



# Plant communication in a changing environment

## The Role of Volatile Organic Compounds

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# Plant Communication in a changing environment. The role of volatile organic compounds.

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## Sammanfattning

Flyktiga organiska föreningar (VOCs) är viktiga sekundära växtmetaboliter som spelar en central roll i växtkommunikation, skydd och ekologiska interaktioner över alla trofiska nivåer. I takt med att klimatförändringarna fortskrider utsätts växter för nya kombinationer av abiotiska stressfaktorer. Dessa förändringar kan påverka ekologiska interaktioner och därmed växters fitness, växtätarens beteenden samt effektiviteten hos naturliga fiender och pollinatörer. I denna litteraturoversikt kommer jag att undersöka under vilka omständigheter VOCs är aktiva på olika trofiska nivåer, samt hur syntesen och funktionen av VOCs påverkas av klimatrelaterade stressfaktorer såsom förhöjda koldioxidhalter, stigande temperaturer, torka, ozon och UV-strålning. Klimatfaktorers påverkan på VOCs är inte generell, utan varierar mellan olika föreningar beroende på växtart, miljö och typ av stress. Till exempel induceras isopren ofta vid värmestress, medan monoterpenener och gröna bladflyktiga ämnen kan hämmas vid långvarig torka eller förhöjda ozonhalter. Eftersom VOCs svarar olika på klimatstress varierar även störningarna i växtkommunikationen, vilket påverkar ekologiska interaktioner mellan växter, växtätare, naturliga fiender och pollinatörer på olika sätt.

Nyckelord: Flyktiga organiska föreningar (VOCs), växtkommunikation, klimatförändringar, ekologiska interaktioner, abiotisk stress.

## Abstract

Across all trophic levels, volatile organic compounds (VOCs) are essential secondary plant metabolites involved in plant communication, protection, and ecological roles. As climate change progresses, plants are facing new combinations of abiotic stresses. These changes may affect ecological interactions, affecting plant fitness, herbivore behaviour, and the efficiency of natural enemies and pollinators. In this literature review I will explore under what circumstances VOCs interact in different trophic levels, and in what conditions VOC synthesis and role, vary upon different climate stresses like, elevated CO<sub>2</sub>, rising temperature, drought, ozone, and UV radiation. Climatic factors do not equally affect VOCs, but it is compound-specific, based on plant species, environment, and combination of stressor. For instance, isoprene is generally induced due to heat stress, while monoterpenes and green leaf volatiles can be repressed due to long duration drought or elevated ozone. Since VOCs respond differently to climatic stress, the resulting disruptions in plant communication are also variable, interfering differently in ecological communication in plants, herbivores, natural enemies, and pollinators.

*Keywords:* Volatile organic compounds (VOCs), plant communication, climate change, ecological interactions, abiotic stress.

# Index

<b>List of Tables</b> .....	<b>5</b>
<b>List of Figures</b> .....	<b>6</b>
<b>Abbreviations</b> .....	<b>7</b>
<b>1. Introduction</b> .....	<b>8</b>
1.1 Aim and Purpose .....	9
1.2 Research Questions .....	9
1.3 Materials and Methods.....	9
1.4 Delimitations.....	10
<b>2. What are VOCs?</b> .....	<b>11</b>
2.1 Ecological Roles of VOCs in Plant Communication and Defense .....	13
2.2 Direct Defenses Against Herbivores .....	14
2.3 Indirect Defenses: Attracting Predators and Parasitoids .....	14
2.4 Plant to plant communication via VOCs .....	16
2.5 Pollinators .....	18
<b>3. Climatic Factors</b> .....	<b>20</b>
3.1 Elevated CO <sub>2</sub> levels .....	22
3.2 Temperature.....	23
3.3 Drought stress.....	24
3.4 O <sub>3</sub> and UV .....	24
3.5 Combined Climate Effects on VOC Emissions .....	25
<b>4. Ecological Consequences of Climate Driven VOC Changes</b> .....	<b>27</b>
4.1 Community Shifts Under Climate Pressure .....	27
<b>5. Discussion</b> .....	<b>30</b>
5.1 Future research.....	31
5.2 Conclusions.....	32
<b>References</b> .....	<b>33</b>

# List of Tables

Table 1: Examples of plant volatile organic compounds with defensive roles against insects, showing active compounds, plant source, and targeted insect species. Adapted from Singh et al., (2021).....	12
Table 2: Overview of floral volatile organic compounds (VOCs), their associated biosynthetic genes, and the plant species in which they have been identified. The table includes examples from major VOC groups such as monoterpenoids, sesquiterpenoids, and benzenoids. It shows which compounds are produced by which plants, and the specific genes that are responsible for their biosynthesis (adapted from Muhlemann et al., 2014).....	18
Table 3: Part of a table (Table1) from Bidart-Bouzat, M. G., & Imeh-Nathaniel, A. (2008), provides an overview of how various plant species alter their production of secondary metabolites, including volatile organic compounds (VOCs), under different environmental stressors such as elevated CO <sub>2</sub> , ozone (O <sub>3</sub> ), UV light, and increased temperature.....	20

# List of Figures

Figure 1: This picture from Razo-Belman and Ozuna (2023) explains the main pathways that plants and microbes use to make volatile organic compounds (VOCs). The different types of VOCs are shown in colored boxes. The four main pathways are the shikimate, methylerythritol phosphate (MEP), mevalonic acid (MVA), and lipoxygenase (LOX) pathways. .... 11

Figure 2: Defense strategies in plants across different organs (above and below ground). The figure illustrates direct (toxic compounds) and indirect responses (VOC-mediated attraction of predators) (Gols 2014). .... 15

Figure 3: Illustrates a range of stressors such as herbivore attack, touch, heat, and drought trigger the release of specific VOC blends. These are distinct signals that can be detected by neighbouring plants, allowing them to prepare for associated environmental stresses (Ninkovic et al., 2020). .... 16

## Abbreviations

VOC	Volatile Organic Compounds, Chemical compounds released by plants.
HIPVs	Herbivore-Induced Plant Volatiles – Gases released by plants when they are attacked by herbivores.
GLVs	Green Leaf Volatiles – Compounds released by plants when their leaves are damaged.
JA	Jasmonic Acid – Plant hormone involved
SA	Salicylic Acid - plant hormone important
MEP	Methylerythritol Phosphate Pathway
MVA	Mevalonate Pathway
LOX	Lipoxygenase Pathway
MeJA	Methyl Jasmonate
CO <sub>2</sub>	Carbon Dioxide
O <sub>3</sub>	Ozone
UV	Ultraviolet Radiation

# 1. Introduction

Plants are one the most important piece in sustaining life on Earth, they contribute to oxygen production, and habitat provision for various organisms. As primary producers, plants have an important role in energy flow processes, as well as sustaining the foundation of the food web. To develop and propagate, plants rely on a variety of abiotic factors, like light, water, and temperature, as well as biotic interactions, such as mutualistic relationships with pollinators and microorganisms (Smith & Smith, 2015).

Plants are in constant interaction with several organisms, like herbivores, pathogens, pollinators and other plants. The most used mechanism in plant interaction with other organisms is the emission of volatile organic compounds (VOCs), released in the atmosphere and perceived by other organisms (Hammerbacher et al., 2019). This VOCs serve variety of functions, including repelling herbivores, signaling natural enemies, attracting plant pollinators and discourage enemy attack from other plants.

According to the IPCC (2021), greenhouse gas emissions from human activities are increasing global temperatures, changing precipitation patterns and a higher frequency of extreme weather events such as droughts and heatwaves. With the ongoing effects of climate change, plants are exposed to stressors that can alter their physiological responses. For example, rising atmospheric CO<sub>2</sub> concentration, as researched by Penuelas & Staudt, (2010) have been discovered to redistribute carbon resource allocation within some plant's species, reallocating metabolic resources from defence compounds to growth, which can reduce VOCs emissions or alter its composition. These changes can impact both the quantity and quality of VOCs, which then could disrupt the ecological functions they serve and as a result, plant interaction with other species may be disrupted or lost entirely (Razo-Belman & Ozuna 2023).

With the essential role VOCs plays in mediating interactions between plants and other organisms, and considering that climatic stressors could alter their production, it's important to understand how these changes affects important ecological processes. As climate change continues to alter environmental conditions, the stability and effectiveness of VOC mediated communication could be disrupted.

## 1.1 Aim and Purpose

The purpose of this thesis is to examine, through a literature review, how plant-emitted volatile organic compounds (VOCs) influence ecological interactions and how these are affected by climate-related environmental changes. The focus is on how stressors such as elevated carbon dioxide levels, increased temperatures, drought, and ozone impact the production and function of VOCs in plants. The aim is to gain a deeper understanding of how VOC-based communication function under changing conditions and what potential ecological consequences could rise as a result.

This review aims to examine:

How do climate-related environmental changes influence the ecological roles of volatile organic compounds (VOCs) emitted by plants?

## 1.2 Research Questions

Specific questions addressed:

What role do VOCs play in plant interactions with herbivores, predators, pollinators, and neighboring plants?

How do climate-related environmental changes affect plant production and ecological functions of plant-emitted volatile organic compounds (VOCs)?

In what ways can changes in VOC production influence ecological interactions and plant communities over time?

## 1.3 Materials and Methods

This thesis is based on a literature review involving scientific articles and reviews in the fields of plant physiology, ecology, biochemistry and environmental science. The sources were collected from Google Scholar and Web of Science as well as through reference tracing in relevant publications. A total of 55 scientific papers were reviewed and the articles and reviews used in this literature study are published between 1990 and 2025, with an emphasis on more recent findings from 2010 onwards. The search terms included combinations of the following keywords: "VOCs", "plant communication", "climate change", "climatic stressors", "ecological interactions".

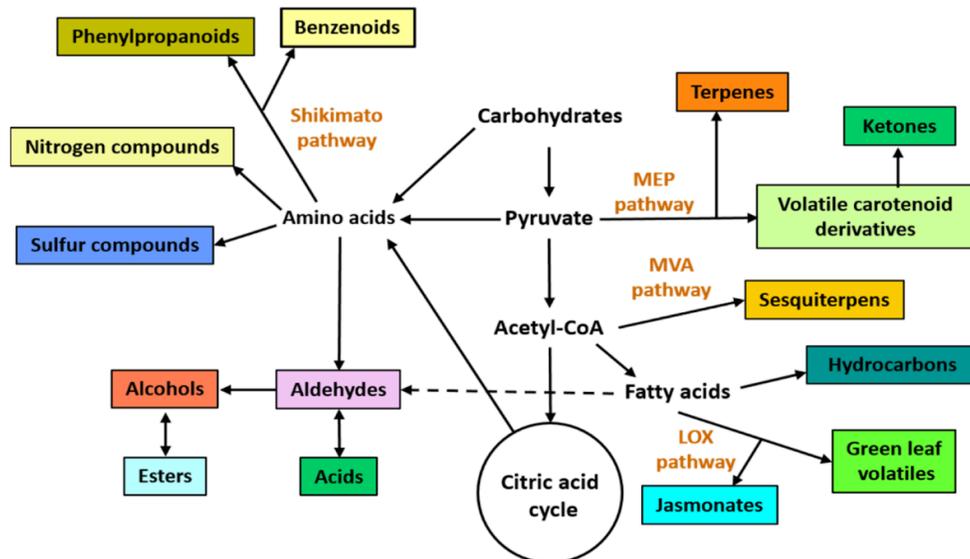
## 1.4 Delimitations

The study is limited to an ecological and physiological perspective on plant VOCs emissions and does not cover emissions from soil microbes. It does not include chemical measurement techniques or genetic regulation in detail. Climate factors are addressed as general stressors (e.g., temperature, CO<sub>2</sub>, drought) without considering specific geographic scenarios or regional climate models. Industrial or technical applications of VOCs are not included.

## 2. What are VOCs?

Picazo-Aragónés et al. (2020) describes volatile organic compounds (VOCs) as lipophilic compounds, low molecular-weight molecules emitted by plants. These compounds are usually secondary metabolites, meaning are not essential for primary functions, like cellular respiration and photosynthesis, but instead fundamental for plant interaction with biotic and abiotic environments. Although VOCs are classified as secondary metabolites Razo and Ozuna 2023 explain that these metabolic pathways need starting material like sugar and fatty acids from primary metabolic processes (Photosynthesis, Glycolysis) to function and so are closely regulated by the plant.

Figure 1: This picture from Razo-Belman and Ozuna (2023) explains the main pathways that plants and microbes use to make volatile organic compounds (VOCs). The different types of VOCs are shown in colored boxes. The four main pathways are the shikimate, methylerythritol phosphate (MEP), mevalonic acid (MVA), and lipoxygenase (LOX) pathways.



VOCs are produced inside plant cells through four main specialised biosynthetic pathways, as shown in Figure 1: MEP, MVA, LOX and shikimate pathway (Razo-Belman and Ozuna 2023). These pathways produce three major classes of VOCs:

Terpenoids: produced through the methylerythritol phosphate (MEP) and the mevalonate MVA pathways, are found in flowers and resins which often is what

gives plants their scent, and includes compounds such as isoprene, monoterpenes, and sesquiterpenes.

Phenylpropanoids and benzenoids: made through the shikimate pathway, are common in floral scents and plant flavours.

Fatty acid derivatives: like green leaf volatiles (GLVs) and jasmonates, synthesised through the lipoxygenase (LOX) pathway, are released when a plant is damaged, for example by insects or mechanical injury (Picazo-Aragonés et al. 2020).

*Table 1: Examples of plant volatile organic compounds with defensive roles against insects, showing active compounds, plant source, and targeted insect species. Adapted from Singh et al., (2021).*

Plant species	Family	Part of the plant	Product	Active principles	Bioassay test	Target Insect	References
<i>Acorus calamus</i> (L.)	Acoraceae	Rhizome	extract	β-Asarone	Contact,	<i>S. zeamais</i>	[76]
<i>Aloysia citrodora</i> (Paláu)	Verbenaceae	Leaves	Essential oils	citronellal and sabinene	Repellent, fumigant, contact	<i>T. castaneum</i> , <i>T. confusum</i>	[100]
<i>A. polystachya</i> (Paláu)	Verbenaceae	Leaves	Essential oils	carvone and limonene	Repellent	<i>T. castaneum</i> , <i>T. confusum</i>	[100]
<i>Artemisia annua</i> (L.)	Asteraceae	Leaves	Essential oils	1, 8-cineole	Fumigant	<i>T. castaneum</i>	[101]
<i>Baccharis salicifolia</i> (Ruiz & Pav.)	Asteraceae	Leaves	Extract	3-Carene	Contact, Repellent	<i>T. castaneum</i> , <i>S. zeamais</i>	[102]
<i>B. salicifolia</i>	Asteraceae	Leaves	Extract	β-Pinene	Contact, Fumigant	<i>T. castaneum</i> , <i>S. zeamais</i>	[73]
<i>Brugmansia suaveolens</i> (Willd.)	Solanaceae	Flowers	Fractions	–	Oviposition deterrent	<i>Zabrotes subfasciatus</i>	[103]
<i>Carum carvi</i> (L.)	Apiaceae	Leaves	Essential oils	Carvone	Contact	<i>R. dominica</i> , <i>S. oryzae</i> , <i>S. zeamais</i>	[104]
<i>Chamaecyparis obtusa</i> (Siebold & Zucc.)	Cupressaceae	Leaves	Essential oils	Limonene, (E)-Anethole	Contact fumigant	<i>S. oryzae</i> , <i>C. chinensis</i>	[105]
<i>Chenopodium ambrosioides</i> (L.)	Amaranthaceae	Leaves	Essential oils	Hexadecane	Contact	<i>T. castaneum</i> , <i>S. granarius</i>	[106,107]
<i>Cinnamomum aromaticum</i> (Nees.)	Lauraceae	bark	extract	Cinnamaldehyde	Contact	<i>T. castaneum</i> , <i>S. zeamais</i>	[108]
<i>Citrus</i>	Rutaceae	Fruit peel	Essential oils	Limonene Eugenol	Fumigant, Antifeedant	<i>T. castaneum</i> , <i>S. oryzae</i>	[109]
<i>Colocasia esculenta</i> var. <i>esculenta</i> (L.) Schott	Araceae	Rhizome	Extracts	2, 3-Dimethylmaleic anhydride	Fumigant	<i>S. oryzae</i> , <i>T. castaneum</i> , <i>C. chinensis</i>	[21]
<i>Convolvulus arvensis</i> (L.)	Convolvulaceae	Leaves	Extracts	Hexadecanoic acid	Contact	<i>R. dominica</i> , <i>S. oryzae</i>	[110]
<i>Coryza discordis</i> (L.) (Desf.)	Asteraceae	Leaves	Extracts	Dicotyhexanedioate	Contact	<i>T. castaneum</i> , <i>S. granarius</i>	[106]
<i>Coriander sativum</i> (L.)	Apiaceae	Seeds	Essential oils	Linalool	Contact	<i>S. oryzae</i> , <i>R. dominica</i> and <i>C. pusillus</i>	[36]
<i>Cupressa lusitanica</i> (Mill.)	Cupressaceae	Leaves	Essential oils	umbellulone and α-pinene	Contact, Fumigant	<i>T. castaneum</i> , <i>A. obtectus</i> , <i>S. cerealella</i> and <i>S. zeamais</i>	[33]
<i>Duguetia lanceolata</i> St.-Hil.	Annonaceae	Leaves	Extract	2,4,5-trimethoxystyrene	Oviposition deterrent	<i>Zabrotes subfasciatus</i>	[111]
<i>Eucalyptus</i> spp.	Myrtaceae	Leaves	Essential oils	α-Terpinene 1, 8-Cineole α-pinene p-Cymene (Cymol)	Fumigant	<i>S. oryzae</i>	[110]
<i>Eucalyptus saligna</i> (Sm.)	Myrtaceae	Leaves	Essential oils		Contact, Fumigant, Repellent	<i>T. castaneum</i> , <i>S. oryzae</i>	[33]
<i>Evoidia ruticarpa</i> (A. Juss.) T.G. Hartley	Rutaceae	Fruit	Essential oils	Triterpenes	Fumigant, Repellent	<i>T. castaneum</i> , <i>S. zeamais</i>	[112]
<i>Foeniculum vulgare</i> (Mill.)	Apiaceae	Fruit	Extract	phenylpropenes (E)-anethole Estragole (+)-Fenchone Citronellol	Contact Fumigant	<i>S. oryzae</i> , <i>L. serricornis</i>	[35]
<i>Juniperus foetidissima</i> (Willd.)	Cupressaceae	Juvenile branches	Essential oils		Fumigant	<i>T. granarium</i>	[113]
<i>Lantana camara</i> (L.)	Verbanaceae	Leaves	Extracts	Coumaran	Fumigant	<i>S. oryzae</i> , <i>T. castaneum</i> , <i>R. dominica</i>	[29]
<i>Melaleuca cajuputi</i> (Powell)	Myrtaceae	Leaves	Essential oils	Terpine-4-ol Terpinolene γ-Terpinene	Contact Fumigant	<i>T. castaneum</i> , <i>S. oryzae</i> , <i>E. kuehniella</i> , <i>R. dominica</i>	[114,115]
<i>Mentha citrata</i> (Ehrh.)	Lamiaceae	Aerial part	Essential oils	Carvone, Menthol, Linalool, Linalyl acetate	Contact, Fumigant	<i>T. castaneum</i> , <i>C. maculatus</i>	[116]
<i>Nardostachys jatamansi</i> (D.Don.)	Caprifoliaceae	Roots	Essential oils	Aristolone	Contact, Fumigant	<i>T. castaneum</i> , <i>S. oryzae</i>	[117]
<i>Ocimum canum</i> (Sims)	Lamiaceae	Dried leaves	Essential oils	Linalool	Fumigant	<i>T. castaneum</i> , <i>S. granarius</i>	[118]
<i>Ocimum kilimandscharium</i> (Gürke)	Lamiaceae	Fresh aerial part	Essential oils	Camphor	Contact	<i>S. oryzae</i>	[119]
<i>Pimenta racemosa</i> (Mill.)	Myrtaceae	Leaves	Essential oils	Linalool	Fumigant	<i>S. zeamais</i>	[120]
<i>Rosmarinus officinalis</i> (Spenn.)	Lamiaceae	Leaves	Essential oils	Camphor	Fumigant	<i>S. oryzae</i>	[121]
<i>Spent hops</i>		Flowers	Extracts	Xanthohumol	Feedant deterrent	<i>S. granarius</i> L., <i>T. confusum</i> and <i>T. granarium</i>	[122]
<i>Tagetes filifolia</i> (Lag.)	Asteraceae	Aerial parts	Essential oils	(E)-anethole and estragole	Fumigant	<i>T. castaneum</i>	[123]
<i>Thespesia populnea</i> (L.)	Malvaceae	Leaves	Extract	Phenol	Fumigant, Contact	<i>C. maculatus</i>	[124]
<i>Zingiber officinale</i> (Roscoe)	Zingiberaceae	Rhizome	Essential oils	1, 8-cineole	Repellent, Fumigant	<i>T. castaneum</i> , <i>S. zeamais</i>	[125]
<i>Z. officinale</i>	Zingiberaceae	Rhizome	Essential oils	β-Zingiberene	Antifeedant, IGR	<i>T. castaneum</i>	[120]

Around 1700 plant VOCs have been identified within different plant species and tissues, varying in structure, function and ecological role. To illustrate this, Table 1, adapted from (Singh et al., 2021), list several plant VOCs and their insecticidal ability. For example, *Ocimum basilicum* (basil) emits linalool and methyl chavicol, two VOCs that have shown fumigant and repellent activity against *Sitophilus oryzae*, a common rice weevil. These compounds disrupt the insect's nervous system and can serve as eco-friendly alternatives to synthetic pesticides (Singh et al., 2021). The production of VOCs can be either constitutive, produced all the time under normal conditions, or induced, triggered by specific stressors such as herbivory, drought, heat, or pathogen attack. Plants tend to utilize induced emissions, since it allows the plant to invest in defence only when danger is perceived and are more specific in composition and timing, being more energy efficient and adaptive, compared to the constitutive emissions. VOCs also vary in volatility, reactivity, and atmospheric lifespan, influencing their range and impact. For instance, light and temperature can alter emission rates, while certain VOCs like isoprene rapidly oxidize in the atmosphere, influencing local air chemistry (Loreto & Schnitzler, 2010).

## 2.1 Ecological Roles of VOCs in Plant Communication and Defense

The ecological functionality of VOCs is broad and extends on different trophic levels, since VOCs are perceived by different organisms. This includes tritrophic interactions, where plants (first trophic level) emit VOCs that influence herbivores (second level), in turn attract herbivore predators or parasitoids (third level) and thereby enhance plant indirect defense (Turlings & Wäckers, 2004).

VOCs can serve as warning signals to activate defense mechanisms in surrounding plants, whether of the same species or different ones. For example, in a study by Ninkovic et al. (2013), it was shown that plants exposed to VOCs released by their neighbours, could activate their own defense responses, even without direct damage. VOCs are also extremely important in attracting pollinators by producing floral scents that guide the insects to the plant reproductive organs.

In these coming sections, the focus will be on how plants utilize VOCs in different ecological interactions, from direct defence against herbivores to pollinator attraction. These interactions are important to define how plants manage stress and how changes in VOC signalling may influence other organisms.

## 2.2 Direct Defenses Against Herbivores

Herbivory stress triggers changes in plant metabolism that result in the release of specific volatile compounds, with direct defensive effects. The compounds are known as herbivore induced plant volatiles (HIPVs), a group of VOCs that are emitted only after herbivore attacks and are dependent on the type of attacker. As explained by War et al. (2012), HIPVs production are regulated through internal defense pathways, like jasmonic acid (JA) and salicylic acid (SA) pathways. In order to respond to herbivore attack, JA and SA signaling pathways induce the activation of enzymes and synthesis of VOCs by specific biosynthesis pathways (Figure 1), which include lipoxygenase (LOX) pathway, green leaf volatiles (GLVs) or methylerythritol phosphate (MEP) and shikimate pathway, which leads to the emission of HIPVs like, terpenoids and phenylpropanoids.

The preferred pathway route, and production type of VOC emitted, is dependent on type of stressor. For example, JA is typically induced by chewing insects like caterpillars, while SA is involved in fighting against piercing/sucking insects such as aphids, (War et al. 2012). Emitted VOC composition also varies based on the degree of tissue damage sustained, for instance, when a plant is exposed to minor insect feeding, it might emit small amounts of GLVs., however, with intense feeding herbivory, the emission becomes a complex blend of different VOCs and higher amounts of for example, terpenes and others stress-induced compounds mix to enhance defence (Niinemets et al., 2013). In a field study, Clancy et al. (2016) looked at tansy (*Tanacetum vulgare*) and found that differences in stored terpene profiles affected how quickly aphids (*Metopeurum fuscoviride*) and their ant partners colonized the plants. The presence of terpenes in the HIPVs blend, in very small amounts, made a difference in whether aphids settled or not. This shows that not only the main volatiles matter, but also other small chemical variations help to shape herbivore choices.

## 2.3 Indirect Defenses: Attracting Predators and Parasitoids

A strategy first described by Turlings et al., (1990) and then later by Engelberth et al. (2004) illustrate that some plant species, like maize (*Zea mays*), cotton (*Gossypium hirsutum*), and lima bean (*Phaseolus lunatus*), take an indirect approach for defending themselves. Rather than directly repel herbivores, those plants instead attract natural enemies of those herbivores and parasitosis, by releasing herbivore induced plant volatiles (HIPVs).

In their study, Davidson-Lowe and Ali (2021) demonstrated that terpenoids released by herbivore damaged *Brassica oleracea*, increased the attraction of predatory Syrphid flies. The attraction was localized, meaning, the flies were attracted by the VOCs released by the plant only to the damaged site, and not to nearby undamaged leaves. This demonstrate that HIPVs release can control predatory activity, within some meters from the damaged, effectively guiding natural enemies to the precise place where the plant is attacked.

Riddick (2020) instead investigated whether specific VOCs could stimulate oviposition in aphidophagous predators.. The study calculated an egg production ratio (EPR) for different predator taxa, revealing that syrphid flies (hoverflies) exhibited the highest EPR(especially to compounds like (E)- $\beta$ -farnesene and 3-methyl-2-butenal).In contrast ladybird beetles showed a weaker response, and lacewings responded minimally.. The study also discovered that the likelihood of egg-laying was higher for VOCs with higher vapor pressure, which evaporate more readily. The physical characteristics of the compounds, such as their ease of evaporation, influence how well they function, and not all predators react to VOCs in the same way. This implies that depending on the kind of volatile organic compound a plant releases, it may be able to draw in specific beneficial insects more successfully.

*Figure 2: Defense strategies in plants across different organs (above and below ground). The figure illustrates direct (toxic compounds) and indirect responses (VOC-mediated attraction of predators) (Gols 2014).*

Just like in direct defences, the volatiles produced in the indirect defence mechanism, can vary depending on the type of damage, plant species, and they usually target specific predator groups. The multitrophic strategy, illustrated in Figure 2, shows how plants utilize direct and indirect chemical defenses in leaves, stems, and roots as a measure against attack by insects' herbivores. Points (1) and (2) represent general chemical features like, non-volatile secondary metabolites

(nvPSMs) that serve roles for direct defense, and volatile compounds (vPSMs) that serve roles of indirect defense and attracting natural enemies. Direct defense is represented by red lines in the figure, blue lines represent indirect, and dashed lines represent additional ecological influences. For example, natural enemies may be affected by plant chemistry (3), and volatiles also control herbivore behaviours (4). There is also an involvement of symbiont microbes (5), where special bacteria aid herbivores in digesting plant defense or silencing plant immunity, while plant-associated microbes like endophytes create anti-herbivore compounds (6). But to what degree these microbes govern volatile emissions and attract predators is not yet well known (7 and 8). In some cases (9) herbivores may sequester plant toxins and use them as protection and finally, (10) and (11) represent how above and below ground interactions, are also able to influence plant defense in other regions of the plant. This picture highlights how complex the plant defense system is, showing how plant defenses are not isolated but rather part of a dynamic multitrophic communication network, that includes chemicals, insects, and microbes, all shaped by internal processes and external stressors.

While most research in this area focuses on insect responses, Amo et al. (2022) investigated the potential role of VOCs in attracting vertebrate predators. Using methyl jasmonate (MeJA) to simulate herbivory in Pyrenean oak trees, they found an increase in VOCs emission and despite the chemical change, no increase in bird predation was observed. The findings suggest that VOCs on their own might not be enough to attract birds, and other factors, such as, what the tree looks like or where it's located, could be more important for attracting herbivory birds.

## 2.4 Plant to plant communication via VOCs

VOCs also serve as airborne signals between plants, allowing one plant to respond to the stress caused to another neighbouring plant (Ninkovic et al. 2016). When some plants are attacked, they emit a specific blend of HIPVs which some nearby plants can detect, through specialized receptors on their leaves, and depending on the signal's intensity and composition, they may activate their own defence pathways in advance.

*Figure 3: Illustrates a range of stressors such as herbivore attack, touch, heat, and drought trigger the release of specific VOC blends. These are distinct signals that can be*

detected by neighbouring plants, allowing them to prepare for associated environmental stresses (Ninkovic et al., 2020).

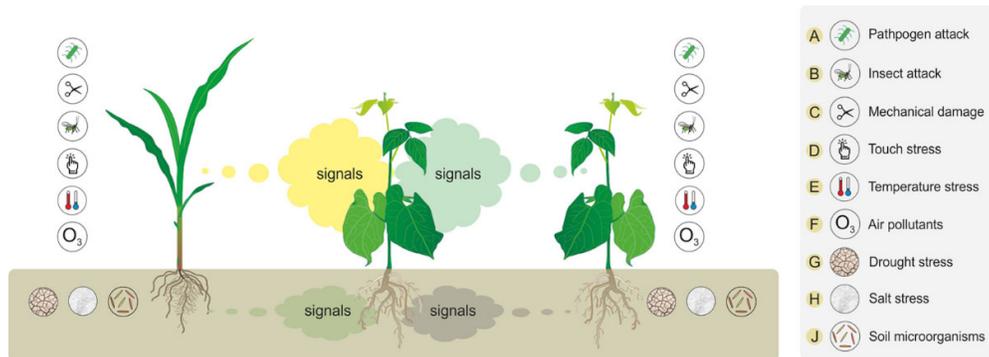


Figure 3 shows how different stressors, herbivore attack, touch, high temperature, and drought, trigger the release of different VOC mixtures, which are "coded messages" to other neighbouring plants. These messages can be interpreted by nearby plants, allowing them to prepare for similar environmental pressures. (Ninkovic et al., 2020). This process is not necessarily an act of helping neighbouring plants, as Ninkovic et al. (2020) explains, the receiving plant directly benefits from the HIPVs detection by becoming "ready" for potential attacks, allowing for faster and stronger response to the possible attack. Rather than an active cooperation, this interaction is usually a defensive eavesdropping, where plants passively (or actively) detect signals to gain survival advantages. This defensive eavesdropping is demonstrated also by Engelberth (2004), who exposed maize and lima bean plants to HIPVs emitted by neighbouring plants under herbivore attack. The plants showed an increased expression of defense related genes and greater resistance to herbivores in later encounters. What makes this process especially efficient is that it avoids that the plants use unnecessary energy, until the threat is confirmed.

Ninkovic et al. (2020) also reviewed how plant-plant signalling is influenced by external factors like light quality, root exudates, and plant spacing. Their work emphasized that plant responses to neighbours are context dependent, and that the ability to detect and react to VOCs is shaped by competition or previous exposure. They propose that plant-plant signalling is not only passive eavesdropping, but can also be an active interaction and adjustment, where a plant may modulate its own VOC emissions or sensitivity based on the identity or behaviour of neighbouring plants. This could occur especially in dense or diverse plant communities, emphasizing how, the ecological role and external environmental input plays a role in detecting and producing VOCs but more study in this subject should be done to be able to understand the complexity of this interaction.

## 2.5 Pollinators

Pollination is a very important ecological service that works as a bridge between different trophic levels, and it relies on VOCs signals to guide these interactions between plants and pollinators. These chemical signals are also known as Floral VOCs and are essential for attracting pollinators and helping plants to ensure reproductive success. Each plant species usually produces its own blend of VOCs that guide insects like bees, moths, and butterflies to the flowers. Floral VOCs are generally synthesized from three major metabolic routes (Figure 1) and these pathways are regulated not only by genetics but also by environmental conditions, such as light, temperature, and the stage of flower opening (Dudareva et al. 2013).

Pollinators rely on visual inspection, like color and shape but scent often is the dominant signal, especially in species that bloom at night or in low light environments where visual signals are limited, in these cases, VOCs need to be emitted in higher concentrations to travel long distances and help insects locate flowers (Muhlemann et al. 2014). The composition and amount of floral scent changes between species and even within the same species, and different pollinators respond to specific blends. For example, benzenoids and terpenoids are often associated with bee and moth attraction, while sulphur containing volatiles are more common in flowers pollinated by bats or carrion flies (Knudsen & Tollsten, 1993).

In some cases, floral VOCs don't just attract, instead according to Muhlemann et al., (2014), some species (*Clarkia breweri* and *Arabidopsis thaliana*) have evolved complex blends that balance attracting pollinators while repelling unwanted visitors like florivores (*Metrioptera bicolor*) or ineffective pollinators such as ants. Compounds like linalool, (E)- $\beta$ -caryophyllene have been shown to repel some florivores while still being attractive to pollinators.

*Table 2: Overview of floral volatile organic compounds (VOCs), their associated biosynthetic genes, and the plant species in which they have been identified. The table includes examples from major VOC groups such as monoterpenoids, sesquiterpenoids, and benzenoids. It shows which compounds are produced by which plants, and the*

specific genes that are responsible for their biosynthesis (adapted from Muhlemann et al., 2014).

Volatiles	Gene	Species	Reference
Monoterpenoids			
1,8-Cineole	<i>CitMTSL1</i>	<i>Citrus unshiu</i>	Shimada et al. 2005
	<i>NsCIN</i>	<i>Nicotiana suaveolens</i>	Roeder et al. 2007
Linalool	<i>CbLIS</i>	<i>Clarkia breweri</i>	Dudareva et al. 1996a
	<i>AmNES/LIS-1</i>	<i>Antirrhinum majus</i>	Nagegowda et al. 2008
	<i>TPS10</i>	<i>Arabidopsis thaliana</i>	Ginglinger et al. 2013
	<i>TPS14</i>	<i>A. thaliana</i>	Ginglinger et al. 2013
Myrcene	<i>Am1e20</i>	<i>A. majus</i>	Dudareva et al. 2003
	<i>AmOc15</i>	<i>A. majus</i>	Dudareva et al. 2003
	<i>AlstroTPS</i>	<i>Alstroemeria peruviana</i>	Aros et al. 2012
<i>E-(β)</i> -Ocimene	<i>Am0e23</i>	<i>A. majus</i>	Dudareva et al. 2003
	<i>CitMTSL4</i>	<i>C. unshiu</i>	Shimada et al. 2005
Sesquiterpenoids			
$\alpha$ -Farnesene	<i>AdAFS1</i>	<i>Actinidia deliciosa</i>	Nieuwenhuizen et al. 2009
Germaacrene D	<i>AdGDS1</i>	<i>A. deliciosa</i>	Nieuwenhuizen et al. 2009
	<i>VvGerD</i>	<i>Vitis vinifera</i>	Lucker et al. 2004
	<i>FC0592</i>	<i>Rosa hybrida</i>	Guterman et al. 2002
Nerolidol	<i>AmNES/LIS-2</i>	<i>A. majus</i>	Nagegowda et al. 2008
	<i>AcNES1</i>	<i>Actinidia chinensis</i>	Green et al. 2012
Valencene	<i>VvVal</i>	<i>V. vinifera</i>	Lucker et al. 2004
Benzenoids/phenylpropanoids			
Benzaldehyde	<i>AmBALDH</i>	<i>A. majus</i>	Long et al. 2009
Benzylacetate	<i>CbBEAT</i>	<i>C. breweri</i>	Dudareva et al. 1998
Benzylbenzoate	<i>PhBPBT</i>	<i>P. hybrida</i>	Boatright et al. 2004
Eugenol	<i>PhEGS</i>	<i>P. hybrida</i>	Koeduka et al. 2006
Isoeugenol	<i>PhIGS</i>	<i>P. hybrida</i>	Koeduka et al. 2006
Isomethyleugenol	<i>CbIEMT</i>	<i>C. breweri</i>	Wang et al. 1997
Methylbenzoate	<i>AmBAMT</i>	<i>A. majus</i>	Murfit et al. 2000
	<i>PhBSMT1</i>	<i>P. hybrida</i>	Negre et al. 2003
	<i>PhBSMT2</i>	<i>P. hybrida</i>	Negre et al. 2003
	<i>CbIEMT</i>	<i>C. breweri</i>	Wang et al. 1997
Methyleugenol	<i>PhPAAS</i>	<i>P. hybrida</i>	Kaminaga et al. 2006
Phenylacetaldehyde	<i>RhPAAS</i>	<i>R. hybrida</i>	Farhi et al. 2010
	<i>RdPAR</i>	<i>R. damascena</i>	Chen et al. 2011b
2-Phenylethanol	<i>PhBPBT</i>	<i>P. hybrida</i>	Boatright et al. 2004
Phenylethylbenzoate	<i>SIGOMT1</i>	<i>Silene latifolia</i>	Gupta et al. 2012
Veratrole			

The production of floral scents is well organised and is controlled by specific genes. As showed in Table 2, linalool in *Antirrhinum majus* is produced through the gene AmNES/LIS-1, while methylbenzoate is linked to the gene AmBAMT in the same species (Muhlemann et al., 2014). The diversity in floral VOCs reflects how plants have evolved specific chemical signals to attract different pollinators. At the same time, it also reveals the biochemical complexity behind VOC mediated communication, where each compound is the result of regulated genetic and metabolic processes (Muhlemann et al., 2014). This variation also shows how carefully processed these scent signals are, since VOCs production depends both on the plant's own biology and the conditions around it, small changes in the environment can shift how flowers smell, how insects respond, and whether pollination happens at all (Dudareva et al. 2013).

### 3. Climatic Factors

Plants are constantly exposed to several climatic stressors, which are expected to intensify as human activities contribute to more extreme weather events (IPCC 2021). In the previous chapter, the focus was on how plants use VOCs to interact with herbivores, predators, and neighbouring plants and as previously mentioned, these interactions are influenced by the surrounding ecological and environmental inputs. In this chapter, the focus will shift on how climatic stressors affect VOC production, which connects to the research question:

*How do climate-related environmental changes influence the ecological roles of volatile organic compounds (VOCs) emitted by plants?*

The environmental factors considered in this thesis are elevated CO<sub>2</sub>, rising temperatures, drought, ozone exposure and UV radiations. Those climatic factors don't work individually, but rather as a whole, creating overlapping conditions which makes plant responses more intricate, especially in the case of VOC biosynthesis and emission (Li et al., 2020). For example, elevated CO<sub>2</sub> has been shown to increase photosynthesis and biomass in many C3 plants like, wheat, rice and soybean (Ainsworth, E. A., & Long, S. P. 2005) but when elevated CO<sub>2</sub> occurs together with high temperature or drought, those effects can reverse, depending on the species and stressor intensity (Leakey et al., 2009; Gray & Brady, 2016)

*Table 3: Part of a table (Table1) from Bidart-Bouzat, M. G., & Imeh-Nathaniel, A. (2008), provides an overview of how various plant species alter their production of secondary metabolites, including volatile organic compounds (VOCs), under different*

environmental stressors such as elevated CO<sub>2</sub>, ozone (O<sub>3</sub>), UV light, and increased temperature.

**Table 1.** Effects of elevated CO<sub>2</sub>, O<sub>3</sub>, UV light and temperature on constitutive levels of plant secondary chemicals

Plant species or community	Secondary chemicals	Environmentally-induced changes in levels of secondary chemicals <sup>a</sup>	References
Elevated CO <sub>2</sub>			
<i>Arabidopsis thaliana</i>	Glucosinolates	+/- or 0	Bidart-Bouzat et al. 2005
<i>Artemisia tridentata</i>	Coumarins	0	Johnson and Lincoln 1990
	Flavonoids	0	Johnson and Lincoln 1990
	Monoterpenes	0	Johnson and Lincoln 1990
	Sesquiterpenes	0	Johnson and Lincoln 1990
<i>Betula pendula</i>	Condensed tannins	+	Kuokkanen et al. 2001
	Flavonol glycosides	+	Kuokkanen et al. 2001, Lavola and Julkunen-Titto 1994
	Terpenoids	+	Kuokkanen et al. 2001
<i>Brassica juncea</i>	Glucosinolates	-	Karowe et al. 1997
<i>Brassica rapa</i>	Glucosinolates	0	Karowe et al. 1997
<i>Raphanus sativus</i>	Glucosinolates	0	Karowe et al. 1997
<i>Brassica napus</i>	Indolyl glucosinolates	-	Hilmanen et al. 2008
<i>Brassica oleracea</i>	Glucosinolates	+/- or 0	Reddy et al. 2004, Schonhof et al. 2007
	Monoterpenes	- <sup>b</sup> or 0	Vuorinen et al. 2004a
	Phenolics	- or 0	Reddy et al. 2004
<i>Bromus erectus</i>	Phenolics (Gallic acid)	+ or 0	Castells et al. 2002
<i>Dactylis glomerata</i>	Phenolics (Gallic acid)	+	Castells et al. 2002
Forest community (12 tree species)	Phenolics	+ or 0	Knapp et al. 2005
<i>Glycine max</i>	Phytoalexins	+ or 0	Braga et al. 2006
<i>Gossypium hirsutum</i>	Condensed tannins	+ or 0	Coviella et al. 2002
	Terpenoid aldehydes	0	Coviella et al. 2002, Agrell et al. 2004
Elevated UV light			
<i>Ascophyllum nodosum</i>	Phenolics (Phlorotannins)	+	Pavia et al. 1997
<i>Betula pendula</i>	Flavonoids	+	Lavola 1998, Lavola et al. 2000
	Phenolic acids	+	Lavola 1998, Lavola et al. 2000
<i>Cannabis sativa</i>	Canabinoid alkaloids	+	Lydon et al. 1987
<i>Caltharantus roseus</i>	Terpenoid Indole alkaloids	+	Ouwkerk et al. 1999
<i>Cistus creticus</i>	Flavonoids	+	Stephanou and Manetas 1997
<i>Festuca rubra</i>	Alkaloids	0	McLeod et al. 2001
<i>Festuca arundinacea</i>	Alkaloids	0	McLeod et al. 2001
<i>Festuca pratensis</i>	Alkaloids	0	McLeod et al. 2001
<i>Glycine max</i>	Terpenoids	-	Singh 1996
	Phenolics	+	Mazza et al. 2000, Mirecki and Teramura 1984, Zavala et al. 2001
	Lignins	-	Zavala et al. 2001
<i>Lolium perenne</i>	Alkaloids	0	McLeod et al. 2001
<i>Nicotiana attenuata</i>	Phenolics	+	Izaguirre et al. 2007
<i>Nicotiana longiflora</i>	Phenolics	+	Izaguirre et al. 2007
<i>Nothofagus pumilo</i>	Phenolics (Gallic acid)	-	Rousseaux et al. 2004
	Flavonoid aglycones	+	Rousseaux et al. 2004
Elevated temperature			
<i>Acer rubrum</i>	Phenolics	0	Williams et al. 2003
<i>Brassica oleracea</i>	Glucosinolates	+/-	Velasco et al. 2007, Matusheski et al. 2004, Perreira et al. 2002
	Indolyl glucosinolate	-	Perreira et al. 2002
<i>Betula pendula</i>	Total phenolics	-	Kuokkanen et al. 2001
	Flavonol glycosides	-	Kuokkanen et al. 2001
	Phenolics (Cinnamoylquinic acid)	-	Kuokkanen et al. 2001
	Polyphenols (Catechin)	-	Kuokkanen et al. 2001
	Flavone aglycones	+	Kuokkanen et al. 2001
<i>Cassiope tetragona</i>	Condensed tannins	+ or 0	Hansen et al. 2006
	Phenolics	- or 0	Hansen et al. 2006
<i>Phragmites australis</i>	Volatile organic compounds	+	Loreto et al. 2006
<i>Picea abies</i>	Terpenes	+	Sallas et al. 2003
	Phenolics	0	Sallas et al. 2003
<i>Pinus ponderosa</i>	Monoterpenes	+	Constable et al. 1999
<i>Pinus sylvestris</i>	Terpenes	+	Sallas et al. 2003
	Phenolics	0	Sallas et al. 2003
<i>Pseudotsuga menziesii</i>	Monoterpenes	+/-	Constable et al. 1999, Snow et al. 2003
<i>Sesbania herbacea</i>	Condensed tannins	0	Hansen et al. 2006
	Phenolics	- or 0	Hansen et al. 2006
<i>Salix myrsinifolia</i>	Phenolics	-	Veillel et al. 2006
<i>Quercus robur</i>	Condensed tannins	-	Dury et al. 1998
<i>Vaccinium vitis-idaea</i>	Condensed tannins	+ or 0	Hansen et al. 2006

<sup>a</sup>(+) increase, (-) decrease or (0) no change in levels of plant secondary chemicals; <sup>b</sup> marginally significant response.

To better understand how different plant species respond to climatic induced stressors, Table 3, which is only part of a long list in the article of Bidart-Bouzat and Imeh-Nathaniel (2008) list findings from a range of experimental articles and shows how the biosynthesis of a range of secondary metabolites, like VOCs, is affected by stressors like elevated CO<sub>2</sub>, temperature increase, ozone, and UV light. Table 3 is relevant since it is not only showing whether emissions increase or decrease, but also if the type of compound affected differs with plant species and stressor. For example, under elevated CO<sub>2</sub>, *Betula pendula* (silver birch) showed an increase production in both condensed tannins and flavanol glycosides, indicating an increase in chemical defense and altered VOC precursor pathways (Kuokkanen et al., 2001). Instead under elevated temperature, *Betula pendula* showed a suppression of phenolic compounds, like flavanol glycosides and catechin-type polyphenols, possibly since warming may suppress the plant's capacity for chemical defense (Kuokkanen et al., 2001). Under increased UV radiation, *Betula pendula* exhibited an increase in phenolic acids and flavonoids, these compounds help in absorbing UV radiation, in diminishing damage and signalling through VOCs (Lavola et al., 2000).

These examples are important to understand the complexity of plant responses to climatic stressors. Each environmental factor (CO<sub>2</sub>, rising temperatures, drought, ozone exposure and UV radiations), will in the coming sections, taken first individually and then as whole, to better grasp the complexity of climatic stresses on volatile organic compounds.

### 3.1 Elevated CO<sub>2</sub> levels

VOCs and CO<sub>2</sub> are both carbon-based compounds but the relationship between those two compounds is not simple and linear. Under elevated CO<sub>2</sub> conditions, plants can shift how they use their internal carbon. For example, Spinelli et al. (2011) observed in spinach (*Spinacia oleracea*), that more of the carbon tends to be directed toward growth and storage, which can affect how much is used for producing secondary compounds like VOCs. This can lead to a possible increase or decrease in emissions, for example, some compounds like monoterpenes are produced more, while others such as isoprene are reduced. The response seems to depend both on the plant species and how the plant balances its growth, defense, and communication under the new conditions (Spinelli et al., 2011). This experiment used atmospheric CO<sub>2</sub> concentrations equivalent to approximately 700 ppm, in line with IPCC predictions for the late 21st century (IPCC, 2021), (relevant to future conditions). In a study on *Arabidopsis thaliana*, a plant from the family Brassicaceae, Zhang et al. (2023) researched that elevated CO<sub>2</sub> altered

the VOC profile, were monoterpenes like limonene and myrcene were upregulated and some sesquiterpenes like farnesene were downregulated, showing a reprioritization of metabolic activity.

Plant interactions can be influenced by even minor variations in VOC composition. Otieno et al. (2023), for example, found that exposure to high CO<sub>2</sub> and ozone caused minor changes in the abundance of VOCs emitted by *Vicia faba* (fava bean), dropping in methyl salicylate and increasing in green leaf volatiles. Although the general VOC emission rates were not much different, these minor variations were enough to lower the visitation of pollinator *Osmia cornuta*, showing how little changes in the floral smell can affect insect detection or the prioritizing of plants.

## 3.2 Temperature

Temperature, with CO<sub>2</sub>, is one of the most important abiotic factors influencing VOC emissions, since VOCs are highly volatile by nature, small increases in temperature can directly enhance their evaporation from plant tissues and warmer conditions also affect the internal processes that regulate VOC production (Peñuelas and Staudt 2010). As a heat stress response, Sharkey and Singaas (1995) explain that VOCs, such as isoprene and monoterpenes increase, since they are components of a plant's defense mechanism, they protect the photosynthetic system and stabilize membranes during short periods of extreme temperature.

Plants from warm environments, such as those found in tropical or Mediterranean regions, usually emit more isoprene than plants growing in cooler climates, likely a physiological strategy evolved under frequent heat stress conditions (Sharkey and Singaas 1995). However, the relationship between temperature and VOCs is not linear. While moderate warming induces VOC emissions, severe or extended heat can suppress them by interfering with photosynthesis and restrict the carbon for VOC biosynthesis. [Table 3](#) also reflects this complexity, were some species, such as *Betula pendula*, showed reduced flavonol and catechin-type phenolic emissions under high temperatures, despite having raised VOC levels under CO<sub>2</sub> or UV conditions. These patterns highlight that the influence of temperature on VOC emissions is not uniform and how it might rely on the species' thermal adaptation as well as the heat intensity (Loreto et al., 2006; Farré-Armengol et al., 2014).

As increased frequency and severity of heatwaves result from climate change, such temperature variation in plant volatiles can be expected to be altered. Changes in VOC profiles can affect plant–insect interactions by changing the chemical cues insects depend on for finding hosts or flowers, as observed by

Peñuelas and Staudt (2010), these changes may contribute to large-scale shifts in ecosystem stability.

### 3.3 Drought stress

Plants under drought stress can alter their internal resource allocation, including the synthesis of volatile organic compounds (VOCs). According to Holopainen and Gershenson (2010), some VOCs, especially monoterpenes, sesquiterpenes, and other isoprenoids, can be released in greater quantities in the early phases of drought, by acting as: antioxidants, that neutralize harmful reactive oxygen species (ROS), as membrane stabilizers, that preserve cellular integrity under heat and dehydration, and as signaling molecules that help control plant reactions and attract beneficial organisms (Loreto & Schnitzler, 2010; Vickers et al., 2009). But with prolonged drought stress, plants will reduce VOC emissions since photosynthesis is reduced, and carbon is limited. Secondary metabolites are not essential for immediate survival, resources are prioritized for vital functions, resulting in decreased synthesis of compounds like, monoterpenes, sesquiterpenes, and green leaf volatiles (GLVs) (Peñuelas & Staudt, 2010; Lerdau et al., 1994). Even stomatal closure, which helps conserve water, can limit the release of some volatiles, depending on how they are transported out of the leaf (Peñuelas & Staudt, 2010).

Sharkey and Loreto (1993) suggested that isoprene emission remains the same even when carbon assimilation is reduced. In some cases, the rate of emissions can recover very quickly under rehydration, indicating greater resistance compared to other chemicals. Isoprene is less dependent on carbon assimilation since it can be produced using alternative carbon sources like stored carbohydrates (e.g., starch breakdown) and intermediates from the methylerythritol phosphate (MEP) pathway (Brilli et al., 2007).

### 3.4 O<sub>3</sub> and UV

Some climatic stressors, even if less commonly known than heat or CO<sub>2</sub>, can still have significant impacts on plant physiology. Ozone (O<sub>3</sub>) and ultraviolet (UV) radiation, for example, also cause plant dysfunction and change the amount and quality of volatile organic compounds emitted. This change can inhibit or enhance VOCs emissions based on intensity, duration of climate factors and plant species (Holopainen and Gershenson 2010).

High ozone exposure causes stress to plant tissues to interfere with biochemical pathways involved in VOC synthesis. According to Holopainen and Gershenson (2010), some species respond to ozone by reducing their VOC emissions, while

others emit more defense-related compounds such as terpenoids and green leaf volatiles. Under high ozone concentrations, photosynthetic tissues can be damaged, leading to reduced carbon availability and ultimately VOC production. Vuorinen et al. (2004) demonstrated that elevated atmospheric ozone concentrations can degrade VOCs after they have been emitted. This atmospheric disturbance will lead to the fact that even if a plant releases the correct volatiles, their effectiveness in ecological communication, e.g. in pollinator or herbivore predators' attraction, can be compromised and VOC molecules breakdown by ozone in the air is an aspect of how human pollution can interfere in plant signalling outside of the leaf surface.

Ultraviolet radiation, particularly UV-B, also effect VOCs emissions in different ways. UV-B functions as a signal that initiates the generation of protective volatile organic compounds at moderate levels. Calfapietra et al. (2009) discussed that moderate UV exposure will more often result in the stimulation of VOC emissions, like isoprene, monoterpenes, and green leaf volatiles as a protection mechanism, stabilizing membranes or enhance resistance to pathogens and herbivores. But when the exposure is excessive or long-term, UV light can cause structural and physiological damage to leaves through damage in DNA and inhibition of photosynthesis. Plants can shift carbon and energy from secondary metabolism to essential survival processes and VOC production usually decreases under these circumstances. As with ozone, prolonged or extreme UV exposure can overwhelm the protective mechanisms of plants and could lead to tissue damage while, in the process, also suppressing VOC production (Vickers et al. 2009).

### 3.5 Combined Climate Effects on VOC Emissions

Climatic stressors like elevated CO<sub>2</sub>, heat, drought, and increased ozone or UV radiation rarely occur in isolation, instead plants are often exposed to simultaneous stressors making VOC responses complex. The combined effects of stressors are not always predictable by just adding up the results from an individual factor. For example, elevated CO<sub>2</sub> may boost carbon availability, but when paired with drought, that same carbon may be redirected toward survival rather than defence, but in other cases, stress combinations can amplify one another for instance, drought and heat together may reduce VOC emissions more strongly than either stress alone, especially when carbon assimilation is suppressed (Peñuelas & Staudt, 2010)

This complexity is demonstrated in recent work by Yang et al. (2024) were several crop species (*Populus tremuloides*, *Ginkgo biloba*, *Pinus*

*tabulaeformis*, and *Larix*) were exposed to elevated CO<sub>2</sub> and ozone (O<sub>3</sub>) but did not match the effects seen under each stressor separately. When these plants were exposed to only elevated CO<sub>2</sub>, VOCs emissions, particularly isoprenoids and green leaf volatiles increased, this probably due to enhanced carbon availability and upregulation of secondary metabolism. When instead Ozone was added, the increased VOCs emissions of isoprenoids and green leaf volatiles was either nullified or reversed. Yang et al. (2024) concluded that this is due to the conflict of CO<sub>2</sub> and O<sub>3</sub> on plant metabolism, since Ozone cause oxidative stress and damage to the photosynthetic organs and while CO<sub>2</sub> stimulate VOC production the result is an unpredictable emission.

These kinds of changes have also been observed in field studies by Pang et al. (2024) in the tropical tree, *Eucalyptus urophylla*, where VOC emissions, specifically isoprene emissions, were repressed at elevated CO<sub>2</sub>. Yet that repression was dependent on other environmental factors like temperature and light intensity. The reduction in VOCs only occurred when other environmental factors, like low light or low temperature, were present with elevated CO<sub>2</sub>, confirming that it is not possible to understand the VOC emission without observing the full environmental context. Many of these experiments are based on model species or controlled experiments, creating a gap in understanding how diverse plant communities respond to realistic climate scenarios. More research is needed to understand the consequences of combined stressors, to be able to predict the VOCs emissions or suppressions.

## 4. Ecological Consequences of Climate Driven VOC Changes

To recap, depending on the context, VOCs can signal herbivore attack, attract predators, warn neighbouring plants, or support pollination. The way they function is based on both, who the interacting partners are and by under which conditions the signals are produced and received. These compounds are part of a complex and active system, and the effectiveness of VOC signalling depends on the surrounding environment. As shown in the previous chapter, factors like temperature, drought, and elevated CO<sub>2</sub> can change both the quantity and quality of VOC emissions. These climatic stressors act differently based on the different combinations of them, altering the VOC profile.

After exploring how VOCs mediate ecological interactions (Chapter 2) and how their production is influenced by climate-related factors (Chapter 3), in this chapter I will bring these perspectives together, showing how environmental changes affect VOCs-based interactions across different trophic levels.

### 4.1 Community Shifts Under Climate Pressure

Muhlemann et al. (2014) explain that plants depend on specific scent blends to attract specific pollinators, and these volatiles do not work in isolation but interact with outside inputs like timing of flowering and insect behaviour. Climate-related environmental changes can alter the production, composition, and perception of plant-emitted VOCs. For instance, alterations in the emission of compounds like linalool or methylbenzoate, triggered by heat or CO<sub>2</sub> fluctuations, can reduce floral attractiveness or change which pollinators are drawn in. This lead not only to lower pollination success, but also to shifts in which plant species dominate a habitat, based on their ability to maintain effective signalling under stress (Muhlemann et al. 2014; Peñuelas, J., & Staudt, M. 2010).

Certain non-native plants, like *Centaurea stoebe* (spotted knapweed), *Solidago canadensis* (Canada goldenrod) and *Chromolaena odorata* have been shown to produce VOCs that are either unusually attractive or chemically unfamiliar to local pollinators. Clavijo McCormick et al. (2023) explain that invasive plants can outcompete natives by drawing more visits from generalist pollinators, particularly when climate conditions alter or weaken the floral cues of native plants. In this scenario, VOC resilience under environmental stress becomes not just a survival trait, but a potential driver of community shifts, giving invasive species a competitive edge over native species.

As documented by Markovic et al. (2014), when VOC mediated interactions start to fail, the consequences don't stop at individual plants or species, instead it can affect pollinator attraction, herbivore pressure, and responses from neighbours. Neighbouring plants that rely on VOCs to prepare their own defences can be affected when those signals change and if the message gets altered or weakened, the result might be less about what's being sent and more about what's no longer being received. Whether it's a missed warning, reduced resistance, or a failure to attract help, the problem is that climate stress doesn't just affect plants under pressure, it also influences how other plants around respond.

Direct and indirect plant defenses mediated by volatile organic compounds (VOCs) are also disrupted by climate change. When drought limits photosynthesis or elevated CO<sub>2</sub> alters internal carbon allocation, the production of defensive volatiles can drop, become delayed, or change in composition. This can weaken the plant's ability to signal distress or confuse the insects that was meant to respond to it and if a predator cannot find its prey because the signal is altered or degraded it could mean that indirect defense system may be disrupted (Peñuelas & Staudt, 2010). While indirect defenses rely on attracting natural enemies like parasitoids or predators through herbivore-induced volatiles (HIPVs), direct defenses release substances that harm or discourage herbivores, such as terpenes or alkaloids. Van Hee et al. (2024) evaluated the impact of environmental context on VOC-mediated defenses against the stink bug *Nezara viridula*. They looked at tomato plants that had been treated with *Trichoderma*, a type of beneficial root fungus that strengthens plant defences by enhancing VOC-mediated signalling. The increase in VOC emissions, however, varied and was influenced by the surrounding environment (including light conditions, nutrient levels, and abiotic stress such as mild drought). In certain cases, the volatiles released were not enough to attract predators, indicating that even when plants are biologically primed to defend themselves, environmental conditions can still prevent VOCs from working properly.

Abbas et al. (2022) suggest that, over time, these small disruptions may create larger changes within communities and maintaining effective VOC signalling under stress, may have a competitive advantage for some species, while others could be disfavoured. One example is the study by Glenney et al. (2018), where the invasive *Potentilla recta* maintained stable pollinator visitation under both drought and elevated CO<sub>2</sub>, particularly when grown alongside native species. In contrast, native plants like *Campanula rotundifolia*, *Erigeron speciosus*, and *Gaillardia aristata* experienced a decline. The VOC profiles of *P. recta* were less affected by climate stress, which may explain its success. This kind of resilience

gives certain species an advantage, especially in mixed communities, where even a little advantage can shift competitive dynamics over time.

## 5. Discussion

The objective of this literature review has been to explore how VOCs emitted by plants determine ecological interactions and how they are modified under climate-related stress. The literature indicates that VOCs have multiple roles in plant communication and that they play a role in direct plant defense against herbivores, in recruitment of beneficial organisms such as pollinators and predators, and in communication between neighbouring plants. VOC production and activity are very responsive to the environment where CO<sub>2</sub> enrichment, rising temperature, drought, and ozone exposure all impact the amount and blend quality of VOCs emitted (Peñuelas & Staudt, 2010). These factors are not direct but vary with plant species, type of stress, and duration of the stress. As an example, Spinelli et al. (2011) showed that elevated CO<sub>2</sub> may lead to a change in carbon allocation within the plant that can reduce the synthesis of VOCs involved in defense. Similarly, a study by Sharkey and Loreto (1993) showed that thermal transition might induce or suppress VOC emission based on the level of heat stress. Temperature and Ozone effects are less predictable; some research shows elevated VOC emission under moderate temperature but inhibitory effect under extreme stress by reduced photosynthesis (Sharkey and Loreto 1993). Ozone similarly can induce or degrade some VOCs, therefore its role in defense and communication becomes complicated.

Changes in VOCs profile, destabilize important ecological relationships. Even small floral scent variation can affect pollinator behaviour, reproductive success in plants and herbivore natural enemies attraction (Muhlemann et al. 2014). War et al. (2012) and Davidson-Lowe and Ali (2021) showed that if such VOC cues are reduced or altered, predator attraction can be reduced, and finally indirect plant defenses will not work. Additional plant-to-plant communication is not only emission driven but also dependent on the ability of neighboring plants to sense and respond to VOCs, which can be disrupted under climatic stress (Ninkovic et al. 2020).

Plant species diversity may affect plant community functions, in terms of how well they can maintain VOC emissions during varying conditions. For instance, Glenny et al. (2018) found that invasive *Potentilla recta* maintained frequent pollinator visits when subjected to drought and high CO<sub>2</sub> than a variety of native species, suggesting that the ability of plants to maintain constant VOCs emission regardless of external climatic variation may be useful under future climates changes but also relevant to species composition and competition.

VOCs processes are also of agricultural importance. Plant VOCs are involved in natural control of pests and pollinator attraction that are essential for crop yields

(Brilli et al. 2019). If climate stress impacts VOC production or diminishes its effectiveness, these ecosystem services become unreliable. According to Bruce et al. (2005), parasitic wasps and other herbivore natural enemies relies on VOCs detection to locate their host and if such signals get chemically altered or destroyed during climate stress, it will disrupt the ability of such helpful insects to find their target and make biological control ineffective. Also, since the VOCs can degrade in polluted air (high O<sub>3</sub>), chemical communication becomes ineffective even if the emission continues and this could become a challenge to already stressed agriculture systems, to provide crop resilience and food security (Holopainen and Blande 2013). Such deterioration affects atmospheric processes and climate regulation in addition to plant signaling and pest defense. According to Zhao et al. (2017), environmental factors have a significant impact on how plant-emitted VOCs affect cloud formation, this implies: air pollution can impair VOCs' ecological function as well as their role in atmospheric particle formation and climate feedback mechanisms. Deteriorating air quality could therefore threaten atmospheric and terrestrial systems, increasing agricultural stress and the stability of larger ecosystems.

In summary, the findings indicate that VOCs are a key to sustaining ecological relationships and ecosystem services which are directly connected to agriculture. The fact that VOCs react to environmental stress, implicate the significance of integrating VOC dynamics into future biodiversity conservation, ecological management, and sustainable agriculture.

## 5.1 Future research

Although the ecological role of VOCs is well documented, their specific responses to combined climatic effects and long-term climate stressors is less explored, particularly in field-based contexts. Since most research so far has examined single factors such as elevated CO<sub>2</sub> or heat separately, fewer examine interactive effects of multi stressors on VOCs across different plant species and communities. Future research could be very valuable in investigating how simultaneous exposures, for example, drought together with ozone or heat stress, affect VOC composition, ecological process, and stability of emission. Finally, it would also be interesting to investigate the function of VOCs in agroecosystems under field relevant climatic conditions and the effect of such emission on crop pollinator relationships or biological control of pests in managed systems.

## 5.2 Conclusions

This review shows that volatiles released by plants have a key function in ecological interactions (plant defense, recruitment of pollinators, and interaction between individuals.). These functions are, however, altered by climate factors (elevated CO<sub>2</sub>, temperature rise, drought, and ozone exposure) which have the possibility to change the quantity and pattern of VOC emissions. These stressors can impact plant-pollinator interactions, natural predators and herbivores. Some plants emit stable VOCs under stress, but other emit deformed or weakened signals, meaning that ecological processes can also be changed. In some cases, changes in VOC mediated interactions can also lead to shifts in species composition, as shown by Clavijo McCormick et al. (2023) and Glenny et al. (2018), where invasive or stress-resistant species outcompeted native species with more stable chemical communication. VOC ecosystem services such as pollination and biological control of pests are essential to yields in crops and in long term, this could weaken food production in already stressed ecosystems. If climate related changes, as predicted by the IPCC, continues to shift, VOC mediated alterations could affect not only single species but also the structure and functioning of whole ecosystems. As noted by Yuan et al. (2009) and Picazo-Aragonés et al. (2020), the emission of VOCs in certain plants may adapt in response to climatic stressors, giving resilience in future ecosystems. One open question remains, which is: can plant VOC emissions evolve over time to match the new climatic conditions, and if so, how quickly these adaptations could occur?

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