



Challenges of climate change and air pollution for volatile-mediated plant–parasitoid signalling

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Herbivore-induced plant volatiles (HIPVs) are reliable cues that parasitoids can use to locate host patches. Interactions mediated by plant volatile organic compounds (VOCs) are vulnerable to disturbance by predicted climate change and air pollution scenarios. Abiotic stress-induced VOCs may act as false signals to parasitoids. Air pollutants can disrupt signalling by degrading HIPVs at different rates and preventing the perception of olfactory signals by reducing the sensitivity of olfactory receptors or by occluding insect sensillae. As essential components of biological control programmes, efforts should be made to assess how different parasitoid species respond and adapt to HIPVs in predicted scenarios. Since providing parasitoid food sources is a promising practice for boosting biological control, parasitoid–flower interactions deserve attention.

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worldwide [1,2]. Additionally, parasitoids have the potential to serve as bioindicators and can be regarded as a monitoring tool for tracking alterations in arthropod diversity within agricultural and forest landscapes [3].

Parasitoids, and insects in general, utilise volatile organic compounds (VOCs) from diverse sources to accomplish vital activities. In addition to pheromones, which are basic intraspecific signals [4] and host-related odours [5,6], parasitoids exploit plant VOCs. For gravid females seeking a suitable host for their offspring, herbivore-induced plant VOCs (HIPVs) are regarded as the most reliable long-distance signals, and they have been extensively studied in the context of tritrophic interactions [7,8]. Starved individuals in search of food also exploit VOCs from flowering and extrafloral nectar-producing plants that do not support their hosts but do provide food resources [9,10], thereby increasing fitness traits such as fecundity and longevity [11–13]. Indeed, the management of habitats with selected nectar-providing flowers has become a promising strategy in the context of conservation biological control for increasing biodiversity and promoting biological control in agricultural landscapes. Although individual compounds act as olfactory stimuli, in nature, insects exploit ratios between compounds to obtain relevant information in complex odour blends [14,15]. In tritrophic interactions, both quantitative and qualitative changes in VOCs emitted upon herbivory are the key to finding hosts. Increases or decreases of individual compounds, even of those emitted in minor amounts, can change the perception of HIPV blends, and alter the responses of parasitoids [16,17].

Introduction

Parasitoids are essential components of insect-dominated food chains. They play a pivotal role in population dynamics and insect community assemblage. The intensive research conducted on the biological and behavioural ecological aspects of parasitoid–host interactions has enabled the successful implementation of numerous biological control strategies using agents, particularly hymenopteran species. Consequently, they have become key components of integrated pest management programmes in open-field and protected crops

Anthropogenic activities are changing the Earth’s environment at an unprecedented rate. Since the advent of the industrial era in the 1850s, the global surface temperature has risen gradually due to higher emissions of greenhouse gases, including carbon dioxide (CO₂). Most critically, since 1970, it has increased faster than in any other 50-year period over at least the last two millennia. Additionally, heatwaves and drought episodes have become more frequent in recent decades [18]. Furthermore, the composition of the atmosphere has been altered due to elevated levels of CO₂ and air pollutants, including ozone (O₃) and its precursors, nitric oxide (NO) and nitrogen dioxide (NO₂), collectively known as NO_x, which primarily originate from the combustion of fossil fuels. In 2019, the levels of atmospheric CO₂ reached 410 parts per million (ppm), and these

concentrations are predicted to double by the end of this century [18]. Ground-level O₃ has increased by 40% since preindustrial times and is expected to continue rising primarily due to the increases in anthropogenic NO_x emissions in South and East Asia [19]. There is evidence that climate change and air pollution have the potential to modify the olfaction-based behaviour of parasitoids (Table 1) by directly affecting the integrity of HIPV signals ('broken' signals) and the olfactory capacities of parasitoids, ('unperceived' signals) or by indirectly altering plant VOC emissions ('false' signals) (Figure 1). Here, we review current knowledge on how climate change-related factors and air pollution impact olfactory signals and insect olfactory perception, with a focus on plant-parasitoid interactions, and identify knowledge gaps in this research area.

False signals: climate change and air pollution induce the emission of plant volatile organic compounds

The emission of VOCs is a common response of plants to stress. Both abiotic and biotic stresses can induce the early emission of fatty acid derivatives (short-chain alcohols, esters and aldehydes, collectively known as green leaf volatiles – GLVs), which are the result of membrane peroxidation. The emission of GLVs is followed by the emission of an array of terpenoids (mono-, sesqui- and homoterpenoids) and phenylpropanoids/benzenoid compounds such as methyl salicylate (MeSA), which may be synthesised *de novo* [20]. Plants subjected to abiotic stress can emit VOCs that overlap, usually partially, with HIPV blends [21]. Induction of VOCs in plants pre-exposed to heat [22•], drought [23] and elevated O₃ levels [24] can enhance the attraction of parasitoids to plants in the absence of their hosts [25]. This may increase time allocation to searching in non-host patches and incur costs for females, including the risk of mortality before locating a host patch. Under herbivory, fine-tuning plant responses to cope simultaneously with abiotic and biotic stress [26] can further alter the composition of the HIPV blends. The aphid, *Myzus persicae*, for instance, induces larger emissions of 6-methyl-5-hepten-2-one in *Arabidopsis thaliana* exposed to temperatures between 17° and 22°C and larger amounts of terpenoids, nitriles and sulfides in plants briefly exposed to temperatures of 27°-32°C [27]. While decreases of ecologically relevant compounds in the odour plume may disrupt the orientation of parasitoids, [28•] abiotic stressors can also enhance the emission of HIPVs and the attraction of foraging parasitoids [23,24]. This suggests that abiotic stressors can facilitate the plant's capacity to respond more rapidly or intensely to subsequent herbivory, a phenomenon known as priming.

Plant responses to both abiotic and biotic stresses include changes in photosynthesis, transpiration and

Table 1

Studies addressing the effects of climate change-related abiotic factors on VOC-mediated plant-parasitoid interactions.

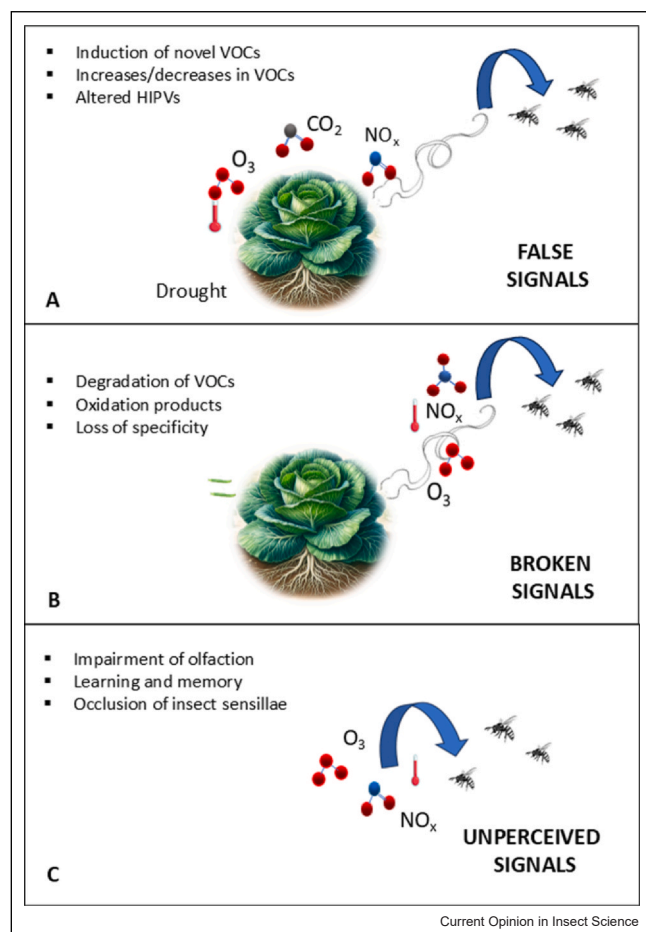
	Parasitoid	Herbivore-plant system	Main Results	Ref.
Elevated T°	<i>Trichogramma chilonis</i>	<i>Phthorimaea operculella</i> -potato	Elevated T° induces the emission of novel compounds in both uninfested and infested plants. [22•] Particularly β-caryophyllene is significantly increased. <i>T. chilonis</i> is more attracted to constitutive odours from plants pre-exposed to elevated T° compared to control plants.	[22•]
Water stress (Drought)	<i>Aphidius colemani</i>	<i>Myzus persicae</i> - Brussels sprouts	Drought increases aphid-induced emissions of several terpenoids but reduces allyl isothiocyanate. <i>A. colemani</i> prefers the odours of well-watered infested plants over those from infested water-stressed plants.	[71]
	<i>Diaeretiella rapae</i>	<i>Brevicoryne brassicae</i> - Brussels sprouts	Drought increases aphid-induced emissions of several terpenoids but reduces allyl isothiocyanate. <i>D. rapae</i> prefers the odours of well-watered infested plants over those from infested water-stressed plants.	[71]
	<i>Microplitis mediator</i>	<i>Mamestra brassicae</i> -Brussels sprouts	Drought induces the accumulation of salicylic acid (SA). Changes in VOCs mainly influenced by herbivory. Plant-parasitoid interactions are not disrupted.	[72]
	<i>Trissolcus basalis</i>	<i>Nezara viridula</i> -broad bean	<i>T. basalis</i> is more attracted to undamaged severely water-stressed plants over well-watered plants. Drought induces the emission of 1,8 cineole, (Z)-β-ocimene, MeSA and hexenal. <i>T. basalis</i> more attracted to severely and moderately water-stressed damaged (feeding+eggs) plants over well-watered damaged plants.	[23]

Table 1 (continued)

Parasitoid	Herbivore-plant system	Main Results	Ref.
<i>Tamarixia radiata</i> <i>M. croceipes</i>	<i>Diaphorina citri</i> -citrumelo <i>Helicoverpa armigera</i> -tomato	Severe drought increases the herbivore-induced emissions of 1,8-cineole and (Z)- β -ocimene and suppresses (E)-2-hexenal and β -pinene. Under water stress, <i>T. radiata</i> does not discriminate between undamaged and damaged plants. Significant interaction herbivory, water treatment and time. Higher total herbivore-induced VOC emissions in water-stressed plants compared to well-watered plants only the first day of herbivory. Well-watered infested plants emit more TMTT, MeSA, (Z)-3-hexenal and (Z)-jasmone. Wasps show attraction for these compounds.	[25] [28•]
CO ₂	<i>Cotesia vestalis</i>	<i>Plutella xylostella</i> -cabbage (cv Rinda and cv Lennox)	[73]
	<i>C. vestalis</i>	<i>P. xylostella</i> -oilseed rape	[34]
	<i>C. vestalis</i>	<i>P. xylostella</i> - cabbage	[50]
O ₃	<i>C. vestalis</i> <i>C. vestalis</i>	<i>P. xylostella</i> - cabbage <i>P. xylostella</i> - oilseed rape	[39] [34]
	<i>Encarsia formosa</i>	<i>Bemisia tabaci</i> -tomato	[24]
	<i>C. glomerata</i>	<i>Pieris brassicae</i> -black mustard	[36]
O ₃ (field) DE ^a + O ₃ (field)	<i>C. vestalis</i> <i>D. rapae</i>	<i>P. xylostella</i> -cabbage <i>B. brassicae</i> -oilseed rape	[74] [49••]

^a Diesel Exhaust (DE).

Figure 1



Potential effects of climate change and air pollution on tritrophic signalling. Changes in the perception of olfactory signals may be the result of (a) altered plant primary and secondary metabolism, (b) reactivity of HIPVs with air pollutants, and (c) direct effects on antennae and olfactory-related processes.

respiration. These fundamental physiological processes determine the carbon partitioning, thereby influencing the availability of carbon for *de novo* biosynthesis of secondary metabolites such as HIPVs. Global warming is anticipated to alter the kinetics of photosynthesis and VOC biosynthesis-related enzymatic activities, the volatility of compounds or the diffusion paths of leaf stomata [20,22•]. The differential temperature dependency of biosynthetic enzymes and volatility of compounds can change the composition of VOC blends and consequently impair foraging of parasitoids at elevated temperatures in comparison to those at lower temperatures [29]. Other climate change–related abiotic factors such as elevated CO₂ [30], drought [23] and air pollutants, namely O₃ [31] and NO_x [32], may promote stomatal closure. This may compromise carbon fixation and assimilation and VOC efflux [20], particularly if the stress

persists. A reduction in constitutive VOC and HIPV emissions, particularly terpenoids, correlates with a reduction in stomatal conductance (ca. 50% and 40%) in broccoli and maize plants grown under elevated CO₂ [30,33]. However, an increase in VOC emissions has been reported in oilseed rape plants grown under elevated CO₂ compared to plants grown under ambient CO₂ concentrations [34]. In maize, chronic exposure to elevated CO₂ decreases the *S. exigua*-induced emissions of three ecologically active compounds [35], namely (*E*)-DMNT, TMTT and (*E*)-β-caryophyllene, but does not compromise their internal levels, which suggests that stomatal closure is at least one of the reasons for decreased HIPV emissions under elevated CO₂ [30]. A reduction in HIPV emissions resulting from a decline in stomatal conductance can translate into a weakening of olfactory signals. In experimental field conditions, *Cotesia glomerata* displays a reduction in the perception of herbivore-infested plants and reduced host-finding abilities under low moisture conditions, which may be attributed to lower emissions of volatiles following stomatal closure [29]. Since the emission of volatiles is related to how dependent a compound or a particular group of compounds are on stomatal control [20], stomatal closure may also alter HIPV composition.

Plant responses to stress are complex and variable in time. They depend not only on plant species and their capacity for acclimation but also on the nature, magnitude and duration of the stress. Water-stressed tomato plants emit larger amounts of HIPVs on the first day, but not on the second day, following the onset of herbivory by *Helicoverpa zea* [28]. Likewise, the enhancement of HIPVs after chronic elevated O₃ exposure observed within the first 24 h after the onset of herbivory by *Plutella xylostella* is no longer evident after 72 h of insect feeding [36]. Plant VOC emissions display a biphasic time and dose response to different stressors, with larger emissions improving tolerance under mild stress and lower emissions under high and long-lasting stress events, suggesting a hormetic response of plant VOCs to stress [20]. Thus, understanding the kinetics of HIPVs in future abiotic scenarios and the responses of natural enemies in different tritrophic systems is crucial to forecast how plants and insects can adapt to future climatic conditions and assess the real effects on plant VOC-mediated ecological processes.

Broken signals: degradation and transformation of herbivore-induced plant volatile organic compound cues in the atmosphere

Once plant VOCs have been released, the distance that the odour plume can travel downwind carrying reliable signals is dependent on factors that affect their persistence in the air. Common HIPVs, particularly terpenoids

and GLVs, are highly reactive with tropospheric oxidants, including O_3 , OH and NO_3 radicals. Consequently, several compounds have short atmospheric lifetimes, which range from several minutes to a few hours [37]. Studies on the impacts of elevated O_3 levels on floral scents indicate that the width of the odour plume and the distance it can travel downwind are both shortened dramatically as the level of O_3 pollution increases [38]. Moreover, the differential degradation of individual compounds alters the composition of the blend as it moves away from a releasing source [38]. The degradation of HIPVs by O_3 can decrease the attraction of parasitoids [39] or can disrupt tritrophic signalling, particularly if HIPV emissions are low [34]. At the atmospheric level, gas-phase and gas/particle partitioning reactions involving plant VOCs may be further sped up in future scenarios of global warming.

The reaction of HIPVs with tropospheric oxidants not only degrades reliable olfactory cues but also increases the concentration of reaction products. Carbonyl species such as aldehydes and ketones produced following O_3 /terpene reactions can elicit electrophysiological responses in insect antennae and alter olfactory preferences [40••]. Oxidation products such as 6-methyl-5-hepten-2-one and geranyl acetone [41] are known to evoke a response in the antennae and alter the behaviour of parasitoids [42,43]. Of these, 6-methyl-5-hepten-2-one has recently been identified as a common product of the oxidation of α -terpinene [44] and α -farnesene [45]. These common oxidation products have the potential to decrease the specificity of olfactory cues or alter the ecological function [44•]. The NO_x fraction of diesel exhaust also reduces the concentrations of parental volatile compounds, enhances those of novel reaction compounds, and can negatively impinge on olfactory signals [46]. Given that some oxidation products are more stable in nature than the parental volatiles from which they are derived, and that some of them have ecological functions, it seems plausible that insects exploit some of these compounds as olfactory cues under natural conditions [36]. Nevertheless, the role of oxidation products as olfactory cues remains largely unknown. The partitioning between the gas-particulate phase following oxidation also results in the formation of low volatility and semivolatile compounds, as well as the formation of secondary organic aerosols. These secondary organic aerosols can be deposited and adsorbed onto plant surfaces and subsequently re-emitted to the atmosphere [47]. Secondary organic aerosols may have repellent properties or may mask relevant olfactory cues [48].

Air pollution may differentially impact parasitoids' responses depending on their degree of specialisation. In field conditions, the abundance of different generalist parasitoids is negatively affected in environments

enriched with O_3 or diesel exhaust, or a combination of both [49••]. O_3 decreases the abundance and parasitism rate of the specialist, *Diaeretiella rapae*. However, the opposite effect has been observed in instances of simultaneous exposure to both pollutants when compared to the ambient treatment [49••]. For specialist parasitoids that rely on specific stimuli innately, the foraging success in polluted atmospheres may be particularly related to the induction and the reactivity of these specific signals, with milder or no effects for less reactive cues [49••,50]. For generalist parasitoids that rely on ubiquitous VOCs, associative learning may facilitate the ability to overcome changes in the composition of HIPV blends or identify novel compounds in the blend, as observed in a Lepidopteran pollinator [51]. Nevertheless, under natural conditions where the insects are expected to be chronically exposed to air pollutants, it is important to consider the potential physiological effects of oxidative stress, which may interfere with the perception and processing of olfactory cues [52].

Unperceived signals: direct effects on the functioning of antennae and olfactory coding

Once odours have reached the antennae of parasitoids, they must first penetrate the cuticular pores on the olfactory sensilla. They then diffuse through the sensillar lymph, bind to an odour-binding protein and finally reach olfactory receptors present on the olfactory receptor neurons (ORN). The combinations of excitatory and inhibitory inputs that generate action potentials can translate several individual chemical stimuli in complex blends into a consistent percept [53]. A variety of climate change-related abiotic factors have the potential to directly affect the perception and processing of olfactory cues. Global warming may affect the sensitivity of olfactory receptors or the signalling of olfactory neurons. For instance, in *Drosophila melanogaster*, warming modulates the response to general odours not only at the receptor level but also at the level of the ORNs [54]. Air pollutants can also alter insect olfactory perception [55] and impair the process of associative learning [56,57••] due to a loss of specificity to the learned conditioned stimuli, which increases olfactory generalisation [52,57••]. The negative effects on insect olfaction resulting from oxidative stress may vary depending on the specific compound and species in question, as well as the duration and dose of O_3 exposure. This is evidenced by observations made in pollinators with different ecological traits [55]. Secondary organic aerosol particles and particulate matter originating from diesel exhaust emissions have the potential to occlude insect sensillae and interfere with olfactory perception [58,59••].

Conclusions and further considerations

Climate change and air pollution can affect plant-parasitoid interactions by degrading olfactory cues by

changing the composition of the odour plume and/or by direct effects on olfaction and olfaction-related processes. Differential impacts on species can alter the abundance of parasitoids and parasitism rates, parasitoid assemblage, herbivore population dynamics and, ultimately, the structure of ecological communities. These effects become economically relevant in the context of biological control practices. Despite the evidence that predicted environmental conditions will alter constitutive VOCs and HIPVs, the number of studies that have assessed the consequences on tritrophic signalling is still rather limited. It is imperative that future studies encompass not only the direct and indirect impact of climate change and air pollution on plant responses and odour plumes but also the perception of olfactory cues by parasitoids in future environmental scenarios. Model systems involving different plants and herbivores are crucial to identify vulnerable and less resilient groups. Studies involving species with different ecological traits, such as longevity, degree of specialisation and diverse abilities to learn novel blends, will help to predict their likelihood of adaptation in the future.

The ability of parasitoids to associate plant VOCs with the presence of prey is enhanced when they exhibit a lower degree of specialisation, in comparison to highly specialised parasitoids [60]. The capacity for associative learning has been put forth as a potential trait that may be exploited by generalist insects to identify and rely on novel compounds or blends in polluted environments. It should be noted, however, that exposure of insects to air pollution can also directly impact on recall processes and impair associative learning. Nevertheless, brief exposures (typically a few minutes) of insects to realistic O_3 levels during behavioural observations in Y-tubes or wind tunnels are insufficient to cause physiological damage to the observed insect. Consequently, studies should adopt a holistic approach encompassing the biosynthesis, emission and reactivity of VOC as well as insect perception to gain a comprehensive understanding of the actual impact of climate change and air pollution on tritrophic signalling.

In contrast to O_3 , which is formed by chemical reactions between VOCs and NO_x in the presence of sunlight, nitrate (NO_3) is the prevailing night-time atmospheric oxidant formed by the reaction of O_3 with NO_2 . Several terpenoids and GLVs can be more reactive with NO_3 than with O_3 , and their degradation can interfere with the behaviour of nocturnal insects [61••,62]. Despite being relatively understudied, many parasitoids display peaks of activity during the scotophase [63]. Assessing the effects of NO_3 on HIPVs and the response of nocturnal parasitoids deserves further investigation. Reactions between VOCs and NO_3 result in the formation of organic nitrates [61••]. Whether parasitoids can exploit products resulting from the reaction of VOCs with

different oxidants in nature or whether it is likely that they can learn to rely on these compounds or degraded scents also deserves attention. In contrast to the existing literature on HIPVs, the role of floral VOCs in parasitoid–plant interactions has been largely overlooked. Floral scents exhibit considerable chemical variability, with terpenoids representing the dominant class of compounds, followed by fatty acid benzenoids and fatty acid derivatives [64]. As with other nectar feeders, such as pollinators, floral scents can be utilised to locate suitable food sources. To optimise the chances of locating a nectar source, starved parasitoids may respond innately to floral volatile cues that are prevalent to many flowering plants, such as linalool or acetophenone [65,66]. Like honey or bumble bees, associative learning can help parasitoids to recognise suitable flowers following rewarding events [66]. A substantial body of research has demonstrated that changes [67–69] or degradation [46,70] of floral scents resulting from climate change and air pollutants can impair pollinator visitation. Such effects may also extend to starved parasitoids in search of food sources, potentially leading to a reduction in fitness traits such as longevity and fecundity. Conservation biological control is based on the premise that diversification of plants and habitats can attract and support natural enemies, thereby enhancing the natural biological control of pests. It is, therefore, important to understand how climate change and air pollution can interfere with the orientation of parasitoids to nectar sources, with a view to ensuring the sustainability of conservation biological control strategies.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

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