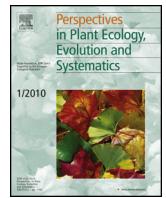




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## Review

# Decoding neighbour volatiles in preparation for future competition and implications for tritrophic interactions



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## ABSTRACT

Plant volatile signals can provide important information about the physiological status and genetic identity of the emitter, and nearby plants can use this information to detect competitive neighbours. The novelty of these signals is that plants eavesdropping to volatiles of undamaged neighbours respond with typical competition responses, even before competition takes place, initiating specific growth responses that can increase their competitive capacity. This preparing for future competition mechanism affects the behaviour and abundance of herbivore pests and their natural enemies. Previously, such responses were only known to occur in response to volatiles released by damaged plants. However, volatile interactions occur only in specific combination of species/genotypes, indicating that plants use volatile signals in the detection and adaption only to substantial competitive neighbours.

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## 1. Plant volatile signals

From its first moment, a growing plant is exposed to various challenges affecting its survival and the plant can respond to this in different ways. Growth condition at the site sets a frame for plant resources to respond to these changes. By spending a lifetime rooted to the same place, as a consequence of their specific nature, neighbouring plants constantly share the same available resources. Thus, coexistence with other plants is permanent and the

most important challenge that individual plants face during their life cycle. In order to prepare for competition with nearby plants and possible upcoming threats, plants monitor and detect reliable signals, to which they respond with great sensitivity and discrimination (Ballarè and Casal, 2000; Clark et al., 2001; Trewavas, 2005). In order for a plant to survive, it must detect the presence of competing individuals, both of the same species (conspecific) and different species (heterospecific), and then adapt appropriately (Hutchings and Dekroon, 1994; Callaway and Aschehoug, 2000; Fridley et al., 2007; Murphy and Dudley, 2009; Ruberti et al., 2012). The consequent signalling that plants perceive forces them to distinguish between crucial signals predicting competitive neighbours from insignificant ones not crucial for their own fitness. Plants

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respond to competitors through physiological and morphological changes that increase their fitness (Callaway et al., 2003; Crutsinger et al., 2006; Violle et al., 2009). They have developed strategies such as competition, confrontation and tolerance (Novoplansky, 2009) to outgrow (Franklin, 2008), suppress (Inderjit et al., 2011) or tolerate (Valladares and Niinemets, 2008) proximate neighbours.

Plants detect neighbouring plants through different kinds of signals, such as quality of light (Izaguirre et al., 2006; Franklin, 2008; Keuskamp et al., 2010), acoustic (Gagliano et al., 2012; Appel and Cocroft, 2014), root exudates (Biedrzycki et al., 2010), root emitted volatile organic compounds (Delory et al., 2016), airborne volatile organic compounds (Ninkovic et al., 2013), floral volatiles (Caruso and Parachnowitsch, 2016) and touch (Braam, 2005; Markovic et al., 2014). Among the crucial signals are airborne volatile signals, which are constantly released by plants into their surroundings. The adaptive strategy of the plants exposed to volatiles depends strongly on the emitter's identity (Ninkovic, 2003; Kellner et al., 2010) and its physiological status (Braam, 2005). Physiological changes in plants responding to volatile signals can cause changes, such as different volatile profiles, which can then be perceived by other plants and organisms (Ninkovic et al., 2013; Dahlin et al., 2015). This paper aims to review the present knowledge on airborne volatile-mediated interactions between plants and the implications of these interactions on different trophic levels. We also identify some research areas that call for increased attention.

## 2. Volatiles as signals in detection of competitive neighbours

Volatile organic compounds (VOCs) can offer important informative value about the physiological stage of each individual in plant communities. The production and emission of VOCs is developmentally regulated, increasing during the early stages of the development when leaves are young and decreasing after maturity (Dudareva et al., 2000). The way in which plants respond to these volatile stimuli depends heavily on the significance of perceived information and neighbour identity, which can be highly related to the age of the receiver. Thus, younger plants are more responsive to future competition than older ones (Novoplansky et al., 1990). Since the emitter plant releases volatile signals constantly in its environment, it can be exploited by nearby plants as a cue for competitive neighbours, thereby initiating growth responses that increase the competitive power of eavesdropping plants (Dicke et al., 2003; Heil and Karban, 2010). The genetic identity of neighbours can have a significant impact on the receiver's growth and development, since the plants share the same available resources but may have different needs. The capacity of an individual plant to recognise nearby kin or strangers and respond differently to their presence represents an important trait that helps plants adjust their competitive ability to a specific neighbour (Fridley et al., 2007; Murphy and Dudley, 2009).

Volatile emissions from undamaged neighbouring plants can be important signals in the process of plant adaption to the presence of potential competitors. For example, Ninkovic (2003) tested two barley varieties that were exposed to each other in laboratory experiments where all other types of interactions were prevented except via volatiles. Plants of the barley variety Kara that had previously been exposed to VOCs of variety Alva allocated more biomass to their roots than unexposed plants or Kara exposed to VOCs of other Kara plants. An increased root biomass in young receiver plants may contribute to their fitness by boosting their capacity for below-ground competition through root proliferation into nutrient-rich patches. A decreased red:far-red light act as the earliest neighbour-detection signal in competition for light (e.g., Dicke and Baldwin, 2010; Pierik and de Wit, 2014) which

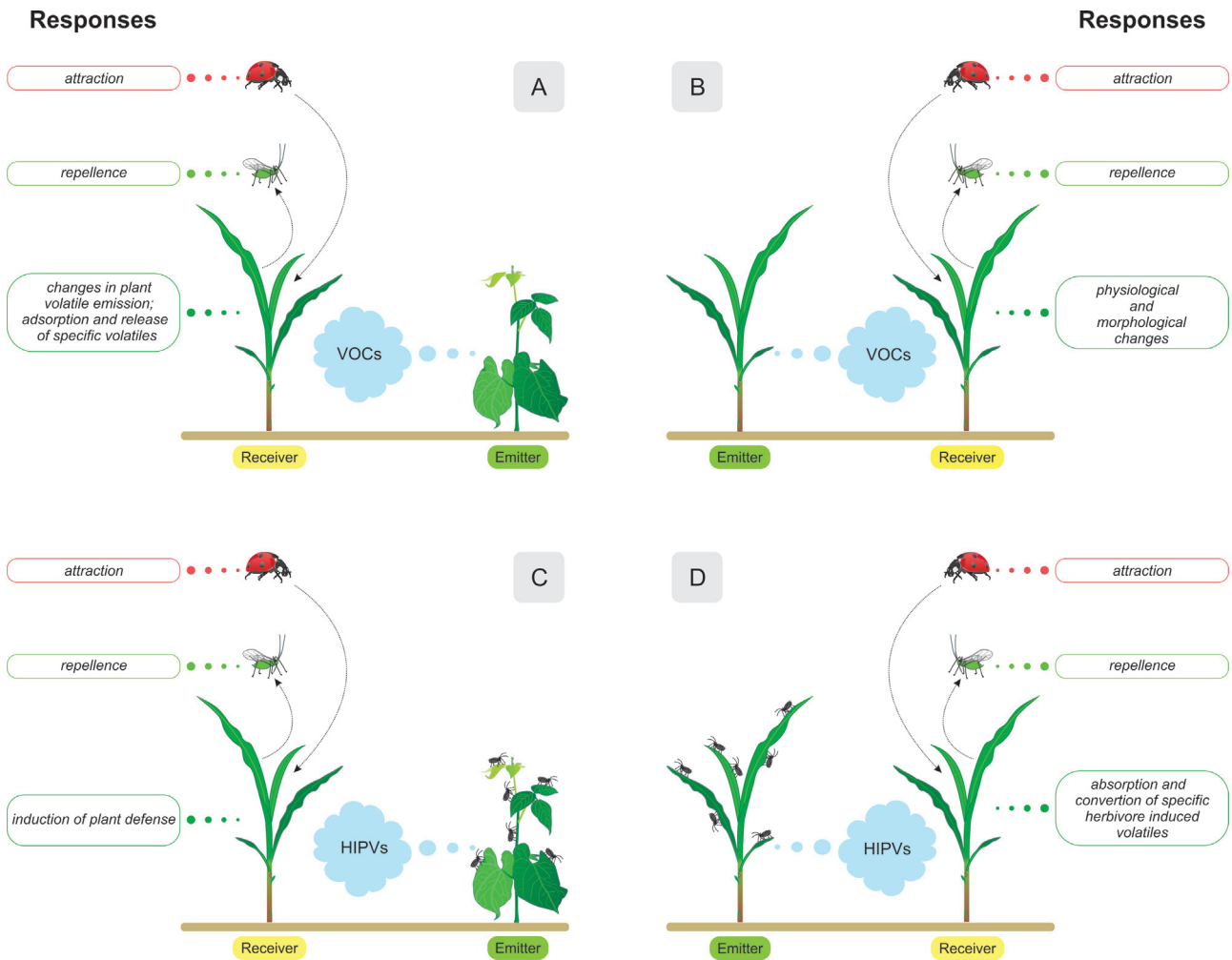
induces elongation and affects the VOCs' emission rate of exposed plants (Kegge et al., 2013). In another experiment, the emitting Alva plants grown in low red:far-red conditions showed typical shade avoidance, increasing in biomass allocation to shoots and changing emission of their volatile blend (Kegge et al., 2015). Such altered volatile emission of Alva induced a typical shade avoidance response of exposed Kara plants that accumulated more resources into shoot- and leaf-biomass than to roots. These examples show that VOCs acts as detecting signals that have important informative value about the physiological status of neighbouring plants, which can induce responses in receiving plants to prepare for future competition. The extraordinary novelty of plants' ability to use volatile cues to predict the existence of forthcoming competitive neighbours is reflected in the response that occurs even before competition takes place. This preparing for future competition mechanism also operates between undamaged neighbours of different species: potato plants that were previously exposed to volatiles from onion plants changed their volatile profile by releasing considerably greater quantities of two terpenoids (Ninkovic et al., 2013). Such responses were previously only known to occur in response to volatiles released by damaged plants (Dicke and Baldwin, 2010; Karban et al., 2014). Thus, VOCs carry information about whether neighbouring plants are under attack, but also about the emitter plants themselves, which enables them to make specific preparations for future competition.

The above examples show that VOCs (a) act as neighbour detection signals, (b) mediate inter- and intraspecific plant interactions, (c) have important informative value about neighbouring plants, and (d) induce responses in receiving plants that prepare for future competition. However, there is a need for further studies to provide knowledge about the underlying mechanisms that are responsible for plants' ability to adapt to competitive neighbours by responding to their volatiles. Interactions between plants are very complex and may have significant ecological implications. The fact that the behaviour of insects can be affected gives this phenomenon even wider ecological significance.

## 3. VOCs induced responses and tritrophic interactions

Volatile interactions between undamaged plants induce changes in receiving plants with the potential to influence organisms at higher trophic levels (Fig. 1A and Table 1) (Glinwood et al., 2011; Ninkovic et al., 2013). The term 'allelobiosis' has been introduced to describe this process and its effects on receiving plants and at higher trophic levels (Pettersson et al., 2003; Ninkovic et al., 2006). In natural habitats, the leaves of birch *Betula* spp. adsorb and then re-release specific herbivore repelling volatiles produced by *Rhododendron tomentosum* Harmaja, reducing their attractiveness to herbivorous insects (Himanen et al., 2010). Broccoli also showed the same ability to adsorb and re-release *R. tomentosum* volatiles, becoming less susceptible to *Plutella xylostella* (L.) oviposition and less favoured and damaged by their larvae (Himanen et al., 2015). The changed volatile emission of onion-exposed potato plants in the above mentioned example resulted in the avoidance of both winged and wingless *Myzus persicae* (Sulzer) morphs (Ninkovic et al., 2013; Dahlin et al., 2015), indicating that active response to volatiles from neighbouring plants may even have effects on herbivorous insects. However, this only occurs in specific combinations of plant species. Thus, volatile chemical interactions between different weed species and barley only affected aphid plant acceptance after exposure of two weed species, indicating that these types of interactions are dependent on the plant species involved (Glinwood et al., 2004; Ninkovic et al., 2009; Dahlin and Ninkovic, 2013).

It has been hypothesised that diversified crops cause a reduction in the abundance of herbivorous insects (Norris and Kogan, 2005).



**Fig. 1.** Volatiles released from nearby undamaged (A) heterospecific and (B) conspecific competitor induce adaptive responses in receiving plant with further implications on other trophic levels. (C) Changed volatile emission after damage (herbivore or mechanical force) of heterospecific or (D) conspecific competitors induce adaptive responses in receiving plants with further implications on other trophic levels.

However, some studies have indicated that diversification had no effect, or increased herbivore densities. In a review of 150 studies on the effects of diverse agro ecosystems on insect herbivores, Risch, Andow and Altieri (Risch et al., 1983) found that 53 per cent of the herbivore species were less abundant in diverse systems, 18 per cent increased, 20 per cent showed a varied response and 8 per cent did not differ between the systems. The variable effect of increased botanical diversity on the occurrence of herbivores could be due to differences in the adaptability of plants to respond to neighbours. The fact that not all plants responded to volatile signals from their specific neighbours suggests that plants may not respond to insignificant signals or may not consider their neighbours as potential competitors. Thus, the ability of plants to adapt to a specific neighbour is dynamic, which can have different outcomes on specific plant–insect interactions (Dahlin and Ninkovic, 2013). Neighbouring plants that are not considered competitors still may have a beneficial role to focal plants due to the processes of associational resistance (Barbosa et al., 2009) which may make plants less exposed to pest attack (Marquis et al., 2002; Himanen et al., 2015).

However, VOCs have been shown to even induce responses in different varieties/genotypes of the same plant species that affect plant defence against herbivores (Fig. 1B). Changes in the growth of receivers and biomass allocation patterns in barley, after exposure to another variety (Ninkovic, 2003), indicate that certain physio-

logical changes within plants could have further implications on herbivores. Pettersson et al. (1999) were the first to show that volatile communication between different barley varieties may reduce the acceptability of exposed plants for *Rhopalosiphum padi* L. Certain combinations of barley genotypes, followed by volatile exposure, significantly reduced aphid acceptance, both in laboratory and field experiments (Ninkovic et al., 2002). As a consequence of the selection process, some barley varieties became good signal emitters while other varieties became better receivers. In general, older barley genotypes displayed a greater tendency to respond to volatile exposure, whereas more recent ones are more likely to be inducers (Kellner et al., 2010). Genotypes that had shown a reduced aphid acceptance also responded to volatile exposure from a particular different genotype with lower aphid growth (Ninkovic and Åhman, 2009). Studies have shown that interaction between plants in diverse wheat variety mixtures reduces *R. padi* performance, affecting mother aphid size that decreased offspring production and lower aphid population (Shoffner and Tooker, 2013; Grettenberger and Tooker, 2016). The empirical results of these studies support the notion that volatile communication represents an effective and rapid means of signalling among plants providing information of the same or different individuals as the emitter.

In plant population, individuals react differently to cues of surrounding plants, which may benefit responders by increasing the

**Table 1**  
Survey of the examples on volatile communication between undamaged plants of the same and different species with the specific effects on tritrophic interactions due to induced responses of the receiving plants.

Author(s)	Emitter plant	Receiver	Induced effects
a) Between different plant species			
Glinwood et al. (2004)	Certain weed species	Barley	Reduced aphid acceptance
Ninkovic et al. (2009)	Certain weed species	Barley	Reduced aphid acceptance
Dahlin and Ninkovic (2013)	Certain weed species	Barley	Reduced aphid population development
Ninkovic et al. (2013)	Onion	Potato	Changed volatile profile, reduced aphid host plant acceptance and aphid immigration rate
Dahlin et al. (2015)	Onion	Potato	Reduced aphid plant acceptance
Himanen et al. (2010)	Rhododendron tomentosum	Betula pendula	Adsorption and re-release of herbivore repelling volatiles
Himanen et al. (2015)	<i>R. tomentosum</i>	Brassica oleracea	Adsorption and re-release of specific volatiles, reduced oviposition and larval feeding
Ninkovic and Pettersson (2003)	Couch grass/thistle	Barley	Increased attractiveness of ladybirds
Vucetic et al. (2014)	Onion	Potato	Changed olfactory responses of aphids, increased attractiveness of ladybirds
b) Between varieties of the same plant species			
Ninkovic (2003)	Barley	Barley	Biomass allocation to roots
Kegge et al. (2015)	Barley in reduced light	Barley	Biomass allocation to shoots
Pettersson et al. (1999)	Barley	Barley	Reduced aphid acceptance and growth rate in certain varieties combinations
Kellner et al. (2010)	Barley	Barley	
Ninkovic and Åhman (2009)	Barley	Barley	
Ninkovic et al. (2002)	Barley	Barley	Reduced aphid acceptance in certain varieties combinations
Shoffner and Tooker (2013)	Wheat	Wheat	Reduced aphid growth rate
Grettenberger and Tooker (2016)	Wheat	Wheat	Reduced aphid offspring production
Ninkovic et al. (2011)	Barley	Barley	Increased attractiveness for ladybirds

inclusive fitness of close neighbours. There is a clear benefit in the VOCs' detection and response to the presence of the "right" neighbour (specific genotype), as it may affect insect behaviour. The above mentioned examples confirm the benefit for signal receivers and strengthen the hypothesis that an increasing genotypic diversity in crop fields could greatly improve insect pest management (Cantelo and Sanford, 1984; Power, 1991; Ninkovic et al., 2002; Tooker and Frank, 2012; Grettenberger and Tooker, 2015). Interactions between plants are context dependent and influenced not only by species or genotype but also by the environment and the physiological state of the plants (Andow, 1991; Barbosa et al., 2009; Barton and Koricheva, 2010).

#### 4. Herbivore predator responses to volatile interactions between undamaged plants

Interactions between undamaged plant species can lead to the alternation of habitat and prey searching behaviour of predatory insects, even when prey were not present (Fig. 1A) (Price et al., 1980; Bottrell et al., 1998; Ninkovic and Pettersson, 2003; Glinwood et al., 2009; Ninkovic et al., 2011). Thus, ladybird occurrence was significantly higher in patches containing either couch grass *Elytrigia repens* (L.) Desv. ex Nevski or thistles *Cirsium arvense* (L.) Scop. then in weedless patches in a barley field (Ninkovic and Pettersson, 2003). Subsequent laboratory studies showed that it was not the VOCs of the weeds by themselves that attracted the ladybirds; instead, ladybirds were more attracted to the VOCs of barley plants that were previously exposed to VOCs from *C. arvense* than to that of unexposed barley (Ninkovic and Pettersson, 2003). These findings are in line with another study showing that ladybirds were significantly more attracted to onion-exposed potato that resulted in an increased emission of two terpenoids than unexposed potatoes (Vucetic et al., 2014). These findings suggest that changed VOCs induced by volatile communication between plants can affect attraction of predators, which can be an underlying mechanism that contributes to an increased abundance of natural enemies in botanically diverse fields (Vucetic et al., 2014).

Effects of volatile communication between genotypes of the same plant species on the third trophic level have also been

reported (Fig. 1B) (Johnson, 2008; Glinwood et al., 2009; Ninkovic et al., 2011). Significantly more ladybirds were found in plots sown with two different barley varieties than in pure plots of either variety alone (Ninkovic et al., 2011). Supporting laboratory studies showed that ladybirds were attracted to VOCs of one variety exposed to another and also to the combined VOCs of two different varieties (Glinwood et al., 2009; Ninkovic et al., 2011). Theory suggests that increased plant species diversity cause a reduction in pest abundance due to an increased number of natural enemies (Andow, 1991; Haddad et al., 2009; Randlkofer et al., 2010). The question remains as to whether decreased pest abundance is caused by higher numbers of their natural enemies or by associational resistance of neighbouring plants that decreases the amount of damage to crop plants (Barbosa et al., 2009; Dahlin and Ninkovic, 2013).

#### 5. Plant volatiles carry information about upcoming threats

Plants' volatiles can also carry information about potential upcoming threats from their surrounding neighbours. Herbivorous insects or mechanical damage rapidly initiate the assaulted plants to substantially change their volatile profile and release herbivore-induced plant volatiles (HIPVs) (Mithöfer et al., 2005; Wasternack et al., 2006; D'Auria et al., 2007; Mumm and Dicke, 2010) that are not typical for undamaged plants (Dicke, 1999; Hare, 2011). These HIPVs have important informative value for undamaged neighbours (Karban and Maron, 2002; Arimura et al., 2010), which helps them predict impending herbivore attack and induce plant defence responses, which make plants less attractive and suitable hosts for herbivores (Fig. 1C) (Heil and Kost, 2006; Baldwin et al., 2006; Karban et al., 2010; Pearse et al., 2013). In such situations, neighbouring unattacked plants may have a huge advantage compared to the signal emitter, which requires resources for defence that would otherwise be used in competition for above- and below-ground resources with undamaged neighbours. However, HIPVs released from a damaged plant also have an important informative role for the emitter itself as within-plant signals that aim to inform other organs of the same plant about the threat. The primary function of HIPVs released after tissue damages is to transmit



signals within the same plant (Heil and Ton, 2008) but not to inform neighbours. This is of particular importance for plants, as the vascular signal transport is much slower than for volatile signalling (Orians, 2005).

Close relatives have more similar chemotypes, confirming that volatile signals from close damaged kin provide more reliable information than those obtained from strangers (Karban et al., 2014). Such individuals of the same chemotype exchange signals more effectively and were significantly less herbivore damaged than individuals of different chemotypes. A recent study showed that tomato plants absorbed (*Z*)-3-hexanol emitted by herbivore attacked conspecific neighbours and converted to (*Z*)-3-hexenyl-vicianoside that is effective in suppressing growth and survival of cutworms (Sugimoto et al., 2014). Also, maize plants infested by *Mythimna separata* (Walker) released a specific blend of volatiles that induce defence responses in conspecific neighbouring plants, reducing larval development immediately after exposure or up to five days later (Ali et al., 2013). The ratio between specific compounds and their concentration is crucial for receiving plants in preparation for upcoming threats. Wounded *Pyrethrum* plants, *Tanacetum cinerariifolium* (Trevir.) Sch. Bip. increased the emission of several terpenoids, which were only effective in the biosynthesis of pyrethrin in neighbouring undamaged plants when all of the five components were included in the blend (Ueda et al., 2012). Many of the inducible and highly reactive HIPVs were shown to have a limited life-time in the atmosphere, ranging from a couple of minutes up to 24 h (Yuan et al., 2009). A greater degree of resistance in receiving plants against herbivores is related to a longer exposure period and a higher accumulation of volatile compounds from infested plants (Choh et al., 2004).

It has been demonstrated that *Trifolium pratense* L. grown together with conspecifics significantly reduced the emission of total and herbivore induced volatiles compared to *T. pratense* grown together with *Dactylus glomerata* L. or growing alone (Kigathi et al., 2013). Such a response of *T. pratense* to the presence of conspecifics was attributed to a reduced possibility of attack by specialist herbivores and minimised eavesdropping of herbivore attack information by neighbours (Fig. 1D). Considering the fact that different plant species emit specific HIPVs blends and grow at different distances from each other, it is reasonable to state that the defence induction in receiving plants is highly correlated to exposure time, emitter relatedness and the reactivity of released HIPVs with atmospheric oxidants. Under natural conditions, volatile exchange between plants of the same species can occur at distances up to 60 cm, while the effective response distance between individuals of different species is much smaller, at 15–20 cm (Karban et al., 2006). It has also been demonstrated that partial defoliation of *Alnus glutinosa* (L.) induced resistance to the beetle *Agelastica alni* (L.) in neighbouring plants of the same species, which declined in the plants with increased distance from defoliated trees (Dolch and Tscharrntke, 2000).

Even mechanically damaged plants can release volatile signals that carry information about upcoming threats. Mechanically damaged sagebrush, *Artemisia tridentata* Nutt. induced resistance to herbivores in neighbouring plants of the same or different species (Karban et al., 2000; Karban and Shiojiri, 2009). Conspecific receivers suffered much less damage after exposure to mechanically damaged sagebrush due to accumulation of defence-related transcripts, which occur in similar ways to that observed in herbivore-attacked plants (Kessler et al., 2006). Volatile signals from genetically related individuals have a much stronger effect, in terms of reducing herbivore damage to exposed plants, than signals from less closely related plants (Karban et al., 2013).

The above examples clearly show that chemical cues from both undamaged and damaged plants induce responses in undamaged

plants. In nature, most plants have to struggle with competing neighbours before they get damaged by herbivores. Therefore, it is expected that plant responses to VOCs of undamaged competitors can have an even wider ecological significance as responses to HIPVs.

## 6. Herbivore predator responses to volatile interactions between damaged plants

Volatiles from damaged plants can also induce responses in neighbouring plants, making them more attractive to herbivore natural enemies (Fig. 1C and D) (Dicke and Van Loon, 2000; Ninkovic et al., 2001; Kessler and Baldwin, 2002; Haddad et al., 2009; Dicke and Baldwin, 2010; Van Wijk et al., 2011). Volatiles released from infested plants are also known to induce changes in neighbouring plants, protecting them indirectly by attracting natural enemies (Bruin et al., 1992; Ninkovic et al., 2001). In a wind-tunnel experiment, unattacked Lima bean plants, *Phaseolus lunatus* L. were exposed to volatiles emitted by lima bean plants that were infested by spider-mites *Tetranychus urticae* Koch. After four to five days, the odour of Lima plants exposed to upwind of infested plants were more attractive to predatory mites *Phytoseiulus persimilis* Athias-Henriot than unexposed Lima beans. The predatory mites responded similarly to cotton plants *Gossypium hirsutum* L. treated in the same way (Dicke et al., 1990).

## 7. Conclusions and future prospects

Research on plant responses to volatile signals has demonstrated the capacity of plants to modify their strategies to meet a diversity of ecological challenges. Experimental evidence has shown that volatile communication between plants plays an important role in responding processes where induced plant traits contribute to mechanisms with tritrophic importance. As these changes are properties of individuals, it is necessary to scale from the level of the individual to the level of communities and ecosystems in order to understand the indirect effects of a plant's adaptive capacity. The present review has shown that volatile signals from undamaged plants mediate similar effects on tritrophic interactions as signals from herbivore-attacked plants. Nevertheless, volatile signals from intact plants have attracted less scientific attention than signals from damaged plants, which have been studied extensively during the last four decades.

With regard to the operating mechanisms, there is still a considerable lack of knowledge and understanding of the consistency of inducible systems to the developmental stage of neighbouring plants. There is currently insufficient knowledge about the limits of inducible responses in relation to necessary costs for successfully growth and reproduction. The role of inducible plant responses and allelobiotic mechanisms calls for an increased understanding of several ecological, biological and genetic aspects. Phenotypes adapted to a certain plant community may express rather epigenetic responses to surroundings that would probably occur in subsequent generations. Recent studies have shown the ability of plants to differentiate volatile signals informing them about possible threats. It is still unknown whether plants respond only to on-going threats or whether they preserve energy to react to signals predicting even more severe forthcoming threats. The more signals point to risk, the greater the chance of a real threat.

## Author contributions

VN, DM and ID wrote the paper and DM constructed and drew figures.

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