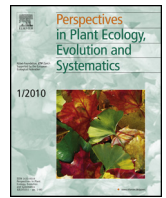




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Review

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).

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