

Review

Ecology of plant volatiles: taking a plant community perspective

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ABSTRACT

Although plants are sessile organisms, they can modulate their phenotype so as to cope with environmental stresses such as herbivore attack and competition with neighbouring plants. Plant-produced volatile compounds mediate various aspects of plant defence. The emission of volatiles has costs and benefits. Research on the role of plant volatiles in defence has focused primarily on the responses of individual plants. However, in nature, plants rarely occur as isolated individuals but are members of plant communities where they compete for resources and exchange information with other plants. In this review, we address the effects of neighbouring plants on plant volatile-mediated defences. We will outline the various roles of volatile compounds in the interactions between plants and other organisms, address the mechanisms of plant neighbour perception in plant communities, and discuss how neighbour detection and volatile signalling are interconnected. Finally, we will outline the most urgent questions to be addressed in the future.

Key-words: defence; growth; herbivore; photoreceptor; phytochrome; signalling.

INTRODUCTION

Plant volatiles play an important role in plant ecology. As sessile organisms, individual plants are at the mercy of mobile attackers such as herbivorous arthropods. Moreover, three quarters of all plant species are also dependent on mobile pollinators for the exchange of gametes, and many plant species even depend on animals for the dispersal of their seeds (Schoonhoven *et al.* 2005). To defend themselves and to reproduce and disseminate their offspring, plants have evolved intricate ways of interacting with their environment and plant volatiles often play crucial roles in these interactions. Plants may produce volatiles to deter herbivores and to attract pollinators, seed dispersers or carnivorous enemies of herbivores (Schoonhoven *et al.* 2005; Dicke & Loreto 2010; Bruce & Pickett 2011). Thus, plant volatiles mediate important interactions with their associated community in the

context of defence and reproduction (Raguso 2008; Kessler & Halitschke 2009; Dicke & Baldwin 2010; Lucas-Barbosa *et al.* 2011).

The majority of research on plant volatiles mediating interactions with the associated community has focused on the responses of isolated plants. However, plants are members of plant communities and interact with neighbouring plants. The interactions of plants with their neighbours may also involve plant volatiles (Dicke & Bruin 2001; Baldwin *et al.* 2006; Heil & Karban 2010; Glinwood *et al.* 2011). Neighbouring plants may act as competitors but also as sexual partners. Through plant volatiles, plants may prime or induce changes in their neighbour's phenotype (Heil & Ton 2008), and this can affect competitive interactions as well as defensive characteristics. Moreover, such changes in a plant's phenotype may also modulate the interactions of plants with their associated animal community (Fig. 1). Here, we will address the role of plant volatiles in interactions of plants with other organisms, with a focus on plants as members of plant communities.

Plant defence

A central paradigm in plant biology is the trade-off between growth/reproduction and defence, which has been dubbed 'the dilemma of plants' (Herms & Mattson 1992; Ballaré *et al.* 2012). To maximize their reproductive success, plants have to make decisions on the relative investments of energy in growth and reproduction on the one hand and in defence on the other hand. The growth–defence dilemma has often been discussed as an allocation trade-off for individual plants, but the decision on the relative investments in growth and defence should also be seen in the context of the plant as a member of a plant community. Moreover, growth and defence may not always be alternative options. For instance, in response to deposition of eggs by a specialist butterfly, black mustard plants enhance growth and flowering (Lucas-Barbosa *et al.* 2013; Pashalidou *et al.* 2013). The caterpillars that hatch from the eggs move towards the plant's flowers and consume the flowers but not the seeds (Lucas-Barbosa *et al.* 2013). Thus, any seeds produced before the caterpillars reach the flowers contribute to the next

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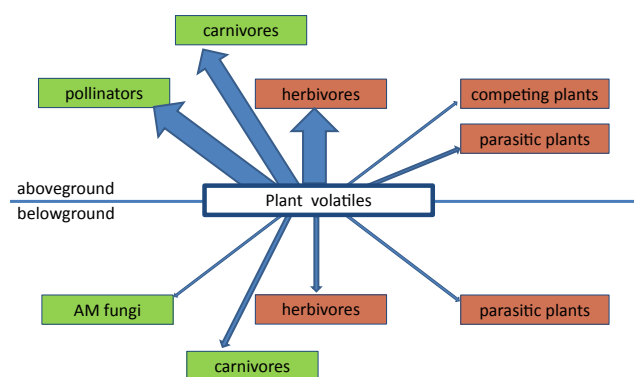


Figure 1. Plant volatiles in interactions with between plants and various members of the associated community. Arrows indicate effects of Volatile Organic Compounds VOCs on different organisms that interact with emitting plants above- and belowground. The thickness of the arrows represents an estimate of the amount of attention received by each type of interaction. AM fungi, Arbuscular mycorrhizal fungi.

generation and the plant growth response to egg deposition can be considered a growth-mediated defence mechanism. It is interesting to note that the plant's growth response does not occur in reaction to oviposition by a generalist lepidopteran herbivore whose caterpillars do not move towards the flowers but are likely to leave the plant due to its high glucosinolate content (Pashalidou *et al.* 2013).

Plants have two types of defences: (1) direct defences, which directly affect an attacker's physiology or behaviour, for example, through hairs, thorns, toxins, digestibility reducers or volatiles (Mithofer & Boland 2012), and (2) indirect defences, which enhance the effectiveness of natural enemies of the attacker, for example, through the provision of alternative food sources or through the production of volatiles that attract the enemies towards their herbivorous victim. These volatile cues include herbivory-induced plant volatiles (HIPVs) and oviposition-induced plant volatiles (OIPVs) (Vet & Dicke 1992; Dicke & Baldwin 2010; Hilker & Meiners 2011). Plant defences can be constitutively present, but many defences are inducible (Kessler & Baldwin 2002; Dicke 2009). The constitutive expression of defence may be costly, resulting in a reduction in seed production (Heidel & Baldwin 2004; van Hulten *et al.* 2006). Moreover, the constitutive expression of defence may also have ecological costs; for instance, volatiles can attract herbivorous insects or may interfere with pollinator attraction (Kessler & Halitschke 2009; Dicke & Baldwin 2010). Finally, inducibility of defences allows plants to adjust their defences to the prevailing conditions.

The effectiveness of plant defence may depend on a plant's neighbours. This has been especially investigated for constitutive defences, and there are many examples of associational resistance or susceptibility (Barbosa *et al.* 2009). Plants may perceive information such as volatiles from their neighbours and may modulate their phenotype in response to this information (Dicke & Bruin 2001; Baldwin *et al.* 2006; Glinwood *et al.* 2011).

Plant competition

Light is the fundamental energy resource for plants as it fuels photosynthesis. Plants have evolved a myriad of mechanisms to optimize light harvesting under a wide variety of suboptimal environmental conditions. Perhaps the most common threat to light harvesting in plants is the proximity of other plants, which can intercept sunlight. In dense plant stands the tallest plants can capture unlimited supplies of light energy, leaving light-depleted conditions for their shaded neighbours. At high plant densities, plants therefore compete for light energy. However, light is certainly not the only resource that plants compete for; belowground there can be severe competition for various nutrients such as nitrogen (N), phosphorus (P) and water (Grime 1979; Keddy 1989; Grace & Tilman 1990).

The complexity of plant competitive interactions requires the integration of resources and information from various plant parts and coordination of responses. Although optimizing growth and phenotypic plasticity to neighbours requires sophisticated information acquisition and integration already, the ecological reality of plants is considerably more complex. Of particular importance are the abundance of herbivorous insects and microbial pathogens that thrive in the canopy microclimate and may spread easily between neighbouring plants. As mentioned earlier, plants carry a variety of mechanisms to protect themselves against such attackers (Vet & Dicke 1992; Glazebrook 2005; Schoonhoven *et al.* 2005; Turlings & Ton 2006; Mumm & Dicke 2010), but these investments need to be balanced against the need to invest in growth to remain competitive in the struggle for the capture of resources. The earlier mentioned growth–defence trade-off has received substantial scientific attention recently (Ballaré *et al.* 2012), and it has been shown convincingly that, at least for shade-intolerant species, plant responses to competition are dominant and can suppress investments in defences against herbivores and pathogens (e.g. Izaguirre *et al.* 2006; de Wit *et al.* 2013).

Plant defence under competition

Studies on the mechanisms of plant defence have been typically carried out using individual plants that neither compete nor experience the conditions that prevail at high plant densities (but see Zavala *et al.* 2004; Glinwood *et al.* 2011). Although this is legitimate from an experimental and mechanistic point of view, it does also mean that information from such single-plant studies cannot always be directly scaled up to predict plant function in plant communities. The effects of changes in light quality brought about by the proximity of neighbouring plants on the expression of direct defences are now fairly well established (see below); however, relatively little is known in this context about indirect defences. Neighbouring plants can eavesdrop on HIPVs and prime their own defence systems (reviewed in Baldwin *et al.* 2006; Heil & Ton 2008; Karban *et al.* 2014). However, although at competitive, high plant densities information transfer between neighbouring plants through constitutive plant volatiles or through

HIPVs could be very effective due to short interplant distances, interactions with other aspects of competition have rarely been addressed.

PLANT VOLATILES AND PLANT–PLANT INTERACTIONS

Within communities, plants usually experience high plant densities and grow with a variety of different neighbouring plants with which they can have an equally varied range of interactions. Neighbours can be genetically related (e.g. offspring) or unrelated (e.g. other species), can deliver services (e.g. pollen source) or pose a fitness threat (competitors, parasitic plants), and either can or cannot be connected through, for example, mycorrhizal hyphae. There is an overwhelming variety of different responses to neighbours of different identity and/or under different conditions. Plants may, for example, respond differentially to the volatiles from undamaged conspecific neighbours of different genotypes with effects on resource allocation to roots and shoots, or defence against insect herbivores (Glinwood *et al.* 2011). A recent study on *Artemisia tridentata* showed that closely related individuals respond more strongly to volatiles from nearby wounded conspecifics than did less closely related individuals, relatedness being assessed using microsatellite markers (Karban *et al.* 2013). Volatile cues from clipped nearby *A. tridentata* plants had been previously shown to induce or prime anti-herbivore responses in nearby neighbours (Farmer & Ryan 1990; Kessler *et al.* 2006). Karban *et al.* (2013) show that the resulting reduction in herbivore damage is strongest in genetically closely related individuals compared with less closely related plants.

Plant volatiles may also guide a parasitic plant to its host: the parasitic plant *Cuscuta pentagona* exploits host–plant volatiles during location of a suitable host. Exposure to the volatiles of tomato plants results in a directed growth response and some of the individual components of this volatile blend had a similar effect (Runyon *et al.* 2006). It remains to be studied if such volatile-mediated host localization by parasitic plants also occurs belowground. However, it has been shown that this can occur through non-volatile, water-soluble root exudates: Strigolactones that plants exude into the rhizosphere to stimulate interactions with arbuscular mycorrhizal (AM) fungi are exploited by parasitic plants and stimulate the germination of their seeds resulting in parasitization of the host plant (Lopez-Raez *et al.* 2011).

Finally, neighbouring plants may be a source of gametes transferred by pollinators. These pollinators may be attracted through floral volatiles (Raguso 2008). However, these volatiles may also attract herbivores and, therefore, the emission of floral volatiles is best restricted to those periods where pollinators are needed and are active (Theis *et al.* 2007). Moreover, to ensure that the pollinators will visit other plants, floral nectar may be endowed with not only sugars and amino acids but also repellents that reduce flower visiting time and nectar feeding, thus enhancing visitation of nearby flowers (Kessler & Baldwin 2007).

PLANT VOLATILES AND DEFENCE

A major response of plants to feeding or oviposition by herbivorous arthropods is the emission of HIPV or OIPV (Dicke & Baldwin 2010; Mumm & Dicke 2010; Hilker & Meiners 2011). Initial studies addressed the effects of these volatiles on the attraction of carnivorous arthropods that attack the herbivores (Dicke & Sabelis 1988; Turlings *et al.* 1990). At present it has become clear that HIPVs are emitted by plants from more than 50 species in 21 families (Mumm & Dicke 2010). They can mediate interactions of plants with herbivores, carnivorous enemies of herbivores, second-order carnivores, pollinators and neighbouring plants (Dicke & Baldwin 2010). HIPVs are emitted in response to aboveground herbivory as well as belowground herbivory (Rasman *et al.* 2005; Dicke & Baldwin 2010). As a result of herbivory, a plant's phenotype changes drastically with consequences for the development of the community of canopy arthropods throughout the growing season (Poelman *et al.* 2008a, 2010). The effects of such herbivore-induced phenotypic changes in community development may override the constitutive effects of genetic differences (Poelman *et al.* 2008b). These effects on community development are partially dependent on HIPV (Dicke & Baldwin 2010) and may extend to interactions between the HIPV-emitting plant and its neighbours. For instance, the emission of HIPV may reduce oviposition by insects on neighbouring undamaged plants and thereby confer associational resistance by influencing ovipositional decisions of herbivorous insects (Zakir *et al.* 2013).

Herbivory-induced changes in a plant's phenotype are regulated by a reticulate hormonal signalling network. The main hormones involved are jasmonic acid (JA), salicylic acid (SA) and ET (Kessler & Baldwin 2002; Pieterse *et al.* 2012; Stam *et al.* 2014). Biting-chewing herbivores especially induce plant responses via the JA/ET pathways while phloem-feeding herbivores especially induce plant responses via the SA pathway (Pieterse *et al.* 2012; Stam *et al.* 2014). Different hormonal signalling pathways interact, which is especially well known for the JA–SA crosstalk (Pieterse *et al.* 2012; Thaler *et al.* 2012). SA interferes with JA signalling and vice versa, and this provides herbivores with opportunities to interfere with induced plant defences. For instance, damage by the phloem-feeding whitefly *Bemisia tabaci*, which is known to activate the SA pathway, interferes with the induction of carnivore-attracting plant volatiles in response to feeding by spider mites on Lima bean plants (Zhang *et al.* 2009). This effect of whitefly feeding was attributed to a reduction in the expression of the JA-inducible gene that codes for ocimene synthase, an enzyme that mediates the rate-limiting step in the biosynthesis of the predator-attracting plant volatile (*E*)- β -ocimene. As a result, spider mites and caterpillars experience a relative enemy-free space on plants infested with the whiteflies and they preferentially select whitefly-infested plants to feed and oviposit on (Zhang *et al.* 2009). ET usually has a positive interaction with JA-inducing plant volatiles. In Lima bean plants, for example, exogenous application of the ET precursor

1-aminocyclopropane-1-carboxylic acid (ACC) enhances the JA-mediated induction of plant volatiles and treatment of Lima bean plants with JA plus ACC resulted in a stronger attraction of the carnivorous mite *Phytoseiulus persimilis* than the treatment with JA only (Horiuchi *et al.* 2001).

PLANT NEIGHBOUR DETECTION AND COMPETITION

Plants are generally assumed to suffer from their neighbours because these neighbours consume resources, thereby increasing the risk of starvation for those resources that are most limiting in a particular system. Plant competition has been studied intensively in plant ecology. There have been a number of excellent recent reviews on this topic (Butterfield & Callaway 2013; Craine & Dybzinski 2013; Hodge & Fitter 2013; Schwinning & Kelly 2013) that point to knowledge gaps and future challenges in this research area (Trinder *et al.* 2013).

In high-density stands, the relative abundance of above-versus belowground resources in any particular ecosystem is thought to determine the optimal pattern of allocation of resources towards above and belowground structures (e.g. Bloom *et al.* 1985). For example, low-nutrient conditions stimulate the relative investments in roots in order to maximize exploration of the soil volume (Poorter *et al.* 2012). On the other hand, shading by neighbouring vegetation typically prompts plants to invest in stem structures to grow their leaves into the best-lit zones of the vegetation and maximize light interception, a response called shade avoidance (Ballaré 1999; Franklin 2008; Casal 2012; Pierik & de Wit 2014). Details on the signalling mechanisms and the various signals and responses were recently reviewed in Pierik *et al.* (2013).

Aboveground, plants respond to the proximity of competitors already before they become shaded, which occurs through the perception of far-red (FR) light reflected by the leaves of neighbouring plants (Ballaré *et al.* 1990). FR light is sensed relative to red (R) light through the phytochrome photoreceptors, with phytochrome B (phyB) playing a predominant role in neighbour detection in plant canopies (reviewed in Ballaré 1999; Smith 2000; Franklin 2008). R activates and FR inactivates phyB and any particular ratio between R and FR, therefore, leads to a relative pool of active (Pfr) and inactive (Pr) phytochrome molecules (reviewed in Smith 2000). The R:FR ratio of natural sunlight is approximately 1.2 (Holmes & Smith 1975), which leads to high phytochrome activity in plants grown in open stands or in canopy gaps, in which the high Pfr pool represses elongation and shade avoidance. As the density of the stand increases or the canopies close, the R:FR ratio drops, leading to phytochrome inactivation and, consequently, induction of shade-avoidance responses (reviewed in Franklin 2008; Casal 2012) in shade-intolerant plants.

The best-studied shade-avoidance traits include stimulation of elongation of hypocotyls, internodes and petioles. Briefly, phytochrome inactivation leads to enhanced accumulation of auxin (Tao *et al.* 2008; Keuskamp *et al.* 2010; Hornitschek *et al.* 2012; Li *et al.* 2012), necessary for

elongation growth. In addition, gibberellin levels are enhanced, leading to degradation of growth-repressing DELLA proteins under low R:FR conditions (Djakovic-Petrovic *et al.* 2007; Pierik *et al.* 2009). The volatile hormone ethylene (ET) can also play a role in shade avoidance, although the mechanisms are less well understood than those mediating auxin and GA effects. The emission rates of ET are mostly elevated in low R:FR conditions (Finlayson *et al.* 1999; Pierik *et al.* 2004a; Foo *et al.* 2006; reviewed in Kegge & Pierik 2010) and genetically engineered, ET-insensitive cultivated tobacco plants have reduced shade-avoidance responses to neighbours (Pierik *et al.* 2003, 2004b). In addition, it has been shown in greenhouse studies that aerial ET levels can be elevated inside a dense tobacco canopy and can induce shade avoidance-like responses in tobacco plants (Pierik *et al.* 2004b), implying that ET could serve as a volatile cue between competing plants. In this light it is interesting that exposure of Lima bean plants to HIPV from spider-mite infested Lima bean plants also results in the induction of ET emission in the undamaged neighbour (Arimura *et al.* 2002). In low R:FR conditions most constitutive VOCs emitted by *Arabidopsis* are suppressed, rather than induced; thus, it is unlikely that these compounds serve as volatile neighbour detection cues among undamaged plants (Kegge *et al.* 2013). Nevertheless, the VOC blend emitted by low R:FR-exposed plants changes compared with high R:FR-exposed individuals and it remains to be studied whether this has consequences for plant-plant signalling.

COMPETITION EFFECTS ON PLANT DEFENCE

As mentioned in the introduction, the expression of plant defences against insect herbivores and microbial pathogens is strongly down-regulated when shade-intolerant plants are exposed to competition or competition-related cues. This down-regulation is thought to help the plant to reduce the investment in defence, thereby freeing up resources that can be directed to growth and the expression of shade-avoidance responses (reviewed in Ballaré 2014). The best documented example of this down-regulation is the repression of direct defences and defence-related genes in plants exposed to low R:FR ratios (reviewed in Ballaré *et al.* 2012). Under conditions of high density and strong competition among neighbouring plants, the reduction of resource availability could conceivably contribute to limit the production of defence-related compounds. For example, in *Arabidopsis* plants grown at high density the accumulation of defence-related proteinase inhibitors was strongly reduced in comparison with plants grown at low density, and this effect was attributed to a limitation imposed by low levels of soil N (Cipollini & Bergelson 2001). Low levels of soil nitrogen were also shown to attenuate elicitor-induced JA and SA bursts in *Nicotiana attenuata*, which correlated with lower expression of several direct defences (nicotine and trypsin proteinase inhibitors, phenolic compounds and diterpene glycosides); the release of volatile compounds (cis- α -bergamotene and germacrene A) was not affected by N limitation (Lou & Baldwin 2004). In maize plants, the emission rates of induced

volatiles were positively affected by fertilization and light intensity (Gouinguene & Turlings 2002). Reduced photosynthetically active radiation (PAR) under conditions of shading can severely limit CO₂ fixation and production of sugars, which could conceivably limit the availability of substrate for the biosynthesis of costly defence-related products, and also down-regulate defence-related signalling (Berger *et al.* 1995; Yanagisawa *et al.* 2003).

Although resource limitation in crowded stands could affect the production of plant defences, it is clear from recent experimental evidence that plant defence is down-regulated in response to proximity cues well before neighbouring plants are engaged in direct competition for resources (Izaguirre *et al.* 2006). A key light signal responsible for regulation of plant defence in canopies is the R:FR ratio, which, as discussed previously in the 'Plant neighbour detection and competition' section, is known to play a central role in modulating adaptive responses to the proximity of other plants. Low R:FR ratios repress both JA and SA signalling (reviewed in Ballaré, 2014). Inactivation of the photoreceptor phyB by low R:FR ratios or by mutation leads to reduced sensitivity to JA in *Arabidopsis* (Moreno *et al.* 2009; Cerrudo *et al.* 2012; de Wit *et al.* 2013) and other species (Izaguirre *et al.* 2013). This reduction in JA sensitivity may occur through a shift in the balance between JAZ proteins (repressors of the JA signalling pathway) and DELLA proteins (positive regulators of JA signalling), in favour of the former (Ballaré 2014); however, the precise mechanism by which Pfr regulates this balance is not well understood yet (Fig. 2). The expression of SA response markers (such as *PR1*) is also reduced under low R:FR ratio (de Wit *et al.* 2013). The mechanisms by which phyB inactivation leads to reduced SA signalling are unknown, but may be associated with down-regulation of SA-induced kinases and consequently insufficient phosphorylation of NPR1, which is a key regulator of SA-mediated defences (de Wit *et al.* 2013). In agreement with the evidence of reduced JA and SA signalling, various studies have documented that plants grown under low R:FR

ratios, or carrying null mutations in the *PHYB* gene, accumulate reduced levels of direct defences and display increased susceptibility to a variety of insect herbivores (McGuire & Agrawal 2005; Izaguirre *et al.* 2006; Moreno *et al.* 2009) and necrotrophic and biotrophic microbial pathogens (Genoud *et al.* 2002; Faigon-Soverna *et al.* 2006; Griebel & Zeier 2008; Cerrudo *et al.* 2012; de Wit *et al.* 2013).

Whereas the effects of competition on the expression of direct plant defences against herbivores is well documented, much less is known regarding regulation of indirect defences involving HIPV-mediated attraction of carnivorous arthropods. Kegge & Pierik (2010) reviewed studies that addressed the effects of competition and resource deprivation on VOC emissions. As could be expected, they found substantial variation among studies regarding changes in VOC emissions, which could be caused by variation among species, intensity of competition, types of resources that were manipulated by the experiments, etc.

Evidence has now accumulated that the emission of most VOCs involved in plant anti-herbivore defence is controlled by JA (Arimura *et al.* 2005; Kost & Heil 2008). Therefore, the growing body of information on environmental regulation of JA signalling could be applied to understand how HIPV emissions are altered by the proximity of neighbouring plants. Under the paradigm that phyB inactivation generally results in reduced JA signalling, it would be expected that low R:FR ratios result in reduced VOC emissions. Indeed, a recent study found that the emissions of many constitutive and JA-inducible VOCs was reduced when *Arabidopsis* plants were exposed to low R:FR ratios, simulating the proximity of other plants (Kegge *et al.* 2013). These altered emission profiles were accompanied by changes in the behaviour of putative targets of the VOCs. Thus, whereas neonates of the specialist herbivore *Pieris brassicae* were attracted by VOCs of *Arabidopsis* plants exposed to MeJA, this attraction effect was attenuated when plants were grown under low R:FR ratios. These results suggest that, as demonstrated for metabolites involved in direct defences, plants perceiving a high risk of competition also down-regulate the emission of VOCs, many of which could have functions as indirect defences (Fig. 2). This conclusion agrees well with the results of studies that evaluated the effects of light quality on other indirect defences, such as JA- and herbivore-induced production of extrafloral nectar (Izaguirre *et al.* 2013). Interestingly, Kigathi *et al.* (2013) found that red clover (*Trifolium pratense*) plants suppress their total and herbivore-induced emissions of VOCs when growing with conspecifics; the nature of the interplant signal involved in this proximity effect was not investigated.

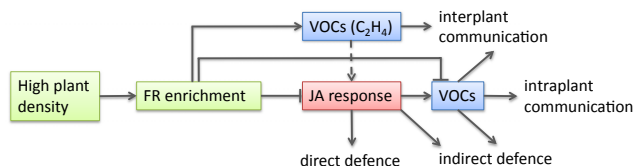


Figure 2. Canopy light conditions affect VOC emissions. Neighbouring vegetation reflects far-red (FR) light, while absorbing R light, which results in inactivation of phytochrome photoreceptors. As a consequence, the emissions of several VOC compounds are reduced, whereas those of others, notably ethylene (ET), are increased. Furthermore, low R:FR conditions reduce jasmonic acid (JA) responses leading to a further decrease of JA-induced VOC emissions and resulting in reduced direct and probably also indirect defences. These changes in VOC emission are also likely to affect inter- and intra-plant communication. Solid arrows indicate positive effects; truncated connectors indicate repression; dashed arrows indicate interactions where the direction of the effect can variable or species specific.

FUTURE PERSPECTIVES

There is extensive information on the effects of VOCs on plant physiology. This has mostly been investigated for isolated plants, although there is an increasing number of field studies addressing volatile-mediated interactions between plants in plant communities. Yet, this research has mostly addressed defence-related aspects. In the context of plant

competition in plant communities, such research should be expanded to integrate two of the most important ecological phenomena, that is, defence and competition that are essential for plant reproductive success and thus Darwinian fitness (Fig. 1).

Light quality–VOC interactions

It has been proposed that plant VOCs might serve as neighbour detection cues in dense stands of undamaged plants, especially because interplant distances are short, allowing VOCs to reach physiologically meaningful concentrations (e.g. Kegge & Pierik 2010; Glinwood *et al.* 2011). Because plants emit often species-specific VOC bouquets, this mechanism of interplant signalling holds potential for species-specific competitor recognition. It is possible that VOCs may be exploited in early phases of stand development, where, depending on plant architecture, changes in light quality may be difficult to detect by plant photoreceptors (e.g. de Wit *et al.* 2012). As the canopy closes, the FR-enriched light environment is expected to inhibit the emissions of several VOCs, but promote the emission of ET (Kegge *et al.* 2013) (Fig. 2). Because VOC concentrations are determined not only by emission rate, but also by the area of emission (i.e. leaf area density) and the gas-exchange characteristics of the whole canopy (canopy boundary layer), it is likely that VOCs continue to play a role as informational cues in dense stands. This is supported by work on plant volatile-mediated interactions between undamaged conspecific plants (Glinwood *et al.* 2011). Further experiments are needed to test this possibility, also for HIPV, and to assess the interplay between light and plant volatiles in real canopies. For example, it will be important to assess if VOC-mediated multitrophic interactions are affected by R:FR ratio and other neighbour cues in plant communities (see, e.g. Glinwood *et al.* 2011; Kigathi *et al.* 2013). To address these ecologically important questions, a blend of field and laboratory studies will be required, combining tools from plant physiology, molecular biology, behavioural biology and chemical ecology. It will, for example, be important to study if under low R:FR conditions VOCs emitted by herbivore-attacked plants still attract natural enemies of the herbivores. This can be studied in the laboratory, but will need to be translated to plant communities. For instance, the parasitoid *Diadegma semiclausum* was equally effective in finding plants infested with caterpillars of *Plutella xylostella* when presented in a low-density or in a high-density set-up of potted uninfested *Brassica oleracea* plants in a greenhouse setting (Gols *et al.* 2005). However, whether light quality can affect the emission of HIPV and consequently parasitoid attraction was not explicitly addressed. To address the effect of R:FR conditions, local manipulation of the light environment by locally adding red light (de Wit *et al.* 2012) or filtering out FR radiation (Ballaré *et al.* 1990) will help assess the relative adaptive value of these interactions. Using genetically silenced plants, for example, R:FR signal transduction can be an alternative way to address the same questions, but this approach will be limited to species for

which the relevant molecular tools and genetic information are available.

An aspect of R:FR signalling in relation to VOC–defence interactions that has not been researched at all is the spatial heterogeneity of the light climate in plant canopies. In dense stands, there are vertical light gradients, with relatively high light intensity and high R:FR in the highest canopy strata, declining to very low light intensity and R:FR down below the canopy (Nagashima & Hikosaka 2012). It was shown recently in a study on passion fruit plants that the local light environment of a plant part can locally modulate JA responses (Izaguirre *et al.* 2013). It is also understood now that VOCs can signal between different parts of the same plant (e.g. between parts that are spatially close, but weakly connected through the vasculature) (Frost *et al.* 2007; Heil & Silva Bueno 2007). A question that would be worth testing is whether shaded, or low R:FR-exposed, branches within a tree produce less JA-induced VOCs in response to attack (Fig. 2) and, because of these reduced emissions are ‘less heard’ by the rest of the tree than well-lit branches. If this is the case, a tempting, yet entirely speculative, interpretation would be that local modulation of VOC emissions by phytochrome results in a systemic (whole plant) response that is more intense when the damage occurs in valuable branches than when it occurs in branches that experience poor light conditions. In cucumber plants, upon spider-mite infestation young leaves are more attractive to a carnivorous mite than mature leaves; this correlates with a change in volatile emission (Takabayashi *et al.* 1994). However, it remains to be investigated whether this was due to differences in light conditions experienced by young and mature leaves.

Above–belowground integration

Another major component in VOC-mediated interactions between plants and their biotic environment is the rhizosphere. Relatively little is known compared with aboveground interactions, but VOCs have been shown to mediate a broad array of interactions. Plants are now known to emit volatiles into the rhizosphere upon herbivory (Van Tol *et al.* 2001; Rasmann *et al.* 2005), with consequences for indirect defence, and root-emitted VOCs may mediate belowground interactions among neighbouring plants (Chamberlain *et al.* 2001; Dicke & Dijkman 2001). The mechanisms behind this are not well understood yet. A particularly challenging task for the future will be to integrate the above- and belowground modes of VOC-based interactions, and the interactions between VOC signalling and additional cues derived from neighbouring plants, such as, for example, light quality, nutrient profiles and soluble root exudates.

Synthesis

As argued in this article, the trade-off between growth/reproduction and defence that plants face should be addressed in the context of a plant community. This implies

that the decision of plants to invest in growth versus defence should be seen in the context of integration of information on (1) attack by, for example, herbivores, parasitic plants and microbial pathogens, (2) competition with neighbouring plants and (3) interactions with beneficial organisms such as mycorrhizal fungi and pollinators. Plant signal transduction pathways that underlie induced responses to attackers, symbionts and competitors converge on important regulatory hubs, which include hormones such as auxin, gibberellin, JA, SA and ET. For instance, herbivore-induced JA may influence auxin homeostasis, JA transiently accumulates in the interaction with mycorrhizal fungi with potential effects on SA-mediated responses to biotrophic pathogens and sensitivity to JA is reduced upon inactivation of the photoreceptor phyB by low R:FR ratios (Cerrudo *et al.* 2012; Erb *et al.* 2012; Pieterse *et al.* 2012). This suggests that there is an exciting hormonal network underlying the trade-off between growth/reproduction and defence that is waiting to be unravelled. Investigating this network will provide important insight into the regulation of a major trade-off in plant biology and is likely to provide a more integrative approach to the ecology of plants within a plant community context. As highlighted in this review, plant volatiles play a role in interactions of plants with their surrounding biota, but this role has so far been studied in isolation for different aspects of plant ecology. Moreover, from a mechanistic point of view, our understanding of the regulation of VOC emissions by hormonal and environmental cues is still very limited. By integrating studies to connect plant defence, plant competition and plant reproduction, and include different levels of biological integration, we expect that exciting new insights into the role of volatiles in plant ecology will be uncovered in the years to come.

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