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PROGRESS REPORT

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Plant scents — mediators of inter-and intraorganismic communication

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The chemical composition of fragrances plays an important role in the communication between organisms. Although the sense of smell in humans is less well developed than in some other mammals, since ancient times odours have been of outstanding importance for cultural and therapeutical reasons. In the past, most fragrances originated from plants, but presently about 90% of the ingredients found in commercial perfumes are chemically produced. But even currently, particularly in the interest of the perfume industry, the search for new plant fragrance compounds continues.

Most plants emit a variety of floral and vegetative scents composed of isoprenoids, benzenoids, phenylpropanoids and fatty acid derivatives. These are compounds with low molecular weight, low polarity and low vapour pressure, properties that facilitate volatility.

The function of emitted volatiles is quite diverse, and most likely our knowledge is too limited to provide a complete picture. Apparently, the most important function is in intra- and interspecific communication (Fig. 1), particularly important for sessile plants since scents have a significantly better transmission range than visual signals.

Odours can have attractive or repellent effects on organisms; some may even function as biocides, and are therefore operative in direct defence mechanisms. Indirect defence is also very well established: primarily after herbivore damage by, for example, caterpillars, plants emit a blend of compounds, whose composition may vary both quantitatively and qualitatively. Two effects may be observed (i) further herbivore attack stops and/or (ii) parasitoid organisms are attracted which attack the herbivores that are causing the damage to the plant (Paré and Tumlinson 1999). Such volatiles can be pre-synthesized and stored in specific glands, trichomes or secretory cavities, and are released after wounding. However, characteristic blends are also synthesized de novo in response to wounding, discriminating between mechanical and herbivore-induced wounding (Alborn et al. 1997). Important inducers for the latter reaction are compounds such as glutamine derivatives present in the spittle of the feeding herbivore. Green-leaf plant volatiles have synergistic effects on the attractiveness of pheromone lures to *Melolontha hippocastani*, and volatiles are also emitted from plants after egg oviposition to attract egg parasitoids (Hilker and Meiners 2002).

Plant–plant interactions via volatile emissions are also documented in the literature. Airborne methyl jasmonate, originally identified as a natural volatile from *Jasminum grandiflorum*, was shown to act by interspecific signaling in proteinase inhibitor (*pin*) expression of tomato leaves following its release from a neighboring sagebrush plant, both kept in a closed chamber. Methyl salicylate is another well-known volatile functioning in plant-to-plant-communication (reviewed by Dicke and Bruin 2001).

The scent composition emitted by injured vegetative tissue appears to be less diverse than scent components emitted by flowers (Knudsen et al. 1993). The emission of floral scent is widespread in angiosperms but does not appear in all species, e.g. *Clarkia breweri* has scented flowers while *Clarkia concinna* is scentless (Raguso and Pichersky 1995). Quality and quantity of fragrance emission may also vary between individual plants of the same species and even between individual flowers of an inflorescence.

The general function of floral scents is the attraction of pollinators. An example is *Cimicifuga simplex*: two of the three subspecies are scentless and are pollinated by bumblebees, while the third emits methyl anthranilate and *iso*eugenol, which specifically attract butterflies for pollination. Similarly, the scented *C. breweri* is pollinated by moths while other *Clarkia* species are not (Raguso and Pichersky 1995). The composition of scents is selective for the pollinator, e.g. fragrances with acyclic

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Fig. 1 A sense of smell: interaction of *Danaus plexippus* and *Lantara camara*. Depicted chemical structures from left to right: methyl salicylate, *trans-β*-ocimene, *iso*eugenol and verbenone

monoterpenes like linalool, esters and nitrogen compounds are believed to be attractive to moths, while short-chain sulfur compounds characteristically attract bats. Further investigations have demonstrated that scent compositions emitted by specific plant species appear to correlate better with the type of pollinator of that plant rather than with the phylogenetic relationships within the plant taxa (Borg-Karlsson et al. 1994).

In some cases the fragrance itself and not nectar is the reward for a pollinator, e.g. the tight and specific interaction between orchids and euglossine bees that use the scent compounds for the species-specific production of pheromones (Dobson 1994). After pollination, the scent profile of many flowers changes, and scent emission often ceases altogether. This allows the pollinator to discriminate between pollinated and non-pollinated flowers. The composition and quantity of emitted volatiles can also vary depending on the developmental stage or the time of day. Some plants emit volatiles diurnally, some nocturnally, while others emit certain volatiles during the day and others during the night (summarized in Dudareva et al. 2000). For example, in *Stephanotis floribunda* the rhythm of emission has a maximum for linalool and methyl benzoate around midnight, while 1-nitro-2-phenyl ethane emission reaches highest levels in the morning (Matile and Altenburger 1988; Pott et al. 2002). *Nicotiana sylvestris* emits phenylpropanoids nocturnally, while terpenoid emission does not oscillate (Loughrin et al. 1990). It is interesting to note that this daytime-specific emission of scent compounds precisely correlates with the activity of the pollinators, e.g. diurnally emitting plants are primarily pollinated by bees, bumblebees, butterflies etc. while nocturnally emitting flowers are pollinated by moths, bats etc., which might be due to co-evolution. It is also possible, although little investigated, that a characteristic floral volatile emission pattern is responsible for repulsion of herbivores, pathogens or 'wrong' pollinators (Schiestl and Ayasse 2001). The precise timing of emission allows the coordinated interaction between organisms but also optimizes the metabolism in respect to energy and carbon expenditures. Storage of the lipophilic volatiles, when continuously synthesized, is unlikely to occur in the hydrophilic vacuoles. To circumvent this problem, compounds can be glycosylated (e.g. *Rosa demascena*; Oka et al. 1999), or are present in lipid particles (*Dianthus caryophyllus*; Hudak and Thompson 1997), or osmophores (e.g., in the orchidaceae and araceae; Vogel 1963; Hadacek and Weber 2001). In *C. breweri* and *A. majus*, the synthesis of scent compounds was shown to occur in epidermal cells, a location which allows immediate emission (Kolosova et al. 2001).

This diurnal or nocturnal scent emission can be regulated by daily light or temperature variations. However, in *Cestrum nocturnum*, *Nicotiana suaveolens*, *N. sylvestris*, *Rosa hybrida*, *A. majus*, and *S. floribunda* (reviewed in Dudareva et al. 2000), a circadian clock is involved and allows precise timing of emission independent of environmental cues. To understand the underlying regulatory mechanisms involved in floral scent emission, it was first necessary to isolate and characterize the genes and enzymes controlling the production of scent compounds. To date, only ca. 15 genes encoding floral scent biosynthetic enzymes have been isolated from six plant species: linalool synthase (LIS; Pichersky et al. 1995), (*iso*)eugenol *O*-methyltransferase (IEMT; Wang et al. 1997), acetyl-CoA:benzylalcohol acetyltransferase (BEAT; Dudareva et al. 1998), *S*-adenosyl-L-methionine:salicylic acid carboxyl methyltransferase (SAMT; Ross et al. 1999), benzoyl-CoA:benzyl alcohol benzoyltransferase (BEBT; D'Auria et al. 2002) from *C.breweri*; *S*-adenosyl-L-methionine:benzoic acid carboxyl methyltransferase (BAMT; Murfitt et al. 2000) from *A. majus*; several methyltransferases and terpene synthases from roses (Guterman et al. 2002); SAMT from *S. floribunda* (Pott et al. 2002); several terpene synthases from *Arabidopsis thaliana* (Chen et al. 2003); SAMT from *Hoya carnosa* and BAMT from *N. suaveolens* (Pott and Piechulla, unpublished). This is still a small number of genes considering that more than 700 different scent compounds have been identified from flowers (Knudsen et al. 1993). A closer inspection of the various scent compounds shows that the majority are methylated derivatives, indicating that methylation reactions are well suited for altering volatile compounds and assisting volatility. The preference for methylation reactions in fragrance synthesis is reflected in the successful isolation of several floral methyltransferases. Such methyltransferase enzymes often accept more than a single substrate, but those that exhibit high substrate specificity also exist. Despite the fact that the floral scent bouquets are filled with numerous terpenoids, not much is yet known about substrate specificity and product synthesis of floral terpene synthases.

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