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Editorial

Chemical diversity and biological functions of plant volatiles

The sessile "life-style" of plants has two main disadvantages. Firstly, plants do not have the option to escape from herbivores, parasites or pathogens by moving away from the locality where they grow. Secondly, interacting with potential mating partners for sexual reproduction over distances is very difficult. Nevertheless, plants have evolved effective strategies to overcome these problems, including an amazing ability for producing a wide array of volatile organic compounds (VOCs).

It is well established that plant VOCs are an important part of the direct and indirect chemical defense systems of plants, including anti-bacterial, anti-fungal, and anti-herbivore defense (Gershenzon and Dudareva, 2007). It has also been suggested that floral volatiles in early angiosperm flowers would have been derived from those used for chemical defense of the reproductive structures against herbivores. These floral volatiles then became signals for attracting animal pollinators (Pellmyr and Thien, 1986).

The importance of plant VOCs for plant interactions with their environment has been recognized for a long time, but progress in the field was hampered due to the complexity of the volatile profiles in both leaves and flowers. A breakthrough, allowing better separation and identification of complex chemical matrices, came with the emergence of new analytical methods, namely gas chromatography-mass spectrometry (GC-MS), in combination with computer-based data processing systems, and affordable bench top GC-MS systems at the beginning of the 1990s. This is also reflected in the increase in the number of publications since 1990 (see below). Modern analytical methods have reached a level of sensitivity that allows for the study of temporal changes in the scent emission (e.g. differences between developmental stages, effect of stress on volatile emission) and better spatial resolution (e.g. differences between flower parts).

Exploring the value of VOCs for their medicinal properties and use in commercial products produced by the flavour and fragrance industries has also become an important field of research.

Currently the research in the field relating to plant volatiles is rapidly growing. In the past 20 years more than 5800 papers were published on essential oils (with more than 900 publications and 11,000 citations in 2009) and more than 2000 papers on floral scent alone (with more than 200 publications and 4500 citations in 2009) (source ISI Web of Sciences search (on 08 August 2010) for the keywords related to topic (A) essential oil* AND topic plant*; (B) volatile* OR odour* OR odor* OR fragrance* OR scent* AND pollinat* OR flower OR floral). The importance of the field is also reflected in the 2009 publication of a Special Issue on this topic in *Functional Ecology* with the title: "Floral scent in a whole plant context".

This Special Issue of the South African Journal of Botany contains 19 full papers (including two reviews) and 3 short communications covering not only different research directions within the fields of plant volatile research but also different groups of organisms including fungi (2 studies), gymnosperms (2 studies), and angiosperms (18 studies). The Special Issue demonstrates not only how the analysis of plant volatiles has become an integral approach for understanding the ecology and evolution of plant–animal interactions but also reports on aspects of essential oil research in the context of their commercially important role in the flavour and fragrance industries and their potential as antimicrobial, anti-oxidant and anti-inflammatory substances.

Southern Africa boasts a unique and diverse botanical heritage of almost 30,000 species. Complementing this unique botanical heritage is South Africa's cultural diversity with traditional healing being integral to each ethnic group. In addition, South Africa represents a global epicenter of aromatic plants, many of which are used in healing rites. Fragrant plant groups such as the Rutaceae (290 species), Lamiaceae (235 species) and the Asteraceae (2300 species) are abundantly distributed throughout the country and remain largely unexplored with respect to the VOC composition. This Special Issue, dedicated to plant volatiles, has the dual aim of documenting some recent studies in this field and to stimulate further research in this fascinating discipline of plant biology.

1. Biochemistry and biochemical pathways of plant volatiles

This Special Issue starts with a review article by Maffei (2010-this issue) giving an overview on the sites of synthesis, biochemistry and functional role of plant volatiles.

Flower scent and flower colour are both important for plant reproductive success (e.g. Majetic et al., 2009) and the combination of visual and the olfactory signals often has a greater influence on pollinator behaviour than either of these cues alone. However, it is possible that the evolution of certain

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scent and colour combinations is not independent because of shared biochemical pathways for pigment and volatile production. To investigate this question, Majetic et al. (2010-this issue) analyzed the biochemical connections between anthocyanin biosynthesis and floral scent production in *Ipomoea purpurea* (Convolvulaceae) by comparing inbred lines of wild type purple flowered plants to lines of two naturally occurring colour mutants.

2. Essential oils and VOCs — chemical diversity and biological activity

South Africa has offered the world two important aromatic plants; *Agathosma betulina* (Buchu) and *Pelargonium graveolens* (and its hybrids) from which geranium oil is obtained. Geraniol, one of the components of rose-geranium imparts the special floral characteristics of this oil. In a review article on the terpene alcohol geraniol (3,7-dimethylocta-trans-2,6-dien-1-ol), one of the most important molecules in the flavour and fragrance industries, Chen et al. (2010-this issue) report and discuss some of the most important applications and biological properties of this compound.

2.1. Chemical diversity — new reports on plant volatiles and essential oils

Kamatou et al. (2010-this issue) describe, for the first time, the chemical composition of the wood and leaf oils of the "Clanwilliam Cedar" (*Widdringtonia cedarbergensis* J.A. Marsh), a critically endangered species in South Africa, and compares these data with other cedars.

2.2. Potential medicinal use of plant essential oils

In a paper on one of the most widely used medicinal plants in African traditional medicine, *Artemisia afra* that is commonly administered in polyherbal combinations to treat respiratory infections, Suliman et al. (2010-this issue) provide evidence for the antimicrobial effect of *A. afra* essential oils in combination with essential oils from three medicinal aromatic plants; *Agathosma betulina*, *Eucalyptus globulus* and *Osmitopsis asteriscoides*. Using the *in vitro* minimum inhibitory concentration (MIC) assays on four pathogens, they show that the individual oils mostly displayed moderate activity. However, predominantly synergistic interactions and, to a lesser extent, additive effects, were noted for all combinations. In a similar study Van Zyl et al. (2010-this issue) investigate the pharmacological interactions of essential oil constituents on the *in vitro* growth of *Plasmodium falciparum* and highlights their potential as adjuvants in the elimination of malaria infections. These two studies make a valuable contribution as a plethora of papers have been published on the bio-activity of essential oils or individual volatile constituents while the possible interactions between VOC's are often neglected.

Using a classical pharmacognostic approach, the multidisciplinary paper by Hulley et al. (2010-this issue) reports on the ethnobotany, leaf anatomy, essential oil variation and biological activity of *Pteronia incana* (Asteraceae).

While most papers reporting the antimicrobial properties of natural products acutely focus on the planktonic form of the pathogens, Leonard et al. (2010-this issue) reports the ability of aromatic plants to inhibit the more resistant biofilms formed by many pathogens.

2.3. Biological activity of essential oils

Essential oils have gained popularity as natural fungicides due to their biological activity against fungal pathogens. Regnier and Combrinck (2010-this issue) completed a commercial trial to determine the efficacy of essential oils for the control of the "wet bubble" disease of *Agaricus bisporus* and demonstrate the potential use of VOCs for the control of this disease on button mushrooms.

2.4. Quality assessment of essential oils

Quality control procedures for herbal raw material are vital to guarantee the authenticity and quality of consumer products. Van Vuuren et al. (2010-this issue) document the volatile composition and antimicrobial activity of frankincense essential oil. The paper illustrates the immense chemical variation in oil composition for 20 commercial oils, all sold under the name of "frankincense". As biological activity is dependent on the chemistry, the authors demonstrate how the oil composition impacts on the antimicrobial activity.

Agathosma betulina ("buchu") is a coveted indigenous ethnomedicinal plant which has gained commercial popularity and is used in flavour and fragrance formulations. Sandasi et al. (2010-this issue) uses vibrational spectroscopy and chemometric computations to discriminate between *A. betulina* and a close taxonomic ally, *A. crenulata*. As a secondary objective the paper explores the potential application of vibrational spectroscopy to rapidly quantify key volatiles in the essential oil of *A. betulina*.

3. Plant volatiles in an ecological context — plant–animal interactions

3.1. Flower volatiles as host signals for flower parasites

Acacia cyclops (Fabaceae), an Australian species, was introduced into South Africa in the nineteenth century and has invasive status in South Africa. For bio-control reasons the gall midge *Dasineura dielsi* (Diptera:Cecidomyiidae) was released in 2001. However, nothing is known about the chemical cues used by the midge for locating its host. Kotze et al. (2010-this issue) investigate the volatiles associated with different flower stages and leaves of *A. cyclops* and discuss the potential role of these volatiles as cues for *D. dielsi* to locate its host plant.

In a second paper on plant volatiles as signals for parasites Augustyn et al. (2010-this issue) found a correlation of volatile profiles of twenty mango cultivars with their susceptibilities to mango gall fly infestation. A chemometric model was developed which was able to predict the susceptibility or resistance of 90% of the cultivars accurately.

3.2. Flower (and cone) volatiles as key signals for insect attraction

In many angiosperm flowers VOCs play a key role for pollinator attraction and it has been suggested that floral volatiles played a key role in early angiosperm evolution (Gottsberger, 1988; Thien et al., 2000) leading to the success of this group. However, information on other plant groups suggests that chemical communication of plants with insects is more universal and probably also precedes the evolution of the angiosperms. In cycads (gymnosperms) scent emission seems to play an important role for attracting insects to female cones and the paper by Suinyuy et al. (2010-this issue) documents the scent chemistry and patterns of thermogenesis in male and female cones of the African cycad *Encephalartos natalensis* (Zamiaceae).

When considering the number of plant species for which data on floral volatiles are available the orchids are by far the most intensively investigated plant group among angiosperms (Knudsen et al., 2006). Their fascinating and often very specialized pollination biology makes them ideal model systems for questions related to phenotypic selection, and specialization. It is therefore not surprising that two papers, in this Special Issue report on orchids. Both papers use an integrative approach combining data on the pollination biology, floral scent chemistry, flower colour, and morphology.

Van der Niet et al. (2010-this issue) investigate the associations between floral traits (scent, colour, and morphology) and pollination systems in four species of the southern African orchid genus *Schizochilus* on population level. Pollinator observations indicate that the presence of distinct pollination systems are associated with subtle, but significant, differences in floral morphology and scent chemistry. Furthermore, the scent chemistry differed not only between species but also between populations of the same species, indicating that diversification is ongoing in this genus.

In a paper by Johnson and Hobbhahn (2010-this issue) floral features (morphology, scent, and colour) of a *Disa* species with a generalized pollination system are analyzed to better understand what are the main factors explaining generalized pollination in the species. *Disa fragrans* subsp. *fragrans* is pollinated by insects belonging to at least four insect orders (flies, beetles, bees, and moths). Nevertheless, its pollination success and pollen transfer efficiency are comparable to those of its close relative, *Disa sankeyi*, which is pollinated by a single genus of wasps. *Disa fragrans* showed a 100 fold greater floral scent emission than *Disa sankeyi* with a wide range of scent compounds which are known to be general attractants for different insects. This case of generalist pollination in *D. fragrans* is an example of how floral advertising traits might evolve during an evolutionary shift from specialized to generalized pollination.

Another plant family well known for their specialized floral morphologies and pollination systems and distinct floral aromas is the Apocynaceae. However, while orchids scents have been intensively investigated our knowledge on Apocynaceae is still relatively limited. The Apocynaceae also evolved remarkably similar mechanisms for pollen transfer via pollinia. The potential of this plant family as model systems for studying ecological and evolutionary questions is supported by the fact that four different publications in this Special Issue (Heiduk et al., 2010-this issue; Johnson and Jürgens, 2010-this issue; Jürgens et al., 2010-this issue; Shuttleworth and Johnson, 2010-this issue) contain data on representatives of this family.

A paper by Jürgens et al. (2010-this issue) presents data on floral scent composition of thirteen species from eight genera of Apocynaceae (Asclepiadoideae and Secamonoideae)

The vast majority of chemicals identified were common components in flower odour bouquets of angiosperms. However, *Cibirhiza albersiana* showed high relative amounts of acetoin (3-hydroxy-2-butanone; 97.6%) in its flower scent. This compound has rarely been reported as a flower scent component and is more commonly found in fermentation odours [see also the two other papers in this Special Issue that report on acetoin: Johnson and Jürgens (2010-this issue) and Steenhuisen et al. (2010-this issue)].

In their paper on the scent chemistry and pollinator attraction in the deceptive trap flowers of *Ceropegia dolichophylla* (Apocynaceae, Asclepiadoideae) Heiduk et al. (2010-this issue) report very unusual chemical compounds (spiroacetals and aliphatic compounds) that are emitted from its flowers. The authors show in bioassays that the common flower visitors, milichiid flies, were attracted by floral scent. Interestingly, milichiid flies are kleptoparasites that feed on the prey (haemolymph or other secretions) of predatory arthropods, e.g. spiders, to which they are attracted by scent and the data thus suggest that the floral scent of *C. dolichophylla* mimics these feeding site odours.

Shuttleworth and Johnson (2010-this issue) found distinct scent profiles when comparing the floral scent composition of seven putatively chafer-pollinated asclepiad species (*Asclepias*, *Pachycarpus* and *Xysmalobium*). This suggests that plants may use different chemical “strategies” to attract beetles. Furthermore, the potential for using floral scent as a tool for studying hybridization in plants is demonstrated (see also the paper by Johnson and Hobbhahn (2010-this issue).

Beetles also play an important role as pollinators in some *Protea* species but nothing has been known about their scent chemistry thus far. To fill this void, Steenhuisen et al. (2010-this issue) investigated the spatial and temporal variation of scent emission of inflorescence volatiles of four South African beetle-pollinated *Protea* species. Their results illustrate how dynamic the emissions from various flower parts are and that the overall floral scent is a blend of spatial scent differences. Although the four species had many scent compounds in common, significant differences in overall scent composition were evident. This was due to various species-specific compounds, such as the unique tiglate esters found in the scent of *P. welwitschii*. The authors also found that typical fermentation products like acetoin and aromatic alcohols were emitted mainly from senescing inflorescences and from nectar and the role of these compounds for attracting pollinators is discussed.

In a paper by Burger et al. (2010-this issue) visual and olfactory floral cues of different *Echium* and *Pontechium* (Boraginaceae) species were compared to those of the closely related *Anchusa officinalis* (Boraginaceae) to reveal whether specific cues may allow oligolectic *Hoplitis adunca* bees (Megachilidae) to recognize its host plants. The authors showed that *Echium*/*Pontechium* provides a specific scent bouquet with some compounds (cis-3-nonenal and 1,4-benzoquinone) being described for the first time as floral scent compounds.

3.3. Plant volatiles as insect attractants in an evolutionary context

Johnson and Jürgens (2010-this issue) demonstrate a pattern of convergent evolution in the volatile emissions of a stinkhorn fungus (*Clathrus archeri*) and seven fly-pollinated angiosperms with foetid floral odours. To further explore the degree of convergent evolution between the fungus and angiosperms the authors analyzed reference scent samples collected from rotting meat, horse dung, dog faeces, and also samples from confamilial species pollinated by other vectors. Both the fungus and the flowering plants seem to attract flies by the same types of chemicals (such as oligosulphides, phenol, indole and *p*-cresol) through mimicry of animal carrion and faeces. In the case of the “stinkhorn” fungi flies are attracted to the fruiting bodies and used as agents of spore dispersal whereas in the case of the sapromyiophilous flowers the flies serve as pollinators.

4. Outlook and perspectives for future research

Species diversity, species interactions (e.g. plant–pollinator, plant–herbivore, and plant–pathogen) and biochemical diversity may be linked at regional scales. Regions of high biodiversity, the so called “biodiversity hotspots”, contain not only valuable medicinal (and other) resources, but are also natural laboratories for studying biochemical diversity in an ecological and evolutionary context. Future challenges will include integrating disparate fields associated with research on plant VOCs like chemotaxonomy, pollination biology, pest-insect research, flavour and fragrance research, and ethnobotany and developing stronger links with molecular biology.

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