#### Ber. d. Reinh.-Tüxen-Ges. 29, 99-107. Hannover 2017

### Evolution and functional diversity of floral volatiles

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#### Abstract

Angiosperms show an astonishing chemical diversity of floral volatiles. More than 1700 floral volatile organic compounds (VOCs) have been described in the literature. This raises the question: why so many? It seems plausible that the high chemical diversity found in angiosperms has played a key role for the evolution of functionally diverse associations with specific pollinator groups. The functional diversity in turn could affect biodiversity via ethological isolation. In this review, I am interested in exploring the link between the chemical diversity of floral volatiles and the functional diversity of plant-pollinator interactions found in angiosperms. To this end, I will discuss how functional diversity may emerge from VOC diversity. To illustrate the different functional aspects of floral VOCs floral mimicry systems will be used because they allow us to interpret the scent in the ecological and evolutionary context of the attracted animal. I will briefly touch on information of plant hybrid systems to explore how changes in the odour composition may lead to a break-down of plant-pollinator associations and/or the formation of new associations (pollinator shifts). Finally, future research avenues are identified which could contribute to a better understanding of the proximate and ultimate causes for the functional diversity of fragrance bouquets in angiosperm flowers.

#### Zusammenfassung

Blütenpflanzen zeichnen sich durch eine erstaunliche chemische Diversität der von ihnen produzierten Blütenduftstoffe aus. Mehr als 1700 verschiedene Duftmoleküle wurden bisher in der Literatur beschrieben. Daraus ergibt sich die Frage: warum so viele? Es scheint plausibel, dass die hohe chemische Diversität leicht flüchtiger Verbindungen, welche wir bei Angiospermen finden, ursächlich mit einer hohen funktionellen Diversität dieser Gruppe verknüpft ist. Die Produktion von Blütendüften ermöglicht Blütenpflanzen die Anlockung spezialisierter Bestäubergruppen. Deshalb erscheint es auch logisch, dass via ethologischer Isolation die Artendiversifizierung mit der funktionellen Diversifikation der Blütenduftstoffe einherging. In diesem Übersichtsartikel wird dieser mögliche Zusammenhang zwischen der chemischen Diversität volatiler Blütenduftstoffe und der hohen funktionellen Diversität der Angiospermen beleuchtet. Zunächst einmal wird dabei die Entstehung funktionaler Diversität im Zusammenhang mit der Spezifität von Duftsignalen analysiert. Anhand von Beispielen wird illustriert wie Veränderungen der Duftstoffzusammensetzung zu funktionell neuen Interaktionen führen können. Die unterschiedlichen funktionellen Aspekte von Blütenduftsignalen werden anhand von Mimikry Systemen erörtert, da diese Systeme einen Zugang zu den ökologischen und evolutiven Ursachen für die Lockwirkung von Blütendüften auf Insekten ermöglichen. Des Weiteren soll anhand von pflanzlichen Hybrid-Systemen der Frage nachgegangen werden, wie sich Veränderungen der Duftstoffzusammensetzung auf die Bestäuberzusammensetzung auswirken kann. Abschließend wird ein kurzer Ausblick gegeben, welche zukünftigen Forschungsfelder zu einem besseren Verständnis der funktionalen Diversität von Blütendüften beitragen können.

#### 1. Introduction

With more than 1700 reported scent compounds (from c. 1000 species) emitted from their flowers angiosperms show an amazingly high diversity of volatile organic compounds (VOCs) (KNUDSEN et al. 2006). The high chemical diversity has been explained to be the result of divergent evolution to a wide range of different pollinating animal species. In the last 30 years, with the advancement of analytical methods (e.g. gas-chromatography coupled to mass spectrometry), evidence has accumulated that the chemical composition, emission rate, and time of scent emission reflect adaptations to the olfactory preferences, sensitivity, and behaviour of their most important pollinators (e.g. KNUDSEN et al. 2006). Chemical similarities in unrelated plants with functional similar pollinator types have been interpreted as convergent evolution of the plants to the sensory preferences of the pollinating animals. This is supported by the findings that plants associated with the same pollinator type, such as moths (KNUDSEN & TOLLSTEN 1993), bats (BESTMANN et al. 1997; KNUDSEN & TOLLSTEN 1995), beetles (JÜRGENS et al. 2000; STEENHUISEN et al. 2010), or carrion flies/beetles (JOHNSON & JÜR-GENS 2010; JÜRGENS & SHUTTLEWORTH 2016), show significant similarities in their floral scent composition. For instance, moth pollinated species emit typical benzenoid esters and aldehydes, e.g. methyl benzoate, phenylacetaldehyde (KNUDSEN & TOLLSTEN, 1993; JÜR-GENS et al. 2002). Whereas flowers pollinated by carrion flies often emit sulphur containing compounds, which for the flies are indicative of bacterial degradation of plant and animal tissue (STENSMYR et al. 2002; JÜRGENS et al. 2006; JÜRGENS et al. 2013; MORÉ et al. 2013).

Among the different floral features, such as colour and rewards, floral scent has been shown to play a key role for mediating the interactions with mutualistic but also antagonistic animals (e.g. RAGUSO 2008a,b; WRIGHT & SCHIESTL 2009). The floral scent composition of single flower can be amazingly diverse in terms of the number of compounds that are produced (RAGUSO 2008a,b). Flower scent may consist of more than 50 different chemicals emitted from a single flower (e.g. JÜRGENS et al. 2006). Yet, the diversity of compounds found in the scent of a flower is not directly correlated to the number of flower visitors that are attracted. This suggests that floral scent is a complex trait where different combinations of VOCs may form adaptive peaks of functional entities in terms of pollinator attraction and that these adaptive peaks need to be analysed in relation to the sensory abilities and information processing of the interacting animals (RAGUSO 2003; RAGUSO 2008a,b; WRIGHT & SCHI-ESTL 2009). The interpretation of floral scent profiles is further complicated by the fact that processing of floral scent information and decision making of flower visitors (based on learning) is strongly affected by the local environmental context of the flower- and flower- visitor community interacting with each other (see BISCHOFF et al. 2015). Thus, information from field observations and lab experiments are needed to disentangle the main factors that affect plant-flower visitor interactions.

In this review I am interested in the question how the high functional diversity observed in angiosperms-flower visitor interactions may be linked to their floral VOC diversity. However, the question – "why do we find so many VOCs in angiosperms?" has some subtle aspects to it. One subtlety is for example that diversity can be defined in different ways. Although diversity could be simply described in terms of the number of compounds that have been reported from angiosperm flowers such a definition would ignore that the (e.g. attractive or repellent) function of a given odour blend is a reflection of the receiver's innate and learned responses to the fragrance bouquet (or a subset of compounds in the scent bouquet).

I have chosen to illustrate the different functional aspects of floral VOCs by using floral mimicry systems because the attractive function of floral scent compounds in these systems

can be interpreted on the background of the sensory ecology and evolution of the pollinator. Furthermore, to explore how changes in the odour composition may lead to a break-down of plant-pollinator associations and/or the formation of new associations (pollinator shifts) I will use information from plant hybrid systems.

## 2. The role of floral volatiles for the interaction with mutualists and antagonists

It is often assumed that the interactions between flowering plants and their pollinators is based on mutualism and coevolution - the idea that adaptive traits evolve by reciprocal selection (see JOHNSON & ANDERSON 2010, and references therein). However, both animals and plants need to be choosy to achieve the highest fitness gain out of the possible interaction partners in a given environment. From the animal's perspective some interaction partners are partly, largely, or completely deceptive (non-rewarding) and should be avoided. The same is true for plants, where a wide range of non-beneficial flower visitors have been reported in the literature (e.g. IRWIN et al. 2001); among them nectar larcenist and pollen feeders/collectors, which exploit the floral resources without any benefit for the plant. However, the diversity of floral VOCs do not only reflect the diversity of pollinator types - each type with a different odour preference - but also other functions (Fig. 1). In this context it seems plausible that selection renders the scent composition of a given flower in such a way that it increases the



Figure 1. Hypothetical fragrance bouquet and its effect on different flower visitors, a butterfly, a fly, and a bee. Different compounds may be attractants for different flower visitors, while the same com-pounds may deter other potential flower visitors. Different flower visitors may overlap in the spec-trum of compounds they are attracted by. Some compounds may have an additional function, such as antimicrobial properties, to protect the flower from pathogens. Note, that not only the odour composition but also the relative amount of each compound in the bouquet may change the attrac-tiveness of the blend.

overall fitness benefit with (mutualistic and antagonistic) floral interaction partners (SCHI-ESTL 2015; Zu et al. 2016; GERVASI & SCHIESTL 2017). In other words a flower should emit VOCs that attract those flower visitors that provide the highest benefit while VOCs associated with interaction partners that lower the fitness benefits should be selected against (GERVASI & SCHIESTL 2017). Indeed, for many VOCs a biological function has been reported and in addition to their role as pollinator attractants, it has been suggested that they deter antagonistic flower visitors (e.g. OMURA et al. 2000). However, there are still wide gaps in our knowledge with respect to pollinator-driven adaptive evolution of floral scent. Only more recently studies by ZU et al. (2016) and GERVASI & SCHIESTL (2017) have demonstrated that floral scent can evolve rapidly under pollinator-driven phenotypic selection.

#### 3. Floral signals and floral cues - the plant and animal perspective

VOCs provide an important information source for animals. There are four main factors that have been demonstrated to play a key role in influencing flower visitor attraction and specialization in angiosperms: (1) the scent composition, (2) the relative ratios of compounds in a given scent, (3) the temporal scent emission patterns, and (4) the spatial scent patterns (e.g. WRIGHT et al. 2005a, 2005b). Among the enormous number of possible scent trait combinations some adaptive peaks have been identified. For instance, to play a role as pollinator attractant the scent emission rate needs to be above the sensitivity level and below the tolerance level of a given pollinator. Some combinations of VOCs may have synergistic effects on the attractiveness of an odour blend, while some compounds repel a specific group of animals (Fig. 1). Finally, other roles of floral VOCs such as antimicrobial properties, and chemical defence against antagonists have been discussed (e.g. THEIS 2006; THEIS et al. 2007). However, the response of an animal for a given scent compound (or combination of compounds) depends on several factors. At the receptor level the animal needs to have the ability to perceive the compound. At the information processing level the animal may receive the sensory input but this information must not necessarily trigger a behavioural response. Furthermore, it is also important to distinguish between innate versus learned responses of animals to VOCs. Flower visitors may learn to overwrite an innate preference for a given scent by learning to avoid it if there are more rewarding alternatives (e.g. CUNNINGHAM et al. 2004).

Several studies have shown that flower-visiting animals use specific VOCs to locate their preferred host plants (e.g. JÜRGENS et al. 2014). However, the scent emitted from a flower is only very indirectly linked to the presence of a food source. Only if the animal receives a reward when visiting the flower the VOC signal can be regarded as an honest signal. Thus, from an animal's perspective it would be better to find food by using olfactory cues that are directly correlated with the quantity and quality of the food source. However, the main macronutrients utilized by most flower visitors carbohydrates (e.g. nectar), protein (e.g. pollen, food bodies), fat (e.g. pollen, some oil producing flowers) are difficult to find based on olfaction because they consist of relatively large molecules with low volatility. Most animals therefore rely on indirect indicators for the presence of these compounds, namely microbial degradation products of the macronutrients. For instance, animals interested in carbohydrates should be sensitive to hydrocarbon alcohols (e.g. ethanol) or hydrocarbon acids (e.g. acetic acid) since they are produced during the fermentation of sugar by microorganisms (see STÖKL et al. 2010; JÜRGENS & SHUTTLEWORTH 2016). From this it becomes clear that the interpretation of VOCs in terms of its function can be quite difficult. Some compounds in the fragrance bouquet may have multiple function while others act as attractants or deterrents only. Furthermore, insects are often opportunistic in their behaviour and may respond differently to the same chemical bouquet depending on the experience they have acquired during

foraging. In such a scenario different chemical strategies might evolve in different populations.

## 4. Plant hybrid systems: a natural laboratory to investigate signal change and signal breakdown

From the above it seems clear that any change in the scent composition or emission rate of a given plant species may affect the attractiveness of a flower for a given flower visitors (WRIGHT & SMITH 2004). Furthermore, what are the kind of changes that can lead to a functional shift of an olfactory signal leading to a functional shift in the pollinator, e.g. from bird to beetle pollination? Theoretically any change in the relative amounts or composition (new compounds, loss of compounds) could produce a functional shift. Curiously, this question has only been addressed in a few studies so far. SHUTTLEWORTH & JOHNSON (2010a) tested in field experiments whether adding sulphur (dimethyl disulphide and dimethyl trisulphide) compounds to flowers can mediate a shift between a fly and a wasp pollinated *Eucomis* (Hyacinthaceae) species. They found that wasp and fly pollination depended on the production or suppression of sulphur compounds in the floral scent (SHUTTLEWORTH & JOHNSON 2010a).

Another possibility to analyse the effects of floral VOC changes is to investigate hybrid species systems where closely related parent species are compared with the hybrid offspring to analyse whether changes in the floral VOC composition and flower visitors can be observed. A couple of such systems have been investigated so far (SALZMANN et al. 2007; VEREECKEN et al. 2010; SHUTTLEWORTH & JOHNSON 2010b; BISCHOFF et al. 2014, 2015; MARQUES et al. 2016). These systems are particularly interesting in the context of floral scent evolution and pollinator shifts because one possible prediction for such systems is that changes in the scent composition might contribute to the ethological isolation of hybrids if they emit unique scent compounds that are not present in the parent species (e.g. VEREECK-EN et al. 2010; MARQUES et al. 2016). For instance, in a study by MARQUES et al. (2016) the role of ethological isolation and its contribution to the potential establishment of two independent naturally occurring hybrid lineages was examined in three autumn-flowering hybridizing Narcissus (daffodils) species. They found that parent species were pollinated by butterflies (N. serotinus and N. miniatus) and bees (N. cavanillesii) respectively, while the two hybrids (N. ×perezlarae, N. ×alentejanus) were mainly pollinated by ants. Interestingly, the authors also reported that the absolute emission rate of floral VOCs in hybrid plants was equal or even higher in parental species and that its scent composition showed some new compounds. MARQUES et al. (2016) explained the pollinator shift occurring in parallel in the two hybrids by a significant increase in nectar production together with changes in the VOC composition. However, the authors state that further research is needed to investigate whether VOCs alone can explain the absence of ant visits to the parental species, either because attractants are missing or because ant repellents are emitted by N. serotinus and N. miniatus.

### 5. Scent evolution in mimicry systems

Flowering plants and their relationship with mutualistic pollinators have often been used as examples for coevolution (see JOHNSON & ANDERSON 2010). Classical examples of coevolution are the morphological adaptations of flower tube/spur length to the tongue length of pollinators (JOHNSON & ANDERSON 2010). Curiously, much less is known about floral scent and there is only very limited evidence that coevolution has played a role for the evolution of floral scent. More recent studies haven even suggested an alternative hypothesis to the coevo-

lution hypothesis, namely that floral scent evolved based on a sensory bias of the receiver (e.g. SCHAEFER & RUXTON 2009; SCHIESTL & DÖTTERL 2012). In other words flowering plants exploit the pre-existing sensory preference of a given animal for the purpose of pollination. In the case of the coevolution hypothesis both partners evolve features (e.g. scent features of the plant and olfactory preferences of the animal) to increase their fitness benefit in the partnership, whereas in the receiver bias model the plant exploits a pre-existing preference that the animal evolved in a different context. The receiver bias hypothesis is not necessarily associated with a deceptive strategy where no reward is offered by the plant. However, receiver bias plays indeed an essential role in deceptive mimicry systems where an animal searches for a food source, a brood site, or sexual partner using olfactory cues/signals (SCHI-ESTL et al. 2003). In such deceptive mimicry systems the plant exploits the chemical communication or the innate/learned preference for a resource by producing the same VOCs or VOCs that are translated by the animal into the same meaning without providing any reward for the pollinator (JOHNSON & JÜRGENS 2010; JERSKOVA et al. 2012a,b; JÜRGENS & SHUTTLEWORTH 2016). Examples for such mimicry systems are sexual deceptive orchids, flowers produce sex pheromones identical to those of female insects (SCHIESTL et al. 1999). In carrion/dung mimicry systems the model is more macabre; these systems imitate the odour of a decomposing carcass or the scent emitted from the faeces of an animal (JÜRGENS & SHUTTLEWORTH 2016).

#### 6. Outlook and future perspectives

Flower scent is probably the most complex among the different floral features involved in flower-visitor attraction. The floral scent composition together with spatial (DÖTTERL & JÜRGENS 2005) and temporal (DÖTTERL et al. 2012; JÜRGENS et al. 2014) scent emission patterns may influence the interaction with mutualistic and antagonistic flower visitors. Is the high functional diversity that we observe in angiosperm flowers the result of their evolutionary potential to produce a diverse array of different VOCs? Many of the VOCs involved in pollinator attraction are produced in plant groups that, from an evolutionary perspective, predate angiosperms (e.g. monoterpenes are found in large amounts in gymnosperms). This suggests that pre-existing biosynthetic pathways changed their function from constitutive defence against herbivores to pollinator attraction (see PELLMYR & THIEN 1986). Such a functional change was possible because angiosperms complete their life cycle much faster than gymnosperms. Thus, under the relaxed selection pressure to protect reproductive tissue angiosperms secondary chemical compounds could change their function from defence against antagonists to attracting mutualists.

There are still wide gaps in our knowledge regarding the evolution of functional scent diversity in angiosperms. VOC diversity can be described at different levels such as the individual, population (e.g. VAN DER NIET et al. 2010), and higher taxonomic levels (e.g. SCHI-ESTL & DÖTTERL 2012; JÜRGENS et al. 2013). Three aspects need more attention in the future: Firstly, evidence for coevolution with respect to the evolution of floral scent and the corresponding sensory apparatus are very limited (see SCHIESTL & DÖTTERL 2012). A global analysis on VOC patterns in angiosperms, using a phylogenetic approach, could provide insights into evolutionary trends for different plant lineages such as convergent and/or divergent evolution of VOCs or the occurrences of novel compounds (biosynthetic pathways). A similar approach could be applied to pollinators that are obligate mutualists, such as yucca moths and fig wasps. It would be interesting to analyse if evolutionary changes in the sensory system of these groups do correlate with the scent signals of their host plants – demonstrating coevolution. Secondly, an important aspect not addressed in this review are the underlying regulatory processes that are responsible for VOC diversity in angiosperms.

Thirdly, the mechanisms how pollinating animals process olfactory information in complex and constantly changing environments needs more attention (SCHRÖDER & HILKER 2008; RIFFELL et al. 2014). It seems likely that the same scent composition may attract different animals at different localities because the meaning of the scent information depends on previous experience (BISCHOFF et al. 2015).

#### References

- BESTMANN, H.J., WINKLER L. & von HELVERSEN O. (1997): Headspace analysis of volatile flower scent constituents of bat-pollinated plants. – Phytochemistry 46: 1169-1172.
- BISCHOFF, M., JÜRGENS, A. & CAMPBELL, D.R. (2014): Floral scent in natural hybrids of *Ipomopsis* (Polemoniaceae) and their parental species. Annals of Botany. **113**(3): 533-544.
- BISCHOFF, M., RAGUSO, R.A., JÜRGENS, A. & CAMPBELL, D.R. (2015): Context-dependent reproductive isolation mediated by floral scent and color. – Evolution, 69: 1-13.
- CUNNINGHAM, J.P., MOORE, C.J., ZALUCKI, M.P. & WEST, S.A. (2004): Learning, odour preferences and flower foraging in moths. J. Exp. Biol. **207**: 87-94.
- DÖTTERL, S. & JÜRGENS, A. (2005). Spatial fragrance patterns in flowers of *Silene latifolia*: Lilac compounds as olfactory nectar guides? – Plant Systematics and Evolution 255: 99-109.
- DÖTTERL, S., JAHREISS, K., JHUMUR, U.S. & JÜRGENS, A. (2012): Temporal variation of flower scent in *Silene otites* (Caryophyllaceae): a species with a mixed pollination system. – Botanical Journal of the Linnean Society 169: 447–460.
- GERVASI, D.D.L. & SCHIESTL F.P. (2017): Real-time divergent evolution in plants driven by pollinators. – Nature Communications 8: 14691.
- IRWIN, R.E., BRODY, A.K. & WASER, N.M. (2001): The impact of floral larceny on individuals, populations and communities. Oecologia 129: 161–169.
- JERSÁKOVÁ, J., JÜRGENS, A., ŠMILAUER P. & JOHNSON, S.D. (2012a): The evolution of floral mimicry: identifying traits that visually attract pollinators. – Functional Ecology 26: 1381–1389.
- JERSÁKOVÁ, J., JOHNSON, S.D. & JÜRGENS, A. (2012b): Deceptive behavior in plants. II. Food deception by plants: from generalized systems to specialized floral mimicry Plant-Environment Interactions, 223-246.
- JOHNSON, S.D. & ANDERSON B. (2010): Coevolution between food-rewarding flowers and their pollinators. – Evo. Edu. Outreach 3: 32–39.
- JOHNSON, S.D. & JÜRGENS, A. (2010): Convergent evolution of carrion and faecal scent mimicry in a stinkhorn fungus and fly-pollinated angiosperm flowers. – South African Journal of Botany 76: 796-807.
- JÜRGENS, A., WEBBER, A.C. & GOTTSBERGER, G. (2000): Floral scent compounds of Amazonian Annonaceae species pollinated by small beetles and thrips. Phytochemistry **55**: 551-558.
- JÜRGENS, A., WITT, T. & GOTTSBERGER, G., (2002): Flower scent composition in night-flowering Silene species (Caryophyllaceae). Biochem. – Syst. Ecol. 30: 383-397.
- JÜRGENS, A., DÖTTERL, S. & MEVE, U. (2006): The chemical nature of fetid floral odours in stapeliads (Apocynaceae-Asclepiadoideae-Ceropegieae). – New Phytologist 172: 452-468.
- JÜRGENS, A., WEE, S.L., SHUTTLEWORTH, A. & JOHNSON, S.D. (2013): Chemical mimicry of insect oviposition sites: a global analysis of convergence in angiosperms. – Ecology Letters 16: 1157–1167.
- JÜRGENS, A., GLÜCK, U., AAS, G. & DÖTTERL, S. (2014): Diel fragrance pattern correlates with olfactory preferences of diurnal and nocturnal flower visitors in *Salix caprea* (Salicaceae). – Botanical Journal of the Linnean Society 175: 624–640.
- JÜRGENS, A. & SHUTTLEWORTH, A. (2016): Carrion and dung mimicry in plants. In: Benbow ME, Tomberlin JK, Tarone AM (eds) Carrion ecology, evolution, and their applications. CRC Press, Boca Raton, pp 361–386.
- KNUDSEN, J.T. & TOLLSTEN, L. (1993): Trends in floral scent chemistry in pollination syndromes: floral scent composition in moth-pollinated taxa. – Botanical Journal of the Linnean Society 113: 263-284.
- KNUDSEN, J.T., ERIKSSON, R., GERSHENZON, J. & STAHL, B. (2006): Diversity and distribution of floral scent. Botanical Reviews 72: 1-120.
- MORÉ, M., COCUCCI, A.A. & RAGUSO, R.A. (2013): The importance of oligosulfides in the attraction of fly pollinators to the brood-site deceptive species *Jaborosa rotacea* (Solanaceae). International

Journal of Plant Science 174: 863-876.

- OMURA, H., HONDA, K. & HAYASHI, N. (2000): Floral scent of Osmanthus fragrans discourages foraging behavior of cabbage butterfly, Pieris rapae. – Journal of Chemical Ecology 26: 655–666.
- PELLMYR, O. & THIEN, L. B. (1986): Insect reproduction and floral fragrances Keys to the evolution of the angiosperms: – Taxon 35: 76-85.
- RAGUSO, R.A. (2003): Olfactory landscapes and deceptive pollination: signal, noise and convergent evolution in floral scent. In: Insect pheromone biochemistry and molecular biology (eds. Blomquist G.J., Vogt Royal), New York, NY, USA: Academic Press, 631-650.
- RAGUSO, R.A. (2008a): Wake up and smell the roses: the ecology and evolution of floral scent. Annual Review of Ecology Evolution and Systematics **39**: 549–569.
- RAGUSO, R.A. (2008b): Start making scents: the challenge of integrating chemistry into pollination ecology. Entomologia Experimentalis et Applicata **128**: 196–207.
- RIFFELL, J.A., SHLIZERMAN, E., SANDERS, E., ABRELL, L., MEDINA, B., HINTERWIRTH, A.J. & KUTZ J.N. (2014): Flower discrimination by pollinators in a dynamic chemical environment – Science 344: 1515-1518.
- SALZMANN, C.C., COZZOLINO, S. & SCHIESTL, F.P. (2007): Floral scent in food-deceptive orchids: Species specificity and sources of variability. Plant Biology 9: 720-729.
- SCHAEFER, H.M. & RUXTON, G.D. (2009): Deception in plants: mimicry or perceptual exploitation? Trends in Ecology and Evolution 24: 676-685.
- SCHIESTL, F. P., AYASSE, M., PAULUS, H. F., LÖESTEDT, C., HANSSON, B. S., IBARRA, F. & FRANCKE, W. (1999): Orchid pollination by sexual swindle. Nature **399**: 421–422.
- SCHIESTL, F. P. & DÖTTERL, S. (2012): The evolution of floral scent and olfactory preferences in pollinators: coevolution or pre-existing bias? – Evolution 66: 2042-2055.
- SCHIESTL, F.P., PEAKALL, R., MANT, J.G., IBARRA, F., SCHULZ, C., FRANKE, S. & FRANKE, W. (2003): The chemistry of sexual deception in an orchid-wasp pollination system. – Science 302: 437-438.
- SCHIESTL F.P. (2015): Ecology and evolution of floral volatile mediated information transfer in plants. New Phytologist **206**: 571–577.
- SCHRÖDER, R. & HILKER, M. (2008) The relevance of background odor in resource location by insects: a behavioral approach. Bioscience, 58, 308–316.
- SHUTTLEWORTH, A. & JOHNSON, SD. (2010a): Floral scents of chafer-pollinated asclepiads and a potential hybrid. South African Journal of Botany **76**: 770-778.
- SHUTTLEWORTH, A. & JOHNSON, S.D. (2010b): The missing stink: sulphur compounds can mediate a shift between fly and wasp pollination systems. Proceedings of the Royal Society of London Series B Biological Sciences **277**: 2811-2819.
- STEENHUISEN, S.L., RAGUSO, R.A., JÜRGENS, A. & JOHNSON, S.D. (2010): Variation in scent emission among floral parts and inflorescence developmental stages in beetle-pollinated *Protea* species (Proteaceae). South African Journal of Botany 76: 779–787.
- STENSMYR, M.C., URRU, I., COLLU, I., CELANDER, M., HANSSON, B.S. & ANGIOY, A-M. (2002): Pollination: rotting smell of dead-horse arum florets. Nature **420**: 625-626.
- STÖKL, J., STRUTZ, A., DAFNI, A., SVATOS, A., DOUBSKY, J., KNADEN, M., SACHSE, S., HANSSON, B.S. & STENSMYR, M.C. (2010): A deceptive pollination system targeting drosophilids through olfactory mimicry of yeast. – Current Biology 20: 1846-1852.
- THEIS N. (2006): Fragrance of Canada thistle *Cirsium arvense* attracts both floral herbivores and pollinators. – Journal of Chemical Ecology 32: 917–927.
- THEIS, N., LERDAU, M. & RAGUSO, R. A. (2007): The challenge of attracting pollinators while evading floral herbivores: Patterns of fragrance emission in *Cirsium arvense* and *Cirsium repandum* (Asteraceae). – International Journal of Plant Science 168: 587–601.
- VAN DER NIET, T., HANSEN, D.M. & JOHNSON, SD. (2011): Carrion mimicry in a South African orchid: flowers attract a narrow subset of the fly assemblage on animal carcasses. – Annals of Botany 107: 981-992.
- VAN DER NIET, T., JÜRGENS, A. & JOHNSON, S.D. (2010): Pollinators, floral morphology and scent chemistry in the southern African orchid genus *Schizochilus*. – South African Journal of Botany 76: 726–738.
- VEREECKEN, N.J., COZZOLINO, S. & SCHIESTL, FP. (2010): Hybrid floral scent novelty drives pollinator shift in sexually deceptive orchids. – BMC Evolutionary Biology 10: 103.

- WRIGHT, G.A., LUTMERDING, A., DUDAREVA, N. & SMITH, B.H. (2005a): Intensity and the ratios of compounds in the scent of snapdragon flowers affect scent discrimination by honey bees (*Apis mellifera*). – Journal of Comparative Physiology A. **191**: 105–114.
- WRIGHT, G. A. & SMITH, B. H. (2004): Variation in complex olfactory stimuli and its influence on odour recognition. – Proceedings of the Royal Society of London Series B 271: 147152.
- WRIGHT, G.A., THOMSON, M.G. & SMITH, B.H. (2005b): Odour concentration affects odour identity in honeybees. Proc. Biol. Sci. 272: 2417–2422.
- WRIGHT, G.A. & SCHIESTL, F.P. (2009): The evolution of floral scent: the influence of olfactory learning by insect pollinators on the honest signalling of floral rewards. – Functional Ecology 23: 841– 851.
- ZU, P., BLANCKENHORN, W. U. & SCHIESTL, F. P. (2016): Heritability of floral volatiles and pleiotropic responses to artificial selection in *Brassica rapa*. – New Phytologist, 209: 1208–1219.

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Zeitschrift/Journal: Berichte der Reinhold-Tüxen-Gesellschaft

Jahr/Year: 2017

Band/Volume: 29

Autor(en)/Author(s): Jürgens Andreas

Artikel/Article: Evolution and functional diversity of floral volatiles 99-107