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MUSTY-EARTHY SCENT IN CACTUS FLOWERS: CHARACTERISTICS OF FLORAL SCENT PRODUCTION IN DEHYDROGEOSMIN-PRODUCING CACTI

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The musty-earthy-smelling sesquiterpenoid dehydrogeosmin (DHG) was found several years ago as a novel compound in flowers of some cactus species, which called attention to the biology of floral scents of the Cactaceae. Our studies showed that the odor bouquet of DHG-producing cactus flowers is dominated by isoprenoids. All floral volatiles were produced by the perianth during the exclusively diurnal anthesis. Volatile emissions were diurnal, as was the daily opening schedule of flowers. Within one species, the odor composition of cultivated specimens varied strongly, whereas little variation was found among individuals of a natural population of the same species. However, field studies revealed that DHG is not produced by all specimens in natural populations. Our results on the timing and location of odor emission support the hypothesis that this unusual volatile may play a role in pollinator-plant interactions.

Keywords: floral scent, floral biology, dehydrogeosmin, geosmin, *Echinopsis*, *Gymnocalycium*, *Mammillaria*, *Parodia*, *Rebutia*, *Turbinicarpus*, Cactaceae.

Introduction

Floral volatiles have been shown to often play important roles in the floral biology of animal-pollinated plants. However, the patterns and diversity of floral scent compounds in cacti have long been neglected. Early references to floral scent in cacti even stated that floral scent in diurnal cacti is mostly absent (Berger 1926; Porsch 1938). Nevertheless, Porsch (1938) mentioned a number of diurnal species with scented flowers. More recently, Rauh (1979) concluded that floral scent is absent or without function in day-flowering cacti. In contrast, Oeser (1978) described the strong musty-earthy scent of the diurnal flowers of several *Sulcorebutia* species, suggesting that geosmin was the responsible substance and discussing its taxonomic value for this genus. Only in 1990 was this unusual musty cactus scent determined to be dehydrogeosmin (DHG; Kaiser and Nussbaumer 1990), a novel natural compound (fig. 1). Subsequently, its synthesis and absolute configuration were clarified by Huber et al. (1993), and its biosynthesis was studied by Feng et al. (1993). Kaiser and Tollsten (1995) presented the first broad survey on the floral scent of cacti, demonstrating different pollination syndromes. This survey revealed a diversity of scent emission patterns and chemical complexities of fragrance compounds (including DHG) among cactus species with distinct pollinator affinities and floral morphologies. These findings compel closer examination of the functional significance of scent chemistry in the Cactaceae.

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Variation in fragrance chemistry occurs on several levels (reviewed by Raguso 2001). The chemical composition of floral scents is thought to be important to specific pollinator classes, and some pollination syndromes are characterized by distinctive odor compounds (Kaiser and Tollsten 1995; von Helversen et al. 2000). Floral scent may also vary between different populations of a species (Knudsen 1994, 2002; Tollsten and Ovstedal 1994). This variation may represent local pollinator preferences (Galen and Kevan 1980; Pellmyr 1986) or neutral genetic drift. Variability of floral scent within populations was shown in several cases (Nielsen et al. 1995; Knudsen 2002) and may be the result of different selective pressures exerted by several sympatric pollinators or pollinator groups (Tollsten and Bergström 1993). Floral scent emission may follow a circadian rhythm, often clearly coinciding with the activity of the respective pollinator or pollinator group. In flowers of *Hoya carnosa* that are open 24 h a day, floral scent is emitted only at night (Matile and Altenburger 1988). In other plants, flowers emit volatiles continuously but with temporal changes in volatile composition (Schiestl et al. 1997).

The unusual volatile DHG has attracted special interest because of its restriction to the Cactaceae, its uncommon perceptual quality, and its low threshold for the human nose. Several authors (Kaiser and Nussbaumer 1990; Feng et al. 1993; Kaiser and Tollsten 1995) have proposed that DHG functions in the reproductive biology of these cacti. Possible functions of floral volatiles in general include attraction (Faegri and van der Pijl 1971; Dobson 1994; Raguso 2001) or repellence (Kennedy and Soerenson 1985; Farrar and Kennedy 1987; Farrar et al. 1992) of floral visitors, antimicrobial properties (Cole et al. 1975; Morris et al. 1979), or influences on pollen germination (French et al. 1979; Hamilton-Kemp et al. 1991). A broad survey in the Cactaceae showed that DHG is produced by only some species of a few genera,

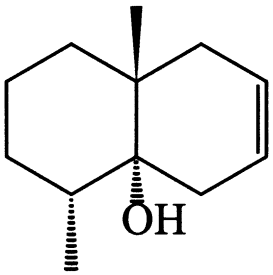

Fig. 1 Chemical structure of dehydrogeosmin

located in different tribes and subfamilies (Schlumpberger 2002). Among more than 500 examined species from 57 genera, DHG-producing flowers were found in only 55 species from seven genera.

As a first approach toward understanding the importance of this unique floral volatile, we studied the scent emission in DHG-producing cacti. The goals of this study were to analyze the emission rate of DHG, identify the floral organs that emit this compound, analyze additional volatile compounds produced by DHG-emitting species, and investigate the kinetics of volatile emission. Intraspecific variation of flower odors, emission rates, kinetics, and location of odor emission have so far never been studied in the Cactaceae, and such data provide a necessary first step in understanding the context in which DHG functions as a component of floral phenotype.

Material and Methods

Plants

The studies were carried out on a variety of DHG-producing cacti from six genera: *Echinopsis* hybrid, *Echinopsis obrepanda*, *Gymnocalycium andreae*, *Gymnocalycium bruchii*, *Gymnocalycium bodenbenderianum* ssp. *intertextum*, *Gymnocalycium monvillei*, *Mammillaria baumii*, *Mammillaria longimamma*, *Mammillaria surculosa*, *Parodia procera*, *Parodia tuberculata*, *Rebutia arenacea*, *Rebutia fabrisii*, *Rebutia marsoneri*, and *Turbinicarpus pseudomacrochele* ssp. *krainzianus*. For the investigations in the laboratory, plants were obtained from a specialized cactus nursery (Uhlig Kakteen, Kernen, Germany). The plants were identified by B. O. Schlumpberger. The field studies on scent production were done in the Sierra Grande, Córdoba, Argentina (31°18′S, 064°49′W, 2000 m above sea level).

Scent Sampling and Analysis

Scent samples were collected from intact plants by using glass desiccators. Sampling was done in a closed-loop system using 12-V vacuum pumps (Fürgut, Tannheim) and carbon traps (1.5 mg; CLSA Filters, Daumazan sur Arize). Filters were eluted twice with 15 μL of acetone, and the samples were stored in glass capillaries at −20°C. Additional samples were taken with solid phase microextraction (SPME) fibers (100 μm; PDMS, Supelco, Bellefont). For odor sampling, the SPME fiber was injected for 15 min into the glass desiccators. In the field, flowers were wrapped in polyester bags (Melitta Toppits Brat-Schlauch, Melitta, Minden).

The samples were analyzed by gas chromatography coupled with mass spectroscopy (GC-MS), using a Finnigan GCQ and a Thermoquest Trace MS (in both, transfer line 265°C, scan range 35–450 Da). The GC-MS was equipped with a DB5 MS ITD (0.25 mm × 30 m, 0.25-μm film thickness) and an AT624 (0.32 mm × 30 m, 3-μm film thickness; Alltech Associates, Deerfield) column, respectively. The carrier gas was helium with a flow rate of 3 mL/min. The temperature program (split) started with 40°C (2 min isotherm), followed by a temperature increase by 10°C/min, up to 200°C, and then with 35°C/min up to 280°C (3 min isotherm). The injector temperature was 260°C. The compounds were identified by their mass spectra and by comparison with standards.

Temporal Patterns in Scent Emissions

To study the timing of scent production, the plants were kept in growth chambers under controlled conditions. Temperatures were 30°C during the day and 8°C during the night. Relative humidity was set to 15% during the day and 50% at night. Depending on the odor intensity, the carbon filters were changed every 2 or 4 h. The temporal patterns of scent emission were studied in *G. andreae*, *G. bodenbenderianum* ssp. *intertextum*, *R. fabrisii*, and *R. marsoneri*.

For the study of the kinetics of scent production, zNose (Electronic Sensor Technology, Newbury Park), a novel method described by Kunert et al. (2002), was applied in addition to traditional GC-MS in order to obtain finer temporal resolution. The zNose is a very sensitive, portable GC that automatically collects and analyzes odor samples in programmed time intervals. The zNose collects volatiles on a Tenax trap and thermally desorbs them. The compounds become separated on a stainless steel DB5 GC column (0.25 mm × 1 m, 0.25-μm film thickness) and are detected by a highly sensitive surface acoustic wave quartz microbalance detector. The cacti were kept in glass desiccators, and a constant stream of purified air (120 mL/min) prevented the accumulation of volatiles. Samples were taken every 30 min. The temperature program started at 40°C, heating up to 180°C by 5°C/s. Because the zNose is not equipped with an MS, additional scent samples were collected at the same time for further qualitative analysis by GC-MS. Therefore, the air stream that constantly passed through the desiccator was directed into a carbon trap for supplemental sample collection. A revolving device with six carbon traps changed the filter automatically every 4 h, allowing the collection of volatiles over a 24-h period without maintenance. The carbon traps were treated as described above but eluted with 2 × 20 μm of dichloromethane instead of acetone. For more detailed description of the methods, see a study by Kunert et al. (2002). DHG was run on the zNose as a standard.

Location of Scent Production

Flowers were dissected in order to collect scent samples from different floral organs, different tepal rows, and different parts of the tepals. Flower parts of several conspecific flowers (preferably from a single specimen) had to be sampled together in order to accumulate enough odor from weakly scented floral organs. The location of scent-producing

tissue was examined in *G. andreae*, *G. bodenbenderianum* ssp. *intertextum*, *G. bruchii*, *R. arenacea*, *R. fabrisii*, *Rebutia heliosa*, and *R. marsoneri*.

Determination of Emission Rates of DHG

Emission rates were investigated in *R. fabrisii*. This species is the epitome of a DHG-producing cactus with only a few other components in its floral scent. The knowledge of total DHG production per hour will facilitate future bioassays with floral visitors. All flowers were in the same developmental stage. Odor samples were taken for 4 h per flower. To quantify the volatile production, 200 μg/mL of 1-bromodecane was added to the samples as an internal standard.

Scent Composition

The composition of the floral scent bouquet was studied in *G. andreae*. The odor bouquet of this species was then compared with the odor of DHG-producing cacti from other species and genera to see whether DHG-producing cacti always have specific compounds in common, i.e., whether there is a typical "DHG odor syndrome." Therefore, the floral volatiles of *G. andreae* were compared with DHG-producing representatives (59 specimens) of six different genera: *Echinopsis* (one species, one hybrid), *Gymnocalycium* (four species), *Mammillaria* (three species), *Parodia* (two species), *Rebutia* (three species), and *Turbinicarpus* (one species).

Variability of Odor Production

To assess the intraspecific variability of floral volatiles, the floral scent composition of 12 specimens of *G. andreae* was studied. In order to check for differences between cultivated plants and specimens in their natural environment, six plants from an Argentine population and six plants from a nursery were randomly chosen and their scent bouquet analyzed and compared.

The cultivated specimens were all grown under identical conditions, and the flowers were of the same age (second day). Samples from the plants growing in the wild were taken in the natural habitat. Cultivated plants were unpollinated. This was not assured for specimens in the wild, but previous tests showed no odor changes after pollination (B. O. Schlumpberger, unpublished data).

To investigate the abundance of DHG in natural populations, an olfactory survey was undertaken among populations of sympatric *G. andreae* ($n = 121$) and *G. monvillei* ($n = 98$) plants. This was possible because of the extremely high sensitivity of the human nose to DHG; the threshold for the human nose is 2×10^{-12} g/L air (Kaiser and Nussbaumer 1990). Three categories were defined: DHG present, absent, or questionable. To confirm the reliability of the olfactory findings analytically, additional scent samples of different specimens (with and without DHG perception) were taken and analyzed by GC-MS.

Results

Temporal Patterns of Scent Production

In all DHG-producing plants studied, floral scents were emitted in a diurnal rhythm. Emission began with anthesis, and the maximum scent production was reached at full anthesis. Flowers of *Gymnocalycium* spp. usually remained open for 5 d, and flowers of *Rebutia* spp. remained open for 3 d. All volatiles were emitted synchronously (figs. 2, 3). The flowers of the examined species closed in the evening, reducing scent emission to the limit of detection.

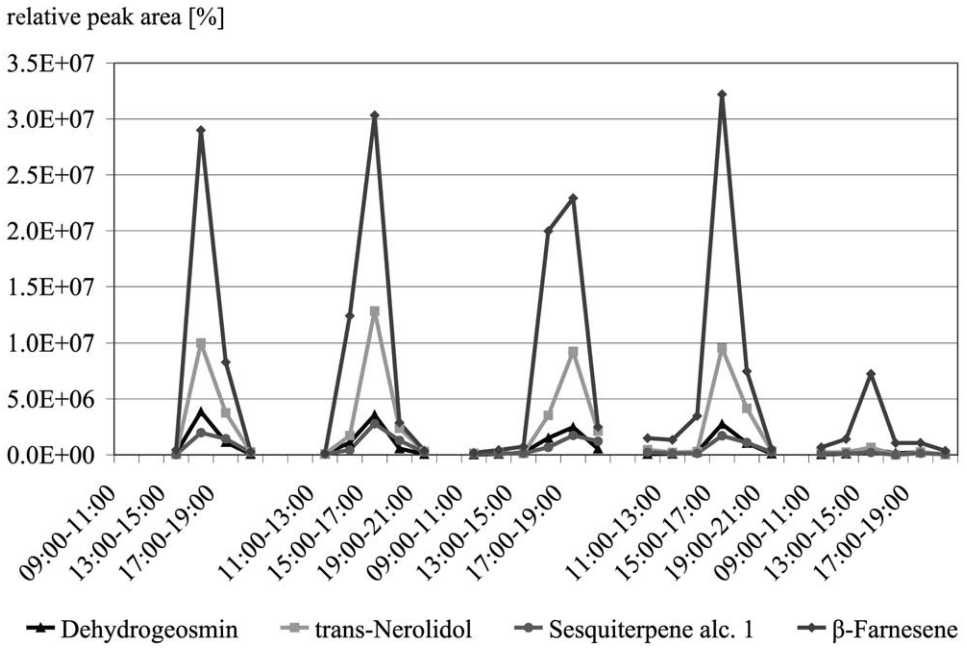

Fig. 2 Diurnal rhythm of scent emission of four compounds in *Gymnocalycium andreae* during the 5-d anthesis, using carbon traps. The flower did not entirely open the fifth day.

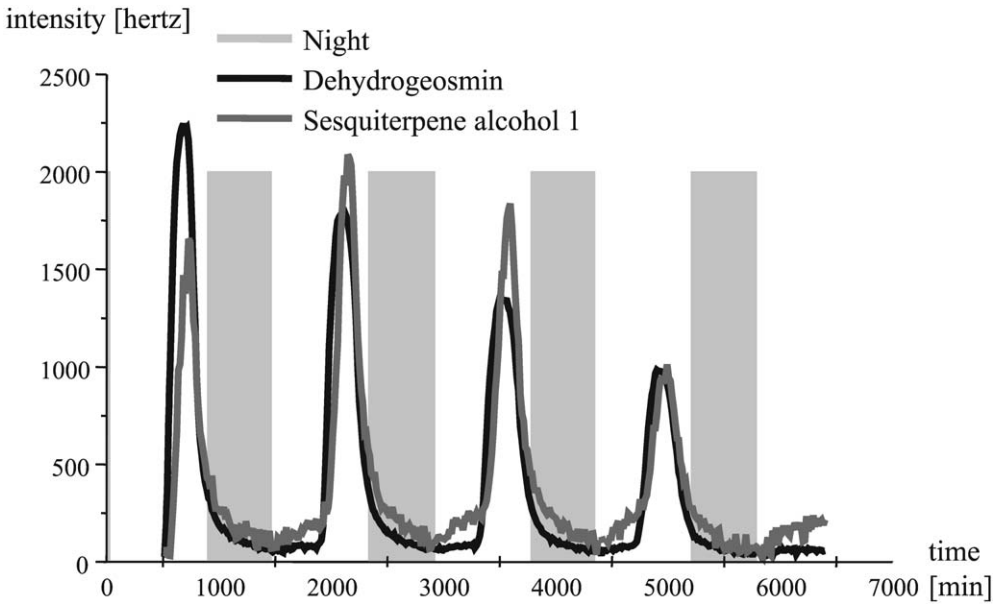

Fig. 3 Diurnal rhythm of emission of dehydrogeosmin and sesquiterpene alcohol 1 in *Gymnocalycium bodenbenderianum* ssp. *intertextum*, using the zNose.

Location of Scent Production

In all species studied, the volatiles were emitted by the perianth. In the pericarpel, including the androecium and gynoecium, we detected no or only small amounts of scent. Neither isolated anthers nor styles showed scent emission. Different parts of the perianth emitted different amounts of volatiles in all species studied; the strongest emission was recorded for the inner and middle tepals, the weakest for the outer ones (fig. 4).

In *Gymnocalycium bodenbenderianum* ssp. *intertextum*, the composition of volatiles emitted from basal and apical parts of the tepals was different; scent emission of the apical 50% was dominated by DHG and an unidentified sesquiterpene alcohol ("sesquiterpene alcohol 1"), while the basal 50% was dominated by β-farnesene (fig. 5).

Emission Rates of DHG

The emission rates of DHG were measured in three flowers of *Rebutia fabrisii*. Emission rates per flower per hour were 66, 112, and 800 ng, respectively.

Scent Composition of DHG-Producing Flowers

The floral scent of *Gymnocalycium andreae* mainly consisted of isoprenoids and, to a lesser extent, fatty acid derivates. Although DHG generally dominated the olfactory perception of the specimens studied, it was rarely the quantitatively dominant component in GC traces of floral headspace. In 19 of 20 individuals of *G. andreae*, the floral scent composition was quantitatively dominated by either β-farnesene or trans-nerolidol; in only one case was DHG the largest GC peak. In addition to these compounds, a number of unidentified terpenoids, one alkane and a series of alkenes, were found (table 1).

Comparison of the floral volatiles found in *G. andreae* with the scent composition of other DHG-producing species showed that two sesquiterpene alcohols with a eudesmane skeleton were present in the headspace of all 59 examined individuals of 14 species (and one hybrid) of six genera (table 1). Another two closely related sesquiterpene alcohols were found in several but not all of the species. These four compounds have a molecular mass of 222 and have a hydroxylisopropyl group in common, and they were never found in the floral scent of cactus flowers without DHG. The other floral volatiles found in *G. andreae* were only occasionally

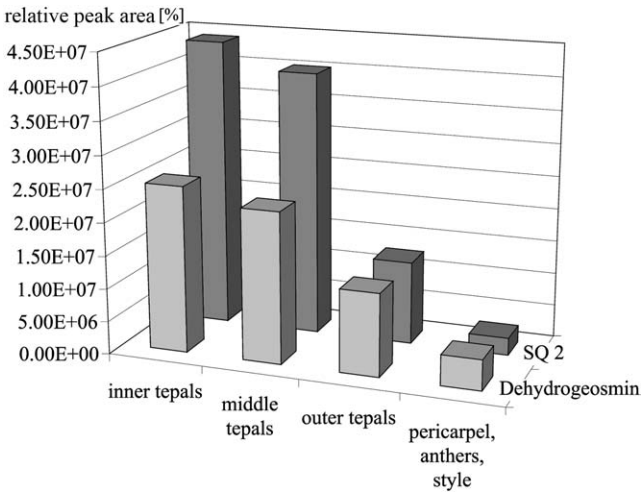

Fig. 4 Volatile emission of dissected flower parts in *Gymnocalycium bruchii* for the two major compounds. Strongest scent is emitted by the inner and middle tepals. Mean value of four flowers is shown. *SQ*2 = unidentified sesquiterpene alcohol 2.

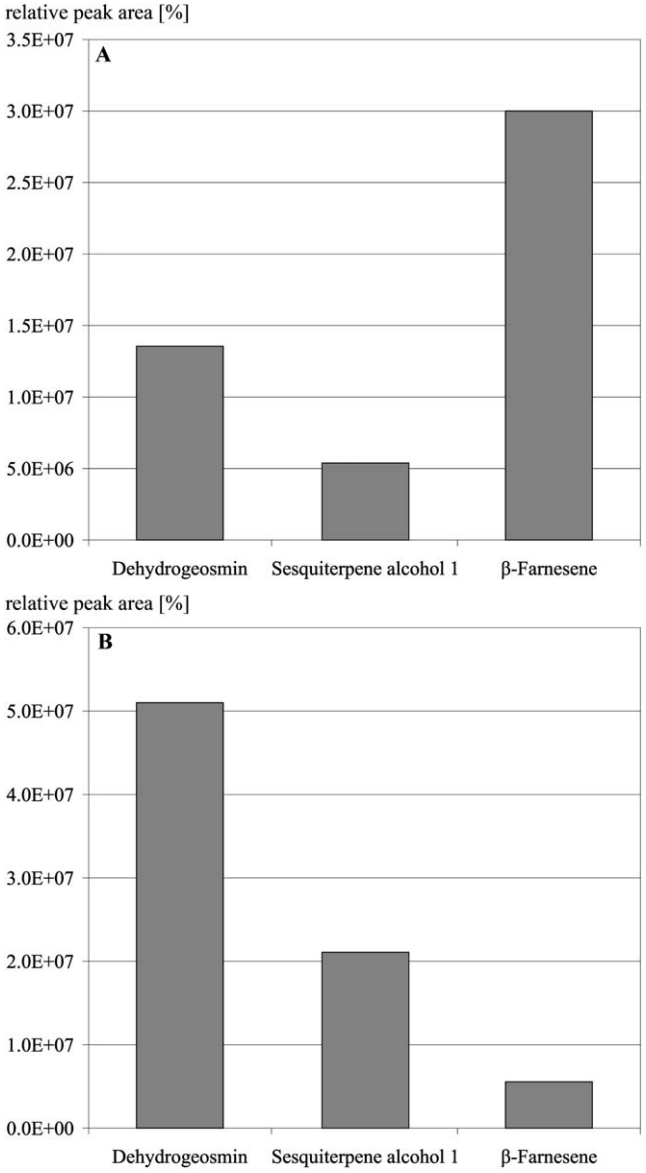

Fig. 5 Different composition of main volatile compounds in apical (*A*) and basal (*B*) parts of the tepals of *Gymnocalycium bodenbenderianum* ssp. *intertextum*.

found in the odor bouquets of other DHG-producing species (table 1). However, the scent profiles of species from different genera occasionally showed striking similarities. This was found in species with very simple odor bouquets dominated by DHG and a sesquiterpene alcohol, e.g., *R. fabrisii* and some specimens of *Gymnocalycium bruchii* (fig. 6). In some cases, DHG could be detected olfactorily, but analysis revealed that it was produced only in trace amounts.

Intraspecific Variability of Scent Production

The composition of floral scent in six randomly chosen cultivated plants of *G. andreae* varied strongly. Either β-farnesene or trans-nerolidol was the dominant compound. Further, the composition of the other studied volatiles was highly variable (fig. 7*a*–7*f*) between individuals. In contrast, six plants from a natural population in Argentina showed a uniform scent composition. Only β-farnesene constantly occurred as the major compound, and trans-nerolidol was mostly absent (fig. 7*g*–7*l*). The relative variation of the other volatiles was also low.

In the olfactory survey in a natural population, DHG was detected in 73% of all observed plants of *G. andreae* ($n = 121$), and it was absent in 15% and questionable in 12% of the specimens. In *Gymnocalycium monvillei*, the odor of DHG was perceived in 85% of all individuals ($n = 98$), absent in 5%, and questionable in 10%. GC-MS analysis of odor samples that were taken from flowers with and without detection of DHG confirmed the olfactory perceptions.

Discussion

In all species studied, the odor emission followed a clear diurnal rhythm. The quantity of volatile emission followed the opening behavior of the flowers, with the highest odor emission during the short time of maximum anthesis. This observation indicates that DHG emissions are correlated with the timing of floral visitation. In contrast, an antimicrobial function appears unlikely, given that a more continuous volatile emission would be expected. This conclusion is consistent with the results of a recent study where DHG showed no effect on selected bacteria and phytopathogenic fungi (Schlumpberger 2002).

The high temporal resolution and automated convenience of the zNose, a novel method for measuring temporal patterns of volatile emission, was a clear advantage over conventional methods, such as using carbon traps or SPME, with time-consuming odor accumulation and protracted GC analysis. However, the sensitivity of the zNose for different compounds depends on their volatility, which makes this method inappropriate for quantitative comparison of volatiles (Kunert et al. 2002). Therefore, the sesquiterpene alcohol is overemphasized in figure 3, which was confirmed by the samples taken with carbon traps simultaneously (data not shown).

In all study species, the entire volatile blend was emitted by the perianth. Because the androecium and gynoecium were always scentless, the participation of DHG in pollen germination as one of the potential functions seems unlikely. Although scented pollen and gynoecial tissues have been reported from several plants (Armbruster 1992; Pichersky et al. 1994; Dobson and Bergström 2000), staminate and carpellate tissues are not scented in the cacti studied here.

Besides DHG, several volatile compounds were identified in the headspace of these cactus flowers, most of which (e.g., β-farnesene and trans-nerolidol) are common substances found in many different plants (Knudsen et al. 1993). The sesquiterpene alcohols, because they are always and exclusively emitted together with DHG, may share a potential function with DHG. However, their chemistry indicates a biosynthetic affinity with DHG, and they are likely to represent precursors or related products of the same pathway (see biosynthesis of DHG in Feng et al. 1993).

Although some species produced DHG only in small quantities, it may still fulfill a function in these plants' reproductive biology. In some cases, trace substances have been

Table 1

Floral Volatiles Identified in *Gymnocalycium andreae,* Subset of Which Was Also Found in Other DHG-Producing Species

	RT	*G. andreae* ($n = 20$)	*Gymnocalycium bruchii* ($n = 7$)	*Gymnocalycium bodenbenderianum* ssp. *intertextum* ($n = 2$)	*Gymnocalycium monvillei* ($n = 5$)	*Echinopsis obrepanda* ($n = 1$)	*Echinopsis* hybrid ($n = 1$)	*Mammaillaria longimamma* ($n = 1$)	*Mammaillaria surculosa* ($n = 2$)	*Mammaillaria baumii* ($n = 1$)	*Parodia tuberculata* ($n = 1$)	*Parodia procera* ($n = 1$)	*Rebutia arenacea* ($n = 3$)	*Rebutia fabrisii* ($n = 5$)	*Rebutia marsoneri* ($n = 7$)	*Turbinicarpus pseudomacrochele* ssp. *krainzianus* ($n = 2$)
Trans-β-ocimene	08:38	S/…	S	…	…	…	…	…	…	…	…	…	…	…	…	…
Dehydrogeosmin	13:53	S/M/…	S/M	M	M/S/…	T	S	S	S	S	M	S	M	M	M	S
Heptadecene	13:55	S/T	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Bergamotene	14:32	S/…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
β-farnesene	14:44	M/T/…	…	S	…	…	…	…	…	…	…	…	…	…	…	…
Sesquiterpene alcohol	14:54	T/…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Alkane	15:24	T/…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Eudesman-3,7-dien?	15:28	S/…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Trans-nerolidol	16:11	M/T/…	M/…	…	…	M	…	…	…	…	…	…	…	…	…	…
Alkene 1	16:31	S/T	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Sesquiterpene alcohol 1	17:06	S/T	S/T	S	S/T	T	T	S	T	T	T	T	S	S	S	T
Sesquiterpene alcohol 2	17:12	S	S/M	M	S	T	S	S	S	S	S	S	S	S	S	S
Alkene 2	17:22	S/…	…	…	…	…	…	…	…	…	…	…	…	…	…	…
Alkene 3	17:35	S/T	……	…	…	…	…	…	…	…	…	…	…	…	…	…

Note. RT = retention time (expressed in minutes and seconds), M = main compound (>10% of total peak area), S = side compound (1%–10% of total peak area), T = trace compound (<1% of total peak area), ellipsis = not found. Different entries within the same field reflect variation between specimens of one species.

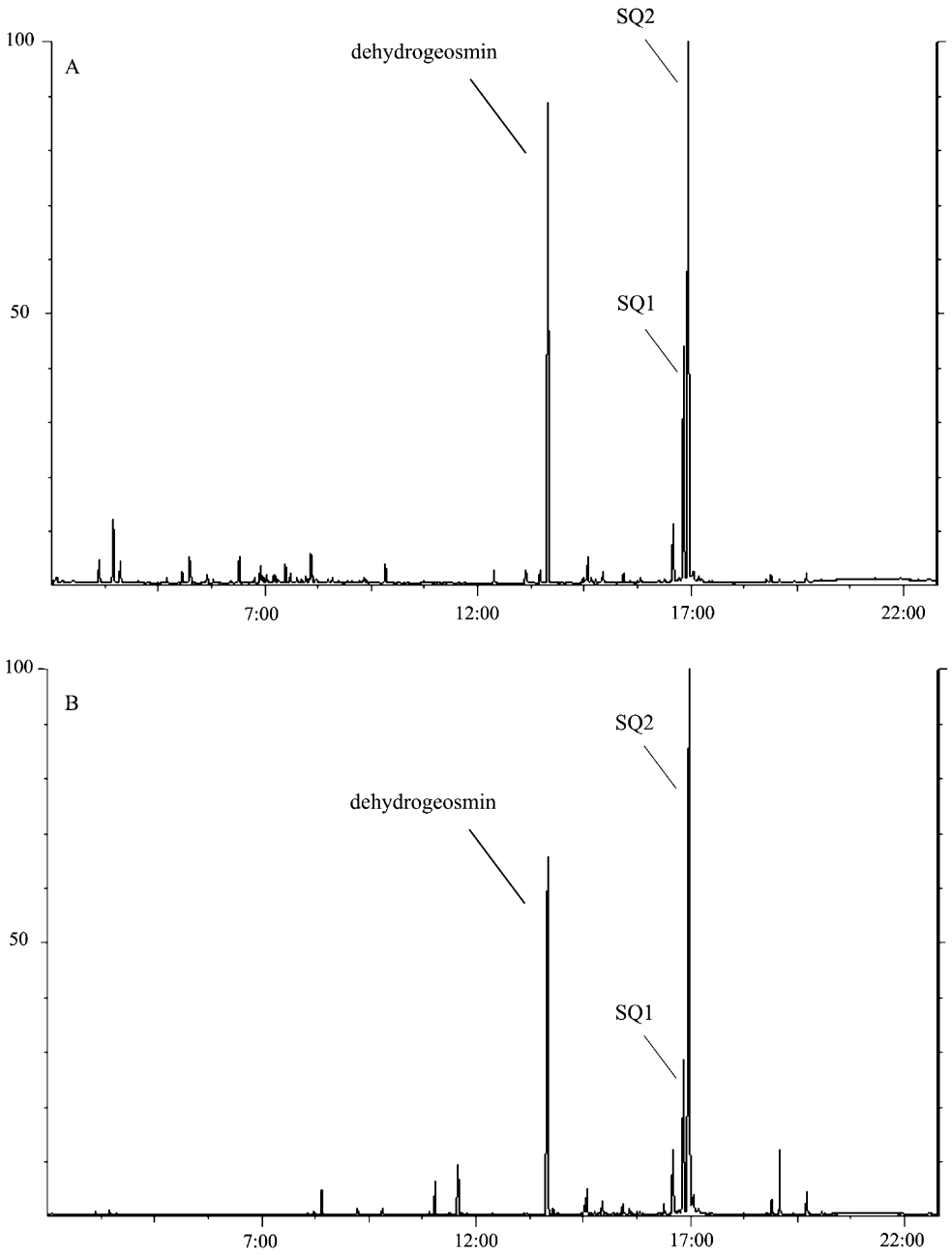

Fig. 6 Similar chromatograms of *Rebutia fabrisii* (*A*) and *Gymnocalycium bruchii* (*B*). *SQ*1 = sesquiterpene alcohol 1, *SQ*2 = sesquiterpene alcohol 2.

shown to be the only biologically active substances in the scent bouquet of certain flowers (Schiestl and Marion-Proll 2002). Experiments with floral visitors and the odor of cactus flowers using a gas chromatograph coupled with an electroantennographic detector may reveal which compounds are biologically active.

The emission rate studies of DHG in *Rebutia fabrisii* showed quantitative variation between individuals, despite the fact that these plants were maintained under identical conditions and the flowers were of the same developmental stage. Also, the observed 12-fold variation of emitted DHG is too big to be explained only by variation of flower size. For further studies on the function of DHG, such as behavioral assays with potential pollinators and synthetic DHG, the knowledge of the emission rates is important in order to use odor amounts comparable with the ones emitted by the flowers.

The variability of floral scent composition in the natural population of *Gymnocalycium andreae* was low in contrast to the variation found in cultivated specimens. This observation can be explained by potentially different odor composition in different populations of this species. The plants

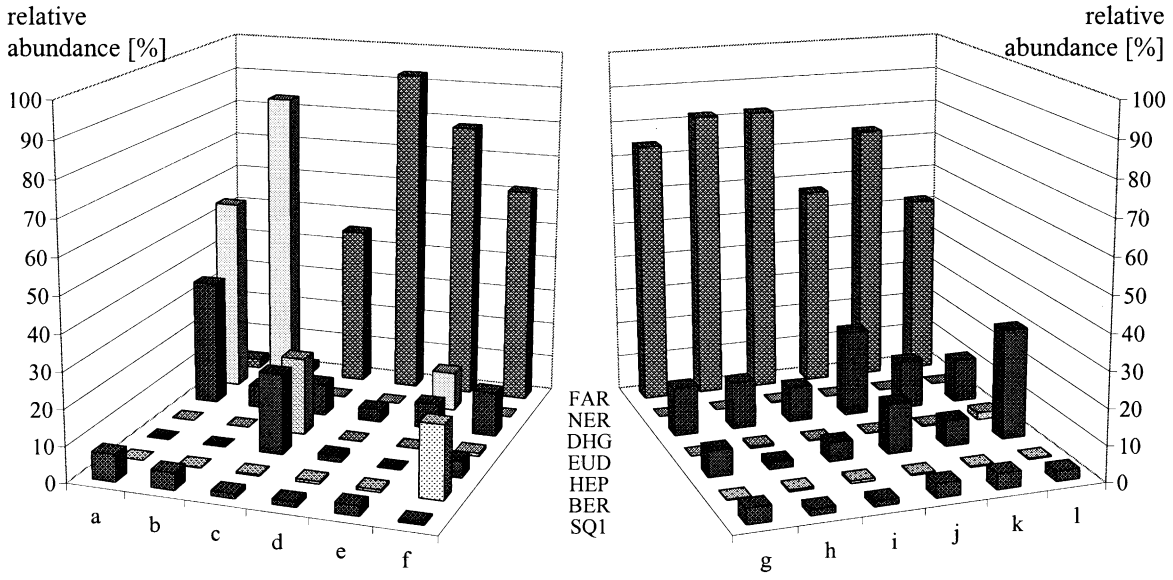

Fig. 7 Intraspecific variation of seven floral volatiles of *Gymnocalycium andreae*. Comparison of the scent bouquet of six cultivated plants (left, *a–f*) and six plants from an Argentine population (right, *g–l*). *FAR* = β-farnesene, *NER* = trans-nerolidol, *DHG* = dehydrogeosmin, *EUD* = eudesmane, *HEP* = heptadecene, *BER* = bergamotene, *SQ*1 = sesquiterpene alcohol 1.

obtained from a nursery are the offspring of plants of an unknown origin. For commercial propagation, usually descendants from different populations across the taxon's range are cross-pollinated. Therefore, the odor variability of cultivated plants may reflect potential population-specific differences. However, further field studies to compare the odors of different populations are required to test this hypothesis. In addition, comparative field studies on the pollination biology may reveal whether differences in scent composition are related to differences in the pollinator spectrum (Galen and Kevan 1980; Pellmyr 1986) or are a result of neutral genetic drift.

Oeser (1978) suggested that the musty odor compound, later identified as DHG, could be used to distinguish species of *Sulcorebutia* (synonym to *Rebutia*). However, this is not possible because of the intraspecific variation of DHG production. The similarities of floral scent composition found in plants of different genera, as in some species of *Gymnocalycium* and *Rebutia* (fig. 6), give further indications that the odor bouquets of these cacti have no taxonomic value. Similar scent compositions more likely reflect convergent adaptations to the same pollinator groups (van der Pijl 1961; Wyatt 1983).

Our studies show that DHG, along with the other floral volatiles in the respective cactus species, is emitted by the perianth in a diurnal cycle during a relatively short time period at full anthesis. Therefore, further studies on the function of this unique volatile should concentrate on the interactions with floral visitors in the field.

Acknowledgments

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Literature Cited

Armbruster WS 1992 Phylogeny and the evolution of plant-animal interactions. BioScience 42:12–20.

Berger A 1926 Die Entwicklungslinien der Kakteen. Gustav Fischer, Jena. 105 pp.

Cole LK, MS Blum, RW Roncadori 1975 Antifungal properties of the insect alarm pheromones citral, 2-heptanone, and 4-methyl-3-heptanone. Mycologia 67:701–708.

Dobson HEM 1994 Floral volatiles in insect biology. *In* EA Bernays, ed. Insect-plant interactions. CRC, Boca Raton, Fla. 176 pp.

Dobson HEM, G Bergström 2000 The ecology of pollen odors. Plant Syst Evol 222:63–87.

Faegri K, J van der Pijl 1971 The principles of pollination ecology. 2d ed. Pergamon, Oxford. 291 pp.

Farrar RR, GG Kennedy 1987 2-undecanone, a constituent of the glandular trichomes of *Lycopersicon hirsutum f. glabratum*: effects on *Heliothis zea* and *Manduca sexta* growth and survival. Entomol Exp Appl 43:17–23.

Farrar RR, GG Kennedy, RM Rose 1992 The protective role of dietary unsaturated fatty acids against 2-undecanone-induced pupal mortality and deformity in *Helicoverpa zea*. Entomol Exp Appl 62:191–200.

Feng Z, U Huber, W Boland 1993 Biosynthesis of the irregular C_{12}-terpenoid dehydrogeosmin in flower heads of *Rebutia marsoneri* Werd. (Cactaceae). Helv Chim Acta 76:2547–2552.

French RC, CL Graham, RA Long, AW Gale 1979 Effect of nonanol and related fungal spore stimulators on germination of pollen of several *Pinus* species. J Agric Food Chem 27: 184–187.

Galen C, PG Kevan 1980 Scent and color, floral polymorphisms and pollination biology in *Polemonium viscosum* Nutt. Am Midl Nat 104:281–289.

Hamilton-Kemp TR, JH Loughrin, DD Archbold, RA Andersen, DF Hildebrand 1991 Inhibition of pollen germination by volatile compounds including 2-Hexenal and 3-Hexenal. J Agric Food Chem 39:952–956.

Huber U, W Boland, WA König, B Gehrcke 1993 Synthesis and absolute configuration of the C_{12}-terpenoid dehydrogeosmin from the flower scents of *Rebutia marsoneri* and *Dolichothele sphaerica* (Cactaceae): a new approach to bis-angularly substituted trans-decalins. Helv Chim Acta 76:1949–1955.

Kaiser R, C Nussbaumer 1990 1,2,3,4,4a,5,8,8a-octahydro-4β,8aα-dimethylnaphthalen-4aβ-ol (=dehydrogeosmin), a novel compound occurring in the flower scent of various species of Cactaceae. Helv Chim Acta 73:133–139.

Kaiser R, L Tollsten 1995 An introduction to the scent of cacti. Flavour Fragrance J 10:153–164.

Kennedy GG, CF Soerenson 1985 Role of glandular trichomes in the resistance of *Lycopersicum hirsutum f. glabratum* to Colorado potato beetle (Coleoptera: Chrysomelidae). J Econ Entomol 78: 547–551.

Knudsen JT 1994 Floral scent variation in the *Pyrola rotundifolia* complex in Scandinavia and western Greenland. Nord J Bot 14: 277–282.

——— 2002 Variation in floral scent composition within and between populations of *Geonoma macrostachys* (Arecaceae) in the western Amazon. Am J Bot 89:1772–1778.

Knudsen JT, L Tollsten, LG Bergström 1993 Floral scents: a checklist of volatile compounds isolated by head-space techniques. Phytochemistry 33:253–280.

Kunert M, A Biedermann, T Koch, W Boland 2002 Ultrafast sampling and analysis of plant volatiles by a hand-held miniaturised GC with pre-concentration unit: kinetic and quantitative aspects of plant volatile production. J Sep Sci 25:677–684.

Matile P, R Altenburger 1988 Rhythms of fragrance emission in flowers. Planta 174:242–247.

Morris JA, A Khettry, EW Seitz 1979 Antimicrobial activity of aroma chemicals and essential oils. J Am Oil Chem Soc 56: 595–603.

Nielsen JK, HB Jakobsen, P Friis, K Hansen, J Møller, CE Olsen 1995 Asynchrounous rhythms in the emission of volatiles from *Hesperis matronalis* flowers. Pergamon 38:847–851.

Oeser R 1978 Blütenduft bei Sulcorebutien: eine Möglichkeit zur Arttrennug? Kakt Sukk 29:192–194.

Pellmyr O 1986 Three pollination morphs in *Cimifuga simplex*: incipient speciation due to inferiority in competition. Oecologia 68: 304–307.

Pichersky E, RA Raguso, E Lewinsohn, R Croteau 1994 Floral scent production in *Clarkia* (Onagraceae). I. Localization and developmental modulation of monoterpene emission and linalool synthase activity. Plant Physiol 106:1533–1540.

Porsch O 1938 Das Bestäubungsleben der Kakteenblüte. I. Cactaceae. Jahrb Dtsch Kakt Ges 1938:1–80.

Raguso RA 2001 Floral scent, olfaction and scent-driven foraging behavior. Pages 83–105 *in* L Chittka, JD Thomson, eds. Cognitive evolution. Cambridge University Press, Cambridge.

Rauh W 1979 Kakteen an ihren Standorten. Paul Parey, Berlin and Hamburg. 230 pp.

Schiestl FP, M Ayasse, HF Paulus, D Erdmann, W Francke 1997 Variation of floral scent emission and postpollination changes in individual flowers of *Ophrys sphegodes* ssp. *sphegodes*. J Chem Ecol 23:2881–2895.

Schiestl FP, F Marion-Proll 2002 Detection of physiologically active flower volatiles using gas chromatography coupled with electroantennography. Pages 173–198 *in* JF Jackson, HF Linskens, R Inman, eds. Molecular methods of plant analysis. Vol 21. Analysis of taste and aroma. Springer, Berlin.

Schlumpberger BO 2002 Dehydrogeosmin produzierende Kakteen: Untersuchungen zur Verbreitung, Duftstoff-Produktion und Bestäubung. PhD diss. University of Tübingen, Grauer. 137 pp.

Tollsten L, LG Bergström 1993 Fragrance chemotypes of *Platanthera* (Orchidaceae): the result of adaption to pollinating moths. Nord J Bot 13:607–613.

Tollsten L, DO Ovstedal 1994 Differentiation in floral scent chemistry among populations of *Conopodium majus* (Apiaceae). Nord J Bot 14:361–367.

van der Pijl L 1961 Ecological aspects of flower evolution. II. Zoophilous flower classes. Evolution 15:44–59.

von Helversen O, L Winkler, HJ Bestmann 2000 Sulphur-containing "perfumes" attract flower-visiting bats. J Comp Physiol 186:145–155.

Wyatt R 1983 Pollinator plant interactions and the evolution of breeding systems. Pages 51–96 *in* L Real, ed. Pollination biology. Academic Press, New York.