Biology *of* Floral Scent

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Biology *of* Floral Scent

Edited by

Natalia Dudareva
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Boca Raton London New York

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Cover image by Liza Pichersky

Published in 2006 by
CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

Printed in the United States of America on acid-free paper
10 9 8 7 6 5 4 3 2 1

International Standard Book Number-10: 0-8493-2283-9 (Hardcover)
International Standard Book Number-13: 978-0-8493-2283-9 (Hardcover)
Library of Congress Card Number 2005058202

Library of Congress Cataloging-in-Publication Data

Dudareva, N.A. (Natal'ia Arnol'dovna)
Biology of floral scent / Natalia Dudareva and Eran Pichersky.
p. cm.
Includes bibliographical references (p.).
ISBN 0-8493-2283-9
1. Flowers--Morphogenesis--Molecular aspects. 2. Flowers--Odor. 3. Plant osomophors. 4. Pollination by insects. I Pichersky, Eran. II. Title.

QK653.D83 2006
575.6--dc22 2005058202

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Contents

Section I Chemistry of Floral Scent

Chapter 1
Detection and Identification of Floral Scent Compounds 3
Dorothea Tholl and Ursula S.R. Röse

Chapter 2
The Chemical Diversity of Floral Scent 27
Jette T. Knudsen and Jonathan Gershenzon

Section II Biochemistry and Molecular Biology of Floral Scent

Chapter 3
Floral Scent Metabolic Pathways: Their Regulation and Evolution 55
Natalia Dudareva and Eran Pichersky

Chapter 4
Biosynthesis of Volatile Terpenes in the Flowers of the Model Plant *Arabidopsis thaliana* 79
Dorothea Tholl and Eran Pichersky

Chapter 5
An Integrated Genomics Approach to Identifying Floral Scent Genes in Rose 91
Alexander Vainstein, Efraim Lewinsohn, and David Weiss

Section III Cell Biology and Physiology of Floral Scent

Chapter 6
Localization of the Synthesis and Emission of Scent Compounds within the Flower 105
Uta Effmert, Diana Buss, Diana Rohrbeck, and Birgit Piechulla

Chapter 7
Examination of the Processes Involved in the Emission of Scent Volatiles from Flowers 125
Reinhard Jetter

Section IV Plant-Insect Interactions and Pollination Ecology

Chapter 8
Relationship between Floral Fragrance Composition and Type of Pollinator 147
Heidi E.M. Dobson

Chapter 9
Floral Scent and Butterfly Pollinators 199
Susanna Andersson

Chapter 10
Floral Scent and Pollinator Attraction in Sexually Deceptive Orchids 219
Manfred Ayasse

Chapter 11
Detection and Coding of Flower Volatiles in Nectar-Foraging Insects 243
Mikael A. Carlsson and Bill S. Hansson

Chapter 12
Learning-Based Recognition and Discrimination of Floral Odors 263
Brian H. Smith, Geraldine A. Wright, and Kevin C. Daly

Chapter 13
Behavioral Responses to Floral Scent: Experimental Manipulations and the Interplay of Sensory Modalities 297
Robert A. Raguso

Section V Commercial Aspects of Floral Scent

Chapter 14
Molecular Engineering of Floral Scent 321
Joost Lücker, Harrie A. Verhoeven, Linus H.W. van der Plas, and Harro J. Bouwmeester

Index 339

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Preface

The sense of smell is the most basic and universal sense. Even bacteria have mechanisms to detect the presence of chemicals in their environment. The scents that emanate from flowers have been noticed by humans since antiquity; a fact that has been documented in ancient texts. In 3000 B.C., when the Egyptians were learning to write and make bricks, they were already making primitive perfumes and using them for religious rituals. Humans' admiration for the fragrances of flowers has made these volatile substances into many commercial products. Volatiles are heavily used in the perfume, cosmetics, and fragrance industries, which are continually researching new and unusual volatile compounds and scents. Consumers are also constantly searching for new scented ornamental crops. However, the biosynthesis of floral volatiles and the roles of floral scents in plants are topics that have only recently begun to receive serious scientific attention. While we can certainly detect scent molecules in the air, the sheer number of such scents, and their complexity, confound us. Our olfactory sense is simply not good enough to separate the components and identify each one with any certainty. The consequences of our inability to clearly and objectively measure smells with our nose mean that, in the absence of appropriate instrumentation, scientific research in this area is greatly impeded.

Recent advances in practical methodologies and affordable instrumentation to collect, separate, and identify volatile compounds have allowed floral scent research to become a standard scientific research topic accessible to many investigators, which in turn has resulted in many exciting new discoveries. Thus the fourteen chapters of this book summarize and represent the progress in our current understanding of the major areas of investigation into floral scent: the techniques used to study it, how the various scent compounds are made, where they are made and how they are emitted from the flower, the effect of floral scent on the various ecological interactions between insects and flowers, and finally, how researchers are using the newly identified scent genes to genetically engineer flowers that will produce new scents. We realize that there is much more to be learned in this area and we hope that this book will stimulate new research to advance our understanding of floral scent biology.

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Editors

Eran Pichersky is the Michael M. Martin collegiate professor in the Department of Molecular, Cellular, and Developmental Biology, University of Michigan, Ann Arbor. Professor Pichersky received his bachelor of science degree from the School of Natural Resources at the University of California, Berkeley, and his Ph.D. from the University of California at Davis. He was a postdoctoral researcher at Rockefeller University from 1984 to 1987, when he moved to the University of Michigan. In 2000 he was a senior Fulbright fellow as well as a senior Alexander von Humboldt fellow while visiting the Max Planck Institute for Chemical Ecology in Jena, Germany.

Professor Pichersky has trained more than 20 graduate students and postdoctoral fellows, and has authored more than 150 scientific papers. His research over the years has involved the biosynthesis of scent volatiles in the flowers of the California annual plant *Clarkia breweri* and in the model plant *Arabidopsis thaliana*. His group has also been studying the volatile compounds that are stored in special glands on the leaves of tomato and basil and are released when the plant is injured by insect herbivores. Such volatiles act as deterrents against the herbivores and also help to attract predators of the herbivores.

Natalia Dudareva is a professor at Purdue University in West Lafayette, Indiana. She received her B.Sc. and M.Sc. in biology and biochemistry at the Novosibirsk State University, Russia, and Ph.D. in molecular biology at the Institute of Biochemistry, Kiev, Ukraine, in 1982. From 1982 to 1991 she worked as a senior scientist in the Institute of Cytology and Genetics of the USSR Academy of Sciences in Novosibirsk and her research focused on the structural organization and transcription of the plant mitochondrial genome. Dudareva then completed her postdoctoral training at the Institut de Biologie Moléculaire des Plantes, Strasbourg, France (1991–1993), and in the Department of Biological Science, Windsor University, Windsor, Ontario, Canada (1993–1995), with emphasis on isolation and characterization of pollen-specific genes in sunflower.

As a postdoctoral research fellow in the laboratory of Professor Eran Pichersky at the University of Michigan, Ann Arbor, she became interested in plant secondary metabolism and biosynthesis of plant volatile compounds. Using *Antirrhinum majus* and *Petunia hybrida* as model systems, she continued the investigation of the regulation of floral volatiles' production at Purdue University, where she became an assistant professor in 1997 and an associate professor in 2001. Dudareva's laboratory is now combining the power of biochemical and genetic engineering approaches with metabolic modeling to gain new insights into the metabolic network leading to volatile secondary metabolites and to obtain a comprehensive understanding of the regulation of their production and emission in *planta*. In 2005 she received Purdue's 2005 Agriculture Research Award for her contributions to the understanding of the biochemistry of floral scent compounds.

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Section I

Chemistry of Floral Scent

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1 Detection and Identification of Floral Scent Compounds

Dorothea Tholl and Ursula S.R. Röse

CONTENTS

1.1 Introduction 3
1.2 Floral Volatile Sampling Techniques 5
1.2.1 Static Headspace Sampling Techniques 5
1.2.1.1 Solid Phase Microextraction 5
1.2.2 Dynamic Headspace Sampling Techniques 7
1.2.2.1 Closed-Loop Stripping 8
1.2.2.2 Pull Systems 9
1.2.2.3 Push-Pull Systems 10
1.2.2.4 Online Volatile Collection Systems 11
1.2.3 Other Headspace Sampling Techniques 12
1.3 Adsorption and Desorption of Volatiles 12
1.4 Gas Chromatographic Separation of Volatiles 13
1.5 Volatile Detection and Identification 14
1.5.1 Enantioselective GC, Multidimensional GC 16
1.6 Structure Elucidation of Volatile Compounds 16
1.7 Volatile Analysis Techniques with High Time Resolution 17
1.7.1 Fast and Transportable GC (zNose) 17
1.7.2 Proton Transfer Reaction Mass Spectrometry 18
1.8 Conclusion 20
References 20

1.1 INTRODUCTION

Any treatment of the subject of floral scent must begin with a description of how its components are detected and identified. Such investigation is often referred to as "headspace" analysis, a term derived from the beer industry, where the analysis of the volatiles in the "head" of the beer was first developed. Floral headspace analyses were developed more than 30 years ago and have since greatly improved as analytical methods have become sensitive enough to collect and analyze volatiles

by gas chromatography (GC) and gas chromatography-mass spectrometry (GC-MS) directly. Several previous reviews have discussed and compared different headspace techniques.[1–7] In this chapter we discuss several practical approaches to floral scent analysis and their advantages and limitations.

The first step in choosing a sample technique should always focus on the biology of the plant system and the purpose of the floral scent analysis. A first consideration is whether volatiles need to be collected in the field or whether the volatiles can be collected in the laboratory without affecting the composition of the blend. While some collection methods are transportable and can easily be taken to the field, other more sophisticated methods may require a complicated setup suitable only for the laboratory. A second consideration should focus on whether the floral scent of the investigated plant is already known and identified, and is only being confirmed (e.g., repetitive insect behavioral experiments), or whether the volatile blend is unknown and needs to be identified completely. Total characterization of a volatile blend often requires additional analytical steps and therefore necessitates more source material for compound identification. Also, if several flowering species are screened for the presence of only one or two compounds, the most appropriate technique may differ from the one necessary for complete identification of a complex volatile blend. Flowers may emit large amounts of volatiles that can easily be detected, even by the human nose, or they may appear rather odorless. Depending on the expected detectability of the floral scent, one may have to choose different types of collection methods that vary in their sensitivity. Flowers of *Arabidopsis thaliana*, for example, which release only very small amounts of volatiles (see Chapter 4),[8] require different collection techniques than flowers that release large amounts of volatiles, such as *Mirabilis jalapa*.[9]

Another important consideration is the developmental stage of the flower and timing when volatiles are collected. Some flowers, such as the orchid *Ophrys sphegodes*, are known to change their odor emission after pollination has occurred.[10,11] The volatile profile emitted by the flowers may also vary depending on the time of day,[9,12–14] as some flowers are mainly pollinated by moths and emit volatiles at night to attract their pollinators, while others are pollinated by insects that are mainly active during the day.[15] While some collection techniques allow for a very high time resolution of the volatile emissions, other techniques require several hours to collect sufficient material for further analysis. Depending on the time intervals during which volatiles should be sampled, some collection methods allow for an easy automated setup for 24 h collections, while others are most appropriate for taking a "snapshot" of the current volatile release.

In the following sections we present a selection of collection methods that range from low-tech, inexpensive, quick sampling methods to high-tech methods that require a complicated laboratory setup and can automatically collect samples in short time intervals over several days. We also present an overview of detection and identification methods for volatiles, including GC-MS, enantioselective GC, and multidimensional GC, and discuss the latest developments in ultrafast volatile analysis techniques, such as zNose™ and proton-transfer reaction mass spectrometry (PTR-MS).

1.2 FLORAL VOLATILE SAMPLING TECHNIQUES

In all volatile collection methods, the used chamber for headspace collection should be free of material that retains volatiles or causes bleeding of compounds that may contaminate the system. Good choices for materials include glass, Teflon, and metal, which are easy to clean and do not show bleeding, whereas materials such as rubber, plastic, glues, adhesives, and wood should be avoided. Details on the materials for the construction of such chambers are discussed by Millar and Sims.[6]

1.2.1 Static Headspace Sampling Techniques

Sampling of volatiles from a static headspace has the advantage of an enrichment of volatiles in a closed tube or chamber. The background impurities that can result from a continuous airstream are reduced, which is an advantage when collecting from low-emitting flowers such as *A. thaliana*. However, for longer sampling times in a static airspace, humidity and a lack of gas exchange may interfere with normal physiological processes and affect the emission of volatiles. If volatiles are sampled in the presence of additional light, a temperature increase in the chamber may affect the emission of volatiles. For applications that require a time course with an expected change in volatile emissions, static headspace sampling does not work well because not all of the emitted volatiles are removed at one sampling time and changes in emission are difficult to determine.

1.2.1.1 Solid Phase Microextraction

Solid phase microextraction (SPME) is a very fast, effective, and simple method for collecting volatiles. The method is based on an adsorption-desorption technique using an inert fiber coated with different types of adsorbents that can vary in polarity and thickness and can be selected according to different types of applications. The adsorbent-coated fiber is mounted to a modified syringe and can be extended out of a needle by pushing the plunger and exposing the fiber to volatiles. The SPME device is available from Supelco (Bellefonte, PA). To collect from the static headspace of a flower sample that is enclosed in a glass container sealed with a septum, the needle of the SPME holder is inserted through the septum and the fiber is extended into the headspace (Figure 1.1). The flower volatiles are then adsorbed by the exposed fiber for several minutes to an hour, until equilibrium is reached. After volatile collection, the fiber is retracted into the needle, which is then transferred to a GC injector where the fiber is exposed to thermal desorption of the compounds. Direct desorption of volatiles from the fiber into a GC injector eliminates the need for solvent-mediated desorption, thereby reducing solvent contaminants in the analysis that may obscure some volatile compound peaks. Limitations of SPME sampling are that samples can be injected only once (no repeated injections), and the amount of material obtained from sampling by SPME is generally sufficient for GC analysis, but not for structure elucidation of unknown compounds.

The amounts adsorbed by the SPME fiber depend on the thickness of the fiber and the distribution constant of the analyte, which generally increases with molecular weight and boiling point. For most volatiles, a thick coating is recommended to

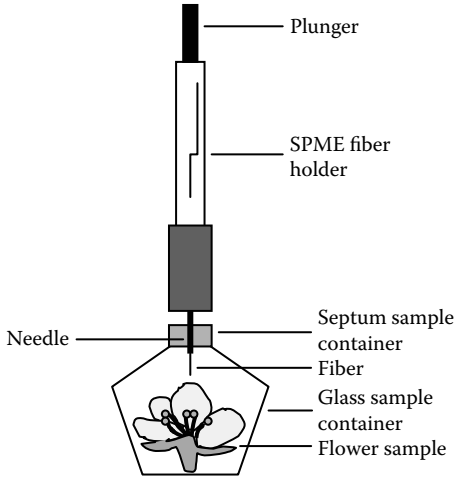

FIGURE 1.1 SPME device to extract volatiles from the headspace of a flower enclosed in a glass sample container. The adsorbent-coated fiber is mounted to an SPME fiber holder, similar to a modified syringe that is injected through the septum of the sample container. By pushing the plunger of the SPME fiber holder, the fiber can be extended out of the needle, exposing the fiber to volatiles. After collection, the fiber is retracted into the needle and the SPME is removed from the container for GC analysis of the absorbed volatiles.

better retain volatile compounds until thermal desorption, whereas semivolatile compounds may be better detected with a thin fiber coating. Thicker coatings desorb analytes more slowly, which increases the risk of carryovers. In general, fibers should be cleaned carefully by heating before reusing them. Thin coatings ensure fast diffusion and release of higher boiling point compounds. The adsorption of volatiles also depends on the polarity and porosity of the surface area. Nonpolar volatile compounds and nonpolar semivolatile compounds are effectively extracted with nonpolar fiber coatings such as polydimethylsiloxane (PDMS). Polar volatiles can be extracted with PDMS/divinylbenzene fibers, and trace level volatiles can be extracted with a PDMS/Carboxen™ fiber.

The effectiveness of SPME extraction is influenced by the volatile concentration relative to the sample volume. At low concentrations, changes in headspace sample volume do not affect responses, because equilibrium is concentration dependent. However, at higher concentrations, the sample volume has a strong effect. In a large sample volume of greater than 5 ml, containing a high concentration of volatile analyte, the amount of analyte removed from the sample is not sufficient to change the concentration. Hence, the response throughout a calibration curve is mostly exponential and is linear only for low concentrations (50 ppb). For the collection of volatiles from flowers, a small volume of 5 ml or less is often not practical. An external or internal calibration for some compounds may be possible, but is often difficult when dealing with a wide range of compounds of different concentrations in one sample. Detailed information on theory, optimization, and different types of fiber adsorbents is available from Supelco. The company also offers a portable field sampler with a Carboxen™/PDMS fiber that has a sealing mechanism to allow storing of samples for later analysis in the laboratory.

Recently the detection of volatiles by SPME has been applied to an increasing number of studies, including a variety of different flowers such as *Ceratonia siliqua*, *Osyris alba*, and different rhododendron species, with a broad range of compounds being extracted from the headspace.[16–18] For a variety of volatile compounds including terpenes and others, we have good experience using a PDMS fiber with a 100 μm film thickness. Although we have observed high selectivity of the fiber for the monoterpene (*E*)-β-ocimene, we found the method very useful for rapid screening of headspace compounds like, for example, from flowers of the butterfly bush (*Buddleja davidii*) (Figure 1.2). However, consistent sampling time, temperature, and sample volume are crucial to obtain comparable results.

1.2.2 Dynamic Headspace Sampling Techniques

Sampling of volatiles from a dynamic headspace eliminates some of the problems that are connected to sampling from static headspace. In general, larger amounts of volatiles can be collected over longer time periods by adsorption (see Section 1.3) in a continuous airstream, allowing not only subsequent detection, but also structure elucidation of compounds. In addition, systems with a continuous incoming airstream provide sufficient temperature and gas exchange and avoid accumulation of compounds in the headspace that may affect the volatile release (pull and push-pull systems). Relative humidity can be adjusted in a push-pull system to a desired percentage by adding a humidified airstream to the incoming air and mixing it with dry air. However, care needs to be taken to avoid background impurities by cleaning the incoming air carefully with filters containing, for example, activated charcoal. The problem of background contaminants resulting from continuous incoming air is reduced in closed-loop stripping systems, where a limited air volume is sampled repeatedly.

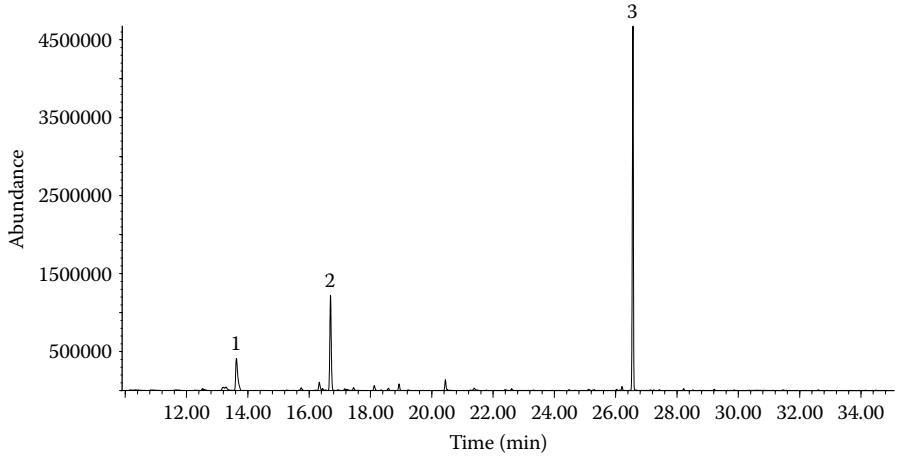

FIGURE 1.2 Volatiles collected by SPME from the headspace of detached flowers of the butterfly bush, *Buddleja davidii* (Scrophulariaceae), enclosed in a glass desiccator for 15 min. Tentative identification of main compounds by GC-MS on a DB-5MS column: (1) (*E*)-β-ocimene; (2) ketoisophorone; (3) (*E,E*)-α-farnesene.

1.2.2.1 Closed-Loop Stripping

In closed-loop stripping systems, volatiles are collected inside closed devices by circulating headspace adsorption. A closed-loop stripping apparatus has been described by Omata et al.[19] for floral scent analysis from oriental orchids. Boland et al.[20] developed a similar system, in which plants or detached plant parts are placed in small glass containers such as 1 l or 3 l desiccators. The top of the container is connected to the odor-collecting device consisting of a circulation pump, stainless steel tubes, and a stainless steel housing containing the volatile trap (Figure 1.3). Headspace air is circulated through the container and the connected trap at flow rates of approximately 3 l/min, allowing continuous quantitative collection of emitted volatiles. The system has been applied not only to the analysis of herbivore-induced volatiles,[21,22] but also to trapping floral volatiles, including collections from flowers with very low emission rates.

Analysis of volatiles from extremely low-scented flowers can be complicated for different reasons. In open headspace systems (see Section 1.2.2.3), often only a proportion of the air passing through the chamber is pulled through the adsorbent filter, thereby reducing the total amount of trapped volatiles. Higher flow rates or extended collection times can compensate for the reduced capture of emitted volatiles; however, these can enhance the trapping of contaminants present in the air or the collection system. The increased noise level in the baseline signal of subsequent GC analyses will complicate the detection of less abundant sample volatiles.[7] One example of a plant with low floral volatile emission rates is the model plant *A. thaliana*. *Arabidopsis* plants emit approximately 200-fold less floral volatiles per hour than strongly scented plants such as *Clarkia breweri*.[8] Closed-loop stripping of monoterpene and sesquiterpene volatiles emitted from *Arabidopsis* flowers was performed by placing 70 to 150 excised inflorescences in small, water-containing, glass beakers inside a sealed 1 l desiccator. Volatiles were collected on traps containing 1.5 mg charcoal or 25 mg Super Q® (Alltech Associates, Deerfield, IL) (see Section 1.3)

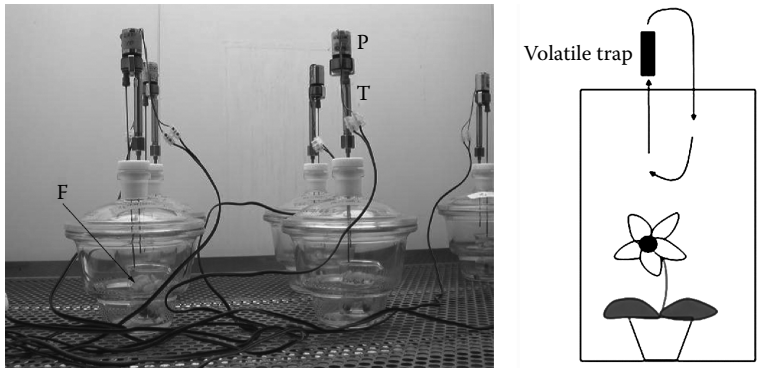

FIGURE 1.3 Volatile collection by the closed-loop stripping procedure. The photograph shows the collection of volatiles emitted from detached snapdragon flowers during feeding with isotope-labeled precursors.[24] P, circulation pump; T, steel housing containing the volatile trap; F, snapdragon flowers.

for 6 to 12 h.[8,23] Floral volatile profiles and compositions analyzed with this method were comparable to those obtained by semiopen headspace volatile trapping from similar numbers of undetached inflorescences, but showed a clearly improved signal:noise ratio, thus allowing a detailed analysis of minor components of the complex terpene volatile mixture.

In addition to qualitative and quantitative analyses of natural floral volatiles, closed-loop stripping procedures have also been used to elucidate the biosynthesis of floral scent components by trapping volatiles from detached flowers treated with biosynthetic inhibitors or supplied with isotope-labeled precursors. For example, cut snapdragon flowers were fed with deuterium-labeled terpene biosynthesis precursors of the mevalonate and methylerythritol phosphate (MEP) pathways, respectively, or inhibitors of these pathways, revealing that mono- and sesquiterpenes emitted from snapdragon flowers are exclusively synthesized via the MEP pathway.[24]

Closed-loop stripping systems can easily be set up in controlled climate chambers. They allow volatile collections from several plants at the same time, which makes them suitable for the analysis of several replicates and screening purposes. A disadvantage of the closed-loop stripping procedure is the strongly reduced air exchange between the inside and outside of the chamber that affects the gas exchange of the plant during longer sampling times. Volatiles that are not adsorbed on the trapping material (e.g., ethylene) or pass through the trap because of a saturated adsorbent surface will accumulate in the chamber and might influence the metabolism of the plant. In addition, transpiration can enhance the relative humidity during collection, requiring intermediate venting of the system between trapping cycles. It is therefore recommended to combine closed-loop stripping analyses with other open headspace sampling techniques for additional result verification and exclusion of potential artifacts.

1.2.2.2 Pull Systems

A simple form of a pull system is an adsorbent trap connected to a vacuum pump that is directly positioned next to a flower.[25,26] This may work well for some flowers that emit large amounts of volatiles; however, the risk is high of trapping ambient air that contains impurities unrelated to the flower and which will obscure minor sample compounds during GC analysis. Enclosure of a flower or flowering branch in a small glass container or a polyacetate cooking bag that releases very little volatiles[3] may reduce the amount of impurities from ambient air. Air enters the container through a purifying filter and is drawn from the chamber by pulling a defined volume of air through an adsorbent trap that can be extracted for further analysis.[7] Although this method is very easy to set up and is portable to the field, it has some drawbacks. Temperature can increase when the chamber is exposed to direct sunlight and the relative humidity inside can increase to nearly 100% within a short time and may lead to condensation on the chamber walls. If a bag is used, it may collapse and damage flower tissue, which may alter volatile emissions. Furthermore, openings in the chamber may provide additional sources of unpurified air entering the system.

1.2.2.3 Push-Pull Systems

In push-pull systems, purified air, which can be humidified to a desired percentage, is pushed into a chamber containing the flowering plant at a controlled flow rate regulated by a flow meter. A defined portion of this air is pulled through a collector trap by a vacuum pump regulated by a second flow meter (Figure 1.4a). Thus a known percentage of the volatiles emitted are collected. To avoid a vacuum or overpressuring of the system, a vent is included in the chamber. Positive-pressure venting prevents ambient air from contaminating the volatiles collected.[27] This positive-pressure venting is also employed in large glass collection chambers on top of a multiport guillotine base. The guillotine base contains concentric gas-sampling ports and two Teflon®-coated removable blades that close the bottom of the chamber around the stem of the plant, leaving an opening for the stem where the blades fit together (Figure 1.4b). This collection system allows for sampling of volatiles from flower parts of intact growing plants, while completely isolating the lower section of the plant including the soil and pot.[9,28,29] Volatiles are subsequently eluted from the trap with solvents such as methylene chloride and analyzed by GC. The technique has been described in detail[30] and was further improved and computer automated to switch traps for drawing samples at predefined time intervals over several days to follow changes in emission of volatiles.[28,31] Such sophisticated automated volatile collection systems can be custom designed by Analytical Research Systems (Gainesville, FL).

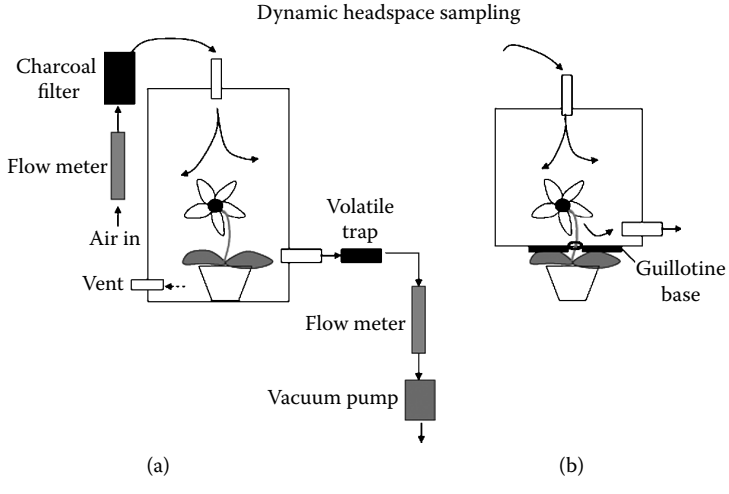

FIGURE 1.4 Example of a push-pull headspace collection system: (a) Air is pushed through a flow meter at a specified rate and cleaned by passing through a charcoal filter before entering the top of the glass chamber containing the flower. After passing over the flower sample, volatiles are pulled through a volatile adsorbent trap on the lower side of the chamber by a vacuum pump at a defined rate, regulated by a second flow meter. Access air for positive pressure venting can escape through the vent on the lower side of the chamber. (b) Example of a push-pull headspace collection chamber following the same principle as (a) for sampling volatiles from parts of a plant. As a modification, Teflon-coated guillotine-like blades close the base of the chamber around the stem of the flower, leaving a small opening for the stem.

Volatiles from flowering *M. jalapa* were identified[28] and their emission over a time course of 48 h was determined with this system.[9] The entire collection chamber can be installed in a greenhouse or in a climate chamber that allows for control of environmental parameters.

1.2.2.4 Online Volatile Collection Systems

Trapping of volatiles on adsorbents and their subsequent elution with organic solvents have been successfully used in many applications (see Section 1.3). However, the sensitivity of the method suffers from the dilution of volatiles by the solvent in the desorption process from the volatile trap. Because only small amounts of the eluted compounds can be analyzed by GC, the sampling times have to be sufficiently long to provide an eluate with enough material for analysis. Therefore precise information on the course of volatile release over short time periods is difficult to obtain. An alternative method is thermal desorption, where volatiles are collected on a trap that is directly inserted into a small oven placed on top of a gas chromatograph. By heating the trap, volatiles are transferred to the analytical column. However, because of interactions between the analytes and the adsorbent surface, higher temperatures may be required for desorption, depending on the compounds. An insufficiently low desorption temperature will result in incomplete release of compounds from the trap, whereas an excessively high desorption temperature can generate artifacts through the formation of degradation products. Tenax® has been successfully used as an adsorbent material in thermal desorption to isolate volatile chemicals[32] (see also Section 1.3), but may lead to interference of degradation products from decomposition of the polymeric skeleton and incomplete desorption of high molecular weight compounds.[33] In comparison to Tenax, the PDMS trapping material, discussed earlier for SPME analysis (Section 1.2.1.1) has been reported to have better properties in preconcentrating the analytes by dissolving them on the bulk of the liquid phase instead of adsorbing them to a porous surface.[34,35] Therefore less energy is necessary to release volatiles from PDMS traps compared to adsorption to Tenax and lower temperatures are sufficient to transfer the sample to a gas chromatography column.

For automated sampling systems, an online thermal desorption method has been described[36,37] that is now commercially available (Gerstel Online-TDS G, Gerstel, Germany). The Gerstel Online-TDS consists of two temperature vaporization chambers placed in series, which are a thermodesorption unit or connected to a temperature-programmable split-splitless injector via a 6-2-way valve mounted on a heated valve chamber. By regulating the mass flow, the system can automatically draw volatile samples with the Online-TDS G. After a cryofocusing step, compounds are flash heated and directly injected on the column. The time resolution of 5 to 60 min depends on the time necessary to collect sufficient amounts of volatiles from the emitting flower for analysis, the compounds themselves, and the time for chromatographic separation on the GC-MS. The TDS G system can be connected to two collecting containers containing the flower samples, as described in detail by Vercammen et al.[35] This method allows for a high time resolution, depending on the compounds, and high sensitivity, but currently requires an extensive laboratory setup.

1.2.3 Other Headspace Sampling Techniques

Besides dynamic headspace sampling, vacuum headspace trapping techniques have been frequently applied in the past for floral fragrance analysis.[38] This method is a form of vacuum steam distillation. Flowers are subjected to a vacuum and volatile compounds are distilled off with the water contained in the plant. Subsequent condensation of the compounds at low temperatures results in a fragrance concentrate which, compared to dynamic headspace sampling, often contains higher proportions of higher boiling point compounds. Because of the improved organoleptic quality of this type of odor concentrate compared to concentrates produced by a dynamic method, the vacuum headspace technique is primarily used in perfume applications. However, it is less applicable for studying the role of floral scent in plant pollinator interactions, since the sampling technique destroys the cellular compartmentation of the plant material and can lead to an additional emission of wound-induced volatile compounds.

1.3 ADSORPTION AND DESORPTION OF VOLATILES

Excellent evaluations regarding the choice and application of volatile adsorbents have been published by several authors in recent years[6,7,39]; therefore, this chapter will primarily summarize the most important practical aspects in the use of different adsorbent materials for volatiles collection.

Matrices used for SPME in static headspace collections have already been described in detail in Section 1.2.1.1. For dynamic headspace volatile collections, adsorbents are usually packed in beds of approximately 2 to 50 mm inside glass or metal tubes between glass wool plugs or metal grids. The amount of adsorbent material used depends on the chemical properties of the compounds to be trapped, the adsorbing capacity of the matrix, the sampling volume, and the flow rate of the collection system. In the case of volatile collections from low-scented flowers, the amount of trapping matrix should be kept low to reduce the volume of solvent required for subsequent compound elution. Smaller amounts of adsorbent also minimize potential artifacts and resistance to air flow. However, if insufficient amounts of trapping media are used, volatile compounds might break through the trap because of adsorbent surface saturation. Breakthrough sampling volumes (per gram of adsorbent) are specified by the supplier or need to be determined by using a series of two traps for collection.

A variety of different adsorbents have been applied for floral volatile trapping. The most common media are the polymer-based Porapak Q® (80 to 100 mesh size; Alltech Associates; Supelco, Taufkirchen, Germany) and its refined version Super Q®, Tenax GC® and its cleaner version Tenax TA® (60 to 80 mesh; Alltech Associates), and activated charcoal. Other carbon-based adsorbents are carbon molecular sieves (Carboxen™, Carbosieve™; Supelco) and graphitized carbon blacks (Carbotrap®; Supelco).[39]

Both porous polymers, Tenax (2,6-diphenyl-*p*-phenylene oxide) and Porapak (ethylvinylbenzene-divinylbenzene), share similar properties. These include a high affinity for lipophilic to medium polarity organic compounds of intermediate molecular

weight and low affinity for polar and low molecular weight compounds such as ethanol and water.

Trapped volatiles are usually eluted from the adsorbents into glass vials with pure solvents or mixtures of low boiling point organic solvents such as pentane, hexane, ether, acetone, or dichloromethane, the latter being preferable with Porapak. A defined amount of one or two standard compounds (e.g., 1-bromodecane, n-octane, nonyl acetate) is generally added to the sample for semi-quantitative analysis. Volatile extracts can be further concentrated by solvent evaporation at ambient temperature or under a nitrogen stream before they are stored at freezing temperatures. Under field conditions, extracts are ideally stored in flame-sealed glass ampoules to exclude sample evaporation.[2] After compound elution, adsorbents are reconditioned by rinsing with clean solvent and dried at room temperature or by flushing with clean nitrogen.

While Tenax appears to have a lower capacity for small molecules compared to Porapak,[40] its thermal stability (350°C) is higher than that of the Porapak polymer (250°C). Therefore Tenax is particularly suited for thermal desorption of volatile compounds in GC analysis. Thermal desorption in combination with cryofocusing (see also Sections 1.2.2.4 and 1.4) allows analysis of the total sample and therefore can enhance the detection limit compared to the analysis of aliquots from solvent-eluted samples. Limitations of thermal desorption include the impossibility of repeated sample injections, the degradation of thermally instable compounds, and artifacts produced from the trapping media.[33,41] Artifacts not only occur with thermal desorption, but can be the result of reactions of the adsorbent material itself or reactions of the adsorbed compounds on the polymer surface. For example, ozone reacts with terpenes on Tenax if ambient air is used in the collection chamber.[42,43] Aromatic ketones and alcohols were identified as artifacts from Porapak,[44,45] and benzaldehyde and acetophenone were found from Tenax, particularly under irradiation with sunlight.[44]

In comparison to Tenax and Porapak, activated charcoal is a cheap adsorbent with high adsorbing capacity. It is used in very small traps (1.5 mg) that are commercially available from different companies (e.g., CSLA-Filter, Le Ruisseau de Montbrun, Daumazan sur Arize, France). Traps can be eluted with small volumes (30 to 40 µl) of an organic solvent such as dichloromethane and reconditioned by extensive rinsing with solvents of different polarity. Artifacts observed with charcoal have been described for the adsorption of terpenes such as ocimene that can be oxidized on the active surface of the adsorbent.[38] Charcoal has been reported to be less efficient than Tenax in trapping aromatic aldehydes.[7] Thus combinations of Tenax and activated charcoal have been applied for trapping the full range of floral volatiles emitted from different orchid species.[46]

1.4 GAS CHROMATOGRAPHIC SEPARATION OF VOLATILES

Gas chromatography is the most efficient chromatographic technique for the separation, identification, and quantification of volatile organic compounds, including plant

volatiles. Numerous research and review articles have been published describing continuous developments and advances in GC analysis technology.[47–53]

Floral volatiles are usually trapped and preconcentrated on adsorbent matrices prior to GC analysis (see Section 1.3). Samples eluted from adsorbents with organic solvents are injected into the column in a split or splitless mode. Split injection provides the advantage of rapidly transferring a small portion of the analytes to the column, resulting in narrow inlet sample bands and chromatographic peaks. In comparison, in the splitless mode, the entire sample is introduced into the column at lower flow rates. This mode is preferred for high-sensitivity analysis of samples with low concentrations.[54] The temperature of the injection liner is typically adjusted to 230 to 250°C to ensure complete vaporization of all sample components. However, adjustments to lower temperatures have to be considered in case of compound decomposition. For example, a conversion of the sesquiterpene germacrene A to β-elemene can be eliminated at an injection temperature of about 150°C.[55]

When samples are thermally desorbed from adsorbents such as Tenax, the solid material is placed directly in a thermal desorption tube that is heated to 250°C to 300°C. In a two-stage thermal desorber, the thermally released volatiles are then transported with the carrier gas to a cold or cryotrap for preconcentration prior to their injection into the GC column. Thermal desorption units are available from different suppliers (Markes, Perkin-Elmer, Gerstel). Despite their still relatively high price, they can save time and money since no manual sample preparation is needed. This advantage has led to the development of online systems combining volatile trapping with automated thermal desorption (see Section 1.2.2.4).

The separation of volatiles in GC analysis is most frequently achieved by the use of fused-silica capillary columns. The most common stationary phases, bound to the inner surface of the column, are the nonpolar dimethyl polysiloxanes, including DB-1, DB-5, CPSil 5, SE-30, and OV-1, and the more polar polyethylene glycol polymers, including Carbowax™ 20M, DB-Wax, and HP-20M. Columns are usually 30 m long and have a stationary phase film thickness of 0.2 to 0.3 μm and an internal diameter of 0.25 mm correlated with a column efficiency of approximately 5000 plates/m.[56] For different stationary phases, retention index data such as the kovats index system have been developed to facilitate compound characterization and identification. Such retention indices have been determined and summarized for several hundred volatile compounds.[57,59]

1.5 VOLATILE DETECTION AND IDENTIFICATION

For the detection of volatile compounds separated by GC, two different types of detectors can be used. The first type, for example, a flame ionization detector (FID), provides only information on retention times, while detectors of the second type, such as MS and Fourier transform infrared (FT-IR) spectroscopy, allow additional structure evaluation. The FID is the most widely used detector in GC analysis. Organic compounds are ionized in a hydrogen/air flame, producing a signal proportional to the mass flow of carbon. FIDs are primarily employed in quantitative analysis because of their wide linear dynamic range (10^6 to 10^8), a very stable response, and high sensitivity, with detection limits on the order of 0.05 to 0.5 ng per compound.

Since isomers with the same molecular formula and carbon content (e.g., sesquiterpene hydrocarbons) principally generate the same FID signal response, relative response factors can be calculated for compounds that are not available in pure form for calibration.

Another detector used in quantitative analysis is the thermal conductivity detector (TCD), which operates by differential thermal conductivity of gaseous mixtures. Compared to FIDs, TCDs do not cause sample destruction, but have only moderate sensitivity (5 to 50 ng per compound). Other detectors applied to the analysis of volatiles are the nitrogen phosphorus detectors (NPDs), which show very high sensitivity for nitrogen- and phosphorus-containing compounds,[60] and photoionization detectors, which have been employed in monitoring plant isoprene and monoterpene emissions.[61,62]

Besides flame ionization detection, MS is one of the most widely used detection techniques in GC analysis. The most common configuration of bench-top GC-MS systems is a gas chromatograph with a single capillary column directly coupled to a quadrupole mass spectrometer with electron ionization (EI). The operating principle of MS relies on the generation of positively charged molecules and molecule fragments from compounds exiting the GC column. The produced ion fragments enter the quadrupole mass spectrometer filter where they are selected according to their mass:charge (m:z) ratio by rapid changes in an electromagnetic field. Following detection of the ions with an electron multiplier, a total ion chromatogram is obtained providing information on the retention time of each compound and its mass spectrum that consists of a characteristic ion fragmentation pattern. Ionization is achieved by either electron impact or chemical ionization that causes less massive fragmentation. MS is a highly sensitive detection method with a minimum detectable quantity in the range of 0.1 to 1 ng per compound. The sensitivity can be further increased in the selected ion monitoring (SIM) mode, in which only selected ions representing particular compounds are scanned. The SIM mode can also be applied for quantification by measuring the most abundant base ion unique to each compound.

Because of the popularity of EI-MS for routine analysis of volatile compounds, several comprehensive mass spectral libraries (Wiley, NIST MS Database, 1998) have been established that are used in EI-MS searches to support compound identification. Other databases for mass spectral comparison of volatile compounds have been developed by Adams[59] and König et al.[63] The MassFinder software, by König et al., allows the comparison of GC-MS data with those of the provided mass spectral library as well as retention indices obtained under identical instrumental and experimental conditions. The MassFinder library contains approximately 2000 spectra of monoterpene, sesquiterpene, diterpene, aliphatic, and aromatic plant volatiles. In addition, MS data for newly identified compounds can be incorporated into the library. Despite the convenient use of mass spectral library data, an umambiguous identification of a compound can only be achieved by the comparison of its mass spectrum with that of an authentic standard analyzed on the same column and the determination of kovats indices on at least two columns with different polarities.

Tandem MS systems have been established to allow separate analyses of single compounds of complex GC peaks.[47] For example, GC-tandem MS was applied to determine the floral scent composition of *Cucurbita pepo* flowers.[64] Moreover,

GC-MS analysis can be complemented by capillary GC-FT-IR, for example, for the differentiation of closely related isomers with very similar EI mass spectra.[47,65] Since FT-IR provides information on the intact molecular structure, unique spectra even for similar isomers can be obtained. The spectroscopic method has been applied for the identification of different floral volatiles.[66,67] Drawbacks of GC-FT-IR are difficulties in quantification and time-consuming data interpretation, although a growing collection of data is provided by the Sadtler database (Sadtler Division of Bio-Rad, Philadelphia, PA, USA).

1.5.1 Enantioselective GC, Multidimensional GC

The chirality of floral scent compounds can be crucial for the olfactory response of pollinators and herbivores. Hence determining the enantiomeric composition of floral volatiles is critical in understanding plant-animal interactions. Since the 1990s, enantioselective capillary columns with chiral phases, such as different hydrophobic cyclodextrin derivatives, have been developed for enantiomer resolution of a variety of chiral volatile compounds, primarily from essential oils.[68,69] As a general rule, polar compounds are better resolved on acylated cyclodextrin derivatives, while nonpolar analytes are better separated on prealkylated cyclodextrin derivatives.[69] König et al. have assembled an enormous amount of data for the identification and enantiomeric recognition of hundreds of sesquiterpene hydrocarbons.[70–73] Other examples for the application of cyclodextrin derivatives in flavor and fragrance analysis were documented by Schreier et al.[74]

In situations where complex volatile mixtures cannot be sufficiently separated on a single chiral column, often two-dimensional capillary GC is employed. In this approach compounds are first separated on a conventional column. Then fractions containing compounds eluting from the first column (heartcuts) are directed to the chiral column as the second dimension. The redirected flow might need to be refocused at the start of the second column by cryotrapping. Borg-Karlson et al.[75] applied a multidimensional GC system to determine the enantiomeric purity of linalool oxides in the floral fragrance of the early flowering shrub *Daphne mezereum*. The system consisted of two gas chromatographs with the first chromatograph housing a DB-WAX column and the second containing two enantioselective β-cyclodextrin columns. The two chiral columns can be used in parallel to ensure optimal enantiomeric resolution. Besides their application in chiral analysis, several other multidimensional GC systems or comprehensive GCxGC systems with directly coupled columns have been developed, particularly in the field of essential oil analysis, allowing increased resolution and improved quantitation or identification of volatile components.[49]

1.6 STRUCTURE ELUCIDATION OF VOLATILE COMPOUNDS

For structure elucidation of unknown volatile compounds usually multiple analytical steps need to be considered. According to König and Hochmuth,[69] in only a few cases might simple mass spectra allow a direct derivation of the corresponding structure.

Most often, sufficient amounts of single compounds need to be isolated for one- and two-dimensional nuclear magnetic resonance (NMR) spectroscopic techniques. Preparative isolation can be accomplished by multiple chromatographic steps including preparative-packed GC columns and thick-film capillary columns with highly selective cyclodextrin matrices. Recently, a simple, efficient NMR sample preparation technique for volatile chemicals has been described using a micropreparative GC system.[76] The absolute configuration of a new compound can be determined by comparison to a synthetic reference compound can be chemical correlation using enantioselective GC. Further details regarding structure elucidation are given elsewhere[69] and go beyond the scope of this chapter.

1.7 VOLATILE ANALYSIS TECHNIQUES WITH HIGH TIME RESOLUTION

A detailed understanding of the regulatory mechanisms governing floral volatile biosynthesis and emissions, such as circadian or diurnal control regimes, require analysis techniques that monitor volatile emission changes with appropriate time resolution. Computer-assisted and online dynamic headspace trapping systems are capable of collecting volatiles in hourly or shorter time intervals (see Section 1.2.2.4). However, trapped volatiles are usually desorbed and subsequently analyzed by GC, which presents a time-limiting factor. Recently new automated analytical systems have been developed that allow highly sensitive, ultrafast volatile analyses and hence represent promising tools for continuous monitoring of plant volatile emissions.

1.7.1 Fast and Transportable GC (zNose)

In recent years, efforts have been made to establish faster GC systems as well as miniaturized GC instruments.[77,78] A recently developed portable GC system, the zNose™ (Electronic Sensor Technology, Newbury Park, CA), has been applied to the analysis of plant volatiles including floral scent[79] (Figure 1.5). The zNose separates compounds by fast GC and operates with a highly sensitive surface acoustic wave (SAW) quartz microbalance detector. The detection principle is based on condensation of the analyte on the surface of an oscillating crystal, leading to an increase in oscillator mass and a reduction in the vibrational frequency proportional to the amount of condensate. The temperature of the SAW detector influences the residence time of the compound on the detector surface and is critical for sensitivity and linear detector response.[79] The high sensitivity of the SAW detector (in the ppbv range) drastically reduces the volatile sampling and preconcentration time of the system. Volatiles are sampled in a small air volume for 20 to 40 sec on a Tenax trap. After rapid thermal desorption, compounds are separated on a capillary 1 or 5 m DB-5 GC column by a defined temperature program before they are monitored and quantified by the SAW detector. The short operation time allows the collection of air samples in time intervals as short as 3 min. Sampling, analysis, and storage of data are fully automated, thus volatile analyses over longer time periods are possible without supervision.

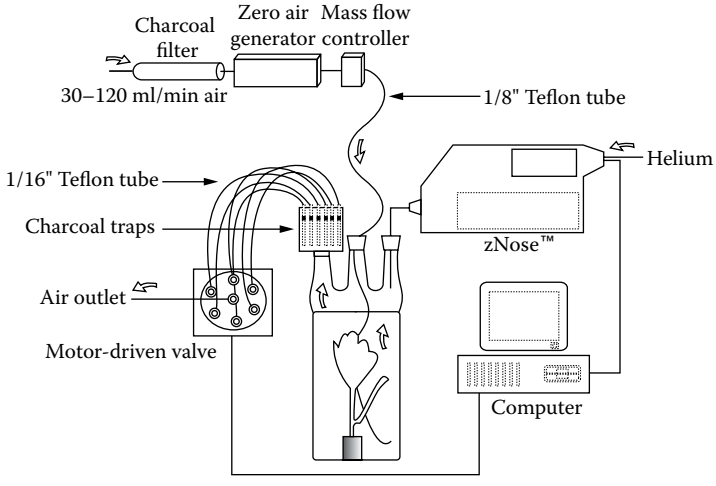

FIGURE 1.5 Volatile monitoring system according to Kunert et al.,[79] combining zNose™ analysis with conventional headspace sampling on activated charcoal traps.

Kunert et al.[79] measured the diurnal emission of volatiles from flowers of the cactus *Rebutia fabrisii* by placing plants in a 2 l glass vessel with a continuous flow of purified air at 30 ml/min. Air samples were taken by the zNose within 40 sec in 30 min intervals. For comparison, volatiles were collected simultaneously in 4 h intervals on charcoal traps for GC-MS analysis. Monitoring the rhythmic emission of floral volatiles with the zNose was comparable to conventional GC analysis, but showed a clearly improved time resolution. An additional advantage of the zNose is its portability, enabling applications not only in the laboratory but also in field experiments. As a drawback of the system, the SAW detector does not allow structure evaluation; therefore, volatiles need to be analyzed by GC-MS prior to calibration of the system with authentic standards. Moreover, the short GC column reduces the compound resolution. Thus monitoring changes of volatiles with similar elution profiles is limited.

In summary, the zNose can be regarded as a tool for quick quantitative estimation of known volatile profiles, making it applicable for high-throughput screenings of natural variants or mutant populations. Given the large time resolution, the system is suitable for monitoring kinetics of volatile emissions from floral and vegetative tissues dependent on diurnal and circadian rhythms and in response to feeding damage or abiotic factors such as light and temperature changes.

1.7.2 Proton Transfer Reaction Mass Spectrometry

Proton transfer reaction mass spectrometry (PTR-MS) analysis technology was developed more than 5 years ago at the University of Innsbruck by Lindinger et al.[80] PTR-MS systems operate independently of GC separation and allow online measurements of volatile organic compounds with concentrations in the pptv range. Originally developed for monitoring changes of volatile organic compounds in the atmosphere, in food control, and in medical analyses, PTR-MS is increasingly applied

for real-time analysis of volatile emissions from plants, although no applications have been reported so far for floral scent analysis. PTR-MS instruments are still relatively expensive and their operation requires extended training by experienced researchers.

For detection by PTR-MS, volatiles undergo a chemical ionization by proton transfer reactions with H_3O^+ ions. Differences in proton affinities allow a proton transfer from H_3O^+ ions to a large number of organic volatiles (e.g., alkenes, aldehydes, ketones, alcohols, aromatics, nitriles, sulfides), but prevent a reaction of H_3O^+ ions with the main constituents of the air. The proton transfer reaction takes place under defined conditions in a homogeneous electric field applied to a drift tube (Figure 1.6). Ions exiting the tube are then mass analyzed by a quadrupole mass spectrometer. The soft ionization of compounds by protonation causes only low fragmentation, hence mainly one product ion species occurs for each reactant. The extremely fast time response of the instrument results from the time the volatiles spend in the drift tube, which is less than 1 sec.

The PTR-MS technique has been applied in recent years to measure fluctuations of volatile emissions from various plants. Usually, whole plants or plant parts are enclosed in glass containers, inert bags, or dynamic cuvette systems with a continuous airstream and controlled temperature, humidity, and light conditions, and aliquots of the exiting air are analyzed by PTR-MS. Emissions of volatiles including isoprene and monoterpenes from trees and other plants have been monitored under laboratory and field conditions in response to changes in abiotic factors, such as light and temperature, or biotic factors such as pathogen attack.[81,82]

Besides its use in online qualitative and quantitative analyses of plant volatile organic compounds, PTR-MS has become a valuable tool for investigating the biosynthesis of volatiles using isotope-labeled precursors. For example, carbon sources other than photosynthetically fixed carbon dioxide (CO_2), involved in the biosynthesis of isoprene in poplar leaves, were identified by online measurements of differentially labeled isoprene isotopes during exposure of the plant to ^{13}C-labeled and unlabeled CO_2 and feeding of ^{13}C-labeled and unlabeled glucose.[83] Similar

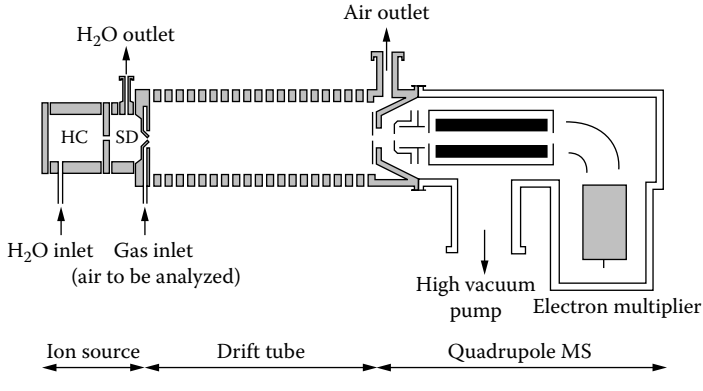

FIGURE 1.6 Principle scheme of the PTR-MS apparatus according to Lindinger et al.[80] (modified). HC, hollow cathode; SD, source drift region.

experimental designs might be applicable to elucidate carbon pools or precursors in biosynthesis pathways of various floral volatiles. In addition, fast metabolic changes in response to enzyme inhibitor applications could be determined.

As a consequence of the ability to perform real-time analyses and measure volatiles with high sensitivity, the PTR-MS system may also qualify as a tool for fast screening of floral emissions from mutants and ecotypes. However, the analysis of volatile mixtures is limited by the ability to determine only the molecular mass of products. Compounds of the same molecular weight cannot be identified separately, therefore additional analysis by GC either in parallel or coupled with the PTR-MS instrument is necessary.[84] Future developments might improve compound identification by combining PTR-MS with an ion trap mass spectrometer, allowing MS/MS performance to distinguish between isomers and other isobars.[85]

1.8 CONCLUSION

The analysis of plant volatiles, including those emitted from floral tissues, has continuously improved over the past 10 to 20 years. The development of materials with high adsorbent capacities for volatile compounds has allowed efficient trapping of volatiles and volatile blends with different chemicophysical properties. Equally important, improvements in gas chromatographic separation, the establishment of highly sensitive spectroscopic detection methods, and expanding mass spectral libraries have laid the foundation for the detection and identification of complex mixtures of volatiles as well as trace amounts of floral volatile components. We have discussed a variety of different volatile collection methods that have been developed, and together they give today's researcher the flexibility of selecting the best method suitable for a particular application. Online analysis techniques are increasingly important for monitoring the kinetics of floral volatile emissions and learning more about the biosynthetic pathways of different scent components. However, greater portability of volatile collection techniques combined with high sensitivity and large time resolution would be desirable to measure floral volatiles in the field in their natural environment, which will further improve our understanding of floral volatile biology.

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