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Volatiles and Food Security

Role of Volatiles in Agro-ecosystems

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Preface

One major challenge for the twenty-first century will be the production of sufficient food – the United Nations Population Fund estimates that the global human population may well reach ten billion by 2050 (www.unfpa.org). This means increasing agricultural productivity of food crops, as plants form the basis of every food chain. If global food production is to keep pace with an increasingly urbanized and growing population, while formulating new food production strategies for developing countries, the great challenge for modern societies is to boost plant productivity in an environmentally sustainable manner. The task of providing food security to our country's burgeoning population is becoming increasingly difficult. This challenge must and needs to be met in the face of the changing consumption patterns, impacts of the climate change and degradation of the finite land and water resources. Management of land resources, in general, and potentially culturable lands, in particular, encompasses crop production methods that will keep pace with a country's food needs, sustaining environment, blunting impacts of climate change, preserving and enhancing natural resources and supporting the livelihood of farmers and rural population in the country. Thus, there is a pressing need for enlarging area under arable lands, by the way of reclaiming degraded lands for sustainable intensification of agriculture, in which crop yields can be increased without compromising and yielding to adverse environmental impacts and without reducing area under forests. The science of crop management and agricultural practices suited to lands exposed to different stresses at present demands a specific orientation for meeting challenges of food insecurity. In this scheme of agricultural development, effective utilization, rejuvenation and management of degraded and wastelands by public and private investments become imperative. In addition to the type and the extent of degradation the lands have undergone or are undergoing, appropriate management strategies need to be designed and implemented in a defined time frame to bring these lands to 'productive health'.

Over the last decade, bacterial volatile emissions under stress and their possible practical applications on plant growth have received increasing attention. We determined bacterial VOC-mediated antifungal activity using NA + PDA agar plates. As shown in the Fig. 1 bacterial culture, SJ-5 was found to be antifungal in nature as it strongly inhibited the growth of fungus mycelia 2 days after inoculation. The same result was obtained in the volatile plate assay, and volatiles produced by SJ-5 inhibited the growth of mycelium.

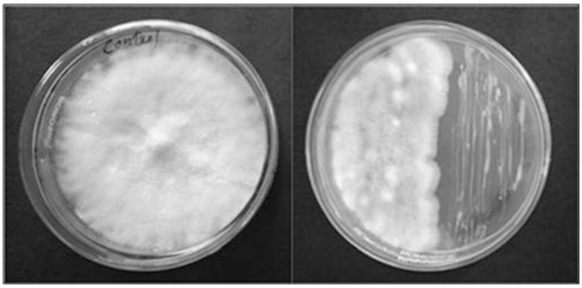

Fig. 1 Volatile activity of *Bacillus* sp. SJ-5 against *Fusarium oxysporum*

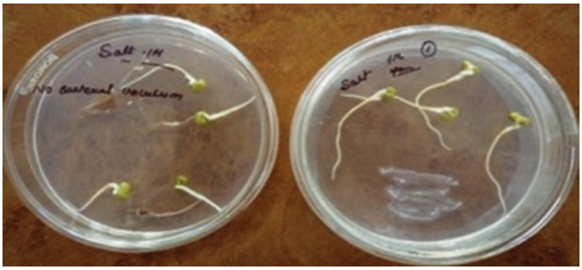

Fig. 2 Effect of bacteria-mediated volatiles on mung bean seed germination under 100 mM NaCl. Left plate, without strain, whereas right plate, with bacterial strain AU. Right plate showed significant radical growth in the presence of bacterial VOCs

In continuation of VOC production, *Pseudomonas simiae* AU (MTCC no. 12057) was grown on nutrient agar media for 24 h before plant experiment and scraped into sterile, distilled water. The liquid suspension culture was diluted with water to yield 10^9 colony-forming units/ml. Bacterial culture were inoculated into one compartment of a petri plate containing half Murashige and Skoog medium amended with 0.8 % agar and 1.5 % sucrose. *Vigna radiata* (mung bean) seeds were surface sterilized with 0.1 % $HgCl_2$ for 1 min and 70% ethanol for 3 min and washed three times after both treatments with Milli-Q water (Millipore, Germany) and transferred to the other compartment of the petri plate. Plates were sealed with Parafilm and arranged in a completely randomized design in a plant growth chamber for 7 days at 27 °C. There were two experimental groups with three replicates (control +100 mM NaCl, without bacterial inoculation; AU inoculated +100 mM NaCl, with bacterial culture inoculation). Seedlings were harvested after 7 days of incubation period and total plant fresh weight, length and protein content were measured (Fig. 2). The sphere of microbial VOCs for rhizobacteria could be within the soil or above ground, and the possibility existed that VOCs are produced at sufficient levels for aerial tissues to perceive and respond to bacterial volatiles. It is interesting to analyse whether VOCs are by-products of various plant processes or they are actively produced and used as a sophisticated ‘language’ by plants to pursue communication with other organisms. Plants are capable of disseminating information to their environment by employing VOCs, and plants have the capacity to change

Fig. 3 Effect of *Pseudomonas simiae*-mediated volatile treatment on soybean seed germination in bipartite petri plates (I-plates). Left plate devoid of strain showed stunted growth, whereas right plate with strain exhibited significant growth

the growth condition employing reactive VOCs. No doubt plants have evolved with the capacity to release and detect VOCs in their environment; the emission of plant odours transmits signals to other organisms and members of its own species.

Case Study Authors and team have performed experiments on bacterial VOC-mediated IST in soybean.

Plant root-associated rhizobacteria elicit plant immunity referred to as IST against multiple abiotic stresses. Among multibacterial determinants, bacterial VOCs that induce IST and promote growth are reported in this study. This research calls attention on the role played by *P. simiae* AU VOCs in salt tolerance in soybean plants directly by the reduction of Na^+ ions in the root and shoot and the induction of proline content in the root and indirectly on the expression of VSPs, GGH and RuBisCO large chain protein. Emissions of AU VOCs significantly increased shoot and root growth. This was attributed to the higher IAA content in the root and lower uptake of Na^+ ions, and the increase in chlorophyll content was related to the up-regulation of chloroplast-specific protein RuBisCO. Furthermore, the up-regulation of GGH protein in salt stress indicates its role in plant metabolism and development through folate homeostasis. Additionally, overexpression of VSPs induced by salt stress suggests its role in salt tolerance by regulating Na^+ homeostasis, maintaining phosphorus content through acid phosphatase activity. Hence, the selected PGPR *P. simiae* have great potential for improving crop yield. Firstly, seed germination was checked on a bipartite petri plate containing half MS incorporated with 100 mM NaCl in one partition and King's B inoculated with strain AU in another partition. All seeds were germinated but could not grow more because of space limitations (Fig. 3).

Over the last decade, bacterial volatile emissions and their possible practical applications on plant growth have received increasing attention. The PGPR strain *P. simiae* AU was previously found to promote seedling growth of *Glycine max* through its plant growth promotion activities like IAA, siderophore production, phosphate solubilization and ACC deaminase activity under salt stress condition. Herein, the study reported for the first time that *P. simiae* produces a volatile blend that can enhance soybean seedling growth and elicit IST against 100 mM NaCl stress condition. To overcome the difficulty encountered with plants of larger size than *Arabidopsis* for studying the effects of bacterial VOCs, in a petri plate, a new VOC assay system, based on a magenta box, was developed. Using this test system, we found that IST elicited by VOCs released from strain AU is mediated by the induction of proteins in plant tissues. After 10 days of seedling growth, the shoot and root length were significantly higher in soybean seedlings treated with strain AU VOCs. It is reported that NaCl caused the depletion and precipitation of available phosphorus that caused restricted growth and impaired the delivery of available phosphate in plant cells. In this study, VOC-treated seedlings showed higher phosphate content in salt stress than non-treated seedlings. It may be caused by the acid phosphatase activity of VSPs that release soluble phosphate from their insoluble compounds inside the cell.

A greater understanding of how plants and microbes live together and benefit each other can therefore provide new strategies to improve plant productivity while helping to protect the environment and maintain global biodiversity. To date, the application of chemicals to enhance plant growth or induce resistance in plants is limited due to some negative effects of chemical treatment and difficulty in determining the optimal concentrations to benefit the plant. For alternative means to solve these problems, biological applications have been extensively studied. Collectively, our description on VOCs eliciting growth promotion suggested that these compounds could be an environmentally sound means to grow and protect plants under greenhouse or field conditions better. From the whole plant perspective, it still remains to be determined whether growth promotion by microbial VOCs occurs in soil or soil-less media. To understand the nature of VOCs and gene expression profiling of plant genes, studies of these compounds can be conducted. It is possible that VOCs produced by microbes while colonizing roots are generated at sufficient concentrations to trigger plant responses. In conclusion, positive or negative effects of VOCs on plant productivity will be dependent upon their specific microbial strains, plant genotype and the presence/absence of abiotic/biotic stresses.

Economic Implications of the Proposed Work

The proposal will have the following long-term socio-economic impact:

- The innovative microbial strategies developed will be employed to plants grown under pathogen-conducive stress in the soil.
- The environment will also benefit from reduced fertilizer and pesticide use.
- The stakeholder will be able to exploit the inoculants developed.
- A dissemination of the proposed book will ensure that the whole agricultural community can benefit from the project.

Hence, in this book, editors compiled researches carried out on volatiles produced by microbes and plants along with their biotechnological implications for sustainable agriculture.

Chapter 1 summarizes the role of plant VOCs produced in various tissues against stresses regarding herbivores, plant viruses, pathogens, temperature, humidity, light ozone, food usability, etc., and their implication for physiological processes such as plant development, seed formation and germination, pollination and fruit ripening.

Chapter 2 briefly describes the VOCs released by bacteria in the air that interact with their surrounding environment. Soil bacterial volatiles are known to contribute to plant interactions, and several studies also identified their influence on plant stress tolerance. This chapter describes the characterization of different bacterial VOCs and their roles in enhancing plant abiotic stress tolerance, a new research area, with potential agriculture applications.

Chapter 3 emphasizes the insight of the phytoextraction and phytovolatilization mechanisms that are involved in the decontamination of the soil. Phytoremediation is a green emerging technology used to remove pollutants from environment components.

Chapter 4 describes techniques like basic chromatography and mass spectrometry to understand the chemical structure and function of plant and microbial VOCs. In addition to this, modern OMICS methods give opportunity to a deep insight of microbial diversity and strengthen the concept of volatile compound function by providing real-time pictures of their expression and signalling. Besides, the incorporation of computational tools with molecular biology techniques incredibly creates a reservoir of knowledge-based database of volatile compound structure, function, diversity, signalling and even prediction through statistical tools.

Chapter 5 highlights the diversity of VOCs present in the plant rhizosphere. The rhizovolatiles discussed here include those produced by plants as well as by microorganisms inhabiting the rhizosphere. The chapter focuses on the role of these volatiles in the establishment of a successful association between plants and other organisms and their beneficial effects on plant growth and development. This will value-add to the present understanding of the chemical cues defining the complexity and dynamism of rhizosphere functioning.

Chapter 6 highlights the current knowledge on the expression patterns and functions of some leguminous plant proteome in response to VOCs released during biotic and abiotic stresses. The biogenesis of VOCs and their functional role in plant-plant signalling and environmental and biological stress responses are highlighted. Experimental evidences revealed that a plant symbiont produces VOCs that induce resistance to phytopathological species and PGPR.

Chapter 7 describes the role of plant VOCs for direct and indirect defence against various abiotic stresses (like temperature, water stress, ozone, salt stress and heavy metals) and biotic stresses (herbivores and pathogen) with above ground and below ground impact.

Chapter 8 briefly describes the importance, chemistry and role of microbial VOCs in defence in general.

Chapter 9 highlights the chemical measures necessary for controlling plant pathogens and their negative impact on human health and/or the environment. It also defines the different sources of essential oils and their antimicrobial activity with particular emphasis on the antifungal properties exhibited against some serious pathogenic fungi and postharvest disease.

Chapter 10 briefly discusses the role of VOCs in microbial-microbial and microbial-plant interactions. The effect of VOCs as inducers for enhancing crop productivity is reviewed. Problems associated with field applications are also highlighted.

Chapter 11 summarizes volatile-mediated interactions in a microbial community mimicking the natural conditions of a heterogeneous soil environment along the rhizosphere as well as the biological and ecological significance of VOC-mediated resistance.

Chapter 12 describes the role of MVOCs wherein they can be exploited as eco-friendly, cost-effective, disease-resistant and sustainable strategies for agricultural practices and aims to provide a comprehensive discussion on below and above ground interactions of microbial volatile diversity and their role against pathogenic fungi.

Chapter 13 elaborately describes the intricate relationship of plant, herbivore and carnivore in this tritrophic ecosystem to determine whether evolution plays any role and to calculate the overall ecological cost to govern this complex machinery of life.

Chapter 14 focuses on the diversity of MVOCs and further discusses their potential in exploiting these bioactive molecules in sustainable eco-friendly agriculture for improving plant growth, production and protection.

Chapter 15 elaborately describes the functionality of herbivore-induced plant volatiles (HIPVs) in communicating with the parasitoids to prey upon attacking herbivores. HIPVs not only help plants to interact with the natural enemies of herbivores but also warn the neighbouring plants of the imminent danger. Thus, HIPVs provide a reliable mechanism for natural control of insect pests.

Chapter 16 describes PGPR-emitted VOCs that can directly and/or indirectly mediate increases in plant biomass, disease resistance and abiotic stress tolerance. Bacterial VOCs promote plant growth by eliciting different hormone signalling pathways. In particular, the volatile components 2,3-butanediol and acetoin were released exclusively from two bacterial strains that trigger the greatest level of growth promotion and induced resistance against fungal pathogens. This chapter focuses on recent research studies and the role of bacterial volatiles in plant growth promotion and protection against pathogens.

Chapter 17 presents an overview of current insights of fungal VOCs on growth and development and the defence system of plants. Numerous fungal VOCs contribute to dynamic processes, leading to myriad interactions between plants, antagonists and mutualistic symbionts. For better understanding of the role of fungal VOCs at field level, more studies will offer further constructive scientific evidences on cost-effective, eco-friendly, and ecologically produced fungal VOCs for crop welfare.

Chapter 18 describes the role of MVOCs as an alternative strategy in lieu of chemicals to protect plants from pathogens which provides a setting for better crop welfare. MVOCs can modulate the physiology of plants and microorganisms and thus can be exploited as eco-friendly, cost-effective, and sustainable strategies for agricultural practices.

Chapter 19 envisages the role of MVOCs with special emphasis on plant defence and health, alluding to the potential of these compounds to control various processes that result in plants' elevated health and defence.

Finally, we would like to express our gratitude to the contributors upon their consent to be a part of this book.

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Plant Volatile Compounds in Growth

1

Demet Altındal and Nüket Altındal

Abstract

Plants synthesise volatile organic compounds (VOCs) in various tissues against stresses regarding herbivores, plant viruses, pathogens, temperature, humidity, light ozone, food usability, etc., and for physiologic processes such as plant development, seed formation and germination, pollination and fruit ripening. These compounds are synthesised in all parts of plants, especially flowers, fruits, roots, xylems and cells, and just as they may be effective in the tissues they are produced, they may be transferred to other parts of the plants and show their effect there.

Plants communicate with living things around them by emitting numerous different volatile compounds. They develop morphological and physiological defence mechanisms by repulsing or attracting their enemies with these compounds. Plants store these compounds produced for defence and release them in the form of volatile gases when needed. Plant volatile compounds include isoprene, terpene, fatty acid derivatives, alcohols, esters, volatile oils, plant development regulators (abscisic acid, auxin, cytokinin, etc.), phenolic compounds and secondary metabolites.

Keywords

Plant • Volatile compounds

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Headings and Heading Numbering

1. Plants produce volatile organic compounds (VOCs).
2. Plants can communicate by releasing volatile compounds.
3. Plant volatile compounds act in physiological processes such as growing, development, seed formation and germination.
4. Plants release volatile compounds they produce for the morphological and physiological defence mechanisms they develop.

1.1 Introduction

Plants, which are sources of food for bacteria, fungi, viruses, insects, nematodes, humans and animals, have developed defence mechanisms against different stress factors, and they regulate these mechanisms by releasing volatile organic compounds (VOCs). Plant volatile compounds may be classified as hydrocarbons, alcohols, aldehydes, ketones, ethers and esters based on their chemical structures. In botany, plant volatiles are usually classified into volatile terpenes, volatile phenylpropanoid/benzenoid and volatile fatty acid derivatives based on their varying biosynthetic functions (Dong et al. 2016).

Volatiles are evaporating compounds with small molecules produced by plants (flowers, fruits, vegetables, herbs, etc.). There are more than 2000 known volatiles in plants to date. Each volatile compound has a different smell. β-Ionone volatile compound is produced in floral, woody, sweet, fruity berry and greens, while dimethyl disulphide sulphurous substance is produced by vegetables, onions, garlic and leeks, and myrcene substance is produced by peppery, spicy berry and plants (Peter 2012). Natural aroma or smell consists of hundreds of volatile compounds.

During their growth and development, plants are exposed to biotic and abiotic stress factors, and thus they develop defence systems. Among these stress factors, herbivores, plant viruses and pathogens are biotic stresses, while temperature, humidity, ozone and food usability are abiotic stresses. Volatile organic compounds (volatiles) are synthesised in different plant tissues. In order for plant volatiles to be released into the atmosphere, secretory cells in sweet basil can release phenylpropanoids, or epidermal cells in mint can release volatiles such as p-methane, diterpenes and monoterpenes (Kant et al. 2009). The places plastid and cytosol volatiles are synthesised are plant cells. These volatiles are secondary metabolites whose place of synthesis is determined biochemically, and they are classified as terpenoids, phenylpropanoids/benzenoids, fatty acid derivatives and amino acid derivatives based on their source of production. Volatile compounds in plants are transferred from primary and secondary roots to leaves, flowers, fruits and the body by way of transpiration. These compounds are released from the living secretion tissue with cells that have abundant cytoplasms and big nuclei.

Table 1.1 Functions of plant volatile compounds in some plants

Process/stress/ interactions	Plant	Volatile compounds	References
Plant growth	*Arabidopsis thaliana*	Brassinosteroid	Zhang et al. (2015)
	Arabidopsis	Abscisic acid, gibberellins	Li et al. (2016)
			Procko et al. (2014)
	Arabidopsis, *Brassica rapa*	Auxin	Altındal and Altındal (2013)
		Sage oil and thyme oil	
	Sainfoin		
Ripening	Maize	Ethylene	Louis et al. (2015)
	Tomato	Ethylene	Kim et al. (2015)
Herbivores	Tomato	Alkaloids, phenolics	Reisenman and Riffell (2015)
	Maize	Terpene	Fiers vd. (2013)
	Cowpea	Thyme oil	Altındal and Altındal (2011)
Pathogens	Tobacco	Flavonoids, phenolics	Büchel vd. (2015)
	Barley	Methyl salicylate	Shulaev vd. (1997)
Pollination	Entomophilous plants	Terpenes and benzenoid	Farre-Armengol vd. (2015)
	Monkey flower	Monoterpenes	Byers et al. (2014)

Plant volatiles which can be stored in the plant cell in liquid form are organic molecules that can evaporate in contact with air and form compounds with carbon atoms. VOCs are exposed to air when mint leaves or pine needles are crushed and they become usable for perfumery. Again, when grass is mown (green leaves are cut), a nice smell is released.

1.2 Types of Plant Volatile Compounds

Plant volatile compounds include different organic classes such as isoprene, terpene, fatty acid derivatives, alcohols, alkanes, esters and acids. These compounds are found in various plants and they serve various physiological purposes (Table 1.1).

1.2.1 Terpenes

They are a broad and diverse class of hydrocarbons which are produced by plants, especially Coniferales. Terpene types are hemiterpenes, monoterpenes, sesquiterpenes, diterpenes, sesterterpenes, triterpenes, tetraterpenes and polyterpenes. Some particular terpenes have well-known functions in plant growth and development; therefore, they are considered primary metabolites.

1.2.2 Alkaloids

They are naturally produced chemical compounds which have amine structures. Alkaloids are seen mostly in Solanaceae and Papaveraceae plant families and found less in Rosaceae, Graminaceae and Labiatae families. The highest amounts of alkaloids are found in plants' roots and leaves, while the lowest amounts are found in skins, seeds and stems. Almost all alkaloids have a bitter, hot taste and they are odourless. Some important alkaloids in plants are piperidine, pyridine and tetrahydropyridine alkaloids.

1.2.3 Glycosides

They are formed by the combination of glycosidic hydroxyl (−OH) in sugar with another substance containing OH such as cellulose, polysaccharide, phenol and extraction of water. These are essential compounds. Glycosides are found extensively in plants. Glycosides with their bitter and hot taste are probably effective for protection against ruminants, and they act in regulation of various biochemical processes. While glycosides exist in plants' leaves too, they are usually found in fruit shells and roots.

1.2.4 Essential Oils

Essential oils in plants are essential compounds for plants as they provide transfer of all chemicals to cells and increase the plants' resistance to diseases and pests by strengthening their defence mechanisms. While they form the structure of hormones in plant cells, they play roles in transfer of information among cells and plants' defence mechanisms.

1.2.5 Plant Volatile Oils

Volatile oils are oil-like mixtures that are obtained from plants and herbal drugs by various methods which are in liquid form in room temperature, crystallisable, pungent and towable by water vapour. The smell of several aromatic, fragrant and scented plants comes from their content of active ingredients (volatile oils). Volatile oils exist in plants' rhizome, body and shells, leaves, fruits and flowers. Many plant volatile oils and monoterpenoid compounds are rapidly degradable in nature, and they do not accumulate in the body or the environment. So, they are used to fight against insects (Tunaz et al. 2009).

Limonene, 1,8-cineole, camphor, linalool, citronellol, citronellal and anethole are chemical compounds with known insect repellent activities, and they are found in volatile oils obtained from plants. Table 1.2 shows volatile oils as insect repellents and their active ingredients.

Table 1.2 Volatile oils as insect repellents and their active ingredients (Öz 2013)

Volatile oil	Active ingredients
Eucalyptus oil	Globulol, epiglobulol, b-pinene, a-pinene,1,8-cineole, limonene, terpinen-4-ol, aromadendrene, piperitone and a-phellandrene
Cedar oil	Cedrol, thujopsene (a ketone), widdrol, cedrene, copaene, thujaplicin, methyl thujate and thujic acid
Fennel oil	Myrcene, a-pinene, trans-anethole, fenchone, anisic aldehyde, limonene, 1,8-cineole and methyl chavicol
Clove oil	Alcohols, phenols (eugenol, acetyl-eugenol), a small amount of esters, ketones and sesquiterpenes (a and b caryophyllenes)
Laurel oil	Myrcene, methyl chavicol, a-terpineol, neral, geranyl acetate, eugenol, chavicol, limonene, linalool, a-pinene and b-pinene
Thyme oil	Camphene, thujone, a-terpinene, b-pinene, p-cymene, borneol, linalool, carvacrol, thymol, b-caryophyllene and a-pinene
Lavender oil	Limonene, 1,8-cineole, cis-ocimene, 3-octanone, camphor, linalyl acetate, terpinen-4-ol, a-pinene, lavandulyl acetate, trans-ocimene, caryophyllene and linalool
Mint oil	Menthol, menthone, menthofuran, limonene, b-pinene, a-pinene, methyl acetate, germacrene-d, trans-sabinene hydrate, isomenthone, 1,8-cineole and pulegone
Basil oil	Limonene, linalool, camphene, a-pinene, b-pinene, myrcene, cis-ocimene, geraniol, camphor, methyl chavicol, eugenol, y-terpineol, camphor, methyl cinnamate and citronellol
Rosemary oil	Borneol, 1,8-cineole, camphor, bornyl acetate, a-pinene, b-pinene, camphene and limonene

1.2.6 Secondary Metabolites

Secondary metabolites produced by plants and assumed to be waste outputs are products of highly complicated mechanisms developed for defence, protection, adaptation and proliferation. All plant metabolisms have phenolic compounds in different quantities and qualities which are considered to act in plants' protection against some pests.

1.2.7 Phenolic Compounds

All plants create phenolic compounds as secondary metabolites in their metabolisms, roles of which are not sufficiently known. This is why all foods of plant origin contain phenolic compounds in different quantities and qualities. Phenolic compounds in plants are phenolic acids (or phenol carbonic acids), flavonoids and compounds with small molecules that are mostly volatile.

1.2.8 Ethylene

It is a colourless alkene gas and an unsaturated hydrocarbon. The reaction capability of ethylene is very high. Plants produce ethylene as a reaction to stresses such as drought, floods, mechanical pressure and infections. Ethylene acts in processes of fruit ripening, conversion of polysaccharide into sugar, defoliation, seed germination and budding.

1.3 Volatile Compounds in Plant Development

Substances that regulate plant development are volatile organic compounds produced by the plant; they regulate growth, development and other physiological processes, and while they can be effective in the parts they are produced, they can be transferred to other parts of the plant and utilised there. Plants produce these fundamental substances needed for their growth, development and transformation. These substances that are produced in the plants' body and regulate growth and development (physiological processes) are called hormones or phytohormones (plant hormones). There are several phytohormones. They are classified in five main groups as gibberellin (GA), abscisic acid (ABA), auxin, cytokinin and ethylene based on their similarities and effects.

1.3.1 Volatile Compounds in Seed Germination and Vegetative Development

Abscisic acid (ABA) and gibberellins (GA) are well-known phytohormones that act in seed germination and regulation. These two hormones affect germination in opposite ways. While ABA inhibits germination, GA catalyses this biological process (Li et al. 2016).

Gibberellins (GA) play an important role in eradicating seed and bud dormancy, as well as controlling and stimulating seed germination. They are found abundantly in developing seeds. Their amount is lower in more developed seeds of especially dicotyledon plants. GA provides that the enzymes taking part in this process are stimulated and play a role in the conversion of polysaccharide into sugar by moving from the embryo to endosperm and stimulating the α-amylase enzyme to provide energy (Zadeh et al. 2015). GA stimulates the growth potential of the embryo and weakens the structures surrounding the embryo. Endo-β-mannanase produced in the endosperm based on GA may help germination by providing degradation of endosperm cell walls (Ogawa et al. 2003). Naturally occurring ABA plays a role in promoting dormancy in seed germination, buds and seeds. Abscisic acid (ABA) prevents germination in seeds by sustaining dormancy and ensures that germination does not take place in arid conditions. The juglone substance that can be found in the roots and leaves of the walnut (*Juglans* sp.) plant prevents germination of some plant seeds.

Naturally occurring ABA plays a preventive role in not only seed germination but also plant growth, especially root development. It is effective in developing an adaptation mechanism against stress. The auxin hormone which produces cotyledon in plants regulates hypocotyl elongation (Procko et al. 2014). Auxins play roles in vertical growth of plants, nutation processes and defoliation. These hormone groups are produced in the plant's terminal bud, and phototropism occurs with the help of these hormones. Cytokinins regulate root and body development by working with auxins in development of seeds, and lead to production of chloroplast, thus preventing yellowing of leaves and ageing. Growth is provided by stimulation of cell division, and growth of offshoots and leaves from buds is induced. Gibberellins induce rapid and abnormal elongation of the body and prevent defoliation. Abscisic acid blocks the pores of the plant in arid conditions and increases adaptation to dry environments by preventing loss of water from leaves. It is observed that young pine seedlings develop very weak in forests containing high numbers of plant species in the Ericaceae family showing allelopathic properties.

While the level of photosynthesis decreases in high temperatures for numerous tree species, resistance to high temperature is achieved by secretion of isoprene in birch leaves (Dong et al. 2016).

1.3.2 Volatile Compounds in Bloom and Fruit Ripening

Gibberellins stimulate bloom and early bloom and promote growth of fruits. Auxins are effective in fruit ripening. ABAs lead to abscission in flowers and fruits, which increases the ripening of the fruits.

Ethylene is one of the volatile compounds that play a role in plant development. Ethylene is secreted in the ripening of climatic fruits; the volatile ethylene regulates gene expression and softens the cell wall. While changes in volatile compounds increase the quality and attractiveness of the fruits, higher ethylene production leads to faster ripening. Chlorophyll loss in the fruit changes the colour, and secondary metabolites such as carotenoids and flavonoids regulated by ethylene and ABA are produced. From the development to the ripening of the fruit, glycose and fructose accumulate, citric and malic acids are created from organic acids, which in turn establish the taste of the fruit. Volatile compounds also determine the flavour of the fruit (Gómez et al. 2014).

About 900 different volatiles were found in fruits and vegetables. Ethylene also plays an important role in flavour creation in climacteric fruits. In a study on grape plants, ester, ketone and lactone compounds emerged after the veraison period, their levels increased up to the point of harvesting, and these compounds' scent activity values were higher than those of others (Chang et al. 2015).

Amount of ester increases starting at postpollination to the postharvest ripeness. Most aldehydes are produced in high amounts in early growth and harvest periods (Beaulieu and Grimm 2001). Aldehydes, hydrocarbons, alcohols, acids and ketones are volatile chemicals which play a part in the smell and flavour of numerous fruits. Volatile esters provide genuine flavour to the fruit.

1.3.3 Volatile Compounds in Promoting Pollinators

Fragrant secondary metabolites secreted in flowers are at least as attractive as colours for many insects, birds and mammals. The most important secondary metabolites responsible for scent in flowers are monoterpenes (such as linalool, limonene, citronellol and geraniol), sesquiterpenes (such as α-bisabolol, β-ionone and farnesol), aromatics (such as vanillin, eugenol and methyl eugenol), aliphatics (such as pentadecane and octanol), monoamines (such as methylamine, ethylamine and propylamine), diamines (such as putrescine and cadaverine) and indole alkaloids (such as indole and skatole). Pollinator insects are highly sensitive about different scent components. Using the scents that attract these insects as pheromones, for example, spraying the plants that are highly dependent on cross-pollination with these chemicals in time of flowering, may increase the amount of pollinator insects, and products can be obtained with higher efficiency and quality.

Plants attract pollinator insects and achieve reproduction with cross-pollination. More than 85% of flowery plants need insects for the pollination to happen. Studies focus on flower scents and plants that attract pollinators. Bees act as pollinators based on smell, rather than flower colour. They also communicate with other bees and find hives based on their sense of smell, instead of following flower colours.

Flowers on plants produce volatile compounds in varying and high amounts for pollination, and benzenoids are found in flower scents as VOCs.

Nectar, which contains volatile primary metabolites (sugars and amino acids) and secondary metabolites (alkaloids, phenolic amino acids that are not proteins with attractive and repulsive properties), is an important component.

1.4 Volatile Defence Against Herbivore Insects and Fungal Pathogens

Plants may be subjected to natural predators such as pests, nematodes, pathogens, fungi, bacteria and viruses, which decrease their yield and quality. Plants have developed various defence mechanisms against these biotic stresses.

While there are still not enough studies about the effective mechanisms of volatile oils and their components which are effective against pests in general, there are some studies about defence mechanisms that prevent feeding or have insecticidal effects (Roy and Das 2015; Shahab-Ghayoor and Saeidi 2015).

Secondary compounds found in plants (volatile oils, alkaloids, glycosides, etc.) are used as raw material for drugs, in addition to being found effective against pests. In the studies conducted (Wang et al. 2015; Degenkolb and Vilcinskas 2016), it was reported that some plants counteract and even kill some pests (nematodes) with the substances they secrete. Repellents which have an important place in biological struggle may be classified in two groups as natural and synthetic. It is reported that some significant natural repellents are *Pyrethrum*, *Artemisia* and *Mentha* species and secondary compounds like volatile oils. Secondary compounds in plants are studied in two groups as repellents and deterrents.

More than 2000 plant species have natural insecticide properties. For example, the pyrethrin substance found in Pyrethrum (*Chrysanthemum cinerariaefolium*) flowers has been used as insecticide material since the nineteenth century. Europeans learnt in the beginning of 1800s that dried flower powders of the Pyrethrum plant used by African natives as an insecticide was significant for Persians, and it was exported from Europe to the United States in the beginning of the twentieth century. These flower powders have been used by Westerners as a source of pyrethrin to produce fly spray for 160 years.

Today, another natural insecticide which is a tropical and subtropical plant is neem tree (*Azadirachta indica*), whose plants are used as a source of azadirachtin. Fruits, seeds and leaves of this plant contain various compounds which kill insects, prevent fungi from growing and developing and restrict the infective abilities of plant viruses.

Again, the volatile oil rich in β-asarone which is derived prom sweet flag plant (*Acorus calamus*) leads to infertility in insects and shows insecticidal properties. Methyl jasmonate is secreted from the wounded tissues of plants attacked by insects and animals, and it leads healthy plants which receive the smell to take precautions against possible attacks by insects and animals. The hordenine alkaloid found in barley (*Hordeum vulgare*), carvacrol found in oregano (*Oreganum* sp.) volatile oil and 1,8-cineole found in eucalyptus (*Eucalyptus* sp.) volatile oil are allomones which have strong allelopathic effects on other plant species.

Combined secretion of terpenoids, phenylpropanoid compounds and acid derivatives with volatile oils shows indirect defensive effects, while proteinase inhibitor, polyphenol oxidase activation and peroxidase play a direct role in the defence mechanism (Huang et al. 2015).

Terpenes play a defensive role in many plants against herbivores, and they are dissuasive for many herbivore mammals and insects because of their toxic effects. This is why they have important roles in plant defence. For example, monoterpene esters known as pyrethroids which are found in leaves and flowers of *Chrysanthemum* species show dramatic insecticidal effects. As they are unstable in nature and they have a negligible toxicity effect on mammals, both natural and synthetic pyrethroids are popular compounds used in commercial insecticides.

Monoterpenes accumulate in resin canals in needles, branches and bodies of coniferous plants like pines and firs, and these compounds have toxic effects on numerous insects including Scolytidae which give great harm to coniferous plants worldwide.

Certain mono- and sesquiterpenes in maize, cotton and wild tobacco are produced and secreted after the insects feed. These chemicals not only repel herbivorous insects that leave their eggs on the plants, but they also attract predatory and parasitic insects that feed on those herbivorous insects. Therefore, they minimise the potential harm, and their functions are not limited, in that they provide help for plants from other organisms.

While essential oil attracts insects and facilitates pollination, it also disperses sun beams by evaporating in the air to protect the plant from heat. In some cases, essential oils act as protective agents against harmful rodents, insects and bacteria which bring disease. Essential oils are chemically heterocyclic, hydroaromatic and fragrant combinations. Just as in fatty combinations, essential oils are composed of carbohydrates, thio acids, phenols, aldehydes, ketones, alcohols, carbonic acids, esters and especially terpenes (mono-, sesqui-, dipolyterpenes), besides causing their scent as oxygen combinations.

As essential oils are effective against pests in an inhalative way because they are composed of volatile compounds, studies focus on fumigant effect mechanisms and mostly storehouse pests (Altındal and Altındal 2011; Hamza et al. 2016; Ja-Eun et al. 2016). These implementations are achieved by fumigation of essential oils in an enclosed environment for a certain time.

Phytoncides are of the volatile essential oil branch (though some are not volatile) and they have a role to kill microbes. They carry antibiotic properties and eliminate many harmful and vector microbes and viruses in the air. They are found in almost all plants in different chemical structures. Particularly some vegetables like onions and cabbages carry significant amounts of phytoncides. Phytoncides are also found in plants such as garlic, horseradish (*Armoracia rusticana* L.), lemon and milfoil.

In contact effect implementations, essential oils are sprayed on pests, and they show their effects by the absorption of the substance by cuticula. Repellent effect occurs by the insect feeling the volatile oil in the air and fleeing the place. This effect may continue until the complete evacuation of the oil from the place based on the properties of volatile oil components.

Feeding inhibitors are compounds that temporarily or permanently prevent feeding based on their potential when they are consumed by insects. Essential oils affect the insect’s peripheral nervous system by their dissuasive effect and prevent the continuation of feeding. Toxic effects disrupt physiological and biochemical activities after consumption by the insect.

Insect repellent effects of volatile oils are well known. There are found frequently in outward facing secretion hairs on plants, and they act as “warning signs” for toxicity as they repel the insect before it even feeds on the plant.

In many studies on phenolic substances (Büchel et al. 2015; Randriamanana et al. 2015), it was reported that phenols form a defensive mechanism in plants’ protection against pathogens and herbivores.

Specific plant hormones such as ethylene are synthesised against most pathogens and pests. As a result of infection with the pathogen, signals which induce defence mechanisms are transmitted, and local and systemic antimicrobial defence is achieved. Ethylene is a signal compound which plays an important role in inducing defence reaction in plants by acting as a signal.

Considering the insect killing effects of plant volatile oils and compounds, their insecticidal effects were studied on *P. americana*, and the highest toxic effect was observed with the carvacrol compound (Ramírez-López et al. 2016). In another study, it was observed that allyl isothiocyanate and garlic volatile oil have high insecticide effect on *Blattella germanica* (L.) (Dictyoptera: Blattellidae) adults, and it may be used as a fumigant against this pest (Tunaz et al. 2009).

A significant portion of herbivore insects prefer plants with high nitrogen content. It is known that herbivore insects, as in Orthoptera, Coleoptera and Lepidoptera orders, usually require equal amounts of proteins and carbohydrates, while phloem and grain insects require higher amounts of carbohydrates. Based on their content of cellulose, plants develop mechanical resistance against digestive enzymes of insects, or the phenolic compounds in the food directly bind with digestive enzymes and affect the insect's digestion activities negatively.

Plants release VOCs against herbivores and attract the predators of herbivores. For instance, maize plant attacked by caterpillar releases terpenoid to repel herbivores and attract bees, which are enemies of herbivores (Fiers et al. 2013).

Defence signals are transmitted as soon as the herbivore insect starts feeding on the plant. Caterpillars affect the leaf tissue damage, quality and amount and remove plant tissue in about the size of leaves. Lima beans (*Phaseolus lunatus*) also release similar compounds against caterpillar damages.

There are an insufficient number of studies conducted on defence systems in different plant species. The studies conducted so far have mostly been on ants and *Spodoptera* larvae that feed on plants like *Arabidopsis*, maize, rice, tomato and tobacco. It was reported that jasmonic acid is produced in high quantities in the tobacco plant as a defence signal against caterpillars (Paré and Tumlinson 1999). It was indicated that *Fusarium* infection transmitted by the soil on leaves and/or roots in maize may induce secretion of volatiles (Piesik et al. 2011). Antifungal activity was found in volatile oils in birch leaves, and it was found to be highly effective against plant pathogens (Yaşar 2005). Conducted studies revealed that substances (β-caryophyllene, linalool) that attract EPNs (entomopathogenic nematodes) are secreted by infected or damaged plant roots (Laznik and Trdan 2016).

There is a very limited amount of information about the roles of plant volatile compounds against pathogens. VOCs make plants resistant to pathogens. Besides their signalling function, volatile compounds may also inhibit the development of pathogens and contribute in resistance (Quintana-Rodriguez et al. 2015). In terms of defence reactions, it was reported that ethylene production is in coordination with plant resistance and it provides warning about disease development (Martínez-Hidalgo et al. 2015).

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Characterization of Bacterial Volatiles and Their Impact on Plant Health Under Abiotic Stress

2

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Abstract

Bacterial released volatile compounds (VOCs) in air enable bacteria to interact with their surrounding environment. Soil bacterial volatiles are known to contribute to plant interactions, and several studies also identified their influence on plant stress tolerance. Plant growth-promoting rhizobacterial (PGPR)-mediated VOCs are reported to increase seedling emergence, plant weight, crop yield, and stress resistance. The present chapter describes the characterization of different bacterial VOCs and their roles in enhancement of plant abiotic stress tolerance, a new research area, with potential agriculture applications.

Keywords

Abiotic stress • Bacterium • Plant growth-ptomoting bacterium • Volatile organic compounds • C4-bacterial volatiles

2.1 Introduction

Plants live naturally with many microorganisms, and the nutrient-rich environment of the rhizosphere is especially conducive to interactions between microorganisms and plants. Plants release different products through the roots into the surrounding

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area that attract a tremendous diversity of microorganisms (Perry et al. 2007). Some of these microorganisms have no observable effects on plant; others enhance or inhibit plant growth. Plant growth-promoting rhizobacteria (PGPR) can stimulate plant growth or increase tolerance by producing nonvolatile substances, such as the hormones auxin and cytokinin, as well as 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which reduces plant ethylene levels, and siderophores, which facilitate root uptake of metal nutrients. In addition, certain PGPR promote plant growth by emitting volatile organic compounds (VOCs) (Vaishnav et al. 2017). Volatile compounds have low molecular weight (<300 Da) and high vapor pressure (0.01 kPa at 20 °C) in nature that can readily evaporate and diffuse through heterogeneous mixtures of solids, liquids, and gasses (Audrain et al. 2015). The spectrum of bacterial VOCs is influenced by heterogeneity of soil, which depends on bacterial/plant-secreted metabolites. Some VOCs are specific for a phylogenetic group and used for taxonomic purposes (Kai et al. 2016). The volatile compounds are generally produced as metabolic end products of anaerobic fermentation processes and extracellular degradation of complex organic molecules. The widely differing species of bacteria were capable of emitting a variety of volatile compounds, comprising of fatty acid derivatives, terpenoids, and aromatic, nitrogenous, and sulfurous compounds. Interestingly, many of the substances found in the bacterial scent spectra have not been identified yet, and their biological roles are also unknown. By referring to a few known examples and by comparison with known functions of scents from other groups of organisms, it is assumed that the bacterial scents serve as signal compounds for interspecies and intraspecies communication or from cell to cell, for the disposal of excess carbon compounds, or as substances that stimulate or inhibit growth (Wenke et al. 2010). Many investigations concerning VOC pattern of soil microorganisms were performed under different treatment conditions. Bolm et al. performed a large screening of volatile-mediated effects on *Arabidopsis thaliana*. The VOC effect was found highly dependent on cultivation medium and the inoculum quantity. The production of beneficial VOC compound butanediol was found higher on the nutrient-rich media LB and MR-VP and less pronounced on MS and Angel. In another study, *P. simiae* strain AU changed VOC pattern in the presence of soybean seeds and sodium nitroprusside (SNP, a nitric oxide donor) treatment. Some compound expression was enhanced in the presence of soybean seedlings, and few compounds like 4-nitroguaiacol and quinolone are newly expressed in the presence of SNP. These compounds were showed significant enhancement of seed germination and higher fresh weight of soybean under 100 mm NaCl stress (Vaishnav et al. 2016). As a result of the increasing interests in VOCs in mediating plant-microorganism interactions, the present chapter focuses on the chemical nature of microbial VOCs, as well as the effects of microbial VOCs on tolerance level of plants under abiotic stresses.