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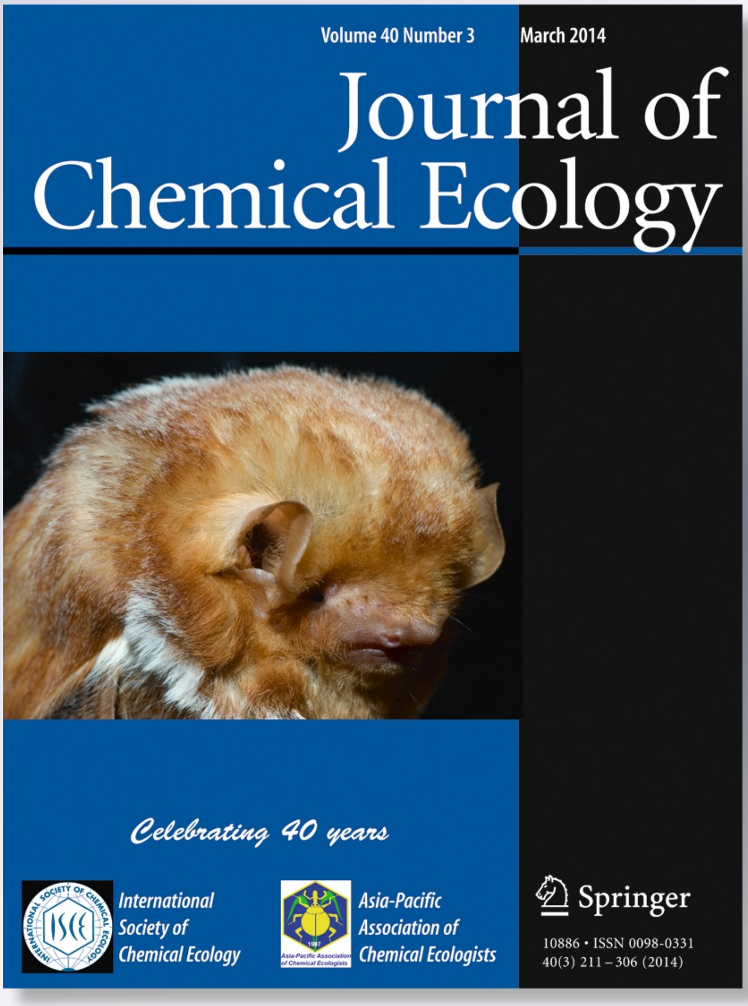

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COMMENTARY: REFLECTIONS ON 40 YEARS

The Importance of Volatile Organic Compounds in Ecosystem Functioning

James H. Tumlinson

In nature, volatile organic compounds (VOCs) abound in air, soil and water, and their use as chemical signals by a large number and broad array of organisms has been well-documented. They have been extracted and distilled from plants and other sources for thousands of years for use in perfumes, but they were considered secondary metabolites, suggesting that they are only by-products of primary metabolism and not essential to the functioning of organisms that produced them. In fact, VOCs are extremely important and critical in mediating intra and interspecific interactions among all organisms in the ecosystem. Since biologically active VOCs often occur in nature in only microgram or smaller quantities, their purification and identification was long hampered by lack of efficient and sensitive analytical methods. Thus, although it has long been known that animals use odors for sexual communication and for location of prey, the first identification of a VOC as a signal that transmitted information between individual animals occurred only a little over 50 years ago. From the abdominal glands of 500,000 female silkworm moths, Adolf Butenandt and colleagues in 1959 purified mg quantities of the sex pheromone, which they identified as (10*E*,12*Z*)-hexadeca-10,12-dien-1-ol, and named bombykol. Since then, analytical techniques and instrument sensitivity have greatly improved, and thousands of biologically active VOCs have been identified, and their roles in signaling mechanisms investigated and elucidated. Thus, our understanding of their functions in chemical ecology has evolved and increased markedly. Yet, it is increasingly clear that we don't fully comprehend the importance and complexity of the vast chemical signaling networks that employ VOCs in nature. Continued exploration and elucidation of these intricate networks is necessary for development of sustainable agricultural practices, fighting diseases and their vectors, and protection of the environment.

Pheromones In the two decades following the discovery of bombykol, studies in the newly emerging field of chemical ecology focused primarily on the isolation, identification and synthesis of insect pheromones. Initially, it was theorized that each insect species would produce and use a single, unique VOC as its specific signal to promote mating communication. This theory was revised when Silverstein, Wood, and colleagues (Silverstein et al. 1966) identified a multicomponent, synergistic blend of compounds serving as the pheromone of the bark beetle *Ips confusus*. Similarly, the compounds in many other beetle pheromones are only active when combined in the correct proportions in a blend. Roelofs and others soon showed that blends were the rule, rather than the exception in numerous species of moths and other insects. Even the domesticated silkworm moth was later shown to produce multiple VOCs in its pheromone gland. Although in moths a single component of the female produced pheromone blend will frequently elicit sexual behaviors in the conspecific males, maximum and complete behavioral activity usually requires complete blends of the pheromone components. As more pheromones were identified it became obvious that although closely related species frequently share pheromone components, speciation is maintained by different proportions of blend components or by variation in geometrical isomers or differences in chirality, when the structure of a compound includes an asymmetric carbon (see following commentary by Mori).

Pheromones, by definition, are chemical signals between members of the same species. They are used not only to attract mates, but also to aggregate both sexes to exploit resources, as in bark beetles that attack trees in mass to overcome tree defenses. They also are used as alarm signals, to mark trails, and to regulate the functioning of the colony in social insects. Of course, while the great majority of pheromone studies have been conducted with insects, VOCs also function as pheromones for other animals including mammals, birds, and reptiles and have even been reported for bacteria and fungi.

Eavesdropping and Mimicry Although a compound or blend of compounds may serve as a very specific pheromone for members of the species releasing it, predators and parasites frequently eavesdrop on these signals that reliably indicate the presence of their prey or hosts. Thus, insects that parasitize the eggs of other insect species may use mating pheromones to guide them to locations where host females oviposit. Alternatively, bolas spiders that prey on moths release moth sex pheromones that lure male moths within range of their bolas. In fact, eavesdropping and chemical mimicry are common in nature. Some orchids produce sex pheromones that lure male bees and thus facilitate pollination. Other flowering plants mimic odors of rotting flesh or animal feces that attract flies and other insects that feed and/or oviposit on these substances. Parasitic insects produce odors that mimic host odors and allow them to invade the colonies of social insects, like ants, without detection.

Plant-Insect Interactions It has long been recognized that floral VOCs play key roles in attracting pollinators. However, the importance of these signals in plant defenses against herbivores only became evident in the 1980s, after Price et al. pointed out the importance of tritrophic interactions among plants, insect herbivores, and natural enemies of the herbivores. Subsequently, several reports showed the importance of herbivore-induced plant VOCs (HIVOCs) as host location cues for parasitoids and predators of the herbivores. This indirect chemical defense is probably as important or more important than direct chemical and physical defenses in reducing herbivore damage.

In response to insect herbivore feeding, damaged plants release a great variety of VOCs. As would be predicted, based on the species diversity of plant biochemical processes, different species produce different blends of HIVOCs. In some plants, VOCs are stored in glands and trichomes and passively released when these structures are damaged by herbivores. In many, if not most plants, herbivore damage also induces *de novo* biosynthesis and release of VOCs. When an herbivore feeds on a plant, several VOC biosynthetic pathways are upregulated. While terpenes and sesquiterpenes are major players, many other classes of volatiles also are produced, depending on the plant species attacked. In addition to species differences in HIVOCs, different plant varieties or ecotypes also

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produce quantitatively and qualitatively different blends. Further, the quality and quantity of the HIVOC blend changes with time of day and growth stage of the plant. Usually nocturnal VOCs differ greatly from those released during the day. In one instance, while diurnal VOCs attract natural enemies of the feeding caterpillar, the same plant releases a nocturnal blend that repels conspecific moth females. One of the most surprising discoveries is that the blend of VOCs released by a plant will change depending on the species of herbivore feeding on it. Parasitoid wasp females can distinguish VOCs from a plant fed on by a host, from those released by the same plant damaged by a non-host of the wasp. VOCs induced by root-feeding insects disperse through the soil and attract nematodes that attack the root herbivores. In addition to feeding damage, oviposition can induce plants to release VOCs that attract egg parasitoids. Thus, the indirect defenses mounted by plants in response to herbivore damage or potential damage are quite comprehensive and effective.

Plant-Plant Communication While animal responses to VOCs have been studied in great depth, particularly in insects, much less is known about communication between plants. In the last 10–15 years it has been clearly demonstrated that plants detect and respond to VOCs, and that this ability is an important defensive mechanism. Plants exposed to VOCs from neighbors damaged by insect herbivores can prime their defenses and respond more quickly and strongly if they are subsequently attacked by the herbivores. Thus, HIVOCs not only attract natural enemies of the herbivores, but also act as "alarm" signals for neighboring plants. In some cases, VOCs act as intra plant signals between damaged leaves and leaves distal to the site of damage. This mechanism is thought to facilitate systemic response in plants where internal signals between leaves are constrained by lack of vascular connectivity. Farmer and Ryan (1990) demonstrated that the plant hormone methyl jasmonate, like ethylene, travels through the air to activate plant defensive responses. The six-carbon aldehydes, alcohols and hexenyl esters, called green leaf volatiles (GLV), as well as methyl salicylate, also have been shown to act as airborne plant-plant signals.

Perhaps the most interesting case is that of the parasitic plant *Cuscuta pentagona* (dodder). A *Cuscuta* seedling must quickly locate a host in order to survive, because it has little photosynthetic ability and must rely on another plant for nutrients. Seedlings of this parasite exhibit foraging behavior, and "select" among potential host plants, by using VOCs as cues for host location (Runyon et al. 2006). They can distinguish between VOCs from tomatoes and wheat and grow preferentially toward the former.

There is evidence that plants perceive and respond to a broad range of phytochemicals, but our knowledge of plant-plant chemical communication is still limited. The scope of volatile compounds that plants can perceive and that affect their growth, development, and defense, is not yet clear.

Microorganisms Bacteria and fungi are abundant and important components of all ecosystems. In microbial communities chemical warfare is prevalent, and VOCs are effective and frequently used weapons. Typical fungistatic VOCs produced by bacteria of the genera *Bacilus* and *Pseudomonas* include 1-octen-3-ol, mono- and sesquiterpenes, nonanal, trimethyl amine, and dimethyldisulfide. Further, VOCs produced by soil fungi can have both positive and negative effects on plants. Volatiles produced by the truffle, *Tuber melanosporum* inhibit the growth of *Arabidopsis thaliana*. Other fungi produce VOCs that promote plant growth. In addition, certain rhizobacteria stimulate plant growth *via* production of VOCs. Two strains of *Bacillus subtilis* that promote growth in *A. thaliana* produce 2,3-butanediol and acetoin. Exposure of the plants to synthetic 2,3-butanediol also induced plant growth, while mutants of these bacteria, in which biosynthesis of these two VOCs was blocked, did not. The chemical ecology of interactions of bacteria and fungi with plants and other organisms has only begun to be explored (See J Chem Ecol, July 2013). There is little doubt that this is a rich field to investigate.

Future Directions Clearly, VOC signals transmit a great variety of messages between and among organisms across the broadest possible range of life forms throughout the world. The same chemical or blend of chemicals can have very different meanings, depending on the receiver. Thus, a sex pheromone may attract a mate and/or a parasite or predator. Further, VOCs may be used to deceive organisms that perceive and respond to them, to the advantage of the organism emitting them. Interestingly they also may facilitate symbiotic interactions, or be used to manipulate a target organism for the benefit of the emitter. They are ubiquitous and essential to the functioning of ecosystems. Although we have investigated the composition and function of VOC signals for 50 years, there are still areas that we know little about. The chemical warfare of microbes and their use of VOCs to interact with and/or manipulate plants and animals provide a good example. In the future we will need to take a more holistic approach to gain a better understanding of the roles of VOCs in mediating the multiorganismal, multitrophic interactions that occur in ecosystems. We also need to explore in greater depth the genetic and biochemical mechanisms that are involved in regulating production and emission, as well as perception of and responses to VOCs. The potential societal benefits are immense.

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