CHAPTER 1

CHEMICAL ECOLOGY

A multidisciplinary approach

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Abstract. Chemical information conveyance is an important phenomenon in the biology of plants and animals. This involves intraspecific chemical communication and its exploitation by heterospecific organisms. As a result food webs are overlaid with information webs that can have important consequences for community processes. A vast amount of research shows that both the emission of chemical information and the responses to it are often genetically controlled, and mediated by numerous interactions between an individual and its environment. Overall, it is argued that ecosystem functioning is much dependent on the responses of various community members to chemical cues, and that therefore knowledge on the chemical communication, from the genetic level to the ecosystem, is critical for our understanding of the functioning of populations, communities and ecosystems.
Keywords: gene; species; population; community; ecosystem; chemical communication

INTRODUCTION

Chemical ecology is the science that addresses the role of chemical cues in the interaction of organisms with their environment. One of the earliest and best-known examples of chemical communication is the use of sex pheromones by insects such as the silk moth *Bombyx mori.* The sex pheromone travels over great distances and attracts male conspecifics (Karlson and Butenandt 1959). Such intra-specific communication is one of the most widespread methods of chemical communication that occurs in all classes of the animal kingdom where sexual reproduction is the main avenue of reproduction. Indeed, sex pheromones have been described in all phyla of animals, including arthropods, fish, birds and mammals (Stoddart 1990). In addition to this example of chemical communication that mediates reproduction, numerous other types of intra-specific chemical communication exist as well, such as those involved in aggregation (Borden 1985; Wertheim et al. 2005), trail-marking (Traniello and Robson 1995) and defence (Brand et al. 1989). Whereas at first attention was paid mostly to the identification of the chemical cues concerned and to the direct behavioural effects these cues elicited, it was rapidly understood how

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important these cues are in the ecology of species. Cues released into the environment are secreted onto a surface area (e.g., scent marking) or as volatiles that travel through space. On their journey to the intended receiver, cues pass through a highly variable environment affected by wind, temperature, moisture and physical obstructions such as plants, animals and rocks. The widespread use of chemical cues to communicate with conspecifics is indicative of the many advantages of this way of information conveyance.

Whilst pheromone communication is a highly important but still relatively limited aspect of chemical ecology, matters become much more complicated when inter-specific interactions are considered. After all, any chemical that is disseminated into the environment may be exploited by any other organism in the environment. Pheromones can be exploited by organisms from other species such as predators or parasitoids (Dicke and Sabelis 1992; Stowe et al. 1995). Moreover, apart from pheromones also other cues can mediate inter-specific interactions. Rudolfs (1922) described how chemical cues from mammals affected the behaviour of mosquitoes, attracting them from a distance. Mosquitoes such as some anopheline species recognize mammalian odours and use these to locate a blood source for food (Takken and Knols 1999). Apart from mammalian (or vertebrate) blood, mosquitoes also feed on plant sugars, and they recognize plant volatiles as well (Thornsteinson and Brust 1962; Healy and Jepson 1988; Foster and Hancock 1994). In higher animals such as reptiles and mammals, olfaction is common in foraging for food. Animals may detect food by smell and many predators locate their prey by chemical cues (Albone 1984; Ylonen et al. 2003). Herbivorous insects generally recognize their food by volatile and non-volatile cues produced by the plant (Visser 1986; Schoonhoven et al. in press). Such cues not only serve as attractants but can also act as repellents or arrestants. As with sex pheromones, early studies on the role of plant volatiles in animal behaviour focused on the identification of the chemicals and bioassay studies that showed their role in plant–herbivore interactions. Since then, a more complex picture of these interactions has emerged.

The chemical interactions discussed above mostly concern bitrophic interactions. More recently, the importance of chemical cues was investigated in multitrophic interactions. For example, the production of plant volatiles following herbivore attack can result in the attraction of carnivorous insects that kill the plant's enemies (Vet and Dicke 1992; Turlings et al. 1995). This was a first step towards appreciating the involvement of chemical information in the ecological context of food webs. Apart from the exclusive involvement of macro-organisms, micro-organisms may also be involved in chemical information conveyance. For instance, microbial organisms were found to affect the odour emission from human sweat that attracts blood-feeding mosquitoes (Braks et al. 2000), and malaria parasites influence the attraction of mosquito vectors so that they can be transmitted to other hosts (Lacroix et al. 2005). All together, these examples show that the interactions of an organism with its environment can be profoundly affected by chemical information conveyance.

Analytical chemistry

The nature of chemical information conveyance mandates that further understanding of the interactions is based upon knowledge of the chemicals involved. These can range from highly volatile to non-volatile compounds. Organisms can produce a vast diversity of chemicals often in small amounts, and modern technology allows for their identification by standard methodology, usually gas chromatography in combination with mass spectrometry (GC-MS) or HPLC and, recently, rapid developments occur in the development of novel, large-scale, metabolomic analytical methods (Fiehn 2002). However, the availability of an analytical chemical profile of the cues produced by an organism does not automatically lead to the discovery of the active compound(s). This requires extensive research including, e.g., sensory physiological and behavioural methods; examples of such research are presented in several chapters of this volume.

Molecular genetics

Rapid developments in the field of genomics result in a fast accumulation of sequenced genomes of various organisms, including *Caenorhabditis elegans, Drosophila melanogaster*, *Anopheles gambiae*, *Arabidopsis thaliana*, *Oryza sativa* and many others (Holt et al. 2002; Adams et al. 2000; Hodgkin et al. 1995). For some of these organisms, such as *Drosophila melanogaster* and *Arabidopsis thaliana,* large numbers of mutants are available in stock centres. These mutants, which may be altered in the production or perception of chemical cues, provide exciting tools to investigate the role of certain genes in chemically mediated interactions. Genes involved in olfaction have been identified in *Drosophila melanogaster* and *Anopheles gambiae.* By the silencing of a gene that is essential in the signal-transduction path of a pheromonal interaction, the organism may no longer be able to respond to the signal and suffer a significant disadvantage (Giarratani and Vosshall 2003). It was found that in mosquitoes the behavioural inhibition following a blood meal is accompanied by down-regulation of olfactory receptor genes on the antennae (Takken et al. 2001; Fox et al. 2001). As the number of fully sequenced genomes is rapidly expanding, it is becoming clear that there is considerable homology in olfactory receptor genes among animal species (Jacquin and Merlin 2004; Robertson et al. 2003; Vosshall 2003). This is likely to further enhance our knowledge about the genetic regulation of chemical communication.

Information on genome sequences may also allow for other manipulative experiments such as the specific down-regulation of certain genes through antisense or RNA-interference techniques (Kessler et al. 2004; Dicke et al. 2004). Therefore, the rapidly expanding knowledge of molecular genetics will provide exciting new tools for ecologists to investigate the function of genes in ecological interactions. This volume presents several of these developments.

Cellular regulation of cue production and perception

The production of chemical signals by animals and plants is regulated through hormones and signal transduction pathways (Jurenka 1996; Rafaeli 2005; Dicke and Van Poecke 2002). Animals perceive chemical cues in specialized organs where the cues bind to receptors, setting a cascade of signal transduction into motion. This is best known from studies in the nematode *Caenorhabditis elegans*, the frog *Xenopus laevis* and the fruitfly *Drosophila melanogaster*, but it is believed that the mechanism of chemical signal transduction is much the same, at least, throughout the animal kingdom (Hildebrand and Shepherd 1997; Dobritsa et al. 2003; Restrepo 2004). Examples of the cellular response to chemical cues in these model organisms may therefore serve as a starting point for investigating this process across a wide range of species. Plants may also perceive chemical cues from their environment, but specialized organs involved have not been reported. How plants perceive chemical signals, however, remains poorly known to date (Dicke and Bruin 2001; Baldwin et al. 2002).

Behavioural responses

We would not know of the existence of chemical communication without having studied the responses of plants and animals (Cardé and Bell 1995; Dicke and Bruin 2001). In animals we can observe typical behavioural responses such as movement towards or away from the chemical cues or a change in behaviour towards subsequent activities. An example of this latter is the observation that female pigs become receptive to boars when exposed to male odour, which is exploited in artificial-insemination methods in pigs through the application of the boar’s pheromone (Gower et al. 1981). It has appeared that many behavioural activities of organisms are mediated by chemical cues. Simple responses to a specific cue have been described, but it is much more common for organisms to respond to a complex blend of chemical cues, sometimes derived from more than one species (e.g. Reddy and Guerrero 2004). Individual components may mediate different behavioural components that together constitute a complex behavioural response (Cardé and Minks 1997). Behavioural responses may be fixed and predictable (e.g., a response to a mate), or phenotypically plastic and subject to learning (e.g., responses to resources that are variable) (McCall and Kelly 2002). A single chemical cue may elicit responses in many different organisms in the environment and, thus, community members are linked in reticulate information webs.

Populations and communities

Animal and plant populations are composed of individuals that each produce chemical information and respond to cues. Population and community processes are not only influenced by direct effects of interactions such as mating, predation and defence but also by behavioural responses to chemical cues. These responses influence spatial distribution and interaction with community members. Therefore, the production of chemical cues and the responses to them are expressions of the phenotype that contribute to processes at the population and community level (Vet 1996; Kessler et al. 2004; Dicke et al. 2004). Individual behaviour can be fixed or phenotypically plastic. Phenotypic plasticity allows individuals to adjust their responses to current environmental conditions and may have important ecological consequences for species interactions and community processes (Agrawal 2001). Investigating the effects of an individual chemical cue on population and community processes may be carried out by comparatively investigating the effects of variation in the expression of a single gene in an otherwise similar genetic background. To do so, knowledge of the mechanisms of gene expression and gene function is essential. This will be highlighted in this volume.

Ecosystems

Processes at the ecosystem level include, for instance, spatial and temporal variation and dispersal of populations and individuals. Ecosystems are spatially complex and organisms with high dispersal capabilities may drive biodiversity patterns and ecosystem functions (Tscharntke et al. 2005). Dispersal capabilities are dependent on physical properties such as speed and mode of displacement, but also on the ability to perceive chemical information. Therefore, chemical cues are likely to influence ecosystem processes as well. This receives attention in several chapters in this volume.

Chemical ecology from gene to ecosystem

From the examples discussed above it is clear that chemical cues that mediate interactions between individuals influence processes at various levels of biological integration. Chemical ecology has often addressed mechanisms but recently interest in the effects of chemical signalling on community and ecosystem processes is rapidly increasing (Thaler 2002; Van Zandt and Agrawal 2004; Kessler et al. 2004; Dicke et al. 2004). To bring these issues together in one volume, we have asked leaders in the field of chemical ecology to discuss their views on this matter from their specific field of expertise. Scientists from as wide a field as molecular genetics to ecosystem analysis have contributed to present a general overview of the cutting-edge knowledge on this topic.

Chemical information conveyance plays a role in the biology of virtually all species. Chemical communication between conspecific individuals may be exploited by individuals of other species and the information web may have consequences for community and ecosystem processes in terrestrial and aquatic systems. In this volume examples are discussed of advances in our understanding of the role of chemical signalling in simple and complex systems as illustrated by recent research on plants (below and above ground) and animals. The cellular aspects of chemical ecology are illustrated by research on parasitic weeds and on members of two different insect orders (Diptera and Hymenoptera) and on nematodes. These examples serve as an illustration of how such processes are regulated and organized and show that there is a good deal of similarity among different species. The relevance of chemical ecology for community ecology is discussed for, e.g., the native tobacco plant *Nicotiana attenuata*. It is clear that chemical communication cannot be viewed from the perspective of a single species but should be placed in a multi-species context. Chemical information mediates interactions in communities and ecosystems. This is presented for plant–plant interactions, plant–animal interactions and inter-specific interactions of aquatic organisms. Finally, the implications of these findings are discussed with a view to the relevance of chemical communication for ecosystem functioning. The main take-home message of this volume is that in order to fully appreciate the influence of chemical signalling on community and ecosystem processes one needs thorough knowledge of the mechanisms of chemical information conveyance from the gene to the individual. Therefore, the highly multidisciplinary approach of modern chemical ecology is likely to make an important contribution to biology in the 21st century.

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