CHAPTER 12

CHEMICAL ECOLOGY FROM GENES TO COMMUNITIES

Integrating 'omics' with community ecology

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Abstract. Chemical cues that convey information are widely used by living organisms. The cues mediate interactions in food webs as well as non-trophic interactions such as interactions between conspecific organisms or between plants and natural enemies of herbivorous organisms. Communities are composed of food webs and each food web is overlaid with a reticulate infochemical web that is more complex than the underlying food web. Chemical ecology has addressed the role of information conveyance in intraspecific and interspecific interactions and has mostly concentrated on elucidating the identity of chemicals and their role in individual interactions of food webs. In addition, the role of infochemicals has been investigated in multitrophic interactions.

Recently, several exciting developments have taken place. On the one hand, chemical ecologists more and more address molecular mechanisms underlying the production of infochemicals and the responses to the cues, such as signal transduction and gene expression. On the other hand, studies on the role of infochemicals in population and community ecology have been initiated. These developments are not independent of each other, and knowledge of mechanisms will provide important tools for investigating the role of infochemicals in populations and communities. This will be discussed especially in the context of insect–plant communities.

Keywords: ecogenomics; phenomics; herbivore-induced plant volatiles; signal transduction; community ecology; behavioural ecology

INTRODUCTION

Chemical information conveyance is omnipresent in biological systems. Chemical cues are a major source of information for very different organisms ranging from micro-organisms to mammals (e.g. Dicke and Grostal 2001; Kats and Dill 1998; Penn 2002; Roitberg and Isman 1992; Tollrian and Harvell 1999), and infochemicals play a role in terrestrial, aquatic and soil ecosystems (Van Tol et al. 2001; Rasmann et al. 2005; Roitberg and Isman 1992; Tollrian and Harvell 1999; Dicke and Takken in press). Chemical information affects various behaviours that underlie population dynamics and food-web interactions, including the selection of food, the selection of

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mates, competition and the avoidance of predators (e.g. Dicke and Vet 1999; Hilker et al. 2002; Kats and Dill 1998; Roitberg and Isman 1992; Sabelis et al. 1999; Turlings and Benrey 1998; Wertheim et al. 2005). Therefore, chemical information is an important factor influencing species interactions and most likely also community processes (Kessler et al. 2004; Van Donk in press; Vet 1999). However, the study of chemical information conveyance has been mostly restricted to studies at the level of individual organisms and the identification of the chemicals that convey the information. The influence of chemical information on food-web processes has received little attention (Hunter 2002; Vet 1999; Wertheim et al. 2005), in contrast to effects of direct trophic interactions (Morin 1999). Yet, circumstantial evidence indicates that chemical information from phenotypically plastic plants can have important influences on food-web dynamics through indirect effects that combine bottom-up and top-down effects (Dicke and Vet 1999; Sabelis et al. 1999). Moreover, pheromones that mediate intraspecific interactions among animals may have important consequences for food-web interactions (Wertheim 2005; Wertheim et al. in press). Empirical support should come from manipulative experiments, such as manipulations of infochemical emission phenotype, that compare food-web processes in the presence and absence of infochemicals. The ability to manipulate the infochemical phenotype in specific and well-known ways is indispensable for this approach. Such experiments have recently come within reach. This provides a modern, novel and exciting interdisciplinary approach to ecology that is possible because of recent breakthroughs at the level of subcellular processes (e.g. Baldwin et al. 2001; Dicke et al. 2004; Dicke and Van Poecke 2002; Fitzpatrick et al. 2005; Jacobs et al. 2005; Kessler et al. 2004; Mitchell-Olds 2001; Van Poecke and Dicke 2004), in metabolomic approaches (Fiehn 2002) and in quantitative food-web analysis (Omacini et al. 2001; Rott and Godfray 2000). For the design of manipulative experiments and for understanding their outcome, information on mechanisms underlying ecological processes is essential (Dicke et al. 2004; Kessler et al. 2004; Wertheim et al. 2005). In this paper I will address the potential of interdisciplinary approaches to the unravelling of the role of chemical information conveyance in community processes.

COMMUNITIES AND FOOD WEBS

Communities are complex compositions of hundreds of interacting species at different trophic levels (Morin 1999). One way of appreciating the complexity of communities is to analyse food webs. This shows that, for example, even a small part of an insect food web may comprise tens of species (Figure 1). Rott and Godfray sampled *Phyllonorycter* leaf-miner moths and their parasitoids on four plant species in a 10,000 m^2 area (Rott and Godfray 2000). They recorded twelve *Phyllonorycter* species and 27 of their parasitoids. The composition of the food web changed in time. Some species that were abundant in the summer were scarce in autumn and vice versa. The estimated total number of *Phyllonorycter* ranged from a few million up to 75 million individuals. Given that the leaf miners are also attacked by predators and pathogens and that the host plants are also attacked by dozens of other herbivore species it is clear that food webs are highly complex in composition and that this complexity is variable in space and time.

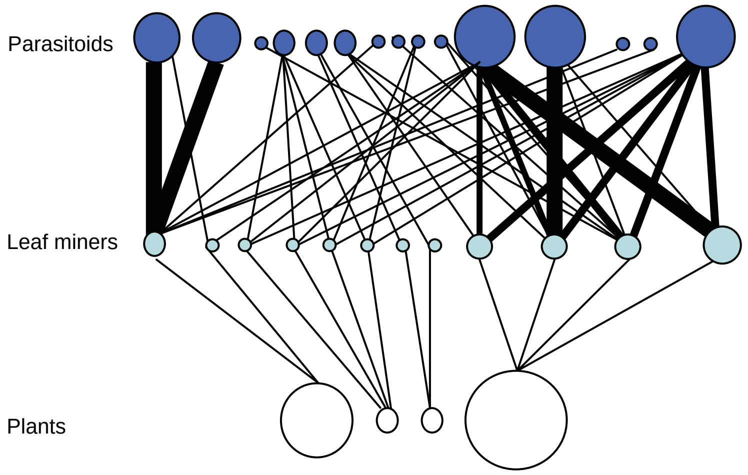

Figure 1. *Schematic representation of a food web consisting of 4 plant species, 12 herbivorous leaf miners and 27 parasitoids. Relative sizes of circles within a trophic level indicate relative population sizes. Lines indicate trophic interactions. Relative thickness of lines between parasitoid species and leaf-miner species indicate relative number of parasitoids involved in the interaction. Figure based on data in Rott and Godfray (2000)*

Food-web analyses address interactions within communities that reflect direct trophic relationships, where one organism feeds on another. Yet, although these interactions are important in shaping communities, they reflect only a part of the interactions in a community. Members of communities also show indirect interactions, i.e., interactions between two organisms that are mediated by a third organism, that connect organisms that do not have a trophic relationship. Such indirect interactions may be important in shaping communities as well.

Major recent developments in our understanding of communities are that:

1. indirect interactions have important effects on food web dynamics (e.g. Abrams et al. 1996; Bonsall and Hassell 1997);
2. top-down and bottom-up forces (enemy-controlled versus resource-controlled forces, respectively) are often integrated rather than mutually exclusive: plants can dramatically influence top-down forces on herbivores, as mediated by carnivorous enemies of the herbivores (Bernays 1998; Dicke and Vet 1999; Sabelis et al. 1999);
3. species characteristics appear to be phenotypically plastic and consequently the effects of species on interactions in a food web are dynamic (Agrawal 2001); ecogenomics can link phenotype to genotypic expression (Baldwin et al. 2001; Dicke et al. 2004; Kessler et al. 2004).

Both direct and indirect interactions are mediated by infochemicals. Communities and food webs are, therefore, overlaid with infochemical webs.

INFOCHEMICAL WEBS

Given that each organism in a community emits and responds to chemical information, it is clear that communities abound with interactions mediated by chemical information. Although chemical information by itself cannot be used to build bodies, it essentially influences interactions between organisms and, thus, fitness of individuals, and most likely also food web and community processes (Dicke and Hilker 2003).

Infochemically mediated interactions can in principle occur between any two organisms in a community, whether conspecific or heterospecific, whether connected by a food-web interaction or not (Dicke and Sabelis 1992; Stowe et al. 1995). For instance, conspecific organisms may interact through pheromones, and these pheromones may be exploited by their natural enemies. E.g., male *Pieris brassicae* butterflies endow a female with an anti-aphrodisiac pheromone during mating. This pheromone renders the females less attractive to other males that might compete with the original male for offspring. However, in addition to the intraspecific interaction, the pheromone also mediates an indirect interaction. The egg parasitoid *Trichogramma brassicae* is attracted to the anti-aphrodisiac pheromone, and after arrival at the mated female butterfly, the wasp mounts the butterfly and hitches a ride to the spot where her transporter deposits her eggs. These eggs are subsequently parasitized by the *Trichogramma* wasp (Fatouros et al. 2005). Thus, an infochemical mediating a non-trophic interaction (mating) can also mediate a trophic interaction (parasitization). Because a single infochemical may mediate many interactions in a food web, the costs and benefits of an infochemical to an emitting organism include the costs and benefits of each of these interactions. Therefore, the evolutionary ecology of infochemicals can only be understood in a community context (Dicke and Sabelis 1992).

Indirect interactions that do not involve trophic relationships are, e.g., those between plants and carnivorous arthropods such as predators and parasitoids of herbivores. In response to herbivory an individual plant produces a complex blend of volatiles. As a result, enemies of the herbivore are attracted to the plant. This is a general phenomenon that has been recorded for a large number of plants (Dicke 1999; 2000; Hilker and Meiners 2002; Turlings et al. 1993). Just as in the case of *Pieris*'s anti-aphrodisiac pheromone, also herbivore-induced plant volatiles can be exploited by many other organisms in a community, including, e.g., herbivores and neighbouring plants (Dicke and Bruin 2001; Dicke and Van Loon 2000; Hilker and Meiners 2002) (Figure 2).

Thus, a food web is overlaid with an infochemical web. Moreover, because each infochemical may mediate many interactions, both trophic interactions and indirect, non-trophic, interactions, the infochemical web is more complex than the food web. Therefore, when investigating communities, infochemical webs should be studied in addition to food webs.

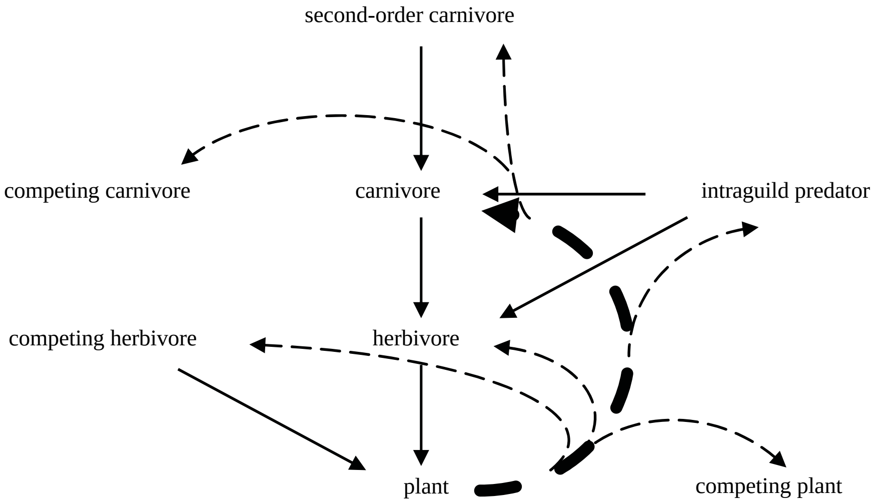

Figure 2. *Herbivore-induced plant volatiles are well-known to attract carnivorous arthropods that feed on the inducing herbivore. Moreover, they may affect the behaviour of many other organisms in a food web, including other plants, herbivores, carnivores and second-order carnivores. Solid lines indicate trophic interactions (food web) and broken lines indicate interactions influenced by herbivore-induced plant volatiles. Note that only one single infochemical blend, viz., the herbivore-induced plant volatiles, is depicted. Each component of the food web may emit infochemicals that similarly affect various other players in the food web*

MECHANISMS OF CHEMICAL INFORMATION CONVEYANCE

Before an infochemical can influence interactions between individual organisms and consequently food webs and community processes, a range of processes has been initiated, from gene expression to mechanisms of storing and releasing the compounds. It is well-known that organisms regulate the production and emission of infochemicals. After all, both the production and the emission come with costs and benefits and organisms are under selection to maximize the returns of infochemical emission. Understanding the mechanisms is essential for understanding the expression of phenotypes in terms of infochemical emission. Moreover, understanding these mechanisms also allows the careful manipulation of infochemical-emission phenotypes (Dicke et al. 2003; Kessler and Baldwin 2004; Kessler et al. 2004; Van Poecke and Dicke 2002), and therefore provides ecologists with important new tools to investigate the ecology of chemical information conveyance.

Apart from variation in infochemical emission, the response to infochemicals may vary as well. Animals are well-known to be phenotypically plastic in their responses to infochemicals (Papaj and Lewis 1993). Moreover, knowledge on genes involved in behavioural responses of animals is rapidly accumulating and this provides exciting new opportunities for manipulative experiments (Fitzpatrick et al. 2005). For instance, the perception of infochemicals, their decoding in the brain and memory processes involved are all processes that are intensively investigated at the molecular level (Fitzpatrick et al. 2005).

At the mechanistic level, systems are characterized by complexity, just as is the case at higher levels of integration (Figure 3). For instance, odour blends are complex mixtures ranging from a few to hundreds of components (Roitberg and Isman 1992; Turlings et al. 1993; Van den Boom et al. 2004), the metabolome of organisms is highly complex with developmental and temporal variation (Fiehn 2002; Rosenthal and Berenbaum 1992), and transcriptomic changes are substantial and dynamic and highly variable with developmental and environmental conditions (De Vos et al. 2005; Heidel and Baldwin 2004; Reymond et al. 2004; Schenk et al. 2000). Thus, connecting ecology with mechanisms is very much a matter of dealing with complexity at different levels. This means that intelligent decisions have to be made at different levels of biological organization so as to unravel the patterns shaping these complex biological systems.

In the remainder of this chapter I will review how knowledge of mechanisms can be exploited to develop new strategies to understanding the effects of chemical signalling on communities.

Genome	10,000s of genes
Transcriptome	1000s to 10,000s of mRNAs
Proteome	1000s to 10,000s of proteins
Metabolome	10,000s of metabolites
Phenome	1000s of phenotypes
Infochemicals	Few to 10s of components in each infochemical; each organism in a community emits infochemicals
Community	1000s of interacting species, each with variable phenotypes

Figure 3. *Degree of complexity at different levels of biological organization, from the genome to the community*

COMMUNITY APPROACH

To understand how chemical information influences community processes it is essential to take an experimental, manipulative approach. Ecologists are well aware of the value of a comparative approach where individuals with different phenotypes are compared. However, it is not always easy to manipulate a phenotype in a biologically realistic way, especially in relation to its infochemical emission or perception. One may apply a synthetic infochemical, and this has been extensively done. However, this option is limited to situations where the infochemical's composition is relatively simple and the components can be synthesized or extracted in pure form. However, in many cases the composition of an infochemical is complex and the components may comprise stereochemically active compounds that are difficult to synthesize *in vitro*. Moreover, if the infochemical emission is phenotypically plastic or temporally dynamic, this may be difficult to mimic realistically. For instance, moths emit a sex pheromone during a restricted period during the night and so the application of a synthetic pheromone in a trap in the environment may be useful for investigating which species respond to the pheromone but it may be less suited for investigating the effect of the pheromone on community processes.

Several approaches have recently been taken to investigate the effect of chemical information on community processes. These manipulative approaches strongly depend on mechanistic information

Drosophila aggregation pheromone

One approach is to distribute the infochemical in synthetic form in a community. Drosophilid fruit flies aggregate on food and oviposition substrates and this behaviour is mediated by an aggregation pheromone (Bartelt et al. 1985; Wertheim et al. in press). Males produce the pheromone and transfer it to the female during mating. The females deposit the pheromone on the oviposition substrate during egg deposition. The emission from the substrate continues for at least several days. The aggregation pheromones of *Drosophila melanogaster* and *D. simulans* consist of a single compound, viz., cis-vaccenyl acetate, which is available in synthetic form. The synthetic pheromone or the naturally deposited pheromone can be used rather easily in manipulative field experiments (Wertheim et al. in press). Laboratory experiments have demonstrated that parasitoids of *Drosophila* larvae exploit this aggregation pheromone and are attracted to the site of oviposition (Hedlund et al. 1996). The application of the pheromone on substrates or fruits in an orchard resulted in the attraction of *Drosophila* flies whose pheromone was applied, as well as the attraction of other, competing *Drosophila* species. The degree of attraction was dose-dependent. In addition, parasitoids of *Drosophila* larvae were attracted (Wertheim et al. in press). Thus, the application of the synthetic pheromone in the field can provide information on its effects on community members and their aggregation. The consequences of the presence of the *Drosophila* aggregation pheromone were both direct effects (attraction of conspecifics and heterospecifics) and indirect effects (for instance, increased interference as a result of higher densities) (Wertheim et al. in press). A similar approach has also been taken for investigating the effects of herbivore-induced plant volatiles (Kessler and Baldwin 2001). This approach will provide the best information if the emission dynamics of the synthetic infochemical sufficiently resemble the natural emission dynamics.

Phytohormonal induction of plant volatiles

Another approach is to manipulate an individual's phenotype by manipulating natural biosynthetic pathways. The phytohormone jasmonic acid is well-known to mediate many phenotypic changes in plants (Dicke and Van Poecke 2002; Kessler et al. 2004). The application of jasmonic acid to tomato plants under field conditions resulted in an increased attraction of parasitic wasps to caterpillar-damaged tomato plants (Thaler 1999) and jasmonic-acid application was found to influence the composition of the insect community on the plants (Thaler 2002; Thaler et al. 2001). However, the disadvantage of this approach is that the single application of an external jasmonic-acid dose is likely to be very different from the natural induction dynamics and concentration. Yet, this approach may provide interesting information, as was clearly shown for the tomato studies (Thaler 1999; 2002; Thaler et al. 2001).

Molecular-genetic approach to plant characteristics

A third approach is to compare two genotypes that differ in identified components of their genetic background. This can relate to a well-characterized mutant and the related wildtype genotype or to a transgenic plant in which one gene is overexpressed or knocked out versus its wildtype. This approach has been taken for the wild tobacco plant *Nicotiana attenuata* (Kessler in press; Kessler et al. 2004). Kessler et al. (2004) knocked out three genes from the jasmonate signal transduction pathway. This pathway leads to the production of jasmonic acid or fatty-acid-derived green-leaf odours. Jasmonic acid is well-known to be involved in induced defences of plants against herbivorous insects, and green-leaf odours are known to influence behaviour of herbivorous insects and their natural enemies (Dicke and Van Poecke 2002). By generating three plant lines, each knocked out for one gene of the jasmonate pathway and bringing these plants into their natural environment, Kessler and colleagues investigated the effects of the genetic modification on herbivory. When planted into their native habitat, lipoxygenase-deficient plants were more vulnerable to *N. attenuata*'s adapted herbivores but were also exploited by a herbivore species that was otherwise not found on *N. attenuata*, which fed and reproduced successfully on the *LOX2*-deficient plants. In addition to observing changes in the insect community as a result of transforming the plants, Kessler and co-workers also assessed the effects at the transcriptomic level through a dedicated microarray analysis and at the level of volatile emission through GC-MS analysis of the headspace of transformed plants (Kessler et al. 2004). This approach is essentially dependent on knowledge of the mechanism underlying induced plant defence, such as the involvement of signal transduction pathways, essential genes in the pathways and the function of their products, as well as knowledge of manipulating the expressed genotype by, e.g., anti-sense knock out, virus-induced gene silencing or RNA interference (Hamilton and Baulcombe 1999; Robertson 2004). Their approach is a major step forward in understanding the role of certain genes and their products in the effects on community ecology. In this case, the effect of the presence/absence of activity of a single gene was compared. Progress in molecular biology is likely to yield other, even more exciting, tools for ecologists as well, including those that allow for quantitative differences (Dicke et al. 2004). This is likely to bring unprecedented progress in our understanding of the role of infochemicals in community processes.

Complementing field studies with laboratory studies

The information from field studies needs to be complemented by laboratory studies to elucidate whether, where and to what extent infochemicals influence the outcome of individual interactions. In the laboratory one can disentangle the complexity of interactions in a directed way by investigating those interactions that are most likely to be influenced. Laboratory information on the effects of individual genes on infochemically mediated interactions is still scarce. For example, potato plants that had been transformed with a linalool synthase gene from strawberry behind a 35S promoter constitutively emitted the monoterpene linalool. These transgenic potato plants attracted the predatory mite *Phytoseiulus persimilis* (Bouwmeester et al. 2003), which is known to be attracted to synthetic linalool (Dicke et al. 1990). Linalool is one of the volatiles induced in lima-bean plants by feeding damage inflicted by the spider mite *Tetranychus urticae,* the prey of *P. persimilis* (Dicke et al. 1990). The parasitoid *Cotesia rubecula* is attracted to volatiles from *Arabidopsis thaliana* that is infested with caterpillars of *Pieris rapae* (Van Poecke et al. 2001). However, the attraction was impaired when Arabidopsis plants were used in which the *LOX2* gene was co-suppressed, which blocks induction of jasmonic acid, or in plants in which a bacterial *NahG* gene was inserted, which results in breakdown of salicylic acid (Van Poecke and Dicke 2002). Moreover, in tomato the attraction of the predatory mite *P. persimilis* to herbivore-damaged plants was impaired in plants with a mutation in the jasmonic-acid signal transduction pathway compared to wildtype plants (Ament et al. 2004; Thaler et al. 2002). These studies show that single biosynthetic genes or genes that interfere with signal transduction pathways can influence infochemically mediated interactions between plants, herbivorous arthropods and their natural enemies.

‘OMICS’ AND COMMUNITY ECOLOGY

In the interaction of organisms with their environment, each individual expresses a complex phenotype that is subject to plasticity in response to the environment or in response to the individual’s phenology (Agrawal 2001). In fact, the phenotype is not a static but a highly dynamic feature. The changes may occur over different spatial scales (from the organelle to the organ) and over different temporal scales (from milliseconds to days or longer). Moreover, the phenotype is influenced by many genetic components. To investigate the contribution of individual traits, one should ideally manipulate that trait so as to affect its expression in the natural – though complex – way. The best way of doing this is to use mutants that are altered in the expression of the trait (Dicke et al. 2004; Dicke and Van Poecke 2002; Kessler et al. 2004; Roda and Baldwin 2003). In fact, comparing mutants with their relevant wildtype allows one to analyse the effects of genetic variation in single traits, and thus to assess the role of these genes in the species' ecology.

To date, a molecular-genetic approach to chemical ecology and community ecology is rapidly developing (Baldwin 2001; Dicke et al. 2004; Kessler et al. 2004). In order to take this novel approach, one needs to have a suitable system that provides all necessary tools. In the past few years we have developed *Arabidopsis thaliana* as a model for a molecular-genetic approach of the ecology of herbivore-induced plant volatiles (e.g. Van Poecke and Dicke 2002; 2003; Van Poecke et al. 2001), and this has also been done for other plant species such as *N. attenuata* (Kessler and Baldwin 2001; 2004; Kessler et al. 2004; Voelckel and Baldwin 2004).

Three major signal transduction pathways are known to be involved in the induction of plant volatiles: the octadecanoid, the salicylic-acid and the ethylene pathways (Dicke and Van Poecke 2002; Kessler and Baldwin 2002, for review). Well-characterized genotypes that are altered in these signal transduction pathways are available for *Arabidopsis* (Pieterse and Van Loon 1999; Reymond et al. 2000; Walling 2000). These genotypes allow the analysis of the involvement of the signal transduction pathways with chirurgic accuracy. A single gene has been modified and thus a single step in signal production or signal perception has been altered. These genotypes have been successfully used in the study of induced resistance against phytopathogenic micro-organisms (Pieterse and Van Loon 1999; Walling 2000). These and other well-characterized *Arabidopsis* genotypes are available to investigate the effect of single traits on interactions mediated by herbivore-induced plant volatiles (Van Poecke and Dicke 2002). This will allow to evaluate the new information in the context of induced responses to other environmental variation such as the attack by pathogens (e.g. De Vos et al. 2005; Pieterse and Van Loon 1999).

The major advantages of using *Arabidopsis* for a molecular-ecological approach are that its genome has been sequenced, that a multitude of well-characterized mutants and transgenics is available and that full-genome microarrays are available that can be used to investigate global transcriptome changes in response to biotic interactions (e.g. De Vos et al. 2005; Reymond et al. 2004; Schenk et al. 2000). Moreover, some of these methodologies or the results of their use with *Arabidopsis* may be transferred to other Brassicaceous plants (e.g. Lee et al. 2004). Therefore, information obtained for *Arabidopsis* may be exploited to develop novel approaches for understanding chemical ecology and community ecology of *Brassica*–insect interactions. This will provide important complementary knowledge on the ecology of *Brassica*–insect interactions as obtained through classical methods (e.g. Geervliet et al. 2000; Harvey et al. 2003; Mattiacci et al. 1995; Shiojiri et al. 2001).

For *Arabidopsis* the connection between transcriptomics and proteomics has been made for several biological contexts (Hirai et al. 2005; Peck 2005). Moreover, the connection between transcriptomics and metabolomics has been made (D'Auria and Gershenzon 2005), also in the context of infochemicals (Mercke et al. 2004). When the connection between gene activity and metabolomics has been made, novel tools will be available to tackle many of the questions that have been addressed for many decades in the ecology of insect–plant interactions, i.e., understanding the function of so-called secondary metabolites (Berenbaum et al. 1989; Fraenkel 1959;

Poppy 1999; Schoonhoven et al. in press). Gaining knowledge of mechanisms in terms of transcriptomics, proteomics and metabolomics provides a solid basis for understanding the expression of phenotypes of an organism under different conditions, also termed 'phenomics' (Edwards and Batley 2004; Kahraman et al. 2005). The field of phenomics addresses the documentation of a phenotypic characteristic to a gene and is so far characterized by a deterministic nature where one gene has a single phenotype. However, ecologists are well aware that phenotypes may change with conditions and as such the input of ecologists in phenomics is badly wanted. It may seem fashionable to invent ever new 'omics' for every new and higher layer of integration. However, at the next level of integration, i.e., understanding the total of interactions within a community, we do not need a new 'omics' term: the term community ecology sufficiently covers this area. Linking 'omics' to community ecology is an exciting challenge because it implies linking two very different ways of looking at biological phenomena, viz., a deterministic and highly technology-driven approach and a stochastic and concept-driven approach. First developments in this area show that linking 'omics' with community ecology can be highly rewarding and is likely to answer questions that were difficult to answer so far (Dicke et al. 2004; Howe and Brunner 2005; Kessler et al. 2004; Shimizu and Purugganan 2005). After all, a major challenge for ecologists has been to understand how individual traits of organisms affect species interactions and community dynamics. Breakthroughs in the 'omics' fields provide ecologists with exciting tools to address this through an ecogenomics approach. This allows the most delicate manipulative studies that one can think of, in which mechanistic knowledge of well-characterized genotypes and phenotypic plasticity can be exploited to study the effect of individual plant traits on interactions in ecosystems.

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