

Ecogenomic approach to the role of herbivore-induced plant volatiles in community ecology

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Summary

1 Linking new developments in genomics with ecology provides interesting novel tools to address ecological questions in ways that have not been possible up to now. In this paper we address this issue for the ecology of infochemicals and plant–insect interactions in a food web context.

2 Plants are at the basis of most terrestrial food webs and insects are a dominant animal group interacting with plants. Insect–plant communities are characterized by direct and indirect interactions, many of which are mediated by infochemicals. Plants respond to insect herbivory with the production of volatiles that attract the enemies of the herbivores, such as insect predators and parasitoids. Moreover, the plant volatiles may be exploited by any organism in the environment and this results in many more infochemically mediated interactions. Thus, a food web is overlaid with an infochemical web.

3 In the past, several manipulative tools have been developed to investigate the role of infochemicals. The rapid advancement of molecular genetics and ‘-omics’ technologies results in interesting new tools. A recent development is the use of well-characterized genotypes that are modified in the mechanisms underlying the induced plant volatiles. These genotypes produce precisely manipulated phenotypes that often differ in only a single gene, and can be used to investigate the effect of particular genes on specific interactions. Moreover, these genotypes can be introduced into a natural community to assess the effects of the genetic change and its resulting phenotypic change on interactions with the entire natural community.

4 Furthermore, with the progress in microarray technology it becomes possible to assess the expressed genotype of plants in the field, which can be exploited to investigate expressed genetic variation under field conditions.

5 These developments are expected to be only the beginning of a successful integration of -omics technologies, such as transcriptomics and metabolomics, with community ecology into the new research field of ecogenomics.

6 In this review we present the current status and discuss the prospects for the future of an ecogenomic approach to the role of herbivore-induced plant volatiles in insect–plant community ecology.

Key-words: community genetics, herbivore-induced plant volatiles, induced defence, infochemicals, insect–plant interactions, manipulative approach, phenotypic plasticity

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Introduction

A principal aim of ecologists is to understand the mechanisms shaping population and community processes. The evolution of species interactions, and

hence their impact on the community, can only be fully understood by the study of the genetics and dynamic processes underlying such interactions. During the last decade, developments in the study of the organization and functioning of genomes have resulted in the acquisition of novel insights into the effects of individual genetic variation and plasticity on community processes. Among

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the plethora of -omics, the relatively recent branch of ecogenomics holds promise for major breakthroughs in linking these two fields (Van Straalen & Roelofs 2006).

Chemical information

Chemical cues are a major source of information for very different organisms ranging from microorganisms to mammals (e.g. Roitberg & Isman 1992; Kats & Dill 1998; Tollrian & Harvell 1999; Dicke & Grostal 2001) that affect various behaviours underlying population dynamics and food web interactions (e.g. Roitberg & Isman 1992; Kats & Dill 1998; Turlings & Benrey 1998; Dicke & Vet 1999; Sabelis *et al.* 1999; Hilker & Meiners 2002). However, the study of chemical information conveyance has largely been 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 (Vet 1998; Van der Meijden & Klinkhamer 2000; Hunter 2002), in contrast to the influence 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 & Vet 1999; Sabelis *et al.* 1999; Kessler & Baldwin 2001).

Herbivore-induced plant volatiles are infochemicals that mediate many interactions in a plant–insect community, both above and below ground (Dicke & Vet 1999; D’Alessandro & Turlings 2005; Rasmann *et al.* 2005). These volatiles that plants produce in response to damage inflicted by herbivores affect various interactions of the plant with community members (Dicke & Vet 1999; Birkett *et al.* 2000; Dicke 2000; Kessler & Baldwin 2001; Strauss *et al.* 2001). For instance, herbivore-induced plant volatiles may deter or attract herbivores, but they also indirectly affect carnivore–herbivore interactions through attraction of carnivores. Differential responses by different carnivore species may mediate the degree to which they compete for the same resource or interact through intraguild predation on each other. Carnivorous arthropods largely rely on herbivore-induced plant volatiles in locating herbivores or their microhabitat from a distance. Moreover, herbivore-induced plant volatiles can also affect herbivore–plant and carnivore–herbivore interactions on neighbouring plants through their effect on the neighbour’s phenotype (Dicke & Vet 1999; Sabelis *et al.* 1999; Dicke *et al.* 2003a). These herbivore-induced plant volatiles (HIPVs) represent phenotypically plastic responses of plants to herbivory that result in changes in interactions among individuals in the insect–plant community.

Insect–plant communities

Approximately 50% of all insect species feed on plants and the other half comprise carnivores and detritivores

(Schoonhoven *et al.* 2005). Insect–plant communities are complex entities that consist of hundreds of species (Rott & Godfray 2000). In addition to the large number of species, genetic variation among species members as well as phenotypic plasticity of individuals add to the complexity of insect–plant interactions in communities (Agrawal 2001).

Insect–plant communities are highly dynamic. Population sizes of insects may quickly change and food webs can show drastic quantitative changes within a season (Rott & Godfray 2000). Moreover, interactions between two community members may influence interactions between various others. Many species show phenotypic plasticity that is induced by the interaction with community members, and phenotypic changes may be specific for the interaction that induces them (Agrawal 2001). Thus, dynamic food web changes can be amplified through their effects on interactions between members of the food web.

When studying a plant–insect community, ecologists may focus on the food web that connects different species in a direct way according to trophic relationships exclusively. Communities also contain indirect interactions between species from different trophic levels, mediated by a third species. For instance, plants may attract the enemies of herbivorous insects with plant volatiles that are induced by feeding damage inflicted by the herbivores.

Both direct and indirect interactions in a community are mediated by chemical information (infochemicals, Dicke & Sabelis 1988). Every member of a community produces infochemicals that can influence direct interactions between the producer of the cues and the organisms that have a trophic relationship with the producer. Moreover, an infochemical that is released into the environment can be exploited by any organism of the community to meet its own needs. As a result, infochemicals mediate ample indirect interactions as well (Turlings & Benrey 1998; Dicke & Vet 1999; Sabelis *et al.* 1999). Thus, a food web is overlaid with an infochemical web. This infochemical web is more reticulate than the food web as the food web only comprises direct interactions whereas the infochemical web also comprises indirect interactions (Dicke & Vet 1999; Shiojiri *et al.* 2001).

A major challenge for biology in the 21st century is to integrate research approaches that address different levels of biological organization, i.e. from subcellular processes all the way to community processes (Fig. 1). A pressing issue in ecology is to understand how interactions among individual organisms influence food webs and community dynamics. Evolutionary ecologists aim to understand how genetic differences affect the fitness of individuals in complex communities. This can now be addressed through a novel integration of approaches: from ecogenomics, through behavioural ecology to community ecology. The major question of evolutionary ecology, i.e. how individual genes affect an individual’s performance, can now for the first

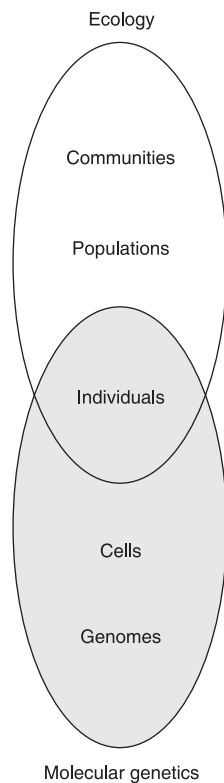


Fig. 1 Molecular genetics and community ecology are involved at different levels of biological integration and overlap at the level of the individual.

time be investigated as such without the confounding influence of other genetic differences between individuals. This is the topic of this review in which we focus on infochemicals and the community ecology of plant–insect interactions.

Manipulative tools for investigating the infochemical web

To develop manipulative tools, knowledge of underlying mechanisms is of great importance. Investigating community dynamics and the role of the infochemical web requires precise manipulative tools. Ideally one should be able to modify individual components of the infochemical web and assess the resulting effects on community processes. Various manipulative tools have been developed over the past decades. Each of these tools is based on mechanistic information on the production of, and response to, the infochemicals (Dicke *et al.* 2003b). Here we will briefly review the different tools developed.

Ecologists initially started to investigate the effects of individual chemicals and mixtures of specific cues (Dicke *et al.* 1990; Whitman & Eller 1990; Turlings *et al.* 1991; Birkett *et al.* 2000). The chemicals used were derived from analytical studies that deciphered the composition of HIPV blends. Surprisingly, individual compounds from HIPV blends were found to attract carnivorous arthropods although the compounds were not specific indicators of their herbivorous prey or

hosts (Dicke *et al.* 1990; Whitman & Eller 1990). This was followed by experiments in which more compounds from the HIPV blend were offered simultaneously (Turlings *et al.* 1991). More recently, HIPV blends were fractionated and the fractions were investigated for their effects on arthropods (Turlings & Fritzsche 1999; Van den Boom 2003; D'Alessandro & Turlings 2005).

In investigations of the effects of infochemicals on individual interactions or overall community effects, the use of (blends of) pure chemicals can be a first step, if the compounds of interest are available as pure compounds. This allows well-defined application of stimuli (Dicke *et al.* 1990; Whitman & Eller 1990; Turlings *et al.* 1991; Kessler & Baldwin 2001; D'Alessandro & Turlings 2005, 2006). Yet, although this can provide valuable information, the application of synthetic chemicals cannot mimic the natural dynamics of volatile emission. For compounds that are not synthetically available or for complex blends the use of elicitors may be a valuable tool to investigate the effect on individual interactions (Dicke *et al.* 1999). Elicitors can induce a subset of the blend of HIPVs (Koch *et al.* 1999). This allows assessment of the role of individual compounds against a complex odour background by supplementing the partially induced blend with individual compounds (De Boer & Dicke 2004; De Boer *et al.* 2004). Yet here, in addition, the natural dynamics of volatile emission will not be mimicked. The use of inhibitors that block specific steps in the signalling pathways or biosynthetic pathways (Zeidler *et al.* 1998; Koch *et al.* 1999) is more likely to leave the non-inhibited signalling and biosynthetic pathways intact. Therefore, the non-affected pathways are likely to retain their natural dynamics. However, a disadvantage may be that chemicals that accumulate in the last step before the inhibited step have physiological side-effects or are redirected into another biosynthetic pathway. A metabolomic analysis may provide more insight in this regard (Bezemer & van Dam 2005).

Plant physiological and biochemical investigations have revealed that induced plant defences are orchestrated by three main signalling pathways, the octadecanoid, the shikimate and the ethylene pathways (Dicke & Van Poecke 2002; Kessler & Baldwin 2002). These three signalling pathways are also involved in the induction of infochemicals (Horiuchi *et al.* 2001; Dicke & Van Poecke 2002; Kessler & Baldwin 2002; Van Poecke & Dicke 2004). Mechanistic knowledge of the biosynthetic and signalling pathways provides interesting options for manipulating the emission of plant volatiles through specific elicitors and inhibitors (Koch *et al.* 1999). Over the last decade molecular genetic information on the induction of plant volatiles has rapidly accumulated. This has allowed the use of mutants or plants that have been genetically modified in the biosynthetic (Kappers *et al.* 2005; Schnee *et al.* 2006) or signalling pathways (Thaler *et al.* 2002; Van Poecke & Dicke 2002; Ament *et al.* 2004; Kessler *et al.* 2004) with consequences for the emission of volatiles.

The most interesting genotypes are those that differ in a limited number of well-defined genes. Such genotypes have often been unavailable, but recent molecular genetic developments are changing this drastically. With the rapidly expanding knowledge of genomics and molecular genetics, specific genotypes are being developed in which the expression of a single gene is modified. These genotypes provide exciting new tools to ecologists. To a large extent this is already true for model plant species of molecular biologists such as *Arabidopsis thaliana*. However, these tools are rapidly being developed for ecological model species as well (Kessler *et al.* 2004; Schmidt *et al.* 2004).

Molecular ecological approach to community ecology

All manipulative tools mentioned in the previous section have been derived from information on mechanisms. We will now address specifically the potential of a molecular genetic approach. This has already yielded interesting results (reviewed by Baldwin *et al.* 2001; Degenhardt *et al.* 2003; Dicke *et al.* 2004) and holds many promises for the future.

Novel transcriptomic developments have allowed the assessment of global responses of plants to environmental changes at the level of gene expression. This has shown that the attack by biotic agents can lead to drastic rearrangements of gene expression (Reymond *et al.* 2000, 2004; Schenk *et al.* 2000; Hermsmeier *et al.* 2001; De Vos *et al.* 2005). Attack results in up-regulation of defence-related genes and down-regulation of genes involved in photosynthesis (Hermsmeier *et al.* 2001), which provides a mechanistic explanation for the growth–defence trade-off that is well known to ecologists (Herms & Mattson 1992). Furthermore, it has become clear that responses of the same plant species to different attacker species can be very different and that induced signal-transduction pathways influence each other (Voelckel & Baldwin 2004; De Vos *et al.* 2005). As a consequence, the effects of combinations of species that attack the same plant can have quite surprising effects on the expressed plant phenotype (De Vos 2006).

The analysis of plant volatiles is undergoing developments that will extensively improve our knowledge of the metabolomic changes in plants in response to attack. With the application of more sensitive analytical equipment the composition of the induced blends appears to be more complex than was previously suspected, and with novel real-time techniques for data sampling and analysis the dynamics of plant volatile emission can now be registered in far greater detail (for a review see Tholl *et al.* 2006). Moreover, the technological developments in metabolomics have resulted in the recording of large sets of metabolites (Fiehn 2002). Combining transcriptomic and metabolomic analyses in plants that are not genomic model species can help to identify genes involved in the biosynthetic pathways

that lead to the production of HIPVs (Mercke *et al.* 2004). Two subtractive cDNA libraries, enriched in cDNA fragments up- or down-regulated by herbivore infestation, can be constructed from the leaves of infested and uninfested conspecific plants. Randomly selected clones from these libraries can be used to make a cDNA microarray. Subsequently, cDNAs prepared from mRNA from plants of several different treatments at different time points can be hybridized to the clones on the microarray. When induced volatile compounds are collected from the same leaves from which the mRNA was collected gene expression profiles can be analysed in combination with volatile production data in order to gain insight into the possible involvement of the studied genes in the synthesis of those volatiles. By grouping clones on the microarray and the herbivore-induced volatiles into a number of clusters, biosynthetic genes clustered with the product of that pathway can be found. The cDNA fragments on the microarray can then be used to screen the cDNA library to clone the gene (Mercke *et al.* 2004).

A logical next step in the -omics development is to link transcriptomics and metabolomics to the assessment of the ecological function of the identified genes and resulting infochemicals (Fig. 2). Transgenics and natural mutants in the genes of ecological interest can be important tools to study the effect of characteristics on the plant–insect community. This can be done by investigating the expression of phenotypes of an organism under different conditions, also termed ‘phenomics’ (Edwards & Batley 2004; Kahraman *et al.* 2005). First steps in this research field have been made, for example related to the behavioural responses by arthropod predators and parasitoids towards altered herbivore-induced volatile production (Van Poecke & Dicke 2002; Bouwmeester *et al.* 2003; Ament *et al.* 2004; Kessler *et al.* 2004; Kappers *et al.* 2005; Schnee *et al.* 2006). Approaches in this research area can roughly be divided into two groups. The first consists of alterations in the biosynthesis of induced plant volatiles (Bouwmeester *et al.* 2003; Faldt *et al.* 2003; Kappers *et al.* 2005; Schnee *et al.* 2006). The second group consists of alterations in the signal-transduction pathways that regulate volatile biosynthesis (Van Poecke & Dicke 2002; Ament *et al.* 2004; Kessler *et al.* 2004).

BIOSYNTHETIC MANIPULATIONS

Molecular genetic information on biosynthetic pathways has accumulated rapidly in recent years (Dudareva *et al.* 2004; Aharoni *et al.* 2005; Fridman & Pichersky 2005). This allows for the manipulation of the plant phenotype in terms of infochemical production (Bouwmeester *et al.* 2003; Degenhardt *et al.* 2003; Arimura *et al.* 2004; Kappers *et al.* 2005; Tholl *et al.* 2005; Schnee *et al.* 2006).

For instance, identification of genes encoding key enzymes in the biosynthesis of herbivore-induced terpenoids has been exploited to transfer these genes to

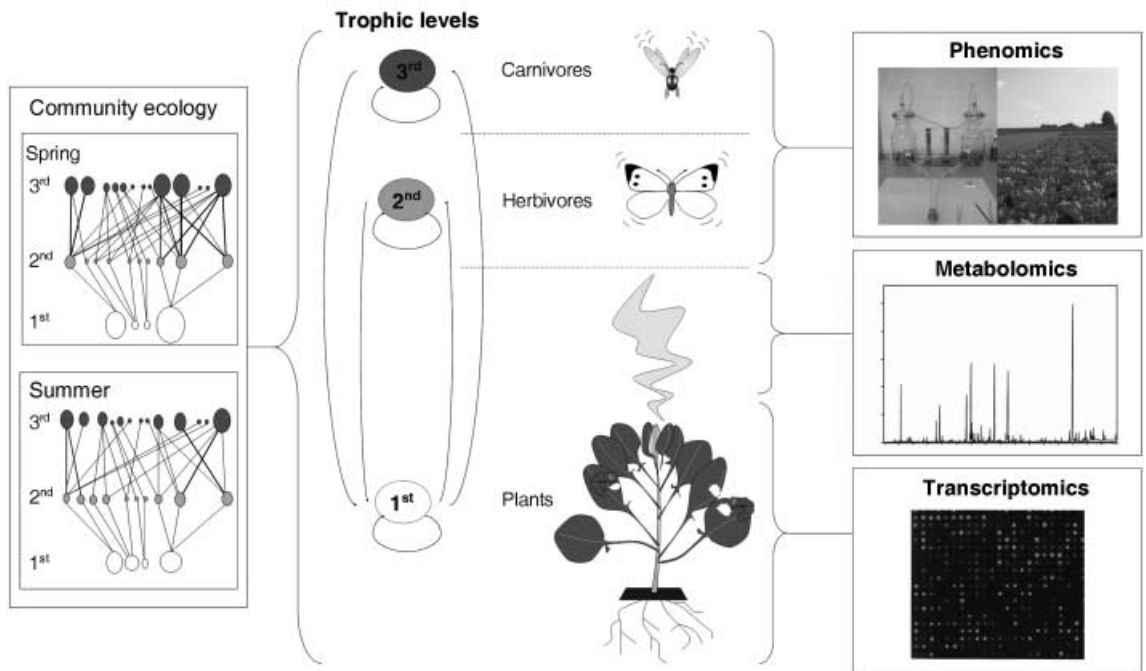


Fig. 2 The application of -omics technologies, such as transcriptomics and metabolomics, and analyses of the range of phenotype expression in individual interactions (phenomics) to the study of community ecology of insect–plant communities. Herbivore damage to plants results in the emission of volatiles that can influence interactions of the plant with organisms at different trophic levels. Interactions (arrows) between members of the same or different trophic levels may be affected by the induced volatiles and this may have consequences for the quantitative food web, in which each species is represented by a circle (circle size indicates population size and the width of the lines connecting species indicates the relative degree of trophic interaction between the two connected species).

Arabidopsis thaliana (Kappers *et al.* 2005; Schnee *et al.* 2006). As a result the transgenic plants emitted one or two (Kappers *et al.* 2005), or six or more terpenoids (Schnee *et al.* 2006). The transgenic plants attracted significantly more carnivorous arthropods such as the predator *Phytoseiulus persimilis* (Kappers *et al.* 2005) and the parasitoid *Cotesia marginiventris* (Schnee *et al.* 2006) than the wild-type. These studies clearly demonstrated the ecological effects of particular terpenoids that are components of a complex blend of HIPVs and thus revealed an ecological function for the genes involved. These results are likely to be a starting point for future studies on the role of these genes in a community context rather than in an isolated ecological interaction. For such studies individuals of the original plant species varying in the degree of gene expression dynamics will be of great value.

SIGNAL-TRANSDUCTION MANIPULATIONS

The signal-transduction pathways underlying induced plant responses, including herbivore-induced volatile production, have been intensively studied in several plant species, especially *Arabidopsis*, tomato and tobacco (Pieterse & Van Loon 1999; Dicke & Van Poecke 2002; Kessler & Baldwin 2002; Van Poecke & Dicke 2004). The natural tomato mutant *def-1* is deficient in jasmonic acid (JA) as a result of a mutation early in the octadecanoid pathway. This mutant does not produce induced metabolites such as proteinase inhibitors

involved in direct defence (Howe *et al.* 1996) or volatile terpenoids involved in indirect defence (Thaler *et al.* 2002; Ament *et al.* 2004). The *def-1* mutant is compromised in the attraction of carnivorous arthropods and this can be restored by the application of exogenous JA (Ament *et al.* 2004; Thaler *et al.* 2002). Knowledge of the molecular genetics of signal-transduction pathways can be used to generate transgenic genotypes that are altered in the underlying mechanism leading to induced plant volatiles. For instance, genotypes changed in certain steps in the octadecanoid (Van Poecke & Dicke 2002; Halitschke & Baldwin 2003; Kessler *et al.* 2004) or shikimate pathways (Van Poecke & Dicke 2002) have been used in studies on the attraction of arthropods to HIPVs. *Arabidopsis* plants compromised in the octadecanoid or shikimate pathways that were infested with caterpillars of the small cabbage white (*Pieris rapae*) were less attractive to the parasitoid *Cotesia rubecula* than caterpillar-infested wild-type plants (Van Poecke & Dicke 2002).

Molecular ecology of HIPVs: two examples

HIPVs have been well studied in crucifers. These studies include the behavioural ecology of crucifer–caterpillar–parasitoid interactions (Wiskerke & Vet 1994; Geervliet *et al.* 2000; Vos *et al.* 2001; Shiojiri *et al.* 2002), as well as molecular genetics and analytical chemistry of induced crucifer volatiles (Geervliet *et al.* 1997; Mattiacci *et al.* 1995; Shiojiri *et al.* 2001; Van

Poecke *et al.* 2001). Over the last decade *A. thaliana*, the model plant of molecular geneticists, has been increasingly used by ecologists (for reviews see Mitchell-Olds 2001; Van Poecke & Dicke 2004). This has yielded novel insight into the role of specific genes in ecological interactions of the crucifer *Arabidopsis* with insects (e.g. Stotz *et al.* 2000; Van Poecke & Dicke 2002; Aharoni *et al.* 2003). Interesting genotypes are now being developed that can no longer produce certain induced plant volatiles (e.g. Chen *et al.* 2003).

However, from an ecological point of view *Arabidopsis* may not be the most interesting plant because of its short life cycle very early in the season. Yet, interesting ecological fieldwork on *Arabidopsis*–attacker interactions has been carried out (Yano & Ohsaki 1993; Mauricio 1998; Arany 2006). Moreover, this plant is a valuable species as a stepping stone towards other brassicaceous plants. For instance, certain types of microarrays developed for *Arabidopsis* can be used to investigate global gene expression in *Brassica* (Lee *et al.* 2004). Moreover, there are many parallels between *Arabidopsis* and other brassicaceous species in the context of HIPVs (Van Poecke & Dicke 2004). Therefore, *Arabidopsis* is an interesting species for investigations of the role of induced plant volatiles on community ecology both from a methodological and a conceptual point of view. In our laboratory we have intimately integrated projects on *Arabidopsis*–attacker interactions with projects on the community ecology of brassicaceous plants and their associated insects. For *Brassica* we have compared the effects of genotypes that differ in the degree of parasitoid attraction on community composition (E.H. Poelman *et al.* unpublished data) and investigated the differences between the genotypes in the underlying mechanisms at the molecular and metabolite levels (E.H. Poelman *et al.* unpublished data; C. Broekgaarden *et al.* unpublished data).

An excellent example demonstrating the value of a molecular approach to community ecology is the work by Kessler, Baldwin and colleagues (Baldwin *et al.* 2001; Kessler *et al.* 2004; Kessler 2006). They have taken the solanaceous species *Nicotiana attenuata* as their ecological model plant and have developed extensive molecular tools to investigate and manipulate mechanisms underlying induced responses to attackers. Their methods and tools include cloned genes, dedicated microarrays, anti-sense (as) knock-out genotypes, in addition to methods to assess changes in secondary metabolites such as nicotine and volatiles (Paschold *et al.* 2006). They have made three plant lines that are knocked out for one of three different genes of the octadecanoid signal-transduction pathway and placed these in a common garden in their native habitat (Kessler *et al.* 2004). This showed that eliminating the functional expression of the *LOX-3* gene results in drastic changes in interactions with the natural insect community: the amount of herbivory increased substantially and the invasion of a new herbivore species, *Empoasca* sp., was the main cause for this. This

herbivore did not feed on wild-type plants under natural conditions. Another new herbivore that had never before been recorded from *N. attenuata* is the western cucumber beetle *Diabrotica undecimpunctata tenella*. In laboratory tests *Empoasca* sp. and *D. undecimpunctata* preferred to feed on *as-lox* plants over wild-type *N. attenuata* plants. The *as-lox* plants had a lower emission rate of the herbivore-inducible terpenoid *cis*- α -bergamotene. However, it remains to be investigated whether the change in herbivore-induced *cis*- α -bergamotene is the cause of the change in acceptance by herbivorous insects. Yet, previous research employing the application of synthetic volatiles or JA as elicitor has shown that plant volatiles are important in the interactions of *N. attenuata* with herbivorous and carnivorous insects under field conditions and result in direct and indirect protection against herbivores (Kessler & Baldwin 2001).

Future prospects

Although the ecogenomics approach clearly holds promise to ecologists, there are some important developments to be made. The most important of these questions plus the ecological questions to which they relate are given below.

1. The most important hurdle to be taken is that, to date, the best genomic model systems do not include the best ecological model systems, either because the ecology of the genomics models is little studied or because important ecological questions cannot be addressed by using the genomics models. Moreover, the ecogenomic approach has so far been applied to a limited number of systems. Two main solutions to this problem exist. One is to investigate an ecological model species that is closely related to a molecular genetic model species and use the latter as a stepping stone. This has been explained for the use of *Arabidopsis* to develop an ecogenomic approach to *Brassica* species. Information on *Arabidopsis* gene sequences can be used to help in cloning of genes for *Brassica* (S.-J. Zheng *et al.* unpublished data) and 70-mer oligonucleotide microarrays developed for *Arabidopsis* can be exploited to investigate global gene expression in *Brassica* (Lee *et al.* 2004). The other solution is to use suppression subtractive hybridization (SSH) to build a library of differentially expressed clones that can be used to develop a dedicated microarray and to clone genes involved in the expression of an induced plant phenotype (Hermsmeier *et al.* 2001; Mercke *et al.* 2004).
2. The technological developments of molecular biology have provided ecologists with a 'digital' tool to compare two genotypes in which a certain gene is either functionally expressed or not. Using the variation between independently transformed lines allows variation of phenotypic expression for candidate genes to be studied (Halitschke & Baldwin 2003). Yet, ecologists are ultimately interested in quantitative natural variation. A major challenge for molecular ecologists is to

identify genotypes that differ quantitatively in the expression of specific genes. This may be done by developing molecular expression markers based on sequence information for the gene(s) of interest. When genotypes have been selected that express quantitative variation in gene expression, novel tools will become available to be used in manipulative experiments under field conditions. The relative effects of community members on these genotypes can be used to assess the effects of the gene on an individual's fitness. This will yield significant information beyond that gained from current qualitative manipulations resulting from knocking out genes.

3. New methodology in quantitative food web analysis has been developed in recent years (Rott & Godfray 2000; Lewis *et al.* 2002; Forup & Memmott 2005). This quantitative food web analysis provides valuable information beyond connectance food webs. This methodology captures community dynamics in space and time (Rott & Godfray 2000) and has proven to be a useful tool for comparative analysis in which the effects of particular phenotype changes are addressed (Omacini *et al.* 2001). This methodology can be used to address issues such as the effect of a single gene on community composition and dynamics. Genotypes that have been characterized in terms of transcriptomic and metabolomic profiles can be quantitatively compared in terms of food web structure. This can be used to evaluate the effects of single genes on food web structure in a manner similar to the evaluation of the effects of an endophytic fungus on the parasitoid–host food web (Omacini *et al.* 2001).

4. In this review, we have illustrated the potential of ecogenomics to understand the consequences of (plasticity in) expression of genes for community processes, assuming that the shape of a particular interspecific interaction is ubiquitous. Although this approach enables the linking of subcellular processes to particular community processes or structures, a challenge for the future lies in the implementation of these results in a spatial framework. Populations are generally highly structured, giving rise to complex mosaic patterns of species interactions (Thompson 2005). This will have consequences for variation across local communities. To address this issue, ecogenomics may again provide important tools. Association and correlation studies (Epperson 1993; Sinervo & Svensson 2002; Purugganan & Gibson 2003), 'natural selection mapping' (Kohn *et al.* 2000), and population genomics (Black *et al.* 2001) enable the estimation of variable selection at (sets of) loci, distinguishing this from processes that act on the whole genome, such as migration and genetic drift. Such an ecogenomics approach provides insights that complement those of the community and ecosystem genetics approach as proposed by Whitham *et al.* (2003). Whereas the latter focuses on the study of patterns of inheritance of traits involved in 'extended phenotypes' (i.e. traits that are likely to have community and ecosystem consequences), ecogenomics provides

an experimental approach, enabling the testing of the involvement of candidate genes in processes affecting the community. It is the integration of these types of studies with the previously described careful dissection of species interactions and their effect on communities that is likely to form both a highly fruitful approach and a major challenge in the search for a unified explanation of community dynamics.

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