MOLECULAR ECOLOGY

NEWS AND VIEWS

PERSPECTIVE

A genomically tractable and ecologically relevant model herbivore for a model plant: new insights into the mechanisms of insect–plant interactions and evolution

DAVID GIRON and ELISABETH HUGUET

Institut de Recherche sur la Biologie de l'Insecte, UMR CNRS 6035, Université F. Rabelais, 37200 Tours, France

Abstract

The availability of model microbial pathogens and plants has been key to characterizing resistance and virulence pathways and to shedding light on the mechanisms of host–parasite interactions and co-evolution (e.g. Allen et al. 2004, Science 306, 1957–1960; Bergelson et al. 2001, Science 292, 2281–2285). However, the absence of genetically tractable arthropod parasites of model plants has impeded so far our ability to gain better insights into the mechanisms, evolution and ecological consequences of plant–herbivore interactions. In this issue of *Molecular Ecology*, Whiteman *et al.* (2011) highlight fascinating features of a drosophilid fly, *Scaptomyza flava*, that feeds on the model plant *Arabidopsis thaliana*. They explore the potential of this system for studying insect–plant interactions with a clever mix of phenotypic and genetic experiments providing a comprehensive and persuasive argument for the validity of this model system. This study sets the ground for key developments in the unravelling of mechanisms involved in (i) plant–insect interactions and co-evolution, and (ii) transition to herbivory in arthropods and evolution of endophagous lifestyles.

Keywords: endophagous lifestyles, herbivory evolution, leaf-miner, plant–insect interactions, signalling pathways.

Received 19 July 2010; revision accepted 31 August 2010

Introduction

Plants constitute key nutritional resources for many organisms on Earth and therefore need to interact with multiple biotic partners ranging from parasites to mutualists. The signalling networks that are activated by plants in response to parasitic, herbivorous and beneficial organisms overlap, which indicates, on one hand, that the regulation of the

Correspondence: Giron David, Fax: +33 (0)2 47 36 69 66;
E-mail: david.giron@univ-tours.fr

adaptive response of the plant must be finely balanced between protection against aggressors and acquisition of benefits (Pieterse & Dicke 2007). On the other hand, the ability to perceive, interpret and manipulate plant signals is likely to provide insects or pathogens novel adaptive capacities, enabling, for example, the ability to expand to new ecological niches (Schultz 2002; Schultz & Appel 2004). So far, the dialogue between insects and plants has been mainly studied from the point of view of the plant, with in-depth characterization of plant responses to attack. Here, Whiteman *et al.* describe a promising model between a drosophilid herbivore and *Arabidopsis* which is likely to provide understanding at the molecular, cellular, ecological and evolutionary levels of the dialogue between plants and insects. It should also help to understand how each partner can adopt an appropriate adaptive response to its biotic environment and generate fundamental insights into co-evolutionary mechanisms in insects, pathogens and hosts.

Insect–plant interactions and signalling pathways

Signalling pathways involved in plant defence against pathogens and insects are known to be complex and ultimately lead to the synthesis of many different secondary metabolites and specialized chemicals such as pathogenesis-related proteins and proteinase inhibitors (Pieterse & Dicke 2007). Induced defences also involve indirect defence mechanisms such as the production of volatiles that attract parasitoids and predators of herbivores feeding on plants and extrafloral nectar that attracts and maintains carnivorous arthropods on herbivore-infested plants. Plant genomic approaches in model plant systems such as *Arabidopsis* have revolutionized our understanding of plant responses to microbial and fungal pathogens and shed light on plant responses to herbivores. The plant hormones salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) emerged as key players in the regulation of signalling networks involved in these responses (Van Peocke & Dicke 2004; Von Dahl & Baldwin 2007). Other plant hormones including abscissic acid, auxin and cytokinin have also been reported to play a role in the plant immune response but with a much lower level of investigations. It is usually assumed that biotrophic pathogens are more sensitive to SA-dependent defence responses, while necrotrophic pathogens and herbivorous insects are mostly affected by JA- and ET-dependent defence responses (Thomma *et al.* 2001). However, among insects, there are also examples of insects that induce the SA pathway, such as sap-feeding insects as opposed to their tissue-chewing counterparts that are known to induce the JA-signalling pathway (Walling 2000).

More precisely, jasmonate-signalling pathways have been shown to control defences against herbivores, such as leaf

eaters, in *Arabidopsis*. Plants lacking the ability to produce jasmonates or tri-unsaturated fatty acids, the precursors of JA, are usually susceptible to various herbivores. JA also shapes the herbivore community, and reduced activity of the oxylipin/jasmonate biosynthesis pathway can cause these plants to be attacked by detrivores or herbivores not normally associated with them (Farmer & Dubugnon 2010). By quantifying variation in *Scaptomyza flava* performance (including adult preference and larval performance) across *Arabidopsis* accessions and a set of canonical *Arabidopsis* defence mutants (mutants of the JA or glucosinolate pathways), and plants pretreated with elicitors of defence responses, Whiteman *et al.* show that known defence pathways in the plant affect the parasitic insect in predictable manners and that the insects respond to these host defence mechanisms both transcriptionally and phenotypically. This proof-of-principle study now opens the door to wide high-throughput analysis of insect manipulation of plant hosts.

Ecology and evolution of plant–insect interactions

Our understanding of the complexity of reciprocal evolution of signalling networks is still relatively limited in plant–insect interactions compared with the well-studied mechanisms involved in the arm races between pathogens and their host plants (Pieterse & Dicke 2007). Owing to the phylogenetic position of *S. flava* within the subgenus *Drosophila*, genomic and genetic tools from this model insect group can be leveraged and combined with the molecular, genomic and transgenic tools available in *Arabidopsis*. Therefore, this insect–plant system explored by Whiteman *et al.* could provide key new insights into the mechanisms at the basis of plant–insect interactions and how the ecology of plant hosts may be shaping insect evolution and adaptation. For instance, how plants respond to insects but also how insects can interfere with and manipulate plant-signalling pathways to allow their development and to enhance their fitness benefits (e.g. Bruessow *et al.* 2010; Kaiser *et al.* 2010) can now be addressed because of such genomically tractable models (Table 1). Because this leaf-miner species feeds on *Arabidopsis* and other crucifers in the wild, both in Europe and in North America, it is also an ecologically relevant model that could help to address questions on mechanisms and evolution of interactions between plants and their community members including other herbivores and pathogenic and beneficial microbes.

Evolution and adaptive significance of the endophagous lifestyle

In spite of a reasonable understanding of the history and origins of the endophagous feeding habit, its evolution and adaptive significance remains unclear (Connor & Taverner 1997; Stone & Schönrogge 2003). Three major hypotheses have been proposed to explain the endophagous feeding life history mode: the nutritional hypothesis, the microenvironment hypothesis and the enemy hypothesis (Connor & Taverner 1997; Stone & Schönrogge 2003). The nutrition

hypothesis states that galling or mining, two major forms of endophytophagy in insects, provides enhanced nutrition over other external feeding modes and allows endophagous organisms to avoid major plant defences. Feeding selectively on the most nutritional tissues is undoubtedly considered as a major advantage and most probably played a major role in the emergence, evolution and/or radiation of the endophagous feeding mode. This behaviour can also be reinforced by manipulating plant physiology. The best documented examples concern gall-inducing arthropods that actively manipulate plant physiology by the differentiation of additional tissues to feed on, the upregulation of protein and/or sugar synthesis *in situ*, and/or the modification of source–sink relationships leading to nutrient translocation towards the insect's feeding site (e.g. Giron *et al.* 2007; Schwachtje & Baldwin 2008) (Fig. 1). Manipulations of plant defensive pathways have also been reported in some galling insect species (e.g. Nyman & Julkunen-Tiitto 2000). However, plant manipulation appears not to be restricted to gall inducers only, as suggested by the autumnal formation of 'green islands' around mining caterpillars in yellow leaves (Fig. 1). In these mining systems, a further level of complexity is attained as endosymbiotic bacteria of insects have been shown to play a key role in the origin of such plant physiological alterations through manipulation of phythormone (cytokinin) levels (Engelbrecht *et al.* 1969; Giron *et al.* 2007; Kaiser *et al.* 2010). Work presented by Whiteman *et al.* in this issue will offer the opportunity to investigate molecular mechanisms on the basis of altered plant physiology in a leaf–miner interaction.

To understand proximal and ultimate mechanisms on the basis of plant–herbivore adaptive lifestyles, and to unravel the evolution and adaptive significance of the endophagous feeding mode, it will be necessary to study the intimate molecular, biochemical and physiological mechanisms underlying these plant–insect interactions, but also to measure fitness consequences for the insect and the plant respectively. This will also require comparing feeding strategies of different arthropod species in an evolutionary framework. By providing relevant genetic, genomic and phylogenetic tools, the *S. flava/Arabidopsis thaliana* model explored by Whiteman *et al.* (2011), could provide key insights into the understanding of the mechanisms and evolution of various feeding strategies, including leaf mining and galling modes. After characterizing the life cycle of *S. flava* on *Arabidopsis*, Whiteman *et al.* describe a large number of experiments to verify that this host plant is indeed infested by the insect, and that the latter can complete its development on the host. The placement of *S. flava* in a phylogenetic context provided in this study, combined with the diversity of feeding habits in drosophilids (from microbes lying on decaying plant tissues, to fungi or living plant tissues—Markow & O'Grady 2005; Hering 1951; Hackman 1959), could undoubtedly shed light on the evolution of plant herbivory in arthropods. Additionally, the comparison of the interaction between *Arabidopsis* and *S. flava* with those obtained on widely studied ectophagous

Table 1 Nonexhaustive list of insect herbivore/host–plant interactions for which genomic data are or soon will be available for both insects and host plants. Information was retrieved from the NCBI genome resources pages. As visible in this table, in the years to come, genomic resources will explode both for insect pests and for their host plants. Data concern sap-feeding and -chewing insects but with only few examples of endophagous organisms (red frame: 1 galler and 1 stem borer—and now 1 leaf miner). The model system described by Whiteman *et al.* has the advantage of dealing with the best characterized model plant, *Arabidopsis*, and the theoretical potential to transfer genetic and functional tools from *Drosophila* to the insect pest, *Scaptomyza flava*

Herbivorous insect	Host range	Genomic data	Examples of host-plants	Genomic data
Acyrthosiphon pisum (Pea aphid)	Large host range	Genome sequence	*Pisum sativum* (Pea)	Plastid genome project
			Medicago sativa (Alfalfa)	Genetic linkage map
			Medicago truncatula (Barrel medic)	Genome sequence in progress
Bemisia tabaci (Sweet potato whitefly)	Large host range	Genome sequence in progress	*Lycopersicon esculentum* (Tomato)	Genome sequence in progress
Ceratitis capitata (Mediterranean fruit fly)	Large host range	Genome sequence in progress	*Citrus sinensis* (Valencia orange)	Genome sequence in progress
Dendroctonus ponderosae (Mountain pine beetle)	15 or more species of pine	EST database	*Pinus contorta* (Lodgepole pine)	Plastid genome
Diaphorina citri (Asian citrus psyllid)	*Citrus* spp.	Genome in progress	*Citrus sinensis* (Valencia orange)	Genome sequence in progress
Heliothis virescens (Tobacco budworm)	Field crop	EST database	*Nicotiana tabacum* (Tobacco)	Genome sequence in progress
		Illumina sequencing of transcripts in progress	*Gossypium hirsutum* (Cotton)	EST database, BAC library
			Glycine max (Soybean)	Genome sequence
Manduca sexta (Tobacco hornworm)	Solanaceous plants	EST database	*Nicotiana tabacum* (Tobacco)	Genome sequence in progress
Mayetiola destructor (The Hessian fly)	Wheat	Genome in progress	*Triticum aestivum* (Wheat)	Genome in progress
Myzus persicae (Green peach aphid)	Large host range	Genome in progress	*Lycopersicon esculentum* (Tomato)	Genome sequence in progress
			Nicotiana tabacum (Tobacco)	Genome sequence in progress
Nilaparvata lugens (The brown planthopper)	Rice	Transcriptome	*Oryza sativa* (Rice)	Draft genome
Ostrinia nubilalis (European corn borer)	Large host range	Mitochondrial genome	*Zea mays* (Corn)	Genome sequence in progress
Pieris brassicae (Cabbage butterfly)	Brassica plants	EST database	*Arabidopsis thaliana*	Genome sequence
Pieris rapae (Small cabbage white butterfly)	Brassica plants	EST database	*Arabidopsis thaliana*	Genome sequence
Scaptomyza flava	Arabidopsis and mustard plants	Transcriptome in progress; Line inbreeding for genome sequencing in progress	*Arabidopsis thaliana*	Genome sequence
Spodoptera frugiperda (Fall armyworm)	Large host range	EST database	*Zea mays* (Corn)	Genome sequence in progress
Spodoptera littoralis (Egyptian cotton worm)	Large host range	EST database	*Phaseolus vulgaris* (French bean)	Genome sequence in progress
Toxoptera citricida (Brown citrus aphid)	*Citrus* spp.	Expressed genes	*Citrus sinensis* (Valencia orange)	Genome sequence in progress

Fig. 1 Remarkable insect-induced plant manipulations. Plant galls (upper panel) are abnormal growths of plant tissues induced by various species of bacteria, fungi and insects. Green islands (lower panel) are also markedly visible signs of leaf physiology alteration induced by various bacteria, fungi, virus and insects. They are characterized by photosynthetically active green patches in otherwise senescing leaves. Pictures: D. Giron.

crucifer specialists, such as the diamondback moth or the cabbage looper, could also provide key information on the origin and mechanisms of evolution of the endophagous lifestyle in arthropods.

Conclusion

The sedentary behaviour of endophagous arthropods makes them ideal systems for interpreting the ecological and evolutionary mechanisms of herbivory and related questions such as plant resistance or physiological manipulation. Such intimate associations are indeed expected to facilitate close interactions between independent genomes leading to molecular and biochemical cross-talk between arthropods and plants. How JA-signalling pathways can shape the herbivore community associated with a specific host plant (Kessler *et al.* 2004) or can constrain certain groups of organisms to change their feeding strategies (Farmer & Dubugnon 2010), how cytokinin gene expression and endosymbiotic communities can shape plant–insect interactions (Kaiser *et al.* 2010), and how other phytohormones and overlapping signalling processes impact plant responses to insects (Pieterse & Dicke 2007) are among questions now made accessible thanks to such new promising genomically tractable and ecologically relevant plant–herbivore systems.

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D. Giron focuses on complex multitrophic systems and their intimate interactions based on a multidisciplinary comprehensive approach ranging from molecular biology, biochemistry and physiology to ecology and evolutionary biology. His laboratory group associates, plant and animal biologists and focuses on behavioural and evolutionary biology of endophagous insects. E. Huguet examines molecular interactions between parasitic insects or pathogens and their hosts with a special emphasis on evolutionary mechanisms involved.