Arthropod Genomics Research impacts on agriculture

- **Insecticide resistance: Uncovering the genetic basis of resistance**
- **RNAi: Pest insect management and control**
- **RNAi: Protection of crustaceans important to aquaculture from disease**
- **Olfactory and gustatory receptors: Discovery of Insect DEET Olfactory Receptor**
- **Insect gut microbes: Sources of enzymes to break down plant materials such as cellulose and lignin**
- **Insect-microbe associations: Discovery and roles of beneficial bacteria residing in arthropods**
- **Community genomics: Discovery of plant resistance mechanisms to insect herbivores**
- **Insect control strategies: Genetic Pest Management**
- **The Argentine ant genome: Potential agricultural applications**

Genetic basis of insecticide resistance (contributed by DeWayne Shoemaker): The evolution of resistance to pesticides represents one of the greatest threats to plant, animal and public health. Unfortunately, the accepted consensus is not a question of if, but when resistance eventually will evolve. Thus, insecticide resistance research focuses on when will it evolve, what mechanisms underlie resistance, do similar mechanisms occur across multiple species, and how the evolution of resistance can be delayed or slowed down. While other novel approaches for combating pest insects exist or are continually emerging, ultimately, the control of arthropod pests in agriculture still heavily relies on the use of chemical insecticides. Recent genetic and genomics studies have provided new insights into the diverse mechanisms by which resistance has evolved in insects.

The widespread use of chemical insecticides and biological toxins for pest control provide the means for continual selection of individuals in insect populations, and is arguably the single most important factor contributing to the evolution of resistance. Efforts to reduce pesticide use is a continual challenge we face, yet the fact remains insecticide use remains necessary to maintain the health and well-being of plants, animals, and humans. Given the importance of understanding insecticide resistance, it perhaps is not surprising there is a large body of literature on this subject. New genome sequencing technologies have greatly advanced scientific understanding of the genetic underpinnings of resistance and the various mechanisms that underlie resistance. The results and patterns emerging from these numerous studies provide a fascinating yet complex picture of the mechanisms underlying resistance in insects. In general, insect adaptation to pesticides involves changes to genes that encode proteins to develop target-site insensitivity, changes in the regulation of enzymes that act to detoxifying chemical insecticides, and increased excretion or reduced absorption. Classic models are based on early discoveries where a single gene mutation conferred insecticide resistance, and are typified by the single amino acid change in the gamma-aminobutyric acid (GABA) receptor that confers resistance to organochlorine insecticides. Interestingly this mutation has occurred multiple times in the same species such that different populations of one insect species can be assumed to have the potential to independently evolve resistance. Furthermore, it has been shown that the same GABA receptor amino acid change has led to organochlorine insecticide resistance in several insect species. This suggests that similar or identical mutations that confer resistance have evolved independently within a species as well as among different insect species. As a result of more recent genomic studies, models have been developed suggesting the additive affects of several gene mutations may be required and indicate that resistance may involve more complex mechanisms.

There also are instances of multiple resistance mechanisms existing within single genomes of a given species. The best example is the aphid *Myzus persicae*, which apparently has at least one example of almost every resistance mechanism currently known. Perhaps the most interesting example of resistance comes from a recent study illustrating that insects are even capable of evolving resistance to compounds mimicking their own natural hormones. The overall messages from these various studies are that resistance mechanisms are diverse and often complex and, disturbingly, that regardless of the novelty of mode of action, resistance always seems to evolve.

The potential utility and power of genomics approaches are illustrated further by recent study that combined biochemical and genomics approaches to identify the molecular basis of resistance to the insecticide DDT in the mosquito *Anopheles funestus*, which is a major vector of malaria. Insecticide-based control represents the major control measure for malaria in Africa. Unfortunately, increasing resistance to insecticides in major malaria vectors, such as the mosquito *An. funestus*, significantly threatens the continued effectiveness of these insecticides. Indeed, insecticide resistance is perhaps the biggest threat to the continued effectiveness of malaria vector control. A recent study demonstrated that a specific single amino acid change in a protein encoded by a gene known as glutathione S-transferase (*GSTe2*) confers high levels of metabolic resistance to DDT. Further, the geographical distribution of *GSTe2* variation correlates with known DDT resistance patterns across Africa. This study provided one of the first DNA-based metabolic resistance markers in mosquitoes. This marker represents a valuable tool for tracking the evolution of resistance in natural populations and for detecting and tracking resistance at early stages, which will facilitate designing of better resistance management strategies.

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Discovery and application of RNAi for pest insect management and control (contributed by DeWayne Shoemaker): Double-stranded RNA-mediated interference (RNAi), one of the most exciting discoveries of the past decade with important applications in functional genomics, is a process in cells that stops the action of specific genes by destroying specific RNA strands, which in turn prevents translation of the gene product into a protein. The first evidence that dsRNA could achieve efficient gene silencing through RNAi came from studies on the nematode *Caenorhabditis elegans*, where degradation of specific nematode RNAs was demonstrated. While RNAi normally plays a role in defending cells against viruses by preventing viral RNA from being translated to proteins within host cells, the above study demonstrated that RNAi could be used as a simple and rapid method for silencing gene expression in a range of organisms. Thus, RNAi is used in functional genomics studies for "knocking out" a particular gene in plants or animals in order to study the gene's function. The discovery of RNAi provided a breakthrough in methodology for functional analysis of genes, and has led to the development of novel methods for treating human diseases and protecting beneficial crops and animals against insect pest damage or disease.

Injection of double-stranded RNA (dsRNA) is the most commonly used method to evoke the RNAi response in insects, but studies have demonstrated that specific suppression of a target gene in can be accomplished by direct feeding or topical application of dsRNA or indirectly by expressing dsRNA in plants that are fed upon by insects. The ability to silence specific genes has stimulated research that exploits RNAi for controlling both agriculturally and medically important insects. Transgenic plants expressing dsRNA of specific insect genes have been developed and demonstrated to be effective in conferring plant resistance against insect pests. Several commercial products using RNAi technologies already are being marketed for control of agricultural insect pests. RNAi also can be used to protect beneficial insects from diseases. As one example, RNAi technology was used to reduce Israeli acute paralysis virus, which is a pathogen of bees, in honey bees in the field.

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Protection of crustaceans important to aquaculture from disease (contributed by DeWayne Shoemaker): Aquatic animal diseases are one of the most significant constraints to the development and management of aquaculture. Although Penaeid shrimp constitute one of the most important groups of species for aquaculture, the spread of viral infections results in huge economic losses in the shrimp farming industry and threatens the viability and long-term sustainability in some areas. Several studies have demonstrated RNAi is a remarkable way to shut down the expression of viral genes and represents a promising approach to the development of antiviral therapies. Also, genomic studies already are providing information regarding diverse biological processes of relevance to shrimp aquaculture, such as immune responses and reproductive physiology. Viral gene-specific knockdown using RNAi represents an attractive tool to inhibit viral replication and protect shrimp from viral infections. RNAi allows gene silencing in a highly sequence-specific manner with little or no risk of undesired off-target effects. Gene silencing by feeding has already been proven as a feasible approach to block viral pathogenesis in living invertebrates, opening the door to the development of RNAi-based aquaculture treatments applicable at a commercial scale.

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Insect olfaction and the discovery of the insect DEET Olfactory Receptors (contributed by DeWayne Shoemaker): Insects rely on olfactory cues to direct diverse behaviors including mating, feeding, egg-laying and host selection to name a few. Largely due to the key role of olfaction in the success of insects that are plant and animal pests and disease vectors (e.g., mosquitoes), the olfactory systems of insects have been studied intensively in efforts to develop or design olfactory-based control technologies. Detailed genomics studies have been crucial for these efforts. A recent genomics study identified the olfactory receptor for the repellent DEET and subsequently used this information to identify safer and more cost effective compounds that mimic DEET (i.e., strongly repellent on mosquitoes) that potentially could be used to combat transmission of vector-borne diseases worldwide.

The olfactory systems of insects characterized by two large gene families, the odorant binding proteins (OBPs) and odorant receptors (ORs). Both gene families have expanded and contracted repeatedly across diverse insect groups. For example, the ORs have undergone a huge expansion in the honey bee genome relative to the genomes of *Drosophila melanogaster* and *Anopheles gambiae*. One hypothesis is that bee-specific expansion of the OR repertoire underlies their remarkable olfactory abilities, including perception of kin recognition signals and diverse floral odors. Other examples of expansion of ORs exist. Generally, such expansions involve emergence of entirely new clades of ORs that are confined to a single insect group. As an example, the OR repertoire of bees, ants, flies, bugs or beetles are all unique and completely non-overlapping with each other.

Progress in studying olfaction in model insect systems has rapidly advanced the study of olfaction in pest insects and insect disease vectors. Molecules and processes involved in the olfactory pathway represent ideal targets for development of more effective products for pest and vector control. For example, blood-feeding insects such as mosquitoes are efficient vectors of human infectious diseases because they are strongly attracted by body heat, carbon dioxide and odors produced by their vertebrate hosts. Numerous mosquito ORs have been identified that are activated by various human volatiles or that lead to avoidance behavior (i.e., repellents). Compounds that activate ORs for attractive behaviors are being used as lures to trap mosquitoes whereas those leading to avoidance may be effective as mosquito repellents.

Progress identifying new mosquito repellents has been facilitated by a recent genomics study that identified the olfactory receptor for DEET. Mosquito repellents containing DEET are highly effective. Unfortunately, DEET is unaffordable and inconvenient for use in Africa and other parts of the world where hundreds of millions of people suffer from vector-borne diseases. After identifying the olfactory receptor for DEET (a major breakthrough in itself), researchers used this information to screen compounds that are found naturally in fruits, plants and animals against the DEET receptor. Several safe compounds that mimic DEET (i.e., strongly repellent on mosquitoes) now have been identified. These repellent compounds represent new, safer, and more affordable alternatives to DEET. Additional detailed molecular and functional genomics studies of insect olfaction across a diverse set of insect species undoubtedly will assist further development of new olfactory-based control technologies.

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Identification of insect gut microbes as sources of enzymes to break down materials such as cellulose and lignin (contributed by DeWayne Shoemaker): Biofuels represent a practical and competitive large-scale solution to widespread petroleum use. However, cost-effective ways to produce fuel from plant biomass are lacking. One component of plant biomass that presents a significant obstacle to biofuel production is lignin. The plant-digesting abilities of insect-gut microbes show promise as natural catalysts to turn plant waste into fuel. Such catalysts may help cutting biofuel production costs and greenhouse gas emission. Recent findings suggest that termites and grasshoppers may be good targets for biocatalyst discovery due to the high activities of cellulytic enzymes in their guts.

The symbiotic gut microbes of plant-eating insects are vital for their ability to utilize and specialize on plants with very different nutrient qualities. For example, termites have specialized digestive systems that efficiently decompose lignocelluloses by degrading cellulose, hemicellulose, and lignin of ingested plant material. Hence, termites represent a potential source for catalyst enzymes for efficient conversion of lignocelluloses to biofuels. Recent studies employing genomics and proteomics approaches identified numerous enzymes important in lignocellulose digestion, including the discovery of two new detoxification enzyme families. These studies provided new insights into novel lignin-targeted enzymatic approaches to enhance biofuel and biomaterial production. Another recent study compared the gut bacteria from three different insect species to examine whether there was a relationship between the diversity and metabolic capability of gut bacteria and host diet. The goal of this study was to use such a relationship for the discovery of biocatalysts for biofuel applications. Metabolic capabilities of the insect gut microbes were correlated with insect adaptation to different food types and life histories at the levels of species, metabolic pathway, and individual genes. Moreover, grasshopper cellulase and xylanase enzymes generally exhibited higher activities than those of cutworms, demonstrating differences in capabilities even at the protein level.

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Discovery and roles of beneficial bacteria residing in arthropods (contributed by DeWayne Shoemaker): Many insects establish intimate and often beneficial symbiotic relationships with bacteria. While some bacteria reside inside the gut or other tissues of insects, other bacteria have established more intimate relationships and actually reside within the cells of their insect hosts (i.e., endosymbionts). Genomics data has transformed our understanding of insect-bacteria relationships and revealed numerous fascinating findings regarding the influences of bacteria on their insect hosts. The varied roles microbes play within host insects include alteration of host insect behavior and reproduction, change of host body color, protection against the natural defenses of plants, protection against attack by other insects and fungi, and resistance to both viruses and protozoa, which in the case of mosquitoes includes Dengue Chikungunya, and West Nile viruses and malarial parasites.

Virtually all insects are attacked by one or more pathogens, parasites or predators. Remarkably, a series of recent studies has revealed that the resistance of many insects to these natural enemies often is modulated by intracellular bacteria. The first example of such resistance to attack was described in aphids. Several wasps that prey on aphids actually inject their eggs inside the aphids. These wasp eggs then hatch within the aphid host and consume their hosts to complete development. Interestingly, variation in susceptibility of aphids to these wasps is linked to the presence or absence of two different bacteria residing within aphids. Although the presence of these bacteria does not prevent attacks from wasps, they do inhibit development of wasp eggs within the aphids.

Detailed molecular studies also have revealed that as many as 20% of all insects harbor intracellular bacteria belonging to the single genus *Wolbachia*. The effects of these bacteria on insects are diverse. In some cases, these bacteria have devised ways to preferentially kill only male offspring. In other insects, these bacteria are necessary for successful egg development. In other cases, several studies found that these bacteria confer resistance toward various viruses that attack insects. Because many plant and animal diseases are caused by insect-transmitted viruses, the discovery of bacteria-mediated protection against viruses has important implications for both plant and animal health. Genomic studies now are underway to uncover the mechanisms of exactly how these bacteria confer resistance to viruses as well as to discover whether additional bacteria also confer resistance toward pathogens.

Bacteria often are beneficial to their hosts but negatively affect associated plants and animals. For example, food plant use of many insects often is enhanced by the presence of intracellular bacteria. Indeed, a common role of many such bacteria is to supply essential nutrients to their hosts, which in turn allows these insects to feed on rather nutrient poor resources such as plant sap. Bacteria also have been found that allow insects to modify and overcome natural plant defenses. One striking example comes from a study that demonstrated bacteria associated with plant-feeding beetles actually prevent the host plant from recognizing it is being attacked by the beetle and, thus, does not turn on its natural defenses against insect predation.

Another fascinating yet troubling finding is that some bacteria can actually confer insecticide resistance to their insect hosts. Chemical insecticides are used globally for controlling agricultural, medical and veterinary pest insects. A major ongoing problem of the widespread use of insecticides is the evolution of resistance. Numerous mechanisms of resistance have been described that are attributable to changes in pest genomes. A recent finding demonstrates a previously unknown mechanism of resistance that is attributed to an insecticide-degrading bacteria residing within insects. The bacteria occur naturally in soils but also reside in the guts of some insects. Once the bacteria are acquired by insects, they become resistant to insecticides almost immediately. The problem is further exacerbated by the fact that these bacteria often increase the fitness of their insect hosts, which can facilitate the spread of the insecticide-resistant bacteria within pest insect populations.

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Discovery of plant resistance mechanisms to insect herbivores (contributed by DeWayne Shoemaker): Community genetics (“genes to ecosystems”) seeks to understand how within-population genetic variation of plants influences species abundance and composition of associated communities. There is a tremendous amount of variation in plant defense mechanisms against herbivores in nature, yet only a small degree of this variation is captured within crop plants. Thus, detailed studies of the varied mechanisms of plant resistance in natural populations holds much promise in understanding how plants deal with herbivores, information which in turn may be used to improve host-plant resistance in important crops. The combination of high-throughput phenotyping of plant toxicity, insect herbivore performance, and genomic study of both plant and herbivore response will allow scientists to uncover the genetic underpinnings of plant resistance to herbivores and corresponding herbivore adaptations, ultimately resulting in the development of crops with increasing effective host-plant resistance.

A recent promising avenue of research in this discipline includes application of association mapping to explore the genetic underpinnings of complex traits in plants, especially traits conferring resistance of plants to insect herbivores. Recent studies indicate that there often is a trade-off between resistance against generalist and specialist insects. A drawback of early studies using a narrow targeted approach is that they often miss important components of insect resistance. However, genome-wide association studies provide a more comprehensive approach and allow exploration of whole arrays of plant defense mechanisms.

Although several biological systems have been explored, including those in agricultural landscapes, it is easy to argue that none have contributed more to advancing the field of community genetics than have tree species in the genus *Populus* and their associated arthropod communities. Recent studies demonstrate that heritable traits in *Populus* have predictable effects on community structure and ecosystem processes. Further, a recent genome-wide association study tested for genome regions that were associated with insect resistance in *Populus*, which revealed three important findings: 1) most of the genomic regions associated with defense were localized to genes involved in a known defense pathway (the shikimate-phenylpropanoid pathway), consistent with the role of phenolic glycosides as defensive compounds. 2) additional genomic regions associated with insect feeding corresponded to two genomic hotspots for leaf traits, indicating that leaf morphology also may influence insect preference; and 3) particular categories of *Populus* genes were over-represented in plants with different types of insect feeding damage, which provided direction for future functional genomic studies. These results provide insight into the genetic components involved in insect community structure in a fast-growing forest tree. Ongoing studies in *Populus* are being conducted in an effort to identify the genomic specific components underlying phenotypic variation in *Populus tremuloides* that determine the abundance and composition of, and damage by, associated insect communities. This “genetical genomics” approach combine phenotypics, genotypic and transcriptomic data in an effort explain mechanisms of tree-insect interactions at a level heretofore inaccessible.

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Genetic pest management (contributed by Brian Rector): Genetic pest management (GPM) represents a new frontier in the control of intractable agricultural, medical, veterinary, or urban insect pest species. The basic premise of GPM is to strategically manipulate the genomes of pest insect populations in order to either cause these populations to crash or to mitigate their pest potential (e.g. by preventing disease vectors from harboring pathogens). State of the art insect genomic resources are vital to the advancement and fruition of GPM studies. Other pests, such as invasive weeds or vertebrate species can also be targeted through GPM.

The primary component of a typical GPM strategy is the deleterious genetic element that is transgenically introduced into laboratory colonies of the pest species to produce the desired effect following exposure to targeted populations. A GPM strategy may be inundative, not unlike sterile insect technique, whereby large number of genetically manipulated individuals of the pest species are released to effect changes in the target population within the first generation(s) after initial contact by the released insects. Under such a strategy, specific pest populations may be targeted by multiple concurrent or consecutive GPM releases with a temporary effect expected. Examples of this approach have included insects modified to bear progeny that produce toxic amounts of an otherwise benign transcriptional activator protein, female progeny that cannot fly, and males that give rise to inviable offspring.

Other GPM strategies seek to incorporate a genetic drive mechanism in tandem with the deleterious transgene in order to produce a self-sustaining and self-spreading effect similar to a classical biological control release. In order to be successful, a genetic drive mechanism must produce super-Mendelian inheritance and predictable expression of the deleterious gene construct without interference from the target species genome. A number of drive mechanisms have been proposed, including insertion of deleterious genes within active transposable elements male-biased populations through distorted segregation of the Y-chromosome or a modified version of the transcriptional activator over-expression model mentioned above, use of homing endonuclease genes to convert heterozygous transgene inserts to the homozygous state prior to meiosis, and the ‘MEDEA’ model of a maternal toxin and zygotic antidote that is lethal to progeny lacking the construct.

In addition to direct genetic manipulation strategies, research is active to better understand the use of *Wolbachia* endosymbionts to either directly cause pest insect population crashes or drive refractory genotypes in disease vectoring insects. Advances in insect genomic knowledge will allow more predictable utilization of this well-known symbiont, just as the development of transcriptomic and metabolomic frameworks for key pest insect species will facilitate the implementation of the aforementioned GPM strategies.

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The Argentine ant genome: potential agricultural applications (Contributed by Monica Poelchau): The Argentine ant is an invasive pest species in the USA. Its presence can result in significant damage to the environment and local ecosystems due to large colony sizes in its invasive range in the USA, and its displacement of other ant species. By providing a near-comprehensive catalog of the Argentine ant gene complement, the Argentine ant genome sequence can help agricultural researchers rapidly identify trends in gene families of relevance to pest control for this species. For example, cytochrome P450 genes are often involved in detoxification and insecticide resistance. The Argentine ant genome has substantially more cytochrome P450 genes (~111) than had been previously recognized in other sequenced Hymenoptera (*Apis mellifera* and *Nasonia vitripennis*). It was speculated that this expansion may relate to the varied diet that the generalist Argentine ant encounters, which includes more toxins. However, this larger complement of cytochrome P450's may have implications in the development of insecticides for this species. Also, increased knowledge of the cytochrome P450 gene sequences in this and other species may help develop more targeted pesticides, resulting in less incidental environmental damage.

Additionally, a genomic understanding of the Argentine ant's use of chemical signals to recognize other ants may have insect control applications. The Argentine ant genome sequence revealed twice as many odorant receptor genes than the honey bee, *Apis mellifera*. These gene sequences may hold the key to chemical recognition between ants, which could lead to avenues to disrupt these signals, provoking the ants to kill each other – obviating the need for pesticides.

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