

IPM-omics: from genomics to extension for integrated pest management of cowpea

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Abstract

Insect pests often develop resistance to insecticides, and such resistance represents a serious management problem. Devising methods that concurrently delay resistance and minimize injury by insects to field crops and stored grain has long been a goal of Integrated Pest Management (IPM). A centerpiece of IPM has been the combined use of biological control agents and prudent application of chemical insecticides. Unfortunately, successful application of IPM has remained a challenge. This chapter describes the use of emerging genomic technologies that may lead to a “systems” perspective of IPM for the control of pests of cowpea and other crops. This emerging field, which we refer to as “IPM-omics”, builds upon recent advances in genome sequencing technologies and detection of large-scale gene polymorphisms, which are becoming economically feasible for pest insect systems. IPM-omics will also need to involve the use of information and communications technologies both to collect critical information on pest populations and to deploy practical IPM solutions. The information obtained on the temporal fluctuations, spatial distribution, and ecological diversification within target, non-target, and natural enemy populations can be overlaid on a geographic information systems (GIS) map to predict pest outbreaks and to decide how to apply control measures. The “systems” perspective of organism communities provided through IPM-omics may also facilitate the effective evaluation, modification, and optimization of IPM strategies. However, any resultant IPM program for crop pests will also require that extension agents, government agencies, and non-governmental organizations (NGOs) have the ability to easily access and deploy the IPM research findings through information and communications technologies. Thus, we also outline the need for an online system that facilitates the sharing and peer review of practical IPM outputs. Many of these tools are currently being developed to help farmers manage insect pests of cowpea in West Africa.

Introduction

The Green Revolution, which introduced modern crop varieties and production techniques (Khush 1995; Evenson and Gollin 2003), greatly affected insect pest control. It caused a shift away from the use of crop rotation, field sanitation, flooding, and manual destruction of damaging insects and/or insect-infested plants (Smith et al. 1976) toward the use of high

intensity monoculture cropping systems that depended on chemical insecticides to suppress pest insect populations. This shift began in industrialized nations in the 1940s and 1960s, and the consequent reliance on synthetic insecticides led to insecticide resistance, the suppression of beneficial insect populations, and the emergence of minor pests as major pests (Norris et al. 2003). Pesticides can provide excellent crop protection, but in addition to selecting for insecticide resistance, they have had numerous negative impacts on human health and the environment (Singh 2000; Wilson and Tisdell 2001; Georghiou 1986). In 1962, Rachel Carson's book "Silent Spring" raised concerns and public awareness of the environmental and ecological impact of pesticide use, and toward the end of the 1970s, this concern and awareness motivated efforts to develop lower impact crop protection methods (Hassan and Bakshi 2005).

The term "Integrated Pest Management" (IPM) was first used by Smith and Van dan Bosch in 1967 to describe concurrent application of multiple control measures to reduce damage caused by insects to crop plants. The development of IPM led to dramatic changes in the technologies available for pest management. Modern IPM approaches aim to provide economically viable and sustainable control of insect damage by relying on biological, chemical, physical, host-plant resistant, and cultural control tools. Conceptually, IPM strategies recognize that many environmental factors interact and work in concert to affect the abundance of insect pests. IPM strategies also strive to exploit the knowledge of the insect pest's biology, location of alternate plant hosts, and natural enemies to achieve more informed pest management decisions. Fundamentally, the application of an IPM strategy involves an holistic or "systems" approach to pest management, where interactions between pests and the community of natural enemies are evaluated in a tiered approach once the scale of the system in question is set (for more detail see Wise and Whalon 2009). The systems approach to IPM requires an in-depth knowledge of how management practices affect the insect's biology and other trophic interactions. It also involves the monitoring of pest populations to identify appropriate control measures as well as aids in making decisions as to how, when, and where to apply them.

Analogous to a systems approach for IPM applications, the genomics "revolution" has led to efforts to understand an organism or community on a genome-wide scale. Recent advances in genomics are now making it possible to better understand pest populations, and are likely to provide new approaches for studying and managing insects. Despite the decreasing costs of DNA sequencing and the development of affordable high-throughput platforms, with which entire genomes can be rapidly sequenced, IPM has not exploited the use of these genomic tools.

Researchers must begin to define how such genomic tools can be used in an inclusive manner with IPM to improve pest management decisions. In addition to the development of genomics, a second parallel "revolution" that has occurred in the past two decades is the ability to deploy pest management concepts through the electronic media. Many of the control strategies that have been developed remain difficult to deploy to extension agents and farmers in Africa and other developing regions because of the remoteness of the regions and the low literacy rates among the farming communities. IPM strategies will have a large-scale impact only if they can be coupled with effective educational deployment tools that can be rapidly updated as new and practical control approaches emerge. We use the term IPM-omics to describe the use of genomic (and other "omics") tools to better characterize

pest populations and to provide a greater depth of knowledge for the development and deployment of IPM strategies. The remainder of this chapter describes how IPM-omics can be used in the management of cowpea insect pests and how IPM-omics has the potential to further cowpea IPM in West Africa.

Advent of the genomics era

Despite the apparent prominence of molecular biology methods within modern laboratories, it is a relatively young discipline. Molecular biology techniques have made gene cloning, sequencing, organism transformation, and genotyping of individuals almost commonplace. Many of these techniques became accessible with the development of polymerase chain reaction (PCR), which essentially is *in vitro* synthesis of millions of copies of defined genome regions. The PCR procedure has been credited to Kary Mullis, and the technique has now been adapted for many different applications such that PCR is now a fundamental and indispensable tool of molecular biology (Bartlett and Stirling 2003).

The development of genomic practices depended on the ability to perform high-throughput DNA sequencing at dramatically reduced costs along with an increased capacity to analyze large data sets. The initial sequencing of DNA by chemical modification and subsequent cleavage of specific nucleotides (i.e., Maxam-Gilbert sequencing; Maxam and Gilbert 1977), and by incorporation of di-deoxynucleotides that resulted in truncation of primer extension reactions at specific bases (i.e., Sanger sequencing; Sanger and Coulson 1975; Sanger et al. 1977) was time consuming. It also required expertise to separate DNA fragments (via denaturing polyacrylamide gel electrophoresis) and to interpret the results. Sequencing throughput was increased by the use of capillary gel electrophoresis platforms that automated the separation of up to 384 individual reaction products at a time and by the use of computers to analyze the data in the form of electropherograms. Despite improving the scale at which DNA fragments could be sequenced, these technologies or “platforms” were still not time- or cost-effective for the sequencing of entire genomes. For example, the human genome project, which was launched in 1990, required more than 10 years to complete at a cost of about three billion USD (Venter et al. 2001). These earlier sequencing platforms were also used to acquire whole genome sequences (WGS) for insects, including the pea aphid, *Acyrtosiphon pisum* Harris (Hemiptera: Aphididae) (The International Aphid Genomics Consortium 2010); the mosquitoes, *Anopheles gambiae* Giles (Diptera: Culicidae) (Holt et al. 2002) and *Aedes aegypti* Linnaeus (Diptera: Culicidae) (Nene et al. 2004); the honey bee, *Apis mellifera* Linnaeus (Hymenoptera: Apidae) (Weinstock et al. 2006); the silkworm, *Bombyx mori* Linnaeus (Lepidoptera: Bombycidae) (International Silkworm Genome Consortium 2008); the fruit flies, *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) (Adams et al. 2000) and *D. pseudoobscura* Fabricius (Diptera: Drosophilidae) (Richards et al. 2005); the wasp, *Nasonia vitripennis* Ashmead (Hymenoptera: Pteromalidae) (Werren et al. 2010); the red flour beetle, *Tribolium castaneum* Herbst (Coleoptera: Tenebrionidae) (Tribolium Genome Sequencing Consortium 2008); and the human body louse, *Pediculus humanus humanus* Linnaeus (Phthiraptera: Pediculidae) (Pittendrigh et al. 2006; Kirkness et al. 2010; Pittendrigh et al. 2011).

More recently, sequence-by-synthesis technologies that use pyrosequencing reactions to obtain DNA sequence data have been developed (Ronaghi et al. 1998; Morozova and Marra 2008; Simon et al. 2009). Adaptations to high-throughput platforms have the capacity

to generate millions of *de novo* DNA base sequences from a single run (Margulies et al. 2005). These next generation sequencing (NGS) platforms have greatly facilitated the collection of DNA sequence data and have been especially useful for genomic research on non-model organisms (McCombie et al. 1992; Ellegren 2009). NGS has contributed to the emergence of insect genomics through the accumulation of WGS data for the wasp species, *Nasonia giraulti* and *N. longicornis* (Werren et al. 2010), and (in ongoing projects) for *Ixodes scapularis* Say (Ixodida: Ixodiade), *Rhodnius prolixus* [Stål](#) (Hemiptera: Reduviidae), *Glossina morsitans* Westwood (Diptera: Glossinidae), *Phlebotomus papatasi* Scopoli (Diptera: Psychodidae), and *Lutzomyia longipalpis* Lutz and Neiva (Diptera: Psychodidae) (Megy et al. 2009). Additionally, NGS has proven useful for the rapid resequencing of wild strains of *B. mori* (Xia et al. 2009) and multiple *Drosophila* species (Hahn et al. 2007), as well as expressed sequence tags (ESTs) (Vera et al. 2008).

EST libraries are collections of short Sanger sequencing- or NGS-derived read data obtained from complementary DNA (cDNA). These sequences are representative of genes that are expressed in a particular tissue, at a specific developmental stage, by a particular phenotype, or under particular treatment conditions under which the libraries were constructed (Adams et al. 1991; Gaines et al. 2002; Nagaraj et al. 2006), and are derived from genomic regions that are actively transcribed. ESTs obviously provide information about gene encoding regions and are considered as low-cost alternatives to a WGS project (Rudd 2003), even though ESTs are subject to sampling bias. More specifically, cDNAs are sampled from a larger pool of potential templates during the cloning and/or DNA sequencing phases, where errors of omission can occur because of stoichiometric differences between libraries (Liu and Graber 2006). Regardless, ESTs are recognized as an effective research approach for discovering genes (Bonaldo et al. 1996; Audic and Claverie 1997), obtaining gene expression information among tissues (Dimopoulos et al. 2000, Porcel et al. 2000), discovering alternate splicing patterns (Gupta et al. 2004), and predicting novel mutations (Coates et al. 2008). Moreover, the quantitative comparison of ESTs within and between libraries is increasingly used for gene expression analysis (RNAseq; Simon et al. 2009; Fu et al. 2009). For further information on these developing aspects of genomics research, we direct the reader to the following review articles: Ungerer et al. 2008; Rokas and Abbot 2009; and Wheat et al. 2010.

The advent of NGS has also been paralleled by the development of molecular marker screening technologies that offer precision and reliability for differentiating allelic variations at single nucleotide positions. Precision and accuracy of allele calling also has been paired with high-throughput capacity that allows for hundreds to thousands of genotyping calls to be made within 24 h (Lyamichev et al. 1999; Tang et al. 1999; Kwok 2001; Tsuchihashi and Dracopoli 2002). These molecular genotyping assays and associated platforms used for detection rely on initial prediction of segregating mutations within individuals or populations of individuals.

Core concepts underlying IPM-omics

IPM-omics, as we envision it, involves five major steps: (1) discover polymorphisms within insect populations (Figure 1), (2) use the polymorphisms to answer critical questions about these pest populations through detailed analysis of sets of individual insects collected from the field (Figure 2), (3) overlay this information with other available data sets (e.g., GIS) (Figures 3 and 4), (4) use the knowledge and outcomes to make better pest management

decisions (Figure 5), and (5) use information and communication technologies to efficiently extend these materials to the target communities (i.e., those involved in the control of pests associated with the target crop) (Bello-Bravo et al.; this volume). These steps are now possible because of the following current conditions. The advent of NGS allows one to sequence genes from a large pool of insects from a given region in order to discover polymorphisms within these populations. The polymorphisms can then be used in high-throughput polymorphism detection systems to investigate details of pest populations. This information on its own or in combination with GIS systems should give us the ability to gain insights into pest populations that have not been previously possible, allowing for better pest management decisions. Finally, the advent of the Internet and cell phones can be used to communicate information on pest populations between farmers and researchers, and these same communication technologies can be used to provide farmers with practical pest management recommendations.

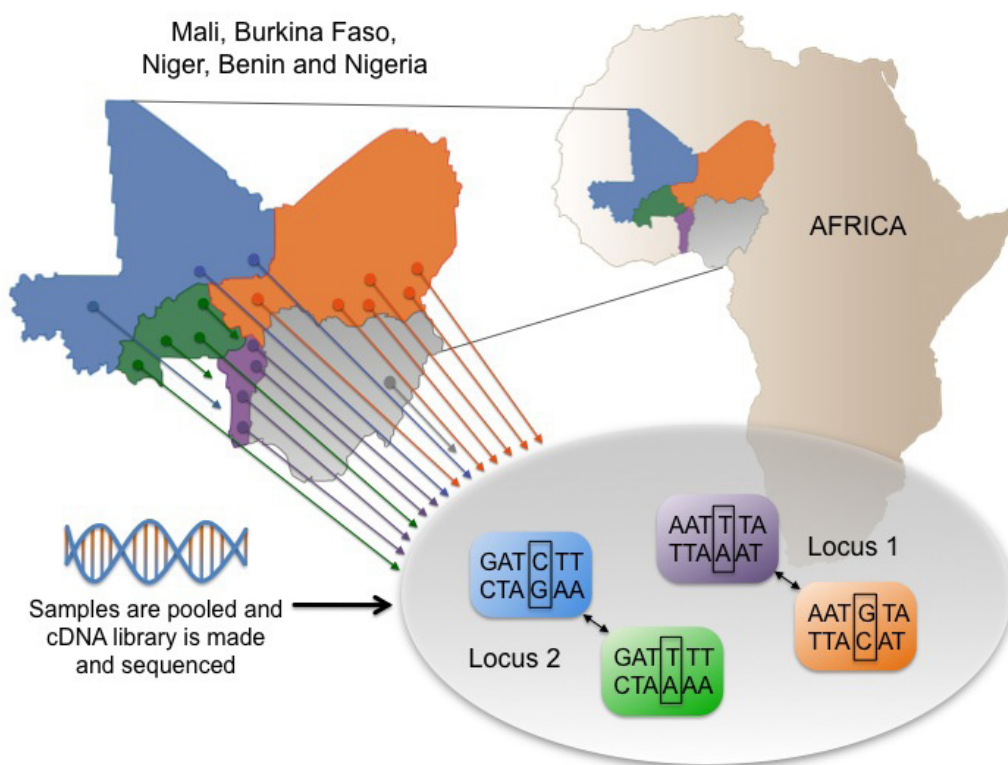


Figure 1. Hypothetical representation of the pooling of insect samples from different cowpea growing areas of West Africa for the construction of cDNA library (the arrows do not represent exact current sampling locations for any given insect species). The insects are taken from a diverse set of geographical locations, and the mRNA is pooled to create a cDNA library. Alignment of subsequent DNA sequence forms a set of expressed sequence tags (ESTs) potentially derived from the same locus, and thus representative of alleles at a locus. The presence of polymorphisms among alleles in the form of single nucleotide polymorphisms (SNPs) can readily be adapted for genotyping individuals with high-throughput systems.

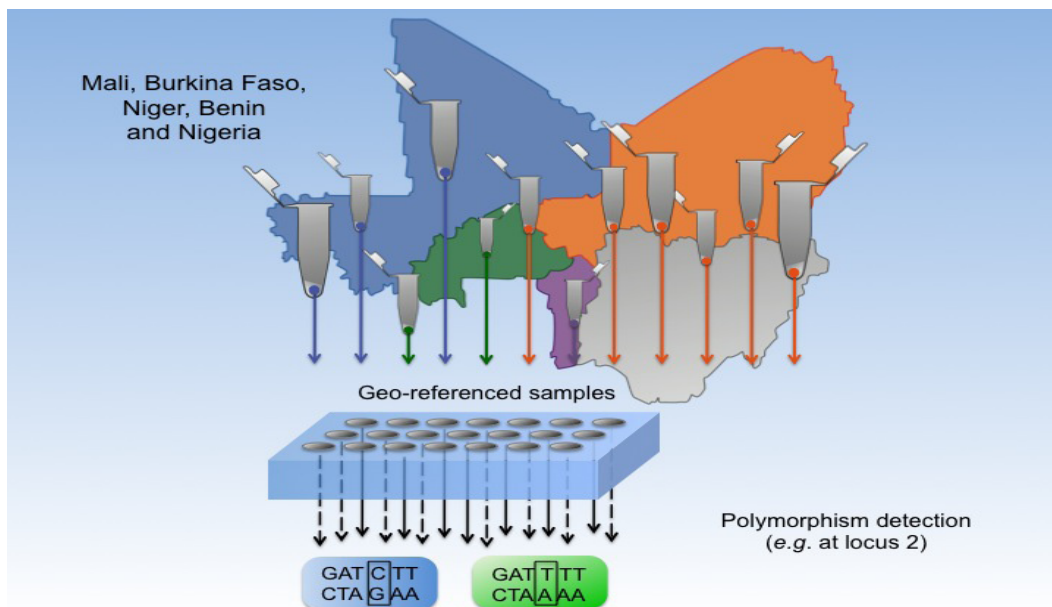


Figure 2. Representation of a hypothetical population genomics study within the scope of IPM-omics in which individual insects from different locations (shown by the tubes) are collected from West Africa. Polymorphisms are detected among individual insect samples with high-throughput system(s) (shown as a blue plate), and are used to differentiate genotypes that are correlated back to geographic location, host plant, ecotype, or other ecological characteristics described at the initial collection. Polymorphisms detected between individual insects are indicated as the C/G to T/A differences at the bottom of the figure.

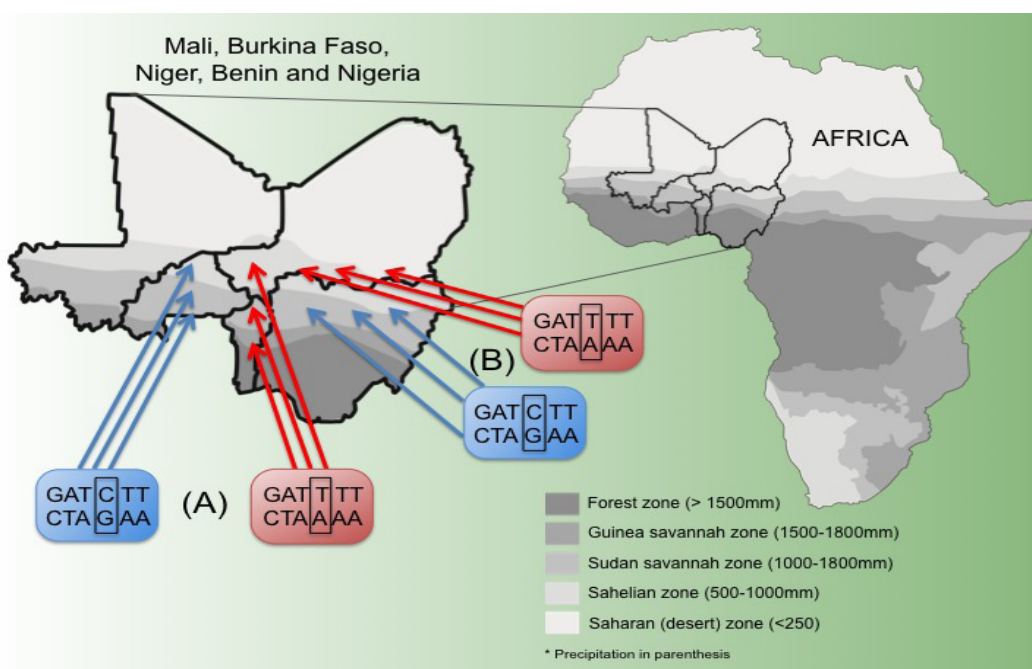


Figure 3. Hypothetical scenario of polymorphisms associated with the insect species in the different agroecological zones in West Africa. Scenario (A) would indicate a longitudinal movement pattern of an insect population, and scenario (B) would be consistent with the hypothesis that the insect populations are endemic in both areas with no major longitudinal movement patterns. These represent hypothetical situations in which polymorphisms could be used to test hypotheses associated with large-scale insect movement patterns.

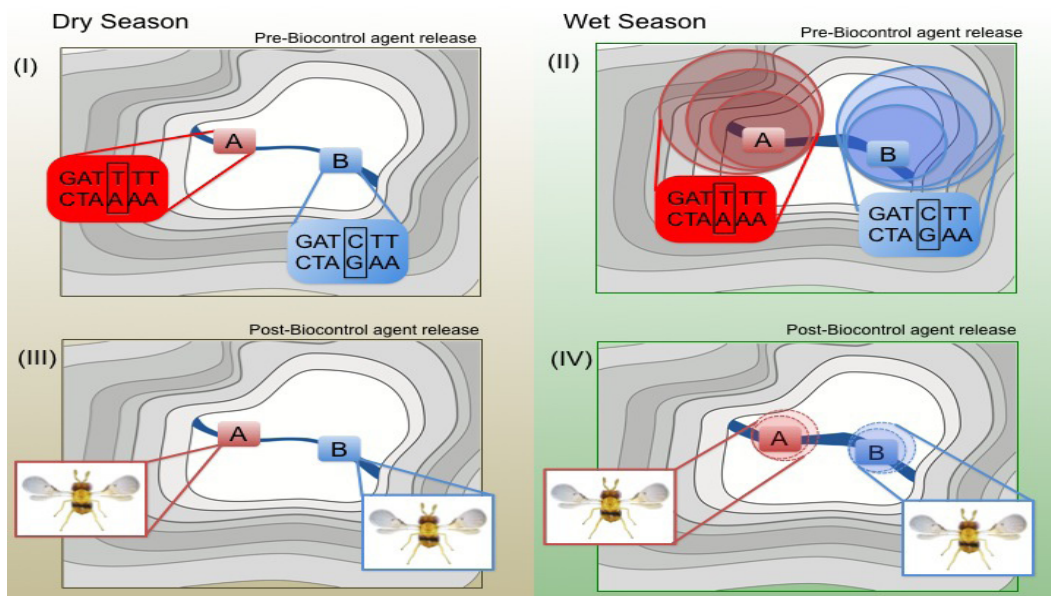


Figure 4. Hypothetical use of molecular markers (short DNA sequences given in the blue and red boxes) for the study of local population structure in a pest population in the dry (I) and wet (II) seasons. When two defined source pest populations remain in the dry season (A and B in I), biocontrol agents are released in the areas where the pest populations are endemic (III) to suppress the pest population in the wet season (IV). During the wet season (II), the pest population without biocontrol agents expands as indicated by the sets of red and blue rings around the A and B source populations. In (IV), the biocontrol agents have reduced the pest population levels as indicated by the smaller and more lightly colored red and blue rings around the A and B source populations.

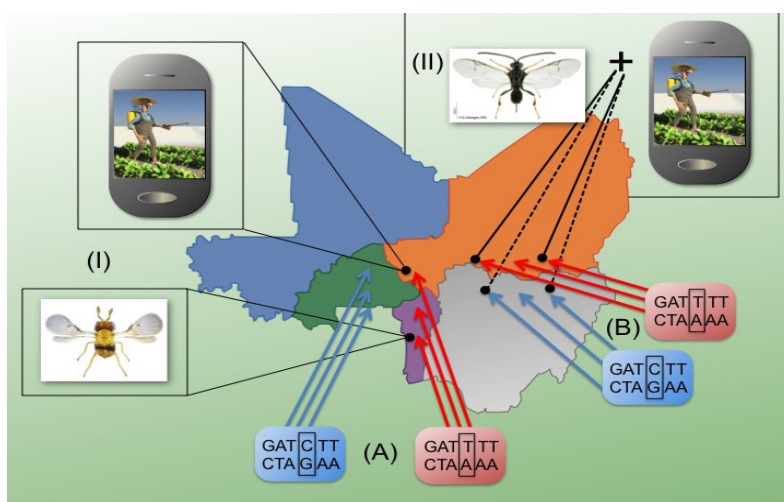


Figure 5. Hypothetical use of information gained from genomic studies of insect populations and how such information could be used in decisions associated with deployment of IPM strategies. Two hypothetical scenarios are illustrated: scenario A with biocontrol approach I and scenario B with biocontrol approach II. In scenario A, the insects move from the south to the north in the rainy season, and biocontrol agents are released in the south (in endemic regions) before migration for long-term suppression of the pest population (biocontrol approach I); temporary control measures (e.g., neem sprays) may be required in non-endemic regions if pest levels become too high. *Apanteles taragamae* is shown as an example of a biocontrol agent. In scenario B, the pest is endemic in both regions, with no significant longitudinal movement patterns. A possible pest control strategy in scenario B could involve the release of parasitoids (in both the south and north regions) (biocontrol approach II) as well as implementation of an education program concerning the temporary control (e.g., with neem sprays) if pest levels become damaging. *Trichogramma eldanae* is shown as an example of a parasitoid. The farmer in the figure is applying a plant-based extract spray and thus does not require personal protection equipment; if a synthetic pesticide were used in this extension material, the farmer would have to be shown with personal protection equipment.

Application of genomic tools to the current pest situation in cowpea

Cowpea, *Vigna unguiculata* (L.) Walp. (Leguminosae: Papilionaceae), is an important grain legume crop in the semi-arid and dry savanna areas of the tropics (Singh and van Emden 1979). Insect pests feed on and damage cowpea at virtually every crop developmental stage and also feed on and damage the stored grain. The pest species that seriously damage cowpea are numerous (Table) and in addition to causing direct feeding damage to vegetative and reproductive tissues, *Aphis craccivora* Koch (Hemiptera: Aphididae) also vectors plant viruses that further decrease crop yields (Singh and van Emden 1979). Although all these insects cause serious damage to cowpea, the pod borer, *Maruca vitrata*, Fabricius (Lepidoptera: Crambidae) is probably the most destructive (Jackai and Singh 1988).

The control of cowpea pests has relied largely on chemical insecticides but the efficacy of this method is variable due to the evolution of resistance to multiple classes of insecticides (Ekesi 1999). In addition, the insecticides are prohibitively expensive or otherwise unavailable to low-income farmers in West Africa (Giga and Biscoe 1989; Alghali 1991; Bottenberg 1995; Alebeek 1996). The effective control of insect pests of cowpea has therefore relied upon conventional methods (see Introduction), which have been enhanced through the introduction of IPM strategies (Jackai and Adalla 1997). IPM-omics is currently being used to identify possible genetic variations in populations of pest species and their related natural enemies, and also to study their geographic distributions and movement patterns. These data are critical for targeting and timing appropriate control measures in the field as well for determining the coincidence of endogenous natural enemy populations.

Although the genomes of a number of insect pests have been sequenced, there is little or no DNA sequence information for most of the cowpea pests. This scenario, however, is quickly changing. Recently, Margam et al. (2011a) used mitochondrial DNA sequence data and molecular genetic markers to determine that *M. vitrata* from West Africa and Puerto Rico represent two distinct groups and even proposed that the samples are possibly a complex of sibling species. Moreover, these data indicated that *M. vitrata* collected from West Africa (Burkina Faso, Niger, and Nigeria), Taiwan, and Australia likely constitute a single species. Previous field studies in West Africa also indicated that *M. vitrata* is more abundant throughout the year in the southern region (Sudanian zone) of the cowpea producing areas, where the rainfall is relatively high, than in the drier northern regions (the Sahelian zone) (Ba et al. 2009; Margam et al. 2010). Furthermore, light trap studies conducted in Burkina Faso (Ba et al. 2009) strongly support the hypothesis that *M. vitrata* adults migrate to the northern drier regions from the south during the rainy season.

To study these movement patterns in greater detail, researchers are developing additional molecular genetic markers from genomic sequence data. EST sequence data were collected from the larval *M. vitrata* midgut and salivary gland tissues as well as from whole adult tissues (Margam et al. 2011b; National Center for Biotechnology Information, NCBI, dbEST accessions HS097571-HS099476). The assembly of these EST data into 3729 contiguous or overlapping contig sequences has also been used to predict the location of ~ 1078 putative single nucleotide polymorphisms (SNPs). Preliminary genotyping data have been collected from Burkina Faso, Niger, and Nigeria at 70 SNP loci, and resulting analyses indicated genetic differences among populations. More specifically, individuals from three sample locations in Burkina Faso (in an East–West pattern of collection) were

Table. Summary of the major pests of cowpea in West Africa, important areas of research for IPM-omics strategies, genomics tools needed in the near future, and genomics tools currently available or currently being developed.

Pest species	Important research areas of immediate concern	Current or potential control strategies	Genomic tools needed (short-term)	Genomic tools available or being developed
<i>Maruca vitrata</i> Fabricius (Lepidoptera: Crambidae)	Local movement patterns <i>Implications</i> 1) Insect resistance management (IRM) 2) Deployment of biological control agents	1) Bt cowpea 2) Biological control 3) Chemical pesticides 4) Biopesticides 5) Viral sprays	1) Greater diversity of ESTs to perform more in depth local studies	1) EST libraries and polymorphisms 2) Studies already performed to show two species in the old and new world 3) microsatellite for characterization of pest populations 4) Mitochondrial genome characterized
<i>Callosobruchus maculatus</i> Fabricius (Coleoptera: Bruchidae)	Regional movement patterns <i>Implications</i> 1) IRM plans for Bt cowpea 2) Deployment of biological control agents 1) Resistance to low oxygen conditions and potential molecular mechanisms	1) Triple bagging 2) Solar treating 3) Fumigants 4) Bio-pesticides	1) RNAi system needs to be developed for functional-omics experiments 2) Continued molecular marker development for population studies	1) Microarrays 2) Bioassay system available 3) EST libraries available and sequenced 4) Studies on the functional genomics of responses to low oxygen conditions (Chi et al. 2011) and genomic and proteomic responses to plant defensive proteins 5) Genome size determination
<i>Megalurothrips sjostedti</i> Trybom (Thysanoptera: Thripidae)	1) Population structure and dynamics 2) Interactions: Host plant resistance/tolerance - biological control 3) Insecticide resistance	1) Host plant resistance/field tolerance 2) Chemical pesticides 3) Biopesticides 4) Biological control 5) Cultural control	1) EST libraries and sequence data generated 2) Molecular marker development for population studies	1) EST libraries in progress
<i>Aphis craccivora</i> Koch (Hemiptera: Aphididae)	1) Population structure and dynamics 2) Interactions: Host plant resistance/tolerance - biological control 3) Insecticide resistance 4) Presence of genetically different populations	1) Host plant resistance 2) Chemical pesticides 3) Biopesticides 4) Biological control	1) EST libraries and sequence data generated 2) Molecular marker development for population studies	1) EST libraries in progress

Pest species	Important research areas of immediate concern	Current or potential control strategies	Genomic tools needed (short-term)	Genomic tools available or being developed
<i>Clavigralla tomentosicollis</i> Stål. (Hemiptera: Coreidae)	1) Population structure and dynamics 2) Interactions: Host plant resistance/tolerance - biological control 3) Insecticide resistance 4) Deployment systems for augmentative biological control	1) Host plant resistance 2) Chemical pesticides 3) Biological control	1) EST libraries and sequence data generated 2) Molecular marker development for population studies	1) EST libraries in progress
<i>Sericothrips adolffridgerici</i> Kamy (Thysanoptera: Thripidae)	1) Population structure and dynamics 2) Interactions: Host plant resistance/tolerance - biological control 3) Insecticide resistance	1) Host plant resistance 2) Chemical pesticides 3) Biological control	1) EST libraries and sequence data generated 2) Molecular marker development for population studies	1) EST libraries in progress
<i>Anoplocnemis curvipes</i> Fabricius (Hemiptera: Coreidae)	1) Population structure and dynamics 2) Insecticide resistance 3) Deployment systems for augmentative biological control	1) Chemical pesticides 2) Biopesticides 3) Biological control	1) EST libraries and sequence data generated 2) Molecular marker development for population studies	1) EST libraries in progress

more genetically different than individuals collected from either Niger or Nigeria (collected in a North–South pattern) (Pittendrigh, unpublished data). These results also suggested that *M. vitrata* populations are isolated by distance in that sample sites most geographically separated show the most genetic divergence. The current and ongoing application of IPM-omics within West Africa has advanced the knowledge of the population structure for pest insects and will likely be used next to investigate the contribution of alternate host plants to the maintenance of population variability. Although cowpea pest dynamics are incompletely understood, the rapid advances in IPM-omics are increasing our understanding. This information should result in better decisions about which pest controls to deploy, and when and where to deploy them.

Several parasitoids have been identified for the biological control of most cowpea insect pests. Although some of these control agents are indigenous, whether they are or can become sufficiently abundant to help control the pest populations is unclear. Non-native species from Taiwan also have been identified as potential biological control agents, and one example is *Apanteles taragamae* Viereck (Hymenoptera, Braconidae), which has already been experimentally released in Benin (Tamò et al. this volume). To verify the success of parasitoid releases, researchers could potentially study the parasitoid and pest populations to determine whether the pests are being controlled by indigenous or exotic parasitoids. Molecular markers with polymorphisms unique to the introduced populations can potentially be used to determine whether parasitoids identified from the field (post-release) are in fact those that were introduced by the biological control program.

Integrating IPM with genomics: IPM-omics

In the last 60 years, the technologies available for pest management have changed dramatically. The previously described genomic tools provide IPM with new ways to understand and develop insect pest control strategies. We are now entering a time when molecular biology, or more precisely the new field of genomics, has the potential to be integrated into IPM to allow practitioners to make better decisions about pest control. The application of molecular genomics to the study of insect population ecology (i.e., ecological genomics) will become increasingly important as insect ecologists discover the power of these new tools (Sunnucks 2000). IPM can increase the durability of chemical and transgenic pest management tools by decreasing the selective pressure on pest populations to evolve resistance. Moreover, resistance management may be enhanced further if other management tools impose fitness costs on insecticide-resistant pests (Pittendrigh et al. 2008; Gassmann et al. 2009a). Fitness costs of resistance arise in the absence of a control agent when those individuals with resistance alleles have lower fitness than homozygous susceptible individuals. Recent research on insects with resistance to insecticidal toxins produced by the bacterium *Bacillus thuringiensis* (*Bt*) indicates that ecological factors can magnify the fitness costs of *Bt* resistance (Gassmann et al. 2009a). This is an example of ecological negative cross-resistance (Pittendrigh et al. 2008). IPM agents that also increase fitness costs of *Bt* resistance include entomopathogenic viruses (Raymond et al. 2007; Sarfarz et al. 2010), entomopathogenic nematodes (Gassmann et al. 2006; Gassmann et al. 2008; Gassmann et al. 2009b; Hannon et al. 2010), entomopathogenic fungi, and host-plant resistance (Raymond et al. 2005; Bird and Akhurst 2007). Computer modeling indicates that IPM agents that magnify fitness costs of resistance can delay or prevent the evolution of insecticide resistance within pest populations (Carrière and Tabashnik 2001; Pittendrigh et al.

2004; Gassmann et al. 2008; Gassmann et al. 2009b). IPM-omics could lead to more efficient and broader application of ecological negative cross-resistance (Gassmann et al. 2009c). By understanding the genetic basis of resistance, it may be possible to predict which IPM practices will elicit the largest fitness costs, thereby maintaining pest susceptibility and preserving the utility of newly developed pest management tools such as Bt crops and biopesticides.

The use of genomics for understanding pest populations can be broadly placed into two categories, functional genomics and population genomics (the latter being a neologism of the term population genetics). Functional genomics (and other related analysis tools such as proteomics, metabolomics, and systems biology analyses) can be and have been used to understand the detailed mechanisms of how insects respond to and evolve specific responses to challenges that they experience in their environment, such as host-plant resistance factors and pesticides (Pedra et al. 2004; Li et al. 2009). Unfortunately, functional “omics” tools are currently resource intensive and are only used in the laboratory. The use of genomics for practical applications like the development of new pesticides or the identification of new host plant-resistance factors is predicted to occur in the future (Grimmelikhuijzen et al. 2007). Additionally, genes known to be critical for insect survival may ultimately be target sites for the expression of RNA interference (RNAi) constructs by transgenic plants. However, the use of transgenic plants expressing RNAi specific to insect target genes for the control of pest insects is still in its infancy, and questions concerning resistance management for this control strategy remain to be resolved. Although little is known about potential RNAi resistance in insects, multiple resistance mechanisms to dietary RNAi have already been identified in *C. elegans* (Winston et al. 2007). It follows that practical insect control measures that may emerge out of functional genomics will probably not occur in the short term.

One of the other challenges for functional “omics” is the general need for complete genome sequencing, annotation, assembly of the genome, and categorization of the gene classes observed. For many insect species, large genomes filled with a high number of repetitive elements may in the short term make the sequencing of these genomes prohibitively expensive, especially for crop pests, for which resources may be limited. Even when resources are sufficient, however, genomes with a large number of repetitive elements may be difficult to reassemble. An additional problem is that an increased availability of genomes will also reduce the availability of individuals able to perform manual assembly and annotation.

With the advent of high-throughput sequencing, population genomics tools have the potential to be useful in insect control in the short and medium term. Knowledge can be rapidly gained about polymorphisms in insect populations, and this information can be used to understand insect population structure and dynamics. Briefly, a large number of insects can be collected from a target region to optimize the amount of polymorphisms observed in a given EST sequencing run. Those polymorphisms identified in the initial sequencing runs can then be used to answer detailed questions about those insect populations. One example within the context of biological control is to use such molecular markers, in conjunction with traditional pest population sampling, to help determine the source populations of the pests during the seasons when the target crop is not grown. By determining the source of host plants or regions where the pest populations originate (e.g., testing the hypothesis that *M. vitrata* migrates from the south to the north during the rainy season), pest managers can decide where to release biological control agents.

Need for effective information sharing systems of polymorphism data and cost-effective, long-term extension strategies

Finally, a mechanism will be needed to facilitate the flow of information in both directions between those scientists who develop IPM-omics strategies and those end users who apply the strategies. The scientists will need such information sharing systems to obtain the large amounts of polymorphic data required to continually and efficiently build on previous efforts. Extension agents will also require a centralized system for information exchange so that they can access information about practical pest control strategies.

Geographic information systems (GIS)

The use of geo-statistics, GIS, satellite and photo aerial images, Geographical positioning systems (GPS), and cellular technologies in combination with the latest advancements in molecular genetic analysis have dramatically changed the level of resolution applied in insect ecology and IPM. The spatial sciences combined with genetic studies of molecular markers such as polymorphisms are now being used to understand the major factors affecting the distribution of insects and to understand the mechanisms of dispersion and migration. These tools are also being used to study the spatial and temporal flow of genetic material within populations and to determine how biotic and abiotic factors along with selection-adaptation strategies may contribute to the genetic structure of an insect population (Lushai and Loxdale 2004).

The use of genomics data requires the development of databases that integrate information on genetic polymorphisms in insect pest populations with geo-referenced information such as geographic coordinates of collected specimens, the time of collection, and environmental conditions of the location. The information collected (or generated in the laboratory) is analyzed using geo-statistical methods and processed into a digital platform or GIS. The information can be displayed in multiple layers as synthetic maps where correlations are visually expressed (Manel et al. 2003; Ribes-Dasi et al. 2005). The revolutionary application of these technologies allows researchers to identify the insects that are being tracked and to track insect displacements at different geographic scales while enhancing the genetic resolution such that the genetics of an individual insect within a population could be characterized (Lushai and Loxdale 2004). From a methods perspective, the use of geo-statistical analysis and GIS programs may simplify the collection, transmission, and handling of large databases. Through the analysis and manipulation of digital data, it is possible to generate scientific predictions based on a number of possible scenarios. A series of thematic maps are usually elaborated. These maps are very powerful application tools because they show values and correlations as visual variables, and this makes them easy to understand by technical personnel, decision makers, and participating producers (e.g., farmers).

If the current trends continue, our ability to access many polymorphisms across many loci and many insect samples will require a data repository that can then be linked with geographic and ecological data sets. These combined databases will allow researchers to answer important questions about insect pest populations and their environment such as: Does the population migrate? Is the population adapted to particular hosts? Is the population resistant to particular insecticides? With the answers to these and similar questions, researchers, governmental agencies, and farmers can make better decisions regarding human and environmental protection through the application of more rational pest management strategies.

Extension systems

Ultimately, the success of any IPM strategy will hinge on the development, adaptation, and rapid deployment of educational materials that inform scientists and farmers about cost-effective pest control strategies. These materials will be developed and used by various stakeholders including scientists, development organizations (e.g., NGOs and Peace Corps volunteers), extension services, farmer organizations, and farmers themselves. For example, live-action videos have been created that describe the best practices for rearing and deploying biological control agents. The sharing of these videos and similar educational materials through the Internet will help institutions in host countries develop effective biological control release programs (Bello-Bravo et al. this volume). Additionally, as innovations in these programs arise, a centralized Internet-based system will be needed so that groups can share these materials for peer review to assure quality and easy access of content.

A centralized Internet-based system is also needed so that practical pest control strategies can be deployed directly to NGOs, extension agents, farmer organizations, and farmers. To this end, an online peer-reviewed system (termed the Sustainable Development Virtual Knowledge Interface) is currently in development to provide for an online platform for the sharing of extension materials in an easily and widely accessible manner (Bello-Bravo et al. 2010). For example, educational videos containing useful information for cowpea farmers and designed for transmission and viewing with cell phones have already been produced. The language of these videos can be easily changed to match the language of the users. In addition, this centralized Internet-based cell-phone system can be used for deploying text, Powerpoint®, audio, and PDF files. Thus, older extension materials can be added to the centralized system and deployed by cell phone to the community of cowpea farmers and extension agents.

Conclusions

Cost-effective educational strategies that produce tangible and useful educational materials will be critical for the long-term sustainability of any IPM program. Such materials will provide various stakeholders with the capacity to easily deploy such information into their communities. It will also allow the end users to provide feedback on the educational materials. Thus, IPM-omics programs will need to integrate not only genomics (to increase the understanding of pest populations) but also GIS and other current tools that facilitate the efficient collection, analysis, and exchange of IPM information.

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References

- Adams, M.D. et al. 2000. The genome sequence of *Drosophila melanogaster*. *Science* 287: 2185–2195.
- Adams, M.D. et al. 1991. Complementary DNA sequencing: expressed sequence tags and human genome project. *Science* 252: 1651–6
- Alebeek, F. 1996. Natural suppression of bruchid pests in stored cowpea, *Vigna unguiculata* (L.) Walp., in West Africa. *International Journal of Pest Management* 42: 55–60.
- Alhali, A.M. 1991. Studies on cowpea farming practices in Nigeria with emphasis on insect's pest control. *Tropical Pest Management* 37: 71–74.
- Audic, S. and J. Claverie. 1997. The significance of digital gene expression profiles. *Genome Research* 7: 986–995.
- Ba, N.M. V.M. Margam, C.L. Dabire-Binso, A. Sanon, J. McNeil, L.L. Murdock, and B.R. Pittendrigh. 2009. Seasonal and regional distribution of the cowpea pod borer, *Maruca vitrata* Fabricius (Lepidoptera: Crambidae) in Burkina Faso. *International Journal of Tropical Insect Science* 29(3): 109–113.
- Bartlett, J.M.S. and D. Stirling. 2003. *PCR Protocols*, 2nd Edition. Humana Press, Totowa, New Jersey.
- Bello-Bravo, J., R. Diaz, S. Venugopal, M. Viswanathan, and B.R. Pittendrigh. 2010. Expanding the impact of practical scientific concepts for low-literate learners through an inclusive and participatory virtual knowledge ecosystem. *Journal of the World Universities Forum* 3:147–164.
- Bird, L.J. and R.J. Akhurst. 2007. Effects of host plant species on fitness costs of Bt resistance in *Helicoverpa armigera* (Lepidoptera: Noctuidae). *Biological Control* 40: 196–203.
- Bonaldo, M.F., et al. 1996. Normalisation and subtraction: Two approaches to facilitate gene discovery. *Genome Research* 6: 791–806.
- Bottenberg, H. 1995. Farmers' perceptions of crop pests and pest control practices in rainfed cowpea cropping systems in Kano, Nigeria. *International Journal of Pest Management* 41: 195–200.
- Carrière, Y. and B.E. Tabashnik. 2001. Reversing insect adaptation to transgenic insecticidal plants. *Proceedings of the Royal Society Biological Sciences Series B* 268: 1475–1480.
- Chi, Y.H., J.E. Ahn, D.J. Yun, S.Y. Lee, T.X. Liu, and Z.S. Keyan. 2011. Changes in oxygen and carbon dioxide environment alter gene expression of cowpea bruchids. *Journal of Insect Physiology* 57(1): 220–30.
- Coates, B.S., D.V. Sumerford, R.L. Hellmich II, and L.C. Lewis. 2008. Mining an *Ostrinia nubilalis* midgut expressed sequence tag (EST) library for candidate genes and single nucleotide polymorphisms (SNPs). *Insect Molecular Biology* 17: 607–620.
- Dimopoulos, G. et al. 2000. *Anopheles gambiae* pilot gene discovery project: Identification of mosquito innate immunity genes from expressed sequence tags generated from immune-competent cell lines. *Proceedings of National Academy of Science* 97: 6619–6624.
- Ekesi, S. 1999. Variability of pathogenic activity of entomopathogenic fungi (Hyphomycetes) towards the legume flower thrips, *Megalurothrips sjostedti* (Trybom) (Thysanoptera: Thripidae) and their potentials for biological control. PhD Thesis. Ahmadu Bello University, Zaria.
- Ellegren, H. 2009. Sequencing goes 454 and takes large-scale genomics into the wild. *Molecular Ecology* 17: 1629–1635.
- Evenson, R.E. and D. Gollin. 2003. Assessing the impact of the Green Revolution, 1960–2000. *Science* 300 (5620): 758–762.
- Fu, X. et al. 2009. Estimating accuracy of RNA-seq and microarrays with proteomics. *BMC Genomics* 10: 161.
- Gaines, P.J. et al. 2002. Analysis of expressed sequence tags from subtracted and unsubtracted *Ctenocephalides felis* hindgut and Malpighian tubule cDNA libraries. *Insect Molecular Biology* 11: 299–306.
- Gassmann, A.J., S.P. Stock, Y. Carrière, and B.E. Tabashnik. 2006. Effect of entomopathogenic nematodes on the fitness cost of resistance to Bt toxin Cry1Ac in pink bollworm (Lepidoptera: Gelechiidae). *Journal of Economic Entomology* 99: 920–926.
- Gassmann, A.J., S.P. Stock, M.S. Sisterson, Y. Carrière, and B.E. Tabashnik. 2008. Synergism between entomopathogenic nematodes and *Bacillus thuringiensis* crops: integrating biological control and resistance management. *Journal of Applied Ecology* 45: 957–966.
- Gassmann, A.J., Y. Carrière, and B.E. Tabashnik. 2009a. Fitness costs of insect resistance to *Bacillus thuringiensis*. *Annual Review of Entomology* 54: 147–163.
- Gassmann, A.J. et al. 2009b. Effects of pink bollworm resistance to *Bacillus thuringiensis* on phenoloxidase activity and susceptibility to entomopathogenic nematodes. *Journal of Economic Entomology* 102: 1224–1232.
- Gassmann, A.J., D.W. Onstad, and B.R. Pittendrigh. 2009c. Evolutionary analysis of herbivorous insects in natural and agricultural environments. *Pest Management Science* 65: 1174–1181.

- Georghiou, G.P. 1986. The magnitude of the resistance problem. Pages 14–43 in *Pesticide Resistance: Strategies and Tactics for Management*, edited by National Research Council. National Academy Press, Washington, DC.
- Giga, D.P. and J. Biscoe. 1989. Treating maize grains for storage with registered protectants in Zimbabwe: technical, practical and economic considerations. *Zimbabwe Science News* 23: 101–103.
- Grimmelikhuijzen, C.J.P., G. Cazzamali, M. Williamson, and F. Hauser. 2007. The promise of insect genomics. *Pest Management Science* 63: 413–416.
- Gupta, S., D. Zink, B. Korn, M. Vingron, and S.A. Haas. 2004. Genome wide identification and classification of alternative splicing based on EST data. *Bioinformatics* 20(16): 2579–2585.
- Hahn, M.W., M.V. Han, and S-G Han. 2007. Gene Family Evolution across 12 *Drosophila* Genomes. *PLoS Genet* 3(11): e197.
- Hannon, E.R., M.S. Sisterson, S.P. Stock, Y. Carrière, B.E. Tabashnik, and A. Gassmann. 2010. Effects of four nematode species on fitness costs of pink bollworm resistance to *Bacillus thuringiensis* toxin Cry1Ac. *Journal of Economic Entomology* 103: 1821–1831.
- Hassan, A.S.M.R. and K. Bakshi. 2005. Pest management, productivity and environment: a comparative study of IPM and conventional farmers of northern districts of Bangladesh. *Pakistan Journal of Social Sciences* 3(8): 1007–1014.
- Holt, R.A. et al. 2002. The genome sequence of the Malaria mosquito *Anopheles gambiae*. *Science* 298: 129–149.
- Jackai, L.E.N. and S.R. Singh 1988. Screening techniques for host plant resistance to insect pests of cowpea. *Tropical Grain Legume Bulletin* 35: 2–18.
- Jackai, L.E.N. and C.B. Adalla. 1997. Pest management practices in cowpea: a review. Pages 240–258 in *Advances in Cowpea Research*, edited by B.B. Singh, D.R. Mohan Raj, K.E. Dashiell, and L.E.N. Jackai. Co-publication of International Institute of Agriculture (IITA) and Japan International Center for Agricultural Sciences (JIRCAS). IITA, Ibadan, Nigeria.
- Khush, G.S. 1995. Breaking the yield frontier of rice. *GeoJournal* 35: 329–332.
- Kirkness, E.F. et al. 2010. Genome sequences of the human body louse and its primary endosymbiont provide insights into the permanent parasitic lifestyle. *Proceedings of National Academy of Science* 107: 12168–12173.
- Kwok, P.Y. 2001. Methods for genotyping single nucleotide polymorphisms. *Annual Review of Genomics and Human Genetics* 2: 235–258.
- Li, C.H., J.M. Yeakley, T.K. McDaniel, and R. Shen. 2009. Medium- to high-throughput genotyping using VeraCode microbeads. *Methods in Molecular Biology* 496: 129–142.
- Liu, D. and J.H. Graber. 2006. Quantitative comparison of EST libraries requires compensation for systematic biases in cDNA generation. *BMC Bioinformatics* 7: 77.
- Lushai, G. and H.D. Loxdale. 2004. Tracking movement in small insect pests, with special reference to aphid populations. *International Journal of Pest Management* 50(4): 307–315.
- Lyamichev, V. et al. 1999. Polymorphism identification and quantitative detection of genomic DNA by invasive cleavage of oligonucleotide probes. *Nature Biotechnology*, 17: 292–296.
- Manel, S., M.K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution* 18(4): 189–197.
- Margam, V.M. et al. 2010. Wild host plants of legume pod borer *Maruca vitrata* (Lepidoptera: Crambidae) in southern Niger and northern Nigeria. *International Journal of Tropical Insect Science* 30(2): 108–114.
- Margam, V.M. et al. 2011a. Geographic distribution of phylogenetically-distinct legume pod borer, *Maruca vitrata* (Lepidoptera: Pyraloidea: Crambidae). *Molecular Biology Reports* (DOI: 10.1007/s11033-010-0182-3).
- Margam, V.M. et al. 2011b. Mitochondrial genome sequence and expression profiling for the legume pod borer *Maruca vitrata* (Lepidoptera: Crambidae). *PLoS ONE* 6(2): e16444. doi:10.1371/journal.pone.0016444.
- Margulies, M. et al. 2005. Genome sequencing in microfabricated high-density picolitre reactors. *Nature* 437: 326–327.
- Maxam, A.M. and W. Gilbert. 1977. A new method for sequencing DNA. *Proceedings of National Academy of Science, USA* 74(2): 560–564.
- McCombie, W.R. et al. 1992. *Caenorhabditis elegans* expressed sequence tags identify gene families and potential disease gene homologies. *Nature Genetics* 1: 124–131.
- Megy, K. et al. 2009. Genomic resources for invertebrate vectors of human pathogens, and the role of VectorBase. *Infection Genetics and Evolution* 9: 308–313.
- Morozova, O. and M.A. Marra. 2008. Applications of next-generation sequencing technologies in functional genomics. *Genomics* 92: 255–264.
- Nagaraj, S.H. et al. 2006. A hitchhiker's guide to expressed sequence tag (EST) analysis. *Brief. Bioinformatics* 8: 6–21.

- Nene, V. et al. 2004. Genome sequence of *Aedes aegypti*, a major arbovirus vector. *Science* 316: 1718–1723.
- Norris, R.F. et al. 2003. Concept in integrated pest management. Prentice-Hall of India Private Ltd, New Delhi.
- Pedra, J.H.F. et al. 2004. Genome-wide transcription profile of field- and laboratory-selected DDT-resistant *Drosophila*. *Proceedings of National Academy of Science USA* 101(18): 7034–7039.
- Pittendrigh, B.R. et al. 2004. “Active” refuges can inhibit the evolution of resistance in insects towards transgenic insect-resistant plants. *Journal of Theoretical Biology* 231: 461–474.
- Pittendrigh, B.R., J.M. Clark, J.S. Johnston, S.H. Lee, J. Romero-Severson, and G.A. Dasch. 2006. Proposed sequencing of a new target genome: the human body louse, *Pediculus Humanus Humanus*. *Journal of Medical Entomology* 43(6): 1103–1111.
- Pittendrigh, B.R. et al. 2008. Negative cross-resistance: past, present, and future potential. Pages 107–124 in *Resistance Management: Biology, Economics, and Prediction*, edited by D.W. Onstad. Academic Press, Burlington.
- Pittendrigh, B.R. et al. 2011. Simplify, simplify. Lifestyle and compact genome of the body louse provide a unique functional genomics opportunity. *Communicative and Integrative Biology* 4(2): In Press.
- Porcel, B.M. et al. 2000. Gene survey of the pathogenic protozoan *Trypanosoma cruzi*. *Genome Research* 10: 1103–1107.
- Raymond, B. et al. 2005. Genes and environment interact to determine the fitness costs of resistance to *Bacillus thuringiensis*. *Proceedings of the Royal Society Biological Sciences Series B* 272: 1519–1524.
- Raymond, B. et al. 2007. Exploiting pathogens and their impact on fitness costs to manage the evolution of resistance to *Bacillus thuringiensis*. *Journal of Applied Ecology* 44: 768–780.
- Ribes-Dasi, M. et al. 2005. The use of Geostatistics and GIS to optimize pest control practices in precision farming systems. *Information and Technology for Sustainable Fruit and Vegetable Production. FRUTIC 05*, 12–16 September 2005, Montpellier, France.
- Richards, S. et al. 2005. Comparative genome sequencing of *Drosophila pseudoobscura*: chromosomal, gene, and *cis*-element evolution. *Genome Research* 15: 1–18.
- Rokas, A. and P. Abbot. 2009. Harnessing genomics for evolutionary insights. *Trends in Ecology and Evolution* 24(4): 192–200.
- Ronaghi, M., M. Uhlén, and P. Nyren. 1998. DNA sequencing: a sequencing method based on real-time pyrophosphate. *Science* 281 (5375): 363–365.
- Rudd, S. 2003. Expressed sequence tags: alternative or complement to whole genome sequences? *Trends in Plant Science* 8: 321–329.
- Sanger, F. and A.R. Coulson. 1975. A rapid method for determining sequences in DNA by primed synthesis with DNA polymerase. *Journal of Molecular Biology* 94(3): 441–8.
- Sanger, F., S. Nicklen, and A.R. Coulson. 1977. DNA sequencing with chain-terminating inhibitors. *Proceedings National Academy of Science USA* 74(12): 5463–5467.
- Sarfaz, R.M., V. Cervantes and J.H. Myers. 2010. Resistance to *Bacillus thuringiensis* in the cabbage looper (*Tricoplusia ni*) increases susceptibility to nucleopolyhedrovirus. *Journal of Invertebrate Pathology* 105: 204–206.
- Simon, S.A. et al. 2009. Short-read sequencing technologies for transcriptional analyses. *Annual Review Plant Biology* 60: 305–333.
- Singh, R.B. 2000. Environmental consequence of agricultural development: a case study from the Green Revolution state of Haryana, India. *Agriculture, Ecosystems and Environment* 82: 97–103.
- Singh, S.R. and H. F. van Emden. 1979. Insect pests of grain legumes. *Annual Reviews of Entomology* 24: 255–278.
- Smith, R.F. and R. Van den Bosch. 1967. Integrated control. Pages 295–340 in *Pest Control: Biological, Physical, and Selected Chemical Methods*, edited by W.W. Kilgore and R.L. Doutt. Academic Press, New York.
- Smith, R.F., J.L. Apple, and D.G. Bottrell. 1976. The origins of integrated pest management concepts in agricultural crops. Pages 1–16 in *Integrated Pest Management*, edited by J.L. Apple and R.F. Smith. Plenum Press, New York.
- Sunnucks, P. 2000. Efficient genetic markers for population biology. *Trends in Evolution and Ecology* 15: 199–203.
- Tang, K. et al. 1999. Chip-based genotyping by mass spectrometry. *Proc. Natl. Acad. Sci. USA* 96: 10016–10020.
- The International Aphid Genomics Consortium 2010. Genome Sequence of the Pea Aphid *Acyrtosiphon pisum*. *PLoS Biol.* 8: e1000313.
- The International Silkworm Genome Consortium. 2008. The genome of a lepidopteran model insect, the silkworm *Bombyx mori*. *Insect Biochem. Molecular Biology* 38: 1036–1045.

- Tribolium Genome Sequencing Consortium. 2008. The genome of the model beetle and pest *Tribolium castaneum*. *Nature* 452: 949–955.
- Tsuchihashi, Z., and N.C. Dracopoli. 2002. Progress in high throughput SNP genotyping methods. *Pharmacogenomics Journal*, 2: 103–110.
- Ungerer, M.C., L.C. Johnson, and M.A. Herman. 2008. Ecological genomics: understanding gene and genome function in the natural environment. *Heredity* 100 (2):178–83.
- Venter, J.C. et al. 2001. The sequence of the human genome. *Science* 291: 1304–1351.
- Vera, J.C. et al. 2008. Rapid transcriptome characterization for a non-model organism using 454 pyrosequencing. *Molecular Ecology* 17: 1636–1647.
- Weinstock, G.M. et al. 2006. Insights into social insects from the genome of the honeybee *Apis mellifera*. *Nature* 443: 931–949.
- Werren, J.H. et al. 2010. Functional and evolutionary insights from the genomes of three parasitoid *Nasonia* species. *Science* 327: 343–348.
- Wheat, C.W. et al. 2010. Rapidly developing functional genomics in ecological model systems via 454 transcriptome sequencing. *Genetica*. 138(4): 433–51.
- Wilson, C. and C. Tisdell. 2001. Why farmers continue to use pesticides despite environmental, health and sustainability costs. *Ecological Economics* 39: 449–462.
- Winston, W.M., M. Sutherlin, A.J. Wright, E.H. Feinberg, and C.P. Hunter. 2007. *Caenorhabditis elegans* SID-2 is required for environmental RNA interference. *Proceedings of National Academy of Science USA* 104: 10565–10570.
- Wise, J. and M. Whalon. 2009. A systems approach to IPM integration, ecological assessment and resistance management in tree fruit orchards. Pages 325–345 in *Biorational Control of Arthropod Pests: Application and Resistance Management*, edited by I.Ishaaya and A.R. Horowitz. Springer Publishing Ltd., Dordrecht, Heidelberg, London, New York.
- Xia, Q. et al. 2009. Complete resequencing of 40 genomes reveals domestication events and genes in silkworm (*Bombyx*). *Science* 326: 433–436.