

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/240518249>

Plant Volatiles-based Insect Pest Management in Organic Farming

Article in *Critical Reviews in Plant Sciences* · March 2010

DOI: 10.1080/07352681003617483

CITATIONS

35

READS

171

5 authors, including:



Mary A. Rogers

University of Minnesota Twin Cities

21 PUBLICATIONS 109 CITATIONS

[SEE PROFILE](#)



Dilip Panthee

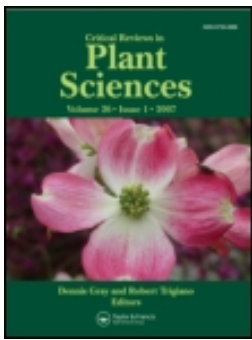
North Carolina State University

90 PUBLICATIONS 841 CITATIONS

[SEE PROFILE](#)

All content following this page was uploaded by [Mary A. Rogers](#) on 08 October 2015.

The user has requested enhancement of the downloaded file. All in-text references [underlined in blue](#) are added to the original document and are linked to publications on ResearchGate, letting you access and read them immediately.



Plant Volatiles-based Insect Pest Management in Organic Farming

Gitika Shrivastava , Mary Rogers , Annette Wszelaki , Dilip R. Panthee & Feng Chen

To cite this article: Gitika Shrivastava , Mary Rogers , Annette Wszelaki , Dilip R. Panthee & Feng Chen (2010) Plant Volatiles-based Insect Pest Management in Organic Farming, Critical Reviews in Plant Sciences, 29:2, 123-133, DOI: [10.1080/07352681003617483](https://doi.org/10.1080/07352681003617483)

To link to this article: <http://dx.doi.org/10.1080/07352681003617483>



Published online: 09 Mar 2010.



Submit your article to this journal [↗](#)



Article views: 590



View related articles [↗](#)



Citing articles: 11 View citing articles [↗](#)

Plant Volatiles-based Insect Pest Management in Organic Farming

Gitika Shrivastava,¹ Mary Rogers,¹ Annette Wszelaki,¹ Dilip R. Panthee,² and Feng Chen¹

¹Department of Plant Sciences, University of Tennessee, Knoxville, TN, USA

²Department of Horticultural Science, North Carolina State University, Mountain Horticultural Crops Research and Extension Center, Mills River, NC, USA

Table of Contents

I. INTRODUCTION	123
II. CURRENT APPROACHES TO INSECT PEST MANAGEMENT IN ORGANIC FARMING	124
A. Prevention	124
B. Biological Control	125
C. Chemical Control	125
III. BIOLOGY OF PLANT VOLATILES	126
A. Plant Volatiles: Chemistry and Biosynthesis	126
B. Ecological Functions of Plant Volatiles in Plant-Insect Interactions	126
IV. INSECT PEST MANAGEMENT IN ORGANIC FARMING BASED ON PLANT VOLATILES	127
A. Cultivars with Enhanced Indirect and/or Direct Defense	127
B. Polyculture	128
C. Association with Beneficial Microorganisms	129
D. Extracted Plant Volatiles for Pest Control	130
V. CONCLUSION AND PERSPECTIVES	130
ACKNOWLEDGMENTS	131
REFERENCES	131

Organic agriculture is increasing in popularity worldwide due to the rapidly growing market for organic products. In organic production, insects present a major pest challenge that negatively impacts crop health and yield. To successfully manage an organic farmland, an effective insect pest management program is key. In this review, we first describe the approaches currently used for pest management in organic farming. Next, we review natural plant defense mechanisms, especially those based on plant volatile organic compounds. Chemically complex, plant volatiles have multiple ecological roles in plant-insect interactions including attracting pollinators, acting as cues for foraging herbivores as well as functioning as direct defense, indirect defense, or interplant priming. Based on the ecological roles of plant volatiles, we then discuss in-depth how pest management may be improved through a variety of strate-

gies including using resistant cultivars, polyculture, using beneficial microorganisms such as mycorrhizal fungi and endophytes, and using plant-derived pesticides, all of which are reviewed in the context of plant volatiles. Lastly, integration of these different strategies based on the trait of plant volatiles for a successful and sustainable pest management program in organic farming is discussed.

Keywords organic farming, insect pests, plant volatiles, plant defenses

I. INTRODUCTION

Promoted early in the 1940s by J. I. Rodale, and spurred by writings of British agriculturalist Sir Albert Howard, organic farming in the U.S. has been politicized and polarizing, despite growing popularity and consumer demand. Organically grown produce is an alternative to conventionally

Address correspondence to Feng Chen, Department of Plant Sciences, University of Tennessee, Knoxville, TN 37996 USA. E-mail: fengc@utk.edu

grown produce. Although sometimes difficult to verify scientifically (Dangour *et al.*, 2009; Woese *et al.*, 1999), organic products are often perceived by consumers as healthier and more environmentally friendly (Yue and Tong, 2009; Williams and Hammitt, 2001; Thompson and Kidwell, 1998). The movement of organic farming in the U.S. was directly related to the indiscriminate use of chemical pesticides, herbicides, and fertilizers. Heavy reliance on synthetic agrochemicals, although undeniably an important factor contributing to increased food production and subsequent food security, led to significant health and environmental concerns. Despite reluctance of certain agricultural communities, organic agriculture gradually began to gain a foothold in U.S. culture. In 1979, the California Organic Food Act was signed into law, which established standardized production practices for organic food products.

In 1990, the Federal Organic Foods Production Act was passed, which established national standards for organic products, thus allowed for consistency in interstate trade. It took twelve years from that date to finalize a set of standards administered by the USDA's National Organic Program. Since 2002, foods that are certified organic are accompanied by the USDA organic label. The USDA currently defines organic agriculture as "an ecological production management system that promotes and enhances biodiversity, biological cycles and soil biological activity. It is based on minimal use of off-farm inputs and on management practices that restore, maintain and enhance ecological harmony." Since the adoption of national standards, organic sales in the U.S. have increased by 20% or more per year, representing one of the fastest growing sectors in agriculture (Oberholtzer *et al.*, 2007).

In a survey of organic farmers administered by the Organic Farming Research Foundation, farmers identified several major challenges faced by organic producers. Among these were issues related to practical weed management, followed by management of insect pests, vertebrate pests, and diseases (Walz, 1999). In this review, we restrict our discussion to management of insect pests. Among the key insect pests of concern, the most significant challenges come from cucumber beetles, flea beetles, Colorado potato beetles, aphids, codling moth, leafhoppers, and grasshoppers (Walz, 1999). These insect pests can cause significant losses in crop yield and produce aesthetics, especially in organic production systems. For example, despite implementation of various organic management efforts, codling moth larvae caused damage levels exceeding 25% in organic apple orchards in British Columbia (Judd *et al.*, 1997). It is important to recognize that insects can cause differing levels of crop damage depending upon both the life stage of the insect pest and the developmental stage of the crop. In addition to direct feeding damage, insects can vector many different plant viruses. Wounds caused by insect feeding also become potential entry points for pathogenic fungi and bacteria. Therefore, adequate management of key insect pests remains critical to the health of organically

grown crops and longevity of perennial plants within an organic production system.

Undoubtedly, insect pests are an important factor in yield and commercial salability of conventional agricultural commodities. Various management strategies have been developed to control insects, including botanical, biorational and synthetic insecticides as well as creation of transgenic pest- and disease-resistant crops, such as Bt corn and cotton. Genetically modified crops are not permitted for use in organic farming systems, and options of chemical insecticide are limited. In light of these constraints, it can be significantly more challenging to sufficiently manage insect pests using approved organic options. In this review, we first discuss approaches currently used to manage insect pest populations in organic production systems. We then review and discuss the potential for volatile compounds produced by plants to optimize or improve insect pest management in organic production.

II. CURRENT APPROACHES TO INSECT PEST MANAGEMENT IN ORGANIC FARMING

A major difference between conventional and organic pest management is the limited choices of pesticides for organic production. Consequently, the focus in organics has been placed on preventative measures, which emphasize an ecosystem approach in pest management. This "agroecosystems" approach drives systems-based research, where relationships between complex elements such as plants and insects are explored. A systems approach to pest management is knowledge-based rather than product-based, which takes the emphasis off therapeutic management, or reactive strategies, and focuses on prevention and proactive strategies for management (Lewis *et al.*, 1997). Additionally, the advance of Integrated Pest Management (IPM) practices focuses on using a variety of strategies to keep pest populations below pre-determined economic or aesthetic threshold levels, rather than targeting pest eradication. In this section we discuss current pest management strategies in organic production, which include prevention, biological control and chemical control.

A. Prevention

Due to limitations of allowable and available insecticides and/or interest in conservation and reducing synthetic inputs, organic farmers must focus on pest prevention by stopping arthropod outbreaks before they occur. This is most commonly attempted through use of crop rotation programs, increasing overall crop biodiversity and potential habitat for beneficial organisms (Lotter, 2003). Besides increasing yields, rotating crops improves soil conditions and fertility, and reduces insect and disease pressure. Crop rotations normally follow a three-year schedule where genetically diverse crops are alternated. Cover crops are ideal for in-between years where vegetable crops are not grown, and can be cultivated to address specific soil needs. For example, oats provide biomass that builds soil organic

matter, while legumes such as clovers and vetch provide nitrogen for the following crop. In addition, cover crops increase the biodiversity of the farm. In particular, by providing a constant supply of nectar, cover crops may help sustain beneficial insect populations. For example, cover crops such as phacelia (*Phacelia tanacetifolia*) and buckwheat (*Fagopyrum esculentum*) provide nectar for hoverflies and bees, which are beneficial insects (Pontin *et al.*, 2006). As a consequence, pest cycles can be broken and pest outbreaks reduced on such farmland.

Timing to avoid pest outbreaks and using resistant varieties can be successful cultural management strategies. The female Hessian fly, *Mayetiola destructor*, has a small window of time after emergence in which to lay eggs and is primarily associated with wheat. However, if this preferred host is not available, eggs may be deposited on other grasses such as oats that do not support larval development (Harris and Rose, 1989). In order to avoid damage by Hessian fly, growers can delay planting wheat to avoid adult emergence. In addition to timing, breeding wheat varieties for resistance to Hessian fly has also been successful (Williams *et al.*, 2003).

Other integrated management practices can involve use of row covers, colored plastic and conventional mulches, physical barriers, sticky traps and barriers, scent lures, and pheromone lures and traps that prevent target insect pests from finding host plants and reproducing. Row covers can be put up and removed fairly easily to provide protection from insect pests. Some research has shown that mulches can reduce insect pest pressure. Whitefly (*Bemisia argentifolii*) colonization was also hindered in zucchini crops when wheat straw and reflective mulches were used (Summers *et al.*, 2004). Sticky traps and pheromone traps are often used for insect monitoring, but can be used in organic systems to attract pests away from crops and disrupt mating. Yellow sticky traps visually stimulate insect pests such as greenhouse whiteflies (*Trialeurodes vaporariorum*) and tarnished plant bugs (*Lygus lineolaris*). When paired with traps, pheromone and scent lures utilize both chemical and visual attractants (Foster and Harris, 1997). These can be sex or aggregation pheromones, or kairomones, which manipulate insect behavior by mimicking chemical cues that elicit a response (Foster and Harris, 1997). Squash vine borer (*Melittia cucurbitae*) is a destructive pest that is difficult to manage in organic systems. Mass trapping using pheromones can lure males away from females that would otherwise mate and lay eggs (Jackson *et al.*, 2005).

B. Biological Control

Biological control is the use of natural enemies to manage pests. There are three different types of biological control recognized: conservation, augmentation and importation. Conservation biological control involves habitat manipulation to increase populations of predators and parasitoids, that can help keep pest populations from building up to injurious levels. An example of conservation biological control is planting strips

of nectar-producing flowers that provide energy-rich sugars to beneficial insects. Dill (*Anethum graveolens*), coriander (*Coriandrum sativum*), and phacelia (*Phacelia tanacetifolia*) produce nectar and pollen, and have adequate flower morphology to support predatory lacewings (*Chrysoperla* sp.), lady beetles (*Coleomegilla maculata*), and syrphid flies (family Syrphidae) in agricultural areas (Landis *et al.*, 2000). These generalist predators eat insect eggs and soft bodied insects, such as aphids. Parasitoid insects lay their eggs in or on a host, and developing larvae exploit host resources eventually causing death. Parasitoid insects are often host-specific, and are adept at finding their hosts. Adult wasps that have access to food sources will live longer and lay more eggs. Adult encyrtid wasps (*Copidosoma koehleri*) lived twice as long as controls when given nectar from buckwheat, faba beans, phacelia, and nasturtium (Baggen *et al.*, 1999). Additional habitat management strategies to conserve beneficial insects are adjusting mowing, height, providing overwintering habitat, and providing alternate hosts (Landis *et al.*, 2000).

Augmentative biological control involves the deliberate release of beneficial species, such as predatory bugs, mites, beetles and midges, parasitic wasps, entomopathogenic nematodes, fungi, bacteria and viruses, to manage pests in a controlled environment. This type of biological control is best applied before pest outbreaks occur. Over 100 different species are commercially available for augmentative biological control, mostly used in greenhouse situations (van Lenteren, 2000).

Importation biological control refers to use of non-native natural enemies that are sought out, imported, reared, tested and introduced from their indigenous habitat to manage an exotic invasive pest. One of the oft-cited successes of this type of biological control is management by the vedalia beetle (*Rodolia cardinalis*) of cottony cushion scale (*Icerya purchasi*), a serious citrus pest. The beetle was imported to the U.S. in 1888 to help control the scale insect and remains effective at managing populations of the pest (Greathead, 1995).

C. Chemical Control

In the past 50 years, insects have mainly been controlled by synthetic insecticides (Kabarou and Gichia, 2001). While many insecticides are not allowed in organic production, there are some "organic" insecticide options that are approved by the Organic Materials Review Institute for use in organic cropping systems. The Organic Materials Review Institute is a nonprofit organization that independently reviews products for compliance with the USDA National Organic Program, and publishes this information for organic certifiers, producers, and manufacturers (www.omri.org). The permitted list of insecticidal products includes plant-based extracts, such as neem oils, pyrethrums, ryania, rotenone, and sabadilla, and microbe-derived chemicals, such as spinosad, which is derived from a naturally occurring soil bacterium called *Saccharopolyspora spinosa*. Soaps, mineral oils, and potassium salts of fatty acids

may also be used to help manage small, soft-bodied insects. Mineral products such as kaolin clay and diatomaceous earth are also allowed. Most organic pesticides have low residual activity, but some are rather stable. For example, veratridine and cevidine, two alkaloid components of *sabadilla*, an organic pesticide, degrade slowly with 50% and 10% of degradation, respectively, when exposed to 22 days of sunlight (Rosen and Zang, 2007). There is much contention and controversy surrounding the safety, risks, and environmental impacts of organic versus conventional pesticides, with many consumers believing that organic foods produced using organic pesticides are safer than conventionally grown foods using synthetic pesticides (Williams and Hammitt, 2001). Scientific data supporting or rejecting this perception are still needed (Dangour *et al.*, 2009).

III. BIOLOGY OF PLANT VOLATILES

Despite availability of a variety of pest control options, efficient and effective insect pest management in organic farming remains challenging. When developing new pest management methods, it is important to fully consider the plant's natural defense mechanisms as well as mechanisms that direct interactions of the host plant with its environment. During a long co-evolutionary timeline, plants have evolved various strategies for defending against or tolerating insect herbivore attack. In the past few decades, there has been tremendous academic and commercial interest in elucidating plant natural defense mechanisms related to enhanced insect resistance with a long-term goal of genetic crop improvement. Some approaches presently used to assist insect management in organic farming described in the previous section are in essence attempts to emulate plant natural defense mechanisms. Plant defense strategies can be broadly categorized into either structural or chemical defense, though these tactics can work in concert. Chemical defenses are characterized by the constitutive or induced production of a myriad of secondary metabolites (Chen *et al.*, 2009b). Some of these secondary metabolites are small molecular weight lipophilic compounds with high vapor pressure and therefore easily volatilize at normal atmosphere. Plant volatiles play important roles for the host plant to interact with its environment, especially plant-insect interactions. In order to effectively utilize plant volatiles for insect management in organic farming, it is necessary to understand the biology of plant volatiles: what they are, how they are synthesized, and what biological/ecological functions they have.

A. Plant Volatiles: Chemistry and Biosynthesis

Approximately 1,700 volatile secondary metabolites have been identified so far from more than 90 plant families and this number is very likely going to increase with studies on more plants and development and application of new analytical methods (Knudsen and Gershenson, 2006). Although very complex, the majority of plant volatiles belong to three groups: terpenoids, fatty acid derivatives, and phenolics (Dudareva *et al.*, 2006).

Volatile terpenoids, including monoterpenes and sesquiterpenes, are synthesized through the nonmevalonate and the mevalonate pathway, respectively (Eisenreich *et al.*, 2001). Terpene synthases are the key enzymes for terpene production. They catalyze the formation of monoterpenes, sesquiterpenes and diterpenes using geranyl diphosphate, farnesyl diphosphate, and geranylgeranyl diphosphate as substrate, respectively. Phenolic volatiles are produced from the shikimic acid pathway (Herrmann and Weaver, 1999). Methyl salicylate is the most important representative in this group. Methyl salicylate is formed from salicylic acid, which is a defense signal, through the action of salicylic acid methyltransferase (Chen *et al.*, 2003). Salicylic acid methyltransferase belongs to a plant-specific protein family called "SABATH" (Zhao *et al.*, 2007, 2008, 2009). Fatty acid-derived volatiles are synthesized through the lipoxygenase pathway. Lipoxygenase catalyzes the dioxygenation of polyunsaturated fatty acids such as linoleate and linolenate to yield hydroperoxides (Porta and Rocha-Sosa, 2002). Hydroperoxides are further metabolized via the hydroperoxide lyase pathway to produce volatile aldehydes and alcohols, which are also known as green leaf volatiles.

Many plant volatiles are produced in specific tissues at specific developmental stages such as flowering, ripening, or maturation and serve various functions (Goff and Klee, 2006). Some plant volatiles are constitutively produced. Some are induced by abiotic stresses such as nutrient stress, drought, UV radiation, and temperature or biotic agents such as fungi, bacteria, and herbivores. Stress factors can activate various biochemical pathways that lead to the production of a single or mixture of different volatile compounds through the regulation of a number of plant signaling molecules, such as jasmonic acid, ethylene (Schmelz *et al.*, 2003), and salicylic acid (Ozawa *et al.*, 2000).

B. Ecological Functions of Plant Volatiles in Plant-Insect Interactions

Flowers of many plants release a complex mixture of volatile compounds and are therefore strongly scented. Floral volatiles are used by many pollinators as an olfactory cue for visitation (Zhuang *et al.*, 2008). Therefore, floral volatiles are important for the reproductive success of many cross-pollinated plants. In addition to attracting pollinators, floral volatiles may function in deterring unwanted floral visitors (Omura *et al.*, 2000). For example, as a floral scent compound of *Nicotiana attenuata*, nicotine has a defense role against herbivores (Euler and Baldwin, 1996). The functions of vegetative volatiles are much more complex. Specialist arthropod herbivores may use vegetative volatiles as the major cue for host finding. Different insect species have preference for different volatile compounds.

Plant volatiles may have multiple functions in defenses against insects: direct defense, indirect defense, and interplant priming. When plant volatiles function as toxins that kill herbivores or reduce plant digestibility, they are called direct defense. Volatiles derived from glucosinolate degradation are a good

example of direct defense against insects (Halkier and Gershenzon, 2006). Several herbivory-induced plant volatiles, such as linalool, were shown to function as a direct defense in nature (Kessler and Baldwin, 2001). The production of plant volatiles for direct defense may be constitutive independent of herbivory. Young and reproductive tissues generally contain large amounts of these defense compounds. In addition to constitutive production, some toxic plant volatiles are induced by herbivory, in which the jasmonic acid signaling pathway plays a key role (Howe and Jander, 2008).

Plants may also defend themselves indirectly. This defense strategy is based on tri-trophic interactions involving plants, herbivores and carnivores (Kessler and Baldwin 2002). When damaged by herbivores, plants emit a diverse array of volatiles, which attract natural enemies, either carnivorous predators or parasitoids, of the herbivores to the herbivore-damaged plants (Takabayashi and Dicke, 1996). These carnivores prey upon the herbivores or lay eggs in them. Further damage to the plant by the herbivores may thus be prevented or reduced. This phenomenon is therefore called “indirect defense.” Since the first time it was demonstrated about two decades ago, plant volatiles-mediated indirect defense has been documented in many systems. Many species of plants, arthropod herbivores and carnivores have been used in different combinations in the studies of herbivore-induced indirect defense (Takabayashi and Dicke 1996). Some investigations were carried out in natural ecosystems (Kessler and Baldwin 2001), and most have been performed in a lab setting (Yuan *et al.*, 2008).

In addition to mediating the interaction of a plant with both its pest arthropod species and their natural enemies, volatile compounds induced by herbivory may also signal adjacent and down-wind plants about a possible herbivore threat. Such signaling may activate the neighboring plant’s defense system. This interplant signaling from herbivore-damaged plants to undamaged neighboring plants is called inter-plant priming (Howe and Jander, 2008). Priming often results in even stronger resistance among undamaged neighboring plants when subsequent herbivory occurs. In addition, undamaged cotton plants become more attractive to predatory mites and less susceptible to spider mites when exposed to volatile compounds emitted by cotton plants damaged by spider mites (Bruin *et al.*, 1992). Most of these studies have been conducted in laboratory conditions and whether these results can be reproduced in field conditions has not been thoroughly studied. A study combining both laboratory and field tests reported that volatiles produced from clipped sagebrush (*Artemisia tridentata*) increased the fitness of native tobacco when they were planted adjacent to each other. Clipped sagebrush emits many volatiles, including methyl jasmonate, methacrolein, terpenoids, and green leaf volatiles. When infested by *Manduca sexta* caterpillars, plants that were already exposed to clipped sagebrush showed an enhanced production of trypsin proteinase inhibitors. This activation of a defense response led to reduced total insect damage on plants activated by clipped sagebrush and also to a higher

mortality rate of young *Manduca* caterpillars (Kessler *et al.*, 2006).

IV. INSECT PEST MANAGEMENT IN ORGANIC FARMING BASED ON PLANT VOLATILES

When underlying mechanisms for insect management approaches currently employed in organic farming are examined, it becomes evident that several emulate either natural defense mechanisms of plants or natural interactions between organisms in agroecosystems. Some of them are fully or partly based upon volatile chemistry of plants, which has many important ecological roles in plant-insect interactions. When we develop new practices to improve the effectiveness of insect management approaches in organic farming, it is important that we fully appreciate the natural defenses that plants employ and implement them in practice to their full potential. In this section, we will discuss various types of existing and prospective approaches for insect control in organic farming taking into the full consideration of the trait of plant volatiles.

A. Cultivars with Enhanced Indirect and/or Direct Defense

Natural preferences of insects for a specific plant species or variety were identified long ago (Guerin and Stadler, 1984; Guerin and Ryan, 1984), which were due to the different volatiles emitted by a specific genotype. However, limited progress has been made in insect resistance breeding (Miklas *et al.*, 2006). With the development of new technologies, it is possible to obtain the entire profile of the volatiles emitted by the plants (Chen *et al.*, 2009; Laothawornkitkul *et al.*, 2008) at a particular growth stage due to internal factors or in response to external factors such as wounding. With the determination of a specific volatile profile that is beneficial for self-defense, it can be manipulated through breeding or genetic transformation (Ng *et al.*, 2008). As an example, responses of wheat varieties Beta (susceptible) and Elands (resistant) to aphids (*Diuraphis noxia*) were evaluated with respect to the application of volatiles from plant essential oils, methyl salicylate, 1,8-cineole and menthol (Prinsloo *et al.*, 2007). *D. noxia* settled less on Elands plants that were exposed to the volatiles, whereas the effect of the volatiles on Beta was not noticeable. The impact of the three chemicals on aphid numbers varied according to the wheat variety, indicating that there was an interaction between those chemicals and wheat genotype.

Volatiles of different genotypes and wild species confer different levels of direct and indirect defense against herbivores. Five commercial and one naturalized cotton varieties were studied for their volatile profiles. Undamaged leaves from all the varieties showed no significant difference in their volatile profiles. However, average volatile emissions from the leaves of naturalized variety damaged by beet armyworm were found to be seven times higher than those from the leaves of commercial varieties even though larvae preferred commercial cultivars to

feed on. These volatiles include monoterpenes, sesquiterpenes, and lipoxygenase products (Loughrin *et al.*, 1995).

These differences in the volatile profile can be utilized by breeders to develop new cultivars with volatile profiles that are repulsive for herbivores or attractive to their natural enemies or a combination of both. Breeding of new crop varieties with increased direct and/or indirect defense based on plants volatiles may be based on existing varieties. The western corn rootworm (*Diabrotica virgifera*) is the most devastating pest of maize in the U.S. Recent study showed that (E)- β -caryophyllene, a sesquiterpene, is emitted by the roots of maize in response to feeding by larvae of western corn rootworm (Rasmann *et al.*, 2005). (E)- β -caryophyllene is highly attractive to entomopathogenic nematodes, which parasitize and kill western corn rootworm larvae effectively (Rasmann *et al.*, 2005). Most North American maize lines lack the ability of emitting (E)- β -caryophyllene from roots (Rasmann *et al.*, 2005). This provides a knowledge base for creating novel maize varieties with improved resistance against western corn rootworm based on the restoration of (E)- β -caryophyllene emission in the roots. Breeding of new crop varieties for organic agriculture should also take advantage of existing genetic diversity in the wild. For example, medium-length methylketones are one class of compounds highly effective in protecting plants against pests (Williams *et al.*, 1980). These compounds are not found in cultivated tomatoes. However, they are highly produced by some wild tomato species (Williams *et al.*, 1980). Transferring the trait of methylketone production from wild tomato species to cultivated elite tomato varieties through breeding may lead to novel tomato varieties with enhanced pest resistance better suited for organic production.

B. Polyculture

When managing insect pests in organic production, it is important to consider natural interactions of a host plant with its environment. The interactions of a host plant with insects as well as the interactions of insects with their natural enemies can be influenced by the diversity of plants in an agroecosystem. Polyculture is an agricultural practice in which multiple plants are grown in the same space. It aims at increasing crop yield by making full use of resources of a given piece of land. In contrast to monoculture, polyculture imitates the diversity of natural ecosystems, which has an important impact on the insect populations. The population density of arthropod herbivores in polyculture is found to be lower than that in monoculture. In contrast, the population density of natural enemies, especially parasitoids, are found to be lower in monoculture (Andow, 1991). Growing plants of different species in close physical proximity may aid insect control in several different ways depending on the volatile traits of various plants (Perrin and Phillips, 1978; Uvah and Coaker, 1984).

Intercropping is one form of polyculture, in which two or more types of crops are cultivated in the same space at the same

time. Examples of intercropping strategies include planting a deep-rooted crop with a shallow-rooted crop, or planting a tall crop with a shorter crop that requires partial shade. The presence of multiple crops in a same agroecosystem provides a habitat for a variety of insects and therefore increases the local biodiversity, especially the beneficial insects, such as parasitic wasps. This can lead to the reduction of outbreaks of crop pests. For example, Colorado potato beetles (*Leptinotarsa decemlineata*) are attracted to volatiles from potato (*Solanum tuberosum*), but are repelled or not attracted by mixtures of potato and tomato (*Lycopersicon esculentum*) (Thiery and Visser, 1986, 1987). Another study was conducted to investigate the effectiveness of combined cropping of cultivated and wild varieties to manage stem borer. Intercropping with nonhost molasses grass (*Melinis minutiflora*) was found to significantly decrease stem borer infestation in the main crop as well as increase larval parasitism by parasitoid *Cotesia sesamiae*. Volatile compounds emitted by *M. minutiflora* were found to repel female stem borers and to attract females of *C. sesamiae* (Khan *et al.*, 2007).

Companion planting refers to the planting of noncommercial plants along with the main crop for the purpose of facilitating nutrient uptake and pollination of the main crop as well as impacting other factors that affect crop productivity. Companion plants may affect crop-insect interactions. For example, when clover was grown as a companion plant for Brussels sprouts (*Brassica oleracea gemmifera*), the infestation of Brussels sprouts by diamondback moth was significantly reduced (Dover, 1986). For many of these studies, the associated resistance has been suggested to be provided by the olfactory effect of volatiles emitted from the nonhost. Some of the companion crops have also been found to increase the number of pests on the main crop. For example, when rue (*Ruta graveolens*), garlic chives (*Allium szechonparum*), and zonal geranium (*Pelargonium × hortorum Bailey*) were grown as companion plants for roses, the first two companion plants had no effect on Japanese beetles in the main crop. Geranium attracted more Japanese beetle and significantly increased the number of beetles on rose instead of reducing it (Held *et al.*, 2002). Therefore, careful selection of companion plants for specific main crops is important for this strategy to work.

Trap cropping is a specific form of companion planting. Being planted around the field to be protected or interspersed among them, trap crops help reduce pest pressure on the main crop by being more attractive to insects than nearby crops. For example, perimeter rows of zucchini (*Cucurbita pepo* 'Elite'), buttercup (*Cucurbita maxima* 'Burgess'), and blue hubbard squash (*C. maxima*) can attract striped cucumber (*A. vittatum*) away from the butternut (*Cucurbita moschata*) main crop (Adler and Hazzard, 2009). Different species of plants may vary in their ability in serving as a trap crop. For example, to control the diamondback moth (*Plutella xylostella*) on cabbage, several plants including glossy and waxy collards, Indian mustard, and yellow rocket, were evaluated as trap crops. Yellow rocket was found to be the best candidate for use as a trap crop for *P. xylostella*

(Fransisco *et al.*, 2004). In addition to the species to grow, other factors that may affect the effectiveness of trap cropping include the proper timing of planting and adequate spacing and size of the trap crop (Hokkanen, 1991).

Weedy species, which are usually undesired, may have some positive impacts on pest control in organic production under certain circumstances. Choice experiments in the laboratory demonstrated that volatiles emitted by ragweed (*Ambrosia artemisiifolia*) interfered with the host finding and feeding behavior of *P. cruciferae* on tomato (Tahvanainen and Root, 1972). Therefore, leaving the ragweed to grow in the tomato field can help control this insect. In addition to growing multiple plants at the same place simultaneously, decomposed plants may also benefit pest control in organic production. This is called biofumigation, which is an agricultural practice for control of soil-borne pests through the toxic substances released from the decomposed plants. Brassica plants are commonly used as biofumigant crops due to the production of secondary compounds especially glucosinolates. When glucosinolates are hydrolyzed, a variety of volatile compounds, including isothiocyanates, nitriles, epithionitriles and thiocyanates, are being produced, many of which are toxic to insect pests (Halkier and Gershenzon, 2006).

Interactions of insect herbivores and their natural enemies mediated by plant volatiles are complex processes. Some of the underlying mechanisms of such interactions are still poorly understood. In addition, these interactions may vary depending on the interacting species. Therefore, fundamental characterization of these interactions, especially in the field conditions, is highly needed. When choosing crops or companion plants for polyculture, in addition to considering their volatile chemical traits, it is also important to bear in mind that these crops should not compete for physical space, nutrients, water, or sunlight when growing together, the factors that are equally important for crop yield.

C. Association with Beneficial Microorganisms

There is a rich diversity of soil organisms that can provide benefits to host plants through association. Growing evidence supports that some of these plant-microorganism associations may impact plant defenses against insect pests. Mycorrhizal fungi are specialized soil fungi that colonize plant roots to form a symbiotic association. Mycorrhizal associations with plant roots are widespread in nature. For example, arbuscular mycorrhizae are found in association with almost 85% of all plant families (Wang and Qiu, 2006). Mycorrhizal fungi gain constant and direct access to carbohydrates from the plant roots. In return, mycorrhizal fungi assist plant in uptake of water and mineral nutrients such as phosphorus. In addition, there is evidence that mycorrhizal association play an important role in the suppression of pests and diseases of associated plants, including herbivores (Gosling *et al.*, 2006). For example, mycorrhizal soybean was found to be more resistant to corn earworm (*Heliothis zea*) and fall armyworm (*Spodoptera frugiperda*) than

non-mycorrhizal soybean (Rabin and Pacovsky, 1985). And mycorrhizal ribwort plantain (*Plantago lanceolata*) is more resistant to attacks by the larvae of *Arctia caja* (Gange and West, 1994). Enhanced pest resistance of mycorrhizal plants might be due to increased availability of soil nutrients through mycorrhizal association, thus improving overall plant health (Gosling *et al.*, 2006). Some studies showed that mycorrhizal plants produce more toxic compounds. For example, significant increase in accumulation of terpenoids was found in cucumber (*Cucumis sativus*) roots upon mycorrhizae inoculation (Akiyama and Hayashi, 2001).

How mycorrhizal association affects the production and emission of volatiles from host plants is, however, little understood. Some studies showed that mycorrhizae colonization can alter a plant's volatile profile. For example, mycorrhizal inoculation led to altered accumulation of certain sesquiterpenes and enhanced emission of limonene and artemisia ketone in *Artemisia annua* plants (Rapparini *et al.*, 2008). In another study, mycorrhizal ribwort plantain (*Plantago lanceolata*) was shown to release one green leaf volatile (Z)-3-hexenyl acetate at a rate that was much higher than that of non-mycorrhizal plants and similar to that of insect-infested plants (Fontana *et al.*, 2009), suggesting this compound may affect direct and indirect defenses. In the same study, it was found that mycorrhizal plants emitted significantly lower quantities of sesquiterpenes than non-mycorrhizal plants when fed by insects, suggesting that indirect defense may be weakened (Fontana *et al.*, 2009). These contradictory implications from the same study highlight the complexity of multi-tropical interactions. In a recent meta-analysis of more than 30 independent studies, it was found that in general the density of chewing insects on mycorrhizal plants were higher than that on non-mycorrhizal plants. However, because herbivore survival on mycorrhizal plants tends to be lower, more consumption did not lead to greater plant damage. Also from this analysis, it was found that while mycorrhizal colonization provides benefits to mono- and oligophagous chewing insects, it negatively affects the performance of polyphagous chewing insects (Koricheva *et al.*, 2009). A number of studies showed that mycorrhizal association negatively affects parasitism (Gange *et al.*, 2003). Whether this is due to altered production of plant volatiles is not yet clear. While mycorrhizal association may benefit crop production in organic farming in many different ways (Gosling *et al.*, 2006), its impact on plant-insect interactions needs to be further investigated.

Endophytes are another type of microorganisms that can affect host plant defense via the alteration of volatile production. An endophyte is a bacterium or fungus that grows systemically in intercellular spaces throughout the plant without causing apparent disease (Clay, 1996). Some endophytes produce mycotoxins. Therefore, plants infested by endophytes are usually more resistant to insects. A study with *Beauveria bassiana* in banana reported reduced crop damage by banana weevil (up to 42–86.7%) (Akello *et al.*, 2008). Some endophytes have been found to alter the volatile profile of host plants. For example, the

presence of endophyte resulted in qualitative and quantitative differences in the production of volatile compounds from tall fescue (*Festuca arundinacea*). Treatment of endophyte-infected and endophyte-free plants with jasmonic acid dramatically altered the volatile compound profile (Yue *et al.*, 2001). The altered production of plant volatiles may be responsible, at least partly, for the increased resistance of endophyte-infected plants against insects. Under certain conditions, the enhanced insect resistance of endophyte-infected plants may be due to the volatiles produced by endophytes. For example, the endophytic fungus *Muscodor vitigenus*, produces naphthalene under certain conditions. This endophyte-derived naphthalene has been found to effectively repel adult wheat stem sawfly (*Cephus cinctus*) in a Y-tube olfactory bioassay (Daisy *et al.*, 2002). *Muscodor albus* is another endophyte that has been known to produce certain antimicrobial volatile compounds. This fungus was tested for its insecticidal activity against Potato tuber moth, *Phthorimaea operculella*. Adults and neonate larvae exposed to the volatile produced by *M. albus* showed significant higher percent mortalities than control (Lacey and Neven, 2006).

Despite the many encouraging results, some plant-endophyte association was found to increase the pest infestation of the host plant. A study examining the interaction between an unspecialized root fungal endophyte *Acremonium strictum* and polyphagous moth *Helicoverpa armigera* provided such evidence. In a bioassay under greenhouse and laboratory conditions *H. armigera* was found to be more attracted to endophyte *A. strictum* inoculated tomato plants as compared to the endophyte-free plants. Endophyte-inoculated plants released significantly lower levels of terpenes as compared to endophyte-free plants. This study demonstrated that *A. strictum* was able to systemically influence the host selection of *H. armigera* moths for oviposition probably mediated by the induced changes in volatile emissions (Jallow *et al.*, 2008). Therefore, endophyte selection is very critical and the impact can be specific to crops and pests.

D. Extracted Plant Volatiles for Pest Control

Based on their biological activities, plant volatiles may be developed into various products for insect control in organic production. They can be developed into organic pesticides. For example, a number of plant-originated monoterpenoids have been found to be more toxic to nematode *Caenorbditis elegans* than a commercial nematicide. Compounds like thymol and carvacrol have been found to be most effective with 100% mortality and eugenol and geraniol moderately effective (Tsai and Yu, 2000). In addition, many plant essential oils have been found to have nematocidal activity. Essential oil of ajowan (*Trachyspermum ammi*), allspice (*Pimenta dioica*) and litsea (*Litsea cubeba*) have been tested against pine wood nematodes and compounds like geraniol, isoeugenol, and methyl isoeugenol have been identified to have good nematocidal activity (Park *et al.*, 2006). Similarly volatile compounds from clove oil have been

found to reduce egg hatch and the viability of hatched juveniles of tomato root knot nematodes (*Meloidogyne incognita*) (Meyer *et al.*, 2008). Altieri *et al.* (1981) studied the application of the extract of the preferred host plant on the less preferred host plant in order to augment parasitoid preference and reported increases in parasitization by *Trichogramma* when *Amaranthus* extract was applied on soybean plants. Aqueous extracts of marigold were also found to trigger oviposition of *Tricogramma* (Ravi *et al.*, 2006). Plant volatiles may also be developed into products for luring insects. For example, traps baited with compounds obtained from Canada thistle (*Cirsium arvense*) floral volatiles have been found to exhibit strong oviposition response from many lepidopteran insect pests. Soybean looper has been found to be attracted significantly to the Canada thistle floral volatiles and more females were trapped than males. Further study showed that phenylacetaldehyde plays the major role in attracting soybean looper, particularly the females (Stringer *et al.*, 2008). Much research is still needed to further develop plant volatiles-based agents for insect control, especially from those plants that are high producer of volatiles, such as *Copaifera* trees (Chen *et al.*, 2009a). Essential oils are often a mixture of many volatiles compounds. The identification of the most active compound will help develop highly effective products. The advance of metabolomics techniques combined with novel approaches for screening of effective volatile compounds (Enan, 2005) will play important roles in such new endeavors.

V. CONCLUSION AND PERSPECTIVES

Pest management is a key component in organic crop production systems. Because synthetic pesticides and genetically modified crops are prohibited in this system, pest management presents a challenging task for the success of organic production. One key strategy currently used for pest management in organic farming involves preventive measures through selection of insect-resistant varieties, planting trap crops, following crop rotation, and nutrient management. Other strategies involve control measures through releasing or attracting natural enemies of herbivores and employing organic pesticides. Facing the challenging task of effective pest management, in this article, we have extensively reviewed and discussed how we may improve current strategies and design new strategies based on the production of volatile organic compounds from various plants.

Plant volatile compounds play important roles in mediating complex interactions between plants and organisms in the same ecosystem (Dudareva *et al.*, 2006). These compounds are of great importance to plant defense as well as reproduction. Volatile production is genetically controlled and can be affected by different biotic (herbivores, microorganisms like mycorrhizae, and endophytes) and abiotic (light, temperature, nutrients) factors. To successfully control pests in an organic system, it is important to understand the interactions of different components in a specific ecosystem. For instance, restriction of use of pesticides may result in increase in the pest pressure in some

crop species or varieties. However, it may positively impact the biodiversity in the crop ecosystem and increase natural enemies' populations. Therefore, it is important to emphasize the integration of different approaches that work synergistically and be in harmony with the nature. In addition to their roles in plant-herbivore interactions, plant volatiles are involved in many other aspects of plant biology and ecology, such as defense against pathogens (Pichersky and Gershenzon, 2002). Volatiles released from below-ground tissues may have synergistic or allelopathic activity on the germination and growth of competitive neighboring plants. When leveraging the benefits of plant volatiles for enhanced defense against insects in organic farming, their potential negative impact also need to be considered. More basic research regarding the functions of plant volatiles, especially in an organic agroecosystem, is still needed. While much research in this area is still in its infancy, a multidisciplinary approach involving molecular biology, biochemistry, plant breeding, entomology, crop management and economics can facilitate the investigation and subsequently provide real world solutions for pest control in organic agriculture.

ACKNOWLEDGMENTS

We thank Dr. William Klingeman for critical reading of the manuscript. Research on plant metabolism and plant-insect interactions in F Chen's lab is supported by the USDA-ARS, the University of Tennessee Experimental Station, the Southeastern Sun Grant Center and the DOE Office Biological and Environmental Research (BER) - Genome to Life Program through the BioEnergy Science Center (BESC). Organic research in A. Wszelaki's lab is supported by the IR-4 Biopesticide Program, the Tennessee Department of Agriculture and the University of Tennessee Cooperative Extension Service. D. Panthee's lab is supported by North Carolina Tomato Growers' Association.

REFERENCES

- Adler L. S. and Hazzard, R. V. 2009. Comparison of perimeter trap crop varieties: effects on herbivory, pollination, and yield in butternut squash. *Environ. Entomol.* **35**: 207–215.
- Akello, J., Dubois, T., Coyne, D., and Kyamanywa, S. 2008. Endophytic *Beauveria bassiana* in banana (*Musa* spp.) reduces banana weevil (*Cosmopolites sordidus*) fitness and damage. *Crop Protection* **27**: 1437–1441.
- Akiyama, K. and Hayashi, H. 2001. Arbuscular mycorrhizal fungus-promoted accumulation of two new triterpenoids in cucumber roots. *Biosci. Biotech. Biochem.* **66**: 762–769.
- Altieri, M. A., Lewis, W. J., Nordlund, D. A., Gueldner, R. C., and Todd, J. W. 1981. Chemical interactions between plants and *Trichogramma* sp. wasps in Georgia soybean fields. *Prot. Ecol.* **3**: 259–263.
- Andow, D. A. 1991. Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.* **36**: 561–586.
- Bagen, L. R., Gurr, G. M., and Meats, A. 1999. Flowers in tri-trophic systems: mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. *Entomol. Exp. Appl.* **91**: 155–161.
- Bruin, J., Dicke, M., and Sabelis, M. W. 1992. Plants are better protected against spider mites after exposure to volatiles from infested conspecifics. *Experientia* **48**: 525–529.
- Chen, F., D'Auria, J. C., Tholl, D., Ross, J. R., Gershenzon, J., Noel, J. P., and Pichersky, E. 2003. An Arabidopsis gene for methylsalicylate biosynthesis, identified by a biochemical genomics approach, has a role in defense. *Plant J.* **36**: 577–588.
- Chen, F., Al-Ahmad, H., Joyce, B., Zhao, N., Köllner, T. G., Degenhardt, J., and Stewart, C. N. 2009a. Within-plant distribution and emission of sesquiterpenes from *Copaifera officinalis*. *Plant Physiol. Biochem.* **47**: 1017–1023.
- Chen, F., Liu, C.-J., Tschaplinski, T. J., and Zhao, N. 2009b. Genomics of secondary metabolism in *Populus*: Interactions with biotic and abiotic environments. *Crit. Rev. Plant Sci.* **28**: 375–392.
- Clay, K. 1996. Interactions among fungal endophytes, grasses and herbivores. *Res. Popul. Ecol.* **38**: 191–201.
- Daisy, B. H., Strobel, G. A., Castillo, U., Ezra, D., Sears, J., Weaver, D. K., and Runyon, J. B. 2001. Naphthalene, an insect repellent, is produced by *Muscodor vitigenus*, a novel endophytic fungus. *Microbiology* **148**: 3737–3741.
- Dangour, A. D., Dodhia, S. K., Hayter, A., Allen, E., Lock, K., and Uauy, R. 2009. Nutritional quality of organic foods: a systematic review. *Am. J. Clin. Nutr.* **90**: 680–685.
- Dover, J. 1986. The effect of labiate herbs and white clover on *Plutella xylostella* oviposition. *Entomol. Exp. Appl.* **42**: 243–247.
- Dudareva, N., Negre, F., Nagegowda, D.A., and Orlova, I. 2006. Plant volatiles: recent advances and future perspectives. *Crit. Rev. Plant Sci.* **25**: 417–440.
- Eisenreich, W., Rohdich, F., and Bacher, A. 2001. Deoxyxylulose phosphate pathway to terpenoids. *Trends Plant Sci.* **6**: 78–84.
- Enan, E. E. 2005. Molecular and pharmacological analysis of an octopamine receptor from American cockroach and fruit fly in response to plant essential oils. *Arch. Insect Biochem. Physiol.* **59**: 161–171.
- Euler, M. and Baldwin, I. T. 1996. The chemistry of defense and apparency in the corollas of *Nicotiana attenuata*. *Oecologia* **107**: 102–112.
- Fontana, A., Reichelt, M., Hempel, S., Gershenzon, J., and Unsicker, S. B. 2009. The effects of arbuscular mycorrhizal fungi on direct and indirect defense metabolites of *Plantago lanceolata* L. *J. Chem. Ecol.* **35**: 833–843.
- Foster, S. P. and Harris, M. O. 1997. Behavioral manipulation methods for insect pest-management. *Annu. Rev. Entomol.* **42**: 123–146.
- Francisco, R. B. P., Shelton, A. M., and Nault, B. A. 2004. Evaluating trap crops for diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *J. Econ. Entomol.* **97**: 1365–1372.
- Gange, A. C., Brown, V. K., and Aplin, M. A. 2003. Multitrophic links between arbuscular mycorrhizal fungi and insect parasitoids. *Ecol. Lett.* **6**: 1051–1055.
- Gange, A. C., and West, H. M. 1994. Interactions between arbuscular mycorrhizal fungi and foliar-feeding insects in *Plantago lanceolata* L. *New Phytol.* **128**: 79–87.
- Goff, S. A. and Klee, H. J. 2006. Plant volatile compounds: sensory cues for health and nutritional value. *Science* **311**: 815–819.
- Gosling, P., Hodge, A., Goodlass, G., and Bending, G. D. 2006. Arbuscular mycorrhizal fungi and organic farming. *Agric. Ecosyst. Environ.* **113**: 17–35.
- Greathead, D. J. 1995. Benefits and risks of classical biological control. In: *Biological Control: Benefits and Risks*. pp. 53–63. Hokkanen, H.M.T. and Lynch, J.M., Eds. Cambridge University Press, Cambridge.
- Guerin, P. M. and Ryan, M. F. 1984. Relationship between root volatiles of some carrot cultivars and their resistance to the carrot fly, *Psila rosae*. *Entomol. Exp. Appl.* **36**: 217–224.
- Guerin, P. M. and Stadler, E. 1984. Carrot fly cultivar preferences - some influencing factors. *Ecol. Entomol.* **9**: 413–420.
- Halkier, B. A. and Gershenzon, J. 2006. Biology and biochemistry of glucosinolates. *Annu. Rev. Plant Bio.* **57**: 303–333.
- Harris, M. O. and Rose, S. 1989. Temporal changes in the egg-laying behavior of the Hessian fly. *Entomol. Exp. Appl.* **53**: 17–29.
- Held, D. W., Gonsisk, D., and Potter, D. A. 2003. Evaluating companion planting and non-host masking odors for protecting roses from the Japanese beetle (*Coleoptera: Scarabaeidae*). *J. Econ. Entomol.* **96**: 81–87.
- Herrmann, K. M. and Weaver, L. M. 1999. The shikimate pathway. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **50**: 473–503.
- Hokkanen, H.M.T. 1991. Trap cropping in pest management. *Annu. Rev. Entomol.* **36**: 119–138.

- Howe, G. A. and Jander, G. 2008. Plant immunity to insect herbivores. *Annu. Rev. Plant Biol.* **59**: 41–66.
- Jackson, D. M., Canhilar, R., and Carner, G. R. 2005. Trap monitoring squash vine borers in cucurbits. *J. Agric. Urban. Entomol.* **22**: 27–39.
- Jallow, M.F.A., Gobena, D. D., and Vidal, S. 2008. Influence of an endophytic fungus on host plant selection by a polyphagous moth via volatile spectrum changes. *Arthropod-Plant Inte.* **2**: 53–62.
- Judd, G.J.R., Gardiner, M.G.T., and Thomson, D. R. 1997. Control of codling moth in organically-managed apple orchards by combining pheromone-mediated mating disruption, post-harvest fruit removal and tree banding. *Entomol. Exp. Appl.* **83**: 137–146.
- Kabaru, J. M. and Gichia, L. 2001. Insecticidal activity of extracts derived from different parts of the mangrove tree *Rhizophora mucronata* (Rhizophoraceae) lam. against three arthropods. *African J. Sci. Tech.* **2**: 44–49.
- Kessler, A. and Baldwin, I. T. 2001. Defensive function of herbivore-induced plant volatile emissions in nature. *Science* **291**: 2141–2144.
- Kessler, A. and Baldwin, I. T. 2002. Plant responses to insect herbivory: the emerging molecular analysis. *Ann. Rev. Plant Biol.* **53**: 299–328.
- Kessler, A., Halitschke, R., Diezel, C., and Baldwin, I. T. 2006. Priming of plant defense responses in nature by airborne signaling between *Artemisia tridentata* and *Nicotiana attenuata*. *Oecologia* **148**: 280–292.
- Khan, Z. R., Nyarko, K. A., Chiliswa, P., Hassanali, A., Kimani, A., Lwande, W., Overholt, W. A., Picketta, J. A., Smart, L. E., and Woodcock, C. M. 1997. Intercropping increases parasitism of pests. *Nature* **388**: 631–632.
- Knudsen, J.T., and Gershenzon, J., 2006. The chemical diversity of floral scent. *In: Biology of Floral Scent*, pp. 27–52. Dudareva, N. and Pichersky, E., Eds., CRC Press, Boca Raton, FL.
- Koricheva, J., Gange, A. C., and Jones, T. 2009. Effects of mycorrhizal fungi on insect herbivores: a meta-analysis. *Ecology* **90**: 2088–2097.
- Lacey, L. A. and Neven, L. G. 2006. The potential of the fungus, *Muscodor albus*, as a microbial control agent of potato tuber moth (*Lepidoptera: Gelechiidae*) in stored potatoes. *J. Invertebr. Pathol.* **91**: 195–198.
- Landis, D. A., Wratten, S. D., and Gurr, G. M. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* **45**: 175–201.
- Laothawornkitkul, J., Moore, J. P., Taylor, J. E., Possell, M., Gibson, T. D., Hewitt, C. N., and Paul, N.D. 2008. Discrimination of plant volatile signatures by an electronic nose: a potential technology for plant pest and disease monitoring. *Environ. Sci. Technol.* **42**: 8433–8439.
- Lewis, W. J., van Lenteren, J. C., Phatak, S. C., and Tumlinson, J. H. 1997. A total system approach to sustainable pest management. *Proc. Natl. Acad. Sci.* **94**: 12243–12248.
- Lotter, D. W. 2003. Organic agriculture. *J. Sustain. Agric.* **21**: 59–128.
- Loughrin, J. H., Manukian, A., Heath, R. R., and Tumlinson, J.H. 1995. Volatiles emitted by different cotton varieties damaged by feeding beet armyworm larvae. *J. Chem. Ecol.* **21**: 1217–1227.
- Meyer, S.L.F., Lakshman, D. K., Zasada, I. A., Vinyard, B. T., and Chitwood, D. J. 2008. Dose- response effects of clove oil from *Syzygium aromaticum* on the root-knot nematode, *Meloidogyne incognita*. *Pest Manag. Sci.* **64**: 223–229.
- Miklas, P. N., Kelly, J. D., Beebe, S. E., and Blair, M. W. 2006. Common bean breeding for resistance against biotic and abiotic stresses: From classical to MAS breeding. *Euphytica* **147**: 105–131.
- Ng, E. C., Dunford, N. T., and Chenault, K. 2008. Chemical characteristics and volatile profile of genetically modified peanut cultivars. *J. Biosci. Bioeng.* **106**: 350–356.
- Oberholtzer, L., Dimitri, C., and Greene, C. 2007. Price premiums hold on as U.S. organic produce market expands. *In: Organic Agriculture in the U.S.* pp.71–95. Wellson, A. J. Ed., Nova Science Publishers, New York.
- Omura, H., Honda, K., and Hayashi, N. 2000. Floral scent of *Osmanthus fragrans* discourages foraging behavior of cabbage butterfly, *Pieris rapae*. *J. Chem. Ecol.* **26**: 655–666.
- Ozawa, R., Arimura, G., Takabayashi, J., Shimoda, T., and Nishioka, T. 2000. Involvement of jasmonate- and salicylate-related signaling pathways for the production of specific herbivore-induced volatiles in plants. *Plant Cell Physiol.* **41**: 391–398.
- Park, I. K., Kim, J., Lee, S. G., and Shin, S. C. 2006. Nematicidal Activity of plant essential oils and components from Ajowan (*Trachyspermum ammi*), Allspice (*Pimenta dioica*) and Litsea (*Litsea cubeba*) essential oils against Pine wood nematode (*Bursaphelenchus Xylophilus*). *J. Nematol.* **39**: 275–279.
- Perrin, R. M. and Phillips, M. L. 1978. Some effects of mixed cropping on the population dynamics of insect pests. *Entomol. Exp. Appl.* **24**: 385–393.
- Pichersky, E. and Gershenzon, J. 2002. The formation and function of plant volatiles: perfumes for pollinator attraction and defense. *Curr. Opin. Plant Biol.* **5**:237–243.
- Pontin, M. D., Wade, M. R., Kehrl, P., and Wratten, S. D. 1998. Attractiveness of single and multiple species flower patches to beneficial insects in agroecosystems. *Ann. Appl. Biol.* **148**: 39–47.
- Porta, H. and Rocha-Sosa, M. 2002. Plant lipoxigenases. physiological and molecular features. *Plant Physiol.* **130**: 15–21.
- Prinsloo, G., Ninkovic, V., van der Linde, T. C., van der Westhuizen, A. J., Pettersson, J., and Glinwood, R. 2007. Test of semiochemicals and a resistant wheat variety for Russian wheat aphid management in South Africa. *J. Appl. Entomol.* **131**: 637–644.
- Rabin, L. B., and Pacovsky, R. S. 1985. Reduced larva growth of two Lepidoptera (Noctuidae) on excised leaves of soybean infected with a mycorrhizal fungus. *J. Econ. Entom.* **78**: 1358–1363.
- Rapparini, F., Llusia, J., and Penuelas, J. 2008. Effect of arbuscular mycorrhizal (AM) colonization on terpene emission and content of *Artemisia annua* L. *Plant Biol.* **10**: 108–122.
- Rasmann, S., Köllner, T. G., Degenhardt, J., Hiltbold, I., Toepfer, S., Kuhlmann, U., Gershenzon, J., and Turlings, T. C. 2005. Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature* **434**: 732–737.
- Ravi, G., Tandon, P. L., Bhakthavasalam, N., Rabindra R. J., Rao, N. S., and Chandrasekaran, B. 2006. Marigold: A Trichogramma friendly crop. *In: Biodiversity and Insect Pest Management*. pp. 163–174. Ignacimuthu, S., and Jayaraj, S., Eds., Narosa Publishing House, New Delhi.
- Rosen, J. D. and Zang, X. 2007. Photolysis of two pesticides used by organic farmers: sabadilla and ryania. *In: Crop Protection Products for Organic Agriculture. ACS Symposium Series*. Vol 947. pp. 222–229. Felsot, A. S., and Racke, K. D. Eds., American Chemical Society, Washington, D.C.
- Schmelz, E. A., Alborn, H.T., and Tumlinson, J. H. 2003. Synergistic interactions between volicitin, jasmonic acid and ethylene mediate insect-induced volatile emission in *Zea mays*. *Physiol. Planta.* **117**: 403–412.
- Stringer, L. D., Sayed, A. M.E., Cole, L. M., Manning, L.A.M., and Suckling, D. M. 2008. Floral attractants for the female soybean looper, *Thysanoplusia orichalcea* (Lepidoptera: Noctuidae). *Pest Manag. Sci.* **64**: 1218–1221.
- Summers, C. G., Mitchell, J. P., and Stapleton, J. J. 2004. Management of aphid-borne viruses and *Bemisia argentifolii* (Homoptera: Aleyrodidae) in zucchini squash by using UV reflective plastic and wheat straw mulches. *Environ. Entomol.* **33**: 1447–1457.
- Tahvanainen, J. O. and Root, R. B. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* **10**: 321–346.
- Takabayashi, J. and Dicke, M. 1996. Plant-carnivore mutualism through herbivore-induced carnivore attractants. *Trends Plant Sci.* **1**: 109–113.
- Thiery, D. and Visser, J. H. 1986. Masking of host odour in the olfactory orientation of the Colorado potato beetle. *Entomol. Exp. Appl.* **41**: 165–172.
- Thiery, D. and Visser, J. H. 1987. Misleading the Colorado potato beetle with an odor blend. *J. Chem. Ecol.* **13**: 1139–1146.
- Thompson, G. D. and Kidwell, J. 1998. Explaining the choice of organic produce: cosmetic defects, prices, and consumer preferences. *Am. J. Agric. Econ.* **80**: 277–287.
- Tsai, R. and Yu, Q. 2000. Nematicidal activity of monoterpenoid compounds against economically important nematodes in agriculture. *J. Essent. Oil Res.* **12**: 350–354.
- Uvah, I.I.I. and Coaker, T. H.1984. Effect of mixed cropping on some insect pests of carrots and onions. *Entomol. Exp. Appl.* **36**: 159–167.

- Van Lenteren, J. C. 2000. Success in biological control of arthropods by augmentation of natural enemies. In: *Biological Control: Measures of Success*. pp. 77–103. Gurr G. and Wratten, S. D., Eds., Kluwer Academic Publishers, Norwell, MA.
- Walz, E. 1999. Third biennial national organic farmer's survey. Organic Farming Research Foundation. Santa Cruz, CA.
- Wang, B., and Qiu, Y. L. 2006. Phylogenetic distribution and evolution of mycorrhizae in land plants. *Mycorrhiza*. **16**: 299–363.
- Williams, C. O., Collier, C. C., Sardesai, N., Ohm, H. W., and Cambron, S.E. . 2003. Phenotypic assessment and mapped markers for H31, a new wheat gene conferring resistance to Hessian fly (Diptera: Cecidomyiidae). *Theo. Appl. Genet.* **107**: 1516–1523.
- Williams, P.R.D. and Hammitt, J. K. 2001. Perceived risks of conventional and organic produce: pesticides, pathogens and natural toxins. *Risk Anal.* **21**: 319–330.
- Williams, W. G., Kennedy, G. G., Yamamoto, R. T., Thacker, J. D., and Bordner, J. 1980. 2-tridecanone: A naturally occurring insecticide from the wild tomato species *Lycopersicon hirsutum* f. *glabratum*. *Science* **207**: 888–889.
- Woese, K., Lange, D., Boess, C., and Bögl, K. W. 1997. A comparison of organically and conventionally grown foods-results of a review of the relevant literature. *J. Sci. Food Agric.* **74**: 281–293.
- Yuan, J. S., Köllner, T. G., Wiggins, G., Grant, J., Jörg, D., and Chen, F. 2008. Molecular and genomic basis of volatile-mediated indirect defense against insects in rice. *Plant J.* **55**: 491–503.
- Yue, C. and Tong, C. 2009. Organic or local? Investigating consumer preference for fresh produce using a choice experiment with real economic incentives. *HortScience* **44**: 366–71.
- Yue, Q., Wang, C., Gianfagna, T. J., and Meyer, W. A. 2001. Volatile compounds of endophyte-free and infected tall fescue (*Festuca arundinacea* Schreb.). *Phytochemistry*. **58**: 935–941.
- Zhao, N., Guan, J., Lin, H., and Chen, F. 2007. Molecular cloning and biochemical characterization of indole-3-acetic acid methyl transferase from poplar. *Phytochemistry* **68**: 1537–1544.
- Zhao, N., Ferrer, J-L., Ross, J., Guan, J., Yang, Y., Pichersky, E., Noel, J. P., and Chen, F. 2008. Structural, biochemical and phylogenetic analyses suggest that indole-3-acetic acid methyltransferase is an evolutionarily ancient member of the SABATH family. *Plant Physiol.* **146**: 455–467.
- Zhao, N., Boyle, B., Duval, I., Ferrer, J., Lin, H., Seguin, A., Mackay, J. and Chen, F. 2009. SABATH methyltransferases from white spruce (*Picea glauca* [Moench] Voss): Gene cloning, functional characterization and structural analysis. *Tree Physiol.* **29**: 947–957.
- Zhuang, X-F, Klingeman, W. E., Hu, J., and Chen, F. 2008. Emission of floral volatiles from Dogwood flowers. *J. Agri. Food. Chem.* **56**: 9570–9574.