

Advances in research of induced resistance to insects in cotton

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Abstract Any change in a plant that occurs following herbivory or environmental factors is an induced response. These changes include phytochemical induction, increases in physical defenses, emission of volatiles that attract predators and parasitoids of herbivores, and reduction in plant nutritional quality for herbivores, which is termed induced resistance. Induced resistance has been demonstrated ubiquitously in plants. It is one of our goals to review what is known about the induced resistance to herbivorous insects in cotton, including three resistance secondary metabolites (terpenoid, tannin, and flavonoids) that are contained at any significant levels of resistance to herbivorous insects in cotton cultivates. In many cases, the quantities or quality of secondary metabolites in plant are changed after attacked by insects. This review focuses on induced plant resistance as quantitative or qualitative enhancement of defense mechanism against insect pests, especially on the abiotic-elicitors-induced resistance in cotton plants. The abiotic-elicitor of cupric chloride, an exogenous inorganic compound, may induce the secondary metabolites accumulation and is referred to as a copper-inducible elicitor (CIE). Finally, we discuss how copper-inducible elicitor may be used in the Integrated Pest Management (IPM) system for cotton resistance control.

Keywords induced resistance, secondary metabolites, abiotic elicitor, herbivorous insect, cotton cultivates

1 Introduction

Before the domestication of plant for agricultural purposes, those susceptible to herbivorous insects died before they could produce seed or before their damaged seeds could germinate. Thus, resistant plants survived subject to laws

of adaptation and natural selection (Smith, 1989; Zhang and Feng, 2000). Higher plants dominate much of the Earth's surface, and yet, as sessile organisms, they must continually resist attacks by various herbivores. In the past 20 years, there have been incredible advances in our understanding of plant defenses, i.e., the mechanisms that plants use to protect themselves from being eaten by their herbivores. Herbivorous insects exploit many different plants or plant parts for food. The number of plants that are suitable for the development of a herbivorous insect is limited, as plants do not wait passively to be ravaged by herbivory, and in fact, most plants produce two types of defenses: physical defenses (such as spines, thorns, tough tissues, sticky resins, and cuticles hairs) on the surface of the plant (Butler et al., 1991; Zhang and Feng, 2000) and chemical defenses (plant biochemicals) against herbivorous insects and other organisms (Waring, 1988; Becerra, 1997; Zhang and Feng, 2000).

Many of these chemicals have been called "secondary metabolites" (Rosenthal et al., 1979; Wink, 1988; Rosenthal and Berenbaum, 1991), because their functions are not part of normal essential (primary) metabolism. More than 10000 types of secondary metabolites have been identified in higher plants, and the majority of those whose function has been identified are alkaloids (such as caffeine and nicotine), terpenoids (terpene and pinene), and polyphenols (tannin and flavonoid) (Navon et al., 1993; Ayres et al. 1997). Thousands of secondary metabolites have been identified in plants, and many have clearly demonstrated defensive functions (Swain, 1977; Zummo et al., 1984; Gatehouse, 2002). Some of these secondary metabolites are fixed (constitutive resistance compounds) in plants, whereas others are only produced (induced resistance compounds) when the plant is attacked by biotic (herbivorous insects or other organisms) or abiotic factors (mechanical wound, ultraviolet, environmental stresses, and other abiotic elicitors) (Edwards and Wratten, 1983; Kang, 1995; Jansen et al., 1998; León et al., 2001; Mahan and Wanjura, 2005).

However, the long-term coevolution of herbivorous insects and plants has led to the development of an array of constitutive and induced resistance that enables plants to protect themselves from the attack of herbivores and other organisms (Becerra, 1997,2007; Rausher, 2001). Induced plant resistance to herbivores has received a great deal of attention, and there are a lot of studies that have documented such induced defenses (Karban and Myers, 1989). From the defensive insect pest's viewpoint, Karban and Myers (1989) suggested that the function of induced resistance was stronger than constitutive resistance strategy in plants.

As a crop plant, the cultivated cotton (*Gossypium hirsutum* L., *G. babardense* L., *G. herbaceum* L., and *G. arboreum* L.) performs through the secondary metabolites resistances to herbivory, and the resistances can also be classified into two types: constitutive and induced resistance. The constitutive secondary metabolites in relation to insect infestation have been discovered by numerous experiments in which the content of constitutive resistance compounds has been found in a cotton plant *in vivo* (Wilson and Szaro, 1989; Wilson et al., 1992; Tang and Wang, 1996a, 1996b; Tang et al., 1996, 1997). Indeed, in artificial cotton breeding, breeders sought out the textile fiber's quality, the low gossypol oil, and available proteins in cottonseeds, which resulted in much lower content of secondary metabolites (such as gossypol) than that in the wild species (Zhang and Feng, 2000). Thus, the high-quality cotton cultivars with the low constitutive resistance level are vulnerable to herbivory. In addition, since the cotton field (agroecosystem) is rich in nutrition for herbivorous insects, the cotton plant suffers from the plague of insect pests. However, biotic or abiotic factors can induce cotton resistance to herbivory, and the biotic factors (such as insect attack) are difficult to be used for pest control; whereas the abiotic factors may also change the physiological and biochemical conditions of cotton plant and increase the resistance level of cotton against herbivory or reduce their normal function or reproduction capacity. Therefore, this review article will discuss induced cotton resistance to herbivorous insects, with a special emphasis on the function of abiotic factors.

2 Chemical-based constitutive resistance to herbivorous insects in cotton

The total number of plant secondary metabolites whose structures have been elucidated is around 50000 (De Luca and St Pierre, 2000), but it may only be the tip of an iceberg in terms of the chemical diversity of the nature. Each plant species produces only a small fraction of this spectrum, but many of these compounds are of importance for the self-defense of plants (Wittstock and Gershenzon, 2002). It has been reported that there are three kinds of secondary metabolites in cotton cultivar (constitutive resistance

compounds) protecting against herbivorous insects and other organisms. They are mainly terpenoid, tannin, and flavone (Liu and Yang, 1990; Bohlmann et al., 1998; Zhang and Feng, 2000).

2.1 Terpenoid

Cotton is highly susceptible to insect feeding, but it has a wide variety of defenses against insects. For example, cotton is rich in terpenoid compounds like gossypol and the even more potent 'heliocides' which are toxic to *Helicoverpa* insects. The terpenoids are in pigment glands that are visible as black dots over most parts of the cotton cultivar (*G. spp.*) and their wild relatives (Gershenzon and Croteau, 1991). The glands in the reproductive organ (cottonseed) and over the entire aboveground portion of the cotton (foliage, stem, bract, sepal, and bell) contain a unique group of terpenes, which include desoxyhemigossypol, hemigossypol, gossypol, hemigossypolone, and the heliocides H₁, H₂, H₃, and H₄ (Altman et al., 1989; Liu and Yang, 1990; Hedin et al., 1992a; Benedict et al., 2004). These compounds have been shown to be important in protecting the plant from cotton insects. For example, the sesquiterpenoid is present in cotton cultivars and wild cotton species. Many experiments demonstrated to the hilt that gossypol is an all-important constitutive resistance compound in cotton (Bottger et al., 1964; Jiang and Yang, 1996). The gossypol can be toxic to many cotton lepidopterous larvae (e.g., *H. armigera*, *H. zea*, and *H. virescens*) (Wang, 1997; Wu et al., 1997; Liu et al., 2008). Gossypol in cotton leaves during the growing seasons can suppress the growth of lepidopterous larvae on high-gossypol cotton lines. The higher the content of gossypol is in cotton plant, the stronger the resistance to cotton insects is. As an example, Elliger et al. (1978) compared gossypol with heliocides H₁, H₂, and hemigossypolone for the preference of *H. virescens* and observed that all four terpenoids evidently inhibited the growth of tobacco budworm larvae. Zhu et al. (2000, 2001) showed that cotton pigment glands had a significant inhibitory effect on the growth and development of cotton bollworms. Moreover, *in vitro*, they also found that when the gossypol dosage was higher than 0.3% of the diet, the cotton bollworm would be poisoned. In addition, gossypol is also toxic to cotton aphids (*Aphis gossypii* Glover). Bottger et al. (1964) reported that gossypol level in the cotton lines that were resistant to aphids was markedly higher than that in the susceptible ones (Meng et al., 1999).

There are also many studies on the mechanism of resistance to insects by gossypol. Meisner et al. (1977, 1978) found that gossypol inhibited protease and amylase activity but did not affect invertase activity in the cotton leafworm (*Spodoptera littoralis*). Gossypol appeared to interact both with the enzyme substrate (i.e., casein) and with the protease enzyme. The study showed that gossypol was largely excreted in the bound form, which thus

decreased the nutritional value of the cotton plant material. Studies with non-ruminant animals showed that gossypol binded to free amino groups in proteins such as in lysine and thereby reduced the nutritional value of the feed. Likewise, the same appeared to be true for the budworm (Meisner et al., 1978). The authors concluded that either or both mechanisms could account for the activity of gossypol. The study by Hedin et al. (1988) strongly supported the view that gossypol acted as both a toxicant and an anti-feedant, especially in the early instar bollworm. Wang (1997) also discovered that gossypol significantly inhibited the activities of some proteinases and growth in cotton bollworm. There is no question that the terpenoid compounds (gossypol) are insurmountable for many cotton insects.

2.2 Tannin and flavonoids

Polyphenols are a large family of natural compounds widely distributed in plants. Tannins have been implicated in plant resistance to insects and diseases. Tannins are produced by plants and stored in plant vacuoles (Chan et al., 1978; Schultz, 1989; Wu and Guo, 2000; Gershenzon and Dudareva, 2007). They also have an important role in plant defense mechanism, and they are toxic to insects because they bind to salivary proteins and digestive enzymes resulting in inactivation of the proteins (Blytt et al., 1988). Insect herbivores that ingest high amounts of tannins fail to gain weight and may eventually die. The pigmented cotton, which is also less prone to bollworms attack, also possesses significantly high levels of condensed tannins that disrupt feeding and growth of chewing insects like *Helicoverpa*, *Heliothis*, and other similar species (Klocke and Chan, 1982; Smith et al., 1992; Navon et al., 1993; Wu and Guo, 2001), and sap-sucking species (Liu and Yang, 1991; Zhang and Liu, 2003; Ma et al., 2005). In addition, Wang (1997) reported that there were significant inhibitions caused non-interactionally by tannic acid and gossypol, in which the inhibition of the former was stronger than that of the latter, on the growth of cotton bollworm larvae.

Flavonoids are also a subclass of polyphenols and are widely distributed in the nature. More than 6000 different flavonoids have been identified. In cotton cultivars, flavonoids are very important chemicals resistant to herbivorous insects. Hedin et al. (1992b) found some prevalent flavonoids in *G. arboreum* and *G. hirsutum* tissues, which were proven to contribute to the resistance

to *Heliothis* feeding. The flavonoid chemicals resistant to pests, which mainly include rutin, isoquercitrin, and quercetin, could be detected and quantitatively analyzed. Their results showed that the contents of rutin, isoquercitrin, and quercetin were higher in petals, but lower in the calyx, bract, and cotton boll (Wu et al., 2000; Wu and Guo, 2001; Zhang et al., 2003). Cotton tannins flavonoids are important compounds associated with the resistance of the host plant to insect pests including *Helicoverpa* spp. and *Heliothis* spp. Wu and Guo (2001) also found the resistances of condensed tannins and flavonoids (gallo catechin, rutin, and isoquercitrin) in upland cotton. Their results demonstrated that these compounds were chronic toxins to the cotton bollworm *H. armigera* (Hübner). The expression of plant resistance belongs to quantitative defense, which is not easily adapted to by insects (Table 1).

3 Induced resistance to herbivorous insects in cotton

The expression of plant resistance to insects is also affected by previous stimuli. Prior wounding by insect or mechanical means induces increased resistance of many crop plants to insect damage. Kogan and Paxton (1983) defined induced plant resistance as “quantitative or qualitative enhancement of a plant’s defense mechanism against pests in response to extrinsic physical or chemical stimuli.” Over the past 20 years, induced plant resistance to herbivores has received a great deal of attention, partly because it has been thought that induced resistance might contribute to the regulation and cyclic fluctuation of insect herbivore populations (Tallamy and Raupp, 1991; Karban and Baldwin, 1997; Agrawal, 1998; Agrawal and Karban, 1999, 2000). Therefore, inducible resistances play a major role in the effects on herbivorous insects such as increased toxicity, delay of larval development, or increased attack by insect natural enemies (Baldwin and Preston, 1999).

3.1 Herbivore-induced volatiles (HIV) in cotton (qualitative defense)

Plant volatile chemicals play a decisive role in the plant–insect chemical communication and regulation of insect behaviors. Leaves normally release small quantities and a few kinds of volatile chemicals, but when a plant is damaged by herbivorous insects, many more volatiles (so-called herbivore-induced volatile (HIV)) are released (Lou

Table 1 Active traits of metabolic substances affecting insect herbivores (from Wu and Guo, 2001)

traits of effects	pre-ingestion	post-ingestion	
active results	deterents or repellence	acute	chronic
approach of effects	feeding behavior	physiologic metabolism	digestibility
expression of plant resistance	anti-xenosis or non-preference	antibiotic (qualitative defense)	antibiotic (quantitative defense)
evolution of plants-insects reaction	easy adaptation by insects	easy adaptation by insects	not easily adapted by insects

and Cheng, 2000; Röse and Tumlinson, 2004). The chemical identity of the volatile compounds varies with the plant species and the herbivorous insect species (Tallamy and Raupp, 1991; Röse and Tumlinson, 2005). These HIVs attract both parasitic and predatory insects that are natural enemies of the herbivores (Agrawal et al., 2000). They may also induce defense responses in neighboring plants. Such chemicals that function in communication among species, as well as those that serve as messengers between members of the same species, are called semiochemicals (León et al., 2001; Dicke et al., 2003; Gershenzon, 2007).

McAuslane and Alborn (1998) noted an increase in HIVs from the damaged cottons. Among the monoterpenes, β -ocimene, and myrcene had the largest increases by more than six-fold and four-fold, respectively; these compounds reacted with hemigossypolone to give off heliocides H₁ and H₄, and heliocides H₂ and H₃, respectively. The α -pinene, β -pinene and limonene increased by 3.2- to 3.6-fold. Damaged glanded plants released more than twice as many terpenes as undamaged ones. The monoterpenes have been shown to repel plant herbivores and in many cases cause herbivore death. Toxicity in some cases is due to the monoterpene volatile rather than direct contact (Paré and Tumlinson, 1997, 1999). The other HIVs, α -pinene, β -pinene, and limonene, among others, can attract natural enemies of herbivorous insect or become a semiochemical to connect neighboring plants (Paré and Tumlinson, 1997, 1999; Kessler and Baldwin, 2001; Kong and Hu, 2003). In addition, Mithöfer et al. (2005) found that controlled and reproducible mechanical damage that strongly resembled the insect's feeding process represented a valuable tool for analyzing the role of the various signals of HIV involved in the induction of plant defense reactions against herbivory. Although the use of plant volatile for monitoring and controlling insect pests, such as simple inexpensive sticky traps, has become standard monitoring tools in recent years, it should be emphasized that the first efforts to apply semiochemicals for crop protection be made with natural plant volatile.

3.2 Herbivore-induced accumulation of constitutive resistance compounds in cotton (quantitative defense)

Resistance of plants to insect herbivores is mediated via constitutive or induced defense mechanisms (Yuan and Xie, 2004). Induced resistance, which is a phenotypic response, happens when plants are attacked and damaged by herbivores and other organisms, which is analogous to immune response as performed in animals (Baldwin and Preston, 1999; Agrawal and Karban, 2000; Zhu and Zhao, 2003; Li et al., 2008). Herbivory-induced chemical defense is very common throughout the plant community. These inducible defenses can take many forms that target a variety of both herbivory and natural enemies. Plant toxins

are often produced in response to herbivory that can either kill the intruders outright or reduce their capacity for normal functioning or reproduction.

Plants respond to herbivory and become less palatable after browsing, due to changes in primary and secondary chemistry, which is known as induced resistance. Such induction has been directly related to foliage loss but has also been regarded as a chemical response initiated by the saliva of the herbivores during feeding. In cotton plant with condense terpenoids, McAuslane and Alborn (1998) also found a 33-fold increase in preference for undamaged terminal leaves from undamaged glanded plants by beet army worm larvae. Extracts from the terminal foliage contained significantly higher concentrations of hemigossypolone, gossypol, and the heliocides. Of these compounds, heliocides H₁ and H₄, which were derived from the reaction of hemigossypolone and β -ocimene, had the largest percentage increase of 351% and 487%, respectively. Hemigossypolone increased by 149%, gossypol increased by 124%, and heliocides H₂ and H₃ increased by 42% and 45% respectively (McAuslane and Alborn, 1998). In response to aphid infestation, the levels of tannin and free proline were increased in the infested cotton plants. All the compounds are important aphid-resistance factors in cotton (Liu and Yang, 1990, 1991). Compounds of constitutive resistance are increased and accumulated markedly in supra experiments. In this way, cotton resistance levels are higher than that prior to inducing.

The mechanism by which a plant becomes resistant after infestation by a pest is not clear. Wang and Wang (2001) detected that polyphenol oxidase (PPO) activity in high resistant cotton increased quickly, but susceptible cultivars increased slowly after aphid feeding. No significant differences in PPO activity were found among all cotton varieties before aphid feeding. Resistance of cotton against aphid was positively correlated with PPO activity. In plants, several defense signaling pathways have been demonstrated to be regulated by low-molecular-weight signal molecules, such as salicylic acid (SA), abscisic acid, jasmonic acid (JA), methyl acrylate (MA), and ethylene (ET). The major aspects of these pathways have been genetically defined, revealing a linkage among them (Hudgins and Franceschi, 2004; Grennan, 2008; Kazan and Manners, 2008). These signal molecules may involve a change in gene expression in the signaling pathways. Herbivore-induced may be a priming agent to initiate plant defense responses signaling pathways.

3.3 Abiotic-elicitor-induced resistance in cotton

Induced responses are changes that occur after herbivores (biotic factors) attack. Many studies have documented negative effects of induced responses on herbivores preference or performance (Tallamy and Raupp, 1991; Karban and Baldwin, 1997). Abiotic factors, including natural and synthetic compounds, can also initiate plant

induced responses to herbivory. A few exogenous abiotic factors (so-called abiotic elicitors) (Benhamou, 1996), as well as some natural endogenous compounds (JA, ET and MA), have been applied in crop plants to protect against future and more damaging attackers (Sembdner and Parthier, 1993; Thaler, 1999). The benzo (1,2,3) thiadiazole-7-carbothioic acid(s) methyl ester (BTH) is another excellent exogenous organic elicitor of the SA activated defensive pathway in cotton, inducing remarkable enzymatic activities both locally and systemically (Inbar et al., 2001; Moshe et al., 2001).

In China, the method of plumular axis cutting was used to induce the resistance of cotton plants to cotton bollworms (*H. armigera*) in a laboratory (Zhang et al., 1998; Li et al., 2000; Wang et al., 2000). The polyphenols and terpenoids of cotton plants after treatment were higher than that of the control. The results suggested that plumular axis cutting could induce the resistance of cotton plants to bollworm and influence the growth and development time of bollworms through retarding their feeding and digestion. These tests can be carried out by wounding-induced resistance to insects in a laboratory but are difficult to be extensively employed in cotton fields.

Metal elements can also promote the accumulation of plant secondary metabolites. For instance, Li et al., (1999) documented that accumulation of taxol as one of a secondary metabolites synthesis in cell suspension cultures of *Taxus chinensis* was measured after elicited by cupric chloride (CuCl_2). Up to now, we still know little about how many variations in the relationship between induced accumulation of secondary metabolites and metal elements elicited exist within plant resistance. However, we can track this clue to lucubrate their internal relationship.

4 A novel concept for induced resistance to insect in cotton

By definition, plant induced resistance differs from constitutive resistance in that induced resistance is activated and expressed only after the plant is attacked by herbivorous insects or otherwise injured; constitutive resistance is expressed independently of injury (Karban and Baldwin, 1997; Agrawal and Karban, 2000). The compounds of constitutive resistance and their spatio-temporal distribution are determined by plant genotype.

In many crops, the secondary metabolites that originally evolved under a natural selection pressure for a specific function have been altered by traditional breeding. For cultivated cotton, traditional plant breeding has often directly or indirectly reduced quantities at the levels of secondary metabolites (e.g., gossypol), though the high fiber quality or low gossypol cottonseed is achieved in the presented cultivars. However, compared with the related wild species, the resistance to insect of cultivated cotton is weakened. At least, the constitutive resistances are weak in

cultivated cotton. In this case, how to enhance the quantities of presented glanded cotton cultivars in constitutive resistance compounds against insect is the issue to be focused on.

In general, as mentioned above, the secondary metabolites can be synthesized during the stationary phase of the growth cycle of cotton, and increased accumulation of the secondary metabolites in cultivated cotton foliage is also a general herbivore-induced response. However, herbivore-induced resistance cannot be controlled, and therefore, it is not a practical tool to use in agriculture because inducing plants with herbivores to protect against future and more damaging attackers is generally not feasible. On the other hand, abiotic-factor-induced resistance may be a novel way to induct resistance to insect in cotton. Based on the fact that accumulated compounds (such as gossypol) are the responses after herbivore-induced resistance or other environmental stirring, there should be an enzyme (or series of enzymes) whose activity must be enhanced in cotton plant.

Chen et al. (1995) and Davila-Huerta et al. (1995) provided a clue for a possible answer. They confirmed that the cotton (+)- δ -cadinene synthase (CDNS) catalyzed biosynthesis of gossypol. The CDNS is a branch point enzyme in the general isoprenoid pathway, and the CDNS multigene family comprises a complex set of genes differing in their temporal and spatial regulation and is responsible for different branches of the cotton sesquiterpene pathway (Davis and Essenberg, 1995; Chen et al., 1996; Luo et al., 2001). As another clue, in *Capsicum*, the CDNS is also found and named sesquiterpene cyclase for the synthesis of phytoalexin (terpenoid compound). He et al. (2001, 2002a, 2002b) reported that the activity of sesquiterpene cyclase could be induced by some abiotic factors (sodium chloride, cupric chloride, mercuric chloride, and ultraviolet ray). With respect to secondary metabolites accumulation, Ti (1999) found a similar result that when cotton leaves were treated by cupric chloride in a special stage, the contents of gossypol and other terpenoid were increased (unpublished data). The results indicated that the CDNS may also be activated by exogenous inorganic compounds. Consequently, cupric ion may be an exogenous elicitor to induce accumulation of terpenoids in cotton and is referred to as a copper-inducible elicitor (CIE).

Our objective in this review is to provide a novel concept for induced resistance to insect in the context of plant-herbivore interactions, suggesting future directions for research of the physiological mechanisms responsible for CIE. The action of CIE differs from herbivore-induced and others-induced resistance, which confers resistance against the herbivorous insect through controlled exogenous compounds and does no harm to the plant. As such, the secondary metabolites accumulated with CIE should be a new way in the Integrated Pest Management (IPM) in cotton plant.

5 Discussion and future prospect

Cotton is the world's leading natural fiber and second largest oilseed crop. In addition to textile manufacturing, cotton and cotton-byproducts are the sources of wealth of consumer-based products. China is one of the largest producers of cotton in the world. Cotton is an important fiber crop that has historically experienced serious insect pest problems. Insect pests such as cotton bollworm, cotton aphid, and mirids are the major factors that contribute to the decrease in cotton production. Traditional control approaches rely on the use of costly insecticides. Chemical insecticide control has been the most common method for the control of these insect pests. Although this method has been effective against many insects, it has serious drawbacks and continued reliance on it is not a sustainable pest control strategy. To reduce harmful impacts on the environment at present, genetic engineering and biotechnology offer great potential in the identification and transfer of resistance genes from distant relatives or even unrelated plant species. Studies are in progress to produce genetically modified organism (GMO) with genes to produce *Bacillus thuringiensis* (*Bt*) toxins and protease inhibitors to make the plants resistant to insect attack. However, results of biosafety research showed that these methods had some potential hazards of gene flow, insect resistance, non-target insects, and so on (Jia and Peng, 2002; Deng et al., 2006). Therefore, to control insect pests, we must search for other novel ways in the functionally related system of the current IPM. IPM has a number of advantages for cotton resistance; one of them is its excellent compatibility. IPM system can help reduce the amount of insecticides.

A number of alternative insect pest control tactics have the potential to supplement and reduce reliance on chemical insecticides. Some of these are already available to growers, but others need further research to become a practical proposition. There are some new approaches for enhancing plant resistance to herbivorous insects in IPM.

First, there is a changing world view from "Save the world from famine and disease" to "Save the world from pesticides and genetically modified (GM) crops" (Kidd, 2002). This view emphasized that the IPM system has an important role in insect pest control. The IPM techniques include using beneficial insects and diseases, cultural control practices, and other methods non-harmful to the environment to the fullest extent if it is possible. Although chemical insecticides are still the most important suppression approach, they should be used selectively and at the proper rate and time.

Second, it should also be emphasized that the approaches to apply semiochemicals or plant-signaling compounds for cotton protection be utilized with natural plant volatiles. Plant volatile chemicals play a decisive role in the plant-insect chemical communication, and they

regulate insect behaviors. For example, some volatile terpenoids that induced by cotton pest can attract natural enemies of these insects or keep these insects away from cotton plant. The technology of using plant volatile in integrated pest management of insect pests appears to have virtually limitless possibilities and can provide the impetus for the development of novel methods of insect pest reagent of suppression. In another way, in *Zea mays*, researchers have induced emission of terpenoids and indole by controlling abiotic factors (soil humidity, air humidity, temperature, light, and fertilization rate in young corn plants) (Gouinguene and Turlings, 2002).

Third, historically, most research has focused on the action of the secondary cotton metabolites and the relation of secondary metabolites in plant and its herbivorous insect. Although many studies have examined the herbivore-induced resistance to herbivorous insect in cotton cultivars (see earlier citations), far fewer studies have examined the abiotic-elicitor-induced resistance to herbivory. However, the mechanisms that caused constitutive resisting compounds' accumulation in cotton plant by CIE-induced synthesis are unknown. There are many questions remaining to be answered. For instance, how does CIE, an exogenous inorganic compound, induce the terpenoids accumulation? Is it in the same pathway as the herbivore-induced resistance? How does the cupric chloride initiate CDNS activity and whether the metal element is a clue to find micro-evolution of cotton and insect with environmental factors concerned?

Finally, it is difficult to investigate the interaction of plants with their herbivorous insects. There are many biotic and abiotic factors that are associated with plant induced resistance. Therefore, to uncover the mechanisms of induced resistances in plants, the research of plant-insect interactions must combine multiple disciplines of sciences, such as botany, entomology, biochemistry, chemistry and agriculture.

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