Chapter 20

MECHANISMS OF COTTON RESISTANCE TO ARTHROPOD HERBIVORY

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1. INTRODUCTION

The cotton crop is host to a wide range of arthropod pests (Hargreaves, 1948; Room, 1979a). Key pests, *i.e.* those that are persistent, occur perennially, and usually reach economically damaging levels (Hearn and Fitt, 1992) have been characterized for most cotton-cropping systems worldwide. The identification and biology of key cotton pests, their economic importance, and methods for their control have been the focus of recent reviews by Frisbie *et al.* (1989), Hearn and Fitt (1992), Fitt (1994), Luttrel (1994), Luttrel *et al.* (1994), Ramalho (1994), Sugonyaev (1994), Vaissayre (1994), Matthews and Tunstall (1994), Hillocks (1995), and Pyke and Brown (1996).

Various terms have been used to describe the different kinds of plant responses to pests (Hooker, 1984). For the purposes of this chapter, we will consider that plant reactions to a given pest grade continuously from full resistance to the extreme sensitivity of those plants that are unprotected and unable to regrow after damage (Painter, 1951; Hooker, 1984; Belsky *et al.,* 1993). In this context, our aim is to analyse the mechanisms of cotton resistance to arthropod herbivory.

This chapter takes a "phytocentric" view of plant-herbivore relationships (Baldwin, 1993). This means that we shall concentrate on physiological and morphological plant and crop traits relevant to herbivory resistance; the effects of the cotton plant on its pests are only considered when necessary to characterise resistance mechanisms. Cotton resistance to arthropod herbivory has been the subject of reviews that emphasised general yield responses to pests (Brook, 1984; Matthews, 1994a), chemical defenses (Bell, 1984b, 1986), breeding for resistance to arthropods (Thomson and Lee, 1980; Thomson, 1987; El-Zik and Taxton, 1989; Smith, 1992; Gannaway, 1994; Jenkins, 1994) and responses to reproductive damage (Sadras, 1995).

Understanding the physiological and morphological adaptations of cotton to arthropod pests is important for the improvement of pest management practices. For instance, a threshold for pest management of z insects per m^2 implies that (i) a fraction, f, of those insects will die due to various factors (*e.g.,* predation); and (ii) that the crop will be able to cope with the damage caused by the surviving $f \times z$ insects. Following with this example, an understanding of the plant and environmental factors that affect the responses of the crop to a given level of damage could assist in developing more precise thresholds for pest management. Thus, assuming that understanding the mechanisms of resistance to pests is important not only for breeding but also for pest and crop management, we have focussed on resistance traits broadly, irrespective of whether or not the traits are relevant for breeding purposes.

Ecological theories provide a valuable background to study the relationships between the cotton crop and its pests (*e.g.,* Gutierrez *et al.,* 1979a; Felton *et al.,* 1989; Sadras, 1996c). We have thus highlighted the ecological principles underlying these relationships. Within this framework, we have analysed the mechanisms of cotton resistance to arthropods including (i) **avoidance**, *i.e.,* escape in space and time, and chemical and morphological defenses; and (ii) **tolerance**, *i.e.,* recovery after damage. We have intentionally emphasised the analysis of tolerance mechanisms. This

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is because, in the past, most research on plant resistance to arthropods has focussed on avoidance traits. For instance, a whole chapter in the previous "*Cotton Physiology*" book dealt with the physiology of secondary products, but none dealt specifically with tolerance to herbivory. Our emphasis on tolerance is therefore not a matter of value, *viz.* we do not consider tolerance to be more or less important than avoidance.

Mechanisms of resistance to arthropods were analysed at various scales, from the molecular to the crop level. The relationship between avoidance and tolerance traits is discussed with emphasis on its implications for breeding varieties with enhanced resistance to pests. Multiple interactions between biotic and abiotic stresses are outlined and directions for further research on cotton responses to herbivory are indicated.

2. ON PLANTS AND THEIR HERBIVORES

This section introduces two contrasting views of plant-herbivore relationships, briefly describes the general responses of crop yield to damage by herbivores, and outlines individual- and population-level mechanisms related to the adaptation of plants to herbivory.

2.1 Antagonism vs Mutualism

The sessile mode of life imposes obvious restrictions for plant survival, *e.g.,* plants cannot run or fly away when threatened by herbivores. Equally obvious is that plants survived because they developed traits for resistance to environmental stresses, including herbivory (Trewavas, 1981). Following this line of thought, relationships between plants and their natural enemies are usually regarded as the result of an antagonism between the ability of herbivores to attack their host and the ability of the host plant to resist such attack (Futuyama and May, 1991; Marquis and Alexander, 1992).

In contrast to this antagonistic view of the relationship between plants and herbivores, it has been proposed that, in some cases, herbivory may increase plant growth and fitness (Owen, 1980; Owen and Wiegert, 1976, 1981; Hilbert *et al.,* 1981; McNaughton 1983a; Paige and Whitham, 1987; Verkaar, 1988; Maschinski and Whitham, 1989; van der Meijden, 1990; Whitham *et al.,* 1991; Vail, 1992; Littler *et al.,* 1995). Owen's (1980) interpretation of the benefits that plants can obtain from their relationships with aphids is an example of this mutualistic view (section 3.2.6). Whether plants and herbivores have evolved a dominantly antagonistic relationship or some form of mutualistic relationship is a highly controversial issue that is out of the scope of this chapter. Readers interested in this debate may refer to Owen (1980), McNaughton (1983a, 1986), Crawley (1987), Aarsen and Irwin (1991), Whitham *et al.* (1991), Bergelson and Crawley (1992), Belsky *et al.* (1993), Mathews (1994), and Vail (1994).

2.2 Crop Yield and Herbivores

General crop yield responses to herbivory have been reviewed by Jameson (1963), Bardner and Fletcher (1974), and Harris (1974). Plant growth and crop yield can be reduced, unaffected, or increased by herbivory. Harris (1974) emphasised the cases in which yield increases have been observed following insect damage. It is of course easier to find examples in which arthropod herbivory reduced rather than increased crop yield (Harris, 1974) but reports of no yield loss or moderate yield increases of cotton crops following pest or artificial damage are not uncommon (*e.g.,* Prokof'ev and Rasulov, 1975; Harp and Turner, 1976; Renou and Aspirot, 1984; Chen *et al.,* 1991; Brook *et al.,* 1992abc; Dyer *et al.,* 1993; see also Table 1 in Sadras, 1995). Physiological mechanisms underlying yield increases after damage in cotton have been discussed by Renou and Aspirot (1984), Gutierrez *et al.* (1979a), Brook *et al.* (1992b), and Sadras (1995). A detailed analysis of the main morphological and physiological responses of cotton plants and crops to different types of damage is presented in Section 3.2.

2.3 How Do Plants Cope with Herbivores?

While ecologists debate whether herbivory is beneficial to plants or not (Section 2.1), cotton growers usually regard pests as detrimental to yield (but see Dyer *et al.,* 1993). From an agronomic perspective, the conservative view of an antagonistic relationship between a crop and its herbivores is not surprising and, in many cases, justified as yield and economic losses due to pests may be quite large. This antagonistic view is, however, a primary obstacle for the implementation of integrated-pest management programmes.

Many schemes have been proposed to characterise the ways in which plants can avoid herbivory and recover after damage. These schemes place emphasis on different aspects of plant-herbivore interactions depending on the objectives of the analysis. For instance, the framework of Painter (1951) is particularly appropriate for entomological studies, the classification of Thomson (Thomson and Lee, 1980; Thomson, 1987) is useful for breeding purposes, while White (1993) emphasises the role of plants as a source of nitrogen for herbivores. A plant-centred approach, is more appropriate for the objectives of this chapter (see Introduction).

Plants may avoid damage via escape in time and space. They may also avoid damage through morphological and chemical defenses. General escape and defense strategies have been discussed in a number of studies (*e.g.,* Painter, 1951; Crawley, 1983; Chapin *et al.,* 1987; Karban and Myers, 1989; Zangerl and Bazzaz, 1992, Tuomi, 1992; Baldwin, 1993) and are further examined in section 3.1.

The strategy of tolerance depends on morphological and physiological traits that, rather than protect the plants from damage, allow them to regrow after damage has occurred (Belsky *et al.,* 1993). Interestingly, both plant- and animal-centred approaches define "tolerance" in similar terms (*cf.,* Belsky *et al.,* 1993 and Painter, 1951). Tolerance traits are important for recovery not only after damage caused by herbivores but also after damage caused by physical factors such as hail, wind, or fire (Belsky *et al.,* 1993). General tolerance traits have been reviewed recently by Belsky *et al.* (1993), Trumble *et al.* (1993) and Rosenthal and Kotanen (1994) and are discussed in section 3.2.

Since damage by pests in field crops is generally heterogeneous in space and time, population-level compensation needs to be considered. Population-level compensation, according to Crawley (1983), occurs when "herbivore attack on one individual allows another individual to grow more rapidly." Section 4 discusses population-level responses to herbivores in cotton.

Despite the commonly accepted view that cotton is highly susceptible to arthropod herbivory, the previous discussion highlights that (i) plants are not passive victims of herbivores, and (ii) in some cases herbivory may be neutral or even positive for plants.

3. RESISTANCE TO HERBIVORY: AT THE PLANT LEVEL

Analysis at the molecular level is required to understand some resistance traits (*e.g.*, chemical defenses). Other traits require to be analysed at the organ level (*e.g.,* okra leaf). Analyses at these levels of organisation are necessary and have been included in this section. They are, however, not sufficient to understand the role of these traits in plant resistance to herbivory, the level of the physiological unit at which they operate, the whole plant, needs to be considered. The discussion about using artificial diets as a method to investigate defensive compounds (section 3.1.2) highlights the risk of taking reductionist approaches in research of plant resistance to arthropod pests.

3.1 Avoidance

Avoidance mechanisms discussed in this section include escape, also referred to as phenological asynchrony and host evasion, and chemical and morphological defenses.

3.1.1 Escape

Earliness is a characteristic often sought in cotton cropping systems due to its implications for pest management. Earliness, however, has also implications for other agronomic outcomes, including yield and quality. It is interesting to note, for instance, that earliness has been favoured during early stages of cotton domestication (Fryxell, 1978) and, more recently, by breeding and selection for high yield potential (Culp, 1994).

Genotype and crop management are the two keys for the manipulation of crop phenological development. Cotton genotypes selected for earliness may allow the plant to avoid pest damage (Smith, 1992). These genotypes are valuable for managing boll weevil, Heliothine (= budworm-bollworm complex; *Heliothis* spp.- *Helicoverpa* spp.) and pink bollworm populations in regions where cultivation of early maturing varieties is feasible (Walker and Niles, 1971; Gannaway, 1994). Fast-fruiting genotypes produce bolls that escape first-generation weevil damage (Walker and Niles, 1971). The resulting reduction in pesticide usage required for boll weevil control may also delay the build-up of Heliothines due to preservation of natural enemies (Smith, 1992). The utilisation of early maturing varieties has been successfully adopted in the U.S. and Brazil (Luttrell *et al.,* 1994; Luttrell, 1994; Ramalho, 1994).

In addition to early maturing varieties, time of maturity can be modulated (and thus pest avoidance can be achieved) through appropriate crop management practices. Watson *et al.* (1978), for instance, indicated that the impact of pink bollworm can be reduced by manipulating the time of last irrigation to terminate crops early. Chu *et al.* (1996) have assessed the results of mandatory short-season cotton management systems in the Imperial Valley of California. The aim of this program, established in 1989, is to reduce pink bollworm populations in the area by optimising the host-free period. The system comprises a number of components, including reference dates for (i) earliest sowing, (ii) defoliation, and (iii) stalk destruction and plow down. The authors of this study regard the short-season cotton system as very effective in reducing pink bollworm abundance and boll damage. These effects were partially confounded, however, with the effects of reduced cotton production in the Imperial Valley during the period of their assessment (Chu *et al.,* 1996).

Plant traits and cropping strategies that affect the fitness of pests have the potential for the selection of "resistance" in the target pest population. Insect resistance to insecticides is the most obvious example of this process (see Section 3.1.2 *Biotechnology and Plant Resistance* below). We are not aware of development of resistance to strategies based on earliness or phenological escape in cotton. Chu *et al.* (1996), however, pointed out that the short-season cotton system mentioned above implies a risk of selection for early diapausing pink bollworm larvae due to diminishing bollworm food sources. An interesting case of "resistance" to cropping strategies based on escape *via* crop rotations has been reported for corn (*Zea maize* L.) rootworm in the central U.S.A. (Karlen *et al.,* 1994). In a monoculture maize production system, rootworm reaches an economic threshold about 30% of the time, but in a 2-year maize/soybean (*Glycine max* L.) rotation, the threshold is reached less than 1% of the time. However, increased use of the 2-year maize/soybean rotation has resulted in selection for rootworms with a 2-year (rather than the normal 1-year) diapause.

3.1.2 Defenses

The development of insect resistance to insecticides has greatly accelerated the emphasis on cotton resistance to herbivores during the last several decades (Smith, 1992). This research has culminated in the identification of scores of morphological and biochemical defenses (Bell, 1984b; 1986; Smith, 1992). It is not our purpose here to review the details of these traits; the reader is referred to several excellent reviews and historical perspectives (Hedin *et al.,* 1976; Thomson and Lee, 1980; Thomson, 1987; Benedict *et al.,* 1988; Jenkins *et al.,* 1991; Wilson, 1991; Gannaway, 1994; Smith, 1992; Summy and King, 1992). Morphological traits such as frego bract, nectariless, glabrousness, pilosity, okra-leaf, rugate bolls, reduced branching, stem-tip stiffness, red leaf coloration and reduced anther numbers are associated with plant resistance (Thomson and Lee, 1980; Thomson, 1987, 1994; Smith, 1992; Gannaway, 1994). Genotypes possessing these traits are often less preferred for feeding and/or oviposition and may be associated with greater arthropod mortality.

The cotton plant possesses a rich abundance of phenolic and terpenoid compounds that may reduce host suitability to arthropod pests. These phytochemicals may be directly toxic and/or interfere with the utilisation of essential nutrients. Phenolic compounds include condensed tannins, flavonoids (*e.g.,* quercetin glycosides, chrysanthemin; Hedin *et al.,* 1983; Hedin *et al.,* 1992), benzoic acids (*e.g.,* syringic acid; Benedict *et al.,* 1988), and cinnamic acids (*e.g.,* chlorogenic acid; Benedict *et al.,* 1988). Among the terpene aldehydes are gossypol, gossypolone, heliocides, and hemigossypol (Stipanovich *et al.,* 1988). Although extensive efforts on identifying sources of resistance to herbivory have been conducted in cotton, there is considerable germplasm, particularly with the Asiatic cottons, that remains to be tested for relevant traits (*e.g.,* Stanton *et al.*, 1994).

Despite these extensive research efforts several complications exist in employing these traits for enhancing plant resistance. First, conference of resistance to one pest may produce increased susceptibility to another. For example the frego bract trait confers resistance to the boll weevil, yet increases susceptibility to plant bugs. Likewise, gossypol may provide resistance to Heliothines, but increase susceptibility to thrips. Part of the contradiction between responses to quantitative traits may arise because ranges of these traits may exist that maximise resistance to a given pest species. This is the case, for instance, for aphids in relation to hairiness: they seem to prefer moderately hairy genotypes over glabrous or pilose surfaces (Jenkins, 1995). The multiple effects of a given resistance trait highlight the need for breeding programs that focus (i) on broad spectrum resistance (*e.g.,* El-Zik and Thaxton, 1989; Calhoun *et al.,* 1994) and (ii) on positive balances whereby the enhancement of resistance associated with certain traits outweighs their detrimental effects. The successful inclusion of the okra-leaf trait in Australian varieties illustrates this point (Thomson, 1994).

Second, reduced quality and/or quantity in yields often accompany expression of these traits. For instance, high amounts of gossypol or tannins in cottonseed are undesirable due to their toxicity in feed and oil products (Yu *et al.,* 1993). Heavy pubescence responsible for enhanced resistance to some arthropods produces commercially unacceptable amounts of "plant trash" in mechanically harvested cotton (Smith, 1992). On the other hand, characters such as nectariless in certain genetic backgrounds do not negatively impact yields (Gannaway, 1994). The "penalties" potentially associated with resistance traits are further considered in section 3.3.

Third, artificial diet bioassays for assessing the toxicity of certain phytochemicals (*e.g.,* phenolics) may be ineffective for assessing their true role in resistance. For example, condensed tannins incorporated into the artificial diet of the bollworm/budworm strongly inhibit larval growth at concentrations above 0.2% dry weight (Reese *et al.,* 1982); however, larvae flourish on cotton tissues where tannin concentrations may exceed 10% dry weight. Furthermore, budworm growth and survival were not affected by several breeding lines selected for elevated tannin concentration (Smith *et al.,* 1992). Another similar discrepancy is with one of the major phenolic acids in cotton, chlorogenic acid. Amount of this phenolic increases significantly in cotton foliage following herbivory by the bollworm or budworm (Bi *et al.,* 1997; G. Felton, unpublished data). Because of this, and because chlorogenic acid is toxic in artificial diet to the budworm or bollworm (at concentrations exceeding 3 mmol g^{-1} wet weight; G. Felton, unpublished data), it is reasonable to suggest that it may have a defensive role in the plant. However, in tobacco (*Nicotiana tabacum* L.) plants which have been transformed to overexpress or underexpress chlorogenic acid, budworm growth is unaffected by this phenolic at concentrations ranging from 0.1 to 6.0 mmol g^{-1} wet weight (J. Bi, G. Felton, R. Dixon, C. Lamb, unpublished data). The discrepancy between plant and artificial diet assays may be due to many reasons including: (i) other phytoconstituents, missing in artificial diets, could interfere with the action of otherwise toxic compounds; (ii) changes in the concentration and/or distribution of putative toxic compounds among plant organs and with ontogeny (*e.g.,* Gubanov, 1966; Lane and Schuster, 1981); (iii) feeding pattern of arthropods in intact plants could allow them to avoid tissues with high concentration of toxic compounds (Parrott *et al.,* 1983); and (iv) behaviour of arthropods may affect the concentration of secondary compounds, *e.g.,* rolling over of leaves by caterpillars may reduce tannin concentration (Sagers, 1992). Whether artificial diets are truly suitable for assaying other cotton phytochemicals (*e.g.,* terpene aldehydes), will require similar tests using transgenic plants that have been specifically transformed for altered expression of the specified biosynthetic pathways. Otherwise, research efforts based solely upon evidence from artificial diets may be futile.

Induced Defenses. Induced defense is defined as situations where herbivory (or other agents) alters the physiology of the plant such that it becomes less suitable for pest feeding, growth, development, survival, and/or reproduction. From a complementary perspective, induced defense is viewed as a strategy that adjusts the defense level to the prevailing risk of herbivory in contrast to constitutive, invariant defense level (Åström and Lundeberg, 1994).

Induced defense in cotton has been established by the pioneering work of Karban and co-workers (Karban and Carey, 1984; Karban, 1987; 1988; Karban *et al.,* 1987; Karban and Meyers, 1989; Brody and Karban, 1989; 1992). They have demonstrated that induced defenses can markedly decrease the population growth of spider mites (Karban and Carey, 1984; Brody and Karban, 1989). Furthermore, defenses induced by one pest (*e.g.,* spider mites) may offer cross protection to multiple insect pests (*e.g., Spodoptera exigua;* Karban, 1988) and phytopathogens (Karban *et al.,* 1987).

Recent work on understanding the biochemical basis for induced defenses may aid in the development of varieties with "heightened" resistance (Hampton, 1990; Bi *et al.,* 1997). Brody and Karban (1992) have already shown that certain genotypes possess high levels of induced defenses, and thus could provide the genetic basis for further selection. Entomologists at the University of have been investigating the biochemical basis of resistance induced by bollworm or budworm feeding. The growth rate of larvae on previously fed-upon plants was significantly reduced compared to those feeding on unwounded plants. Bi *et al.* (1997) have found that herbivory on foliage or squares/bolls results in an extensive change in plant metabolism, as indicated by a decline in the nutritive content of cotton tissues accompanied by a shift to a more oxidative, antibiotic state. They have identified at least three proteins (*i.e.,* ascorbate oxidase, diamine oxidase, and peroxidase) that are strongly induced by herbivory. If these proteins are causally linked to defenses, then amplification of the genes encoding these proteins could be used to produce varieties with enhanced resistance. Overall, research on cotton proteins associated with arthropod or phytopathogen resistance has lagged behind most major crops (Liu *et al.,* 1995).

Furthermore, knowledge of the systemic signalling pathways for inducible defenses may offer an additional avenue for exploitation. For instance, in the tomato (*Lycopersicon esculentum* L.) plant, expression of the gene for the translocatable peptide, systemin, promotes the expression of defense genes for protease inhibitors and polyphenol oxidases resulting in enhanced insect resistance (Orozco-Cardenas *et al.*, 1993; Constabel *et al.*, 1995). In this case, expression of one gene may in fact lead to multicomponent resistance. Greater knowledge of the defense-signalling pathways in cotton is needed.

Another interesting approach for employing induced defenses involves the use of chemical elicitors. Several large agro-biotech firms are developing chemical elicitors (*e.g.* benzothiadiazole, 2,6-dichloroisonicotinic acid) for systemic acquired resistance to phytopathogens (Ward *et al.*, 1991; Gorlach *et al.*, 1996). A similar approach may be feasible for insect resistance. Preliminary data with cotton has shown that the application of minute concentrations of the signal compound, jasmonic acid, to cotton enhances resistance to the bollworm (G. Felton, unpublished data). This compound is essentially nontoxic and has been used for years as a component of many perfumes. Levels of the putative defense compound, gossypol, are increased by foliar applications of cytokinins (Hedin and McCarty, 1994b). Furthermore, defenses can be induced by application of spores from *Bacillus* spp. (Benedict *et al.*, 1988).

Price *et al.* (1980) suggested that enemies of herbivores may be considered "plant defenses." Following Price *et al.* (1980), the release of herbivory-induced volatile chemicals that attract parasitoids and predators to damaged plants (McCall *et al.*, 1994; Turlings and Tumlinson, 1992; Turlings *et al.*, 1995; Röse *et al.*, 1996) can also be considered, broadly, as a form of "induced defense". Thus, induced resistance may not only be directly targeted against the pest, but may also be indirect such that the impact of natural enemies on pest populations is increased (Turlings *et al.*, 1995). The chemical nature of compounds released by cotton plants in response to damage by insects and/or manual damage have been investigated in several laboratory studies (*e.g.* Röse *et al.*, 1996). There are, however, many questions remaining about the effectiveness of this form of indirect resistance, notwithstanding the question whether these same volatiles may attract herbivores. The defensive role of volatile chemicals is further discussed in section 4.1.

Biotechnology and Plant Resistance. Striking successes in enhancing plant resistance are possible with the advent of biotechnology. The development of transgenic cotton expressing the endotoxins from *Bacillus thuringiensis* (= Bt cotton) has been a remarkable story of years of basic research on microbial, plant, and insect biology, culminating in its commercial release (Perlak *et al.*, 1990; Benedict *et al.*, 1992, 1996; Wilson *et al.*, 1992, 1994; Carlton and Gawron-Burke, 1993; Fitt *et al.*, 1994; Cannon, 1995; Halcomb *et al.*, 1996). Nevertheless, the utilisation of Bt cotton is not without concerns, some emotional, but some scientifically valid (Fitt *et al.*, 1994; Raybould and Gray, 1994; Lefol *et al.*, 1995; Nap *et al.*, 1996). The potential for development of insect resistance to Bt cotton is a major, well recognised problem (Whalon and McGaughey, 1993; McGaughey, 1994; Tabashnik, 1994a). Strategies to manage or delay resistance to Bt have been delineated in several excellent reviews (Tabashnik, 1994b; Tabashnik *et al.*, 1991; Gould *et al.*, 1994; Forrester, 1994; Roush, 1994ab; Kennedy and Whalon, 1995) and will not be further addressed in this chapter. Other problems associated with the commercial use of Bt cotton that remain to be solved include changes in pest status associated with altered patterns of pesticide use, the declining Bt expression during the late stages of the crop cycle (Fitt *et al.*, 1994) and transient decline in Bt efficacy probably associated with environmental stresses (*e.g.,* Forrester and Pyke, 1997). Importantly, the introduction of *Bacillus thuringiensis* genes into cotton does not seem to have reduced the considerable capacity of the crop to tolerate insect damage (Sadras, 1998). Tolerance to damage in Bt cotton is obviously important as the crop remain vulnerable to non-lepidopteran insects and, when the efficacy of Bt toxins falls because of ontogenetic and/or environmental factors, to lepidopteran pests also.

Bt cotton is only the beginning. The continued identification of genes encoding insecticidal proteins will lead to new products as the cultivation of cotton continues through the 21st century. The fungal enzyme, cholesterol oxidase, has been shown to be a potent toxin against the boll weevil (Purcell *et al.*, 1993; Greenplate *et al.*, 1995) and to offer partial resistance to lepidopteran larvae (Purcell *et al.*, 1995). Whether cultivars expressing the cholesterol oxidase gene are ever commercially acceptable, of course, depends upon a host of factors such as health concerns regarding ingestion of cholesterol oxidation products in food or feed products, reduced crop yields, environmental impact, and non-target effects on natural enemies, pollinators, etc. This example, however, illustrates the enormous possibilities awaiting discovery and employment of new defense genes.

Expression of the gene for tryptophan decarboxylase from *Catharanthis roseus* into *Petunia hybrida* offers potential for resistance against the whitefly *Bemisia tabaci* and related pests (Thomas *et al.*, 1996). Expression of the gene in cotton is a goal of this research (J. Thomas, personal communication). However, one drawback may be that expression of this enzyme [in potato *Solanum tuberosum* L.)] results in suppression of phenolic biosynthesis (Yao *et al.*, 1995). The altered metabolism has the disastrous consequence of greatly increasing the susceptibility of potato to the pathogen *Phytophtora infestans* (Yao *et al.*, 1995). This illustrates an important concept; whenever plant metabolism is genetically redirected towards expression of novel gene products or towards overexpression of incumbent genes, there is a metabolic cost. This cost may translate to a reduction in primary metabolism resulting in reduced growth and yield and/or in altered secondary metabolism potentially causing increased susceptibility to other pest organisms. Trade-offs among various plant functions have been widely investigated and are beyond the scope of this chapter. For "trade-offs" or "costs" related to defenses readers are refereed to Gershenzon (1994), who reviewed chemical defenses in general, and Baldwin and colleagues, who emphasised inducible defenses (Baldwin and Ohnmeiss, 1994; Baldwin and Schmelz, 1994; Baldwin *et al.*, 1994; Ohnmeiss and Baldwin, 1994). Costs associated with improved resistance to herbivores in cotton are further discussed in section 3.3.

3.2 Tolerance

Plant recovery after damage depends on various physiological and morphological mechanisms that are at the core of this section. Nevertheless, due to the wide range of arthropod species that feed on cotton crops, general plant responses to damage are not straightforward. Differences in timing of attack, distribution of individuals on the plant, production of toxins, and feeding habit are some of the pest-specific characteristics that may generate variable plant responses. Despite this diversity, generalisations are necessary and possible, as shown by McNaughton (1983b), Boote *et al.* (1983), and Johnson (1987) in general and by Gutierrez *et al.* (1981), Sadras (1995), and Matthew (1994a) in cotton. Gutierrez *et al.* (1981) demonstrated that separating the effects of *Anthonomus grandis* and *Heliothis zea* was irrelevant to predicting final yield of cotton crops. Similarly, Sadras (1995) analysed cotton responses to reproductive damage and found that changes in the patterns of dry matter and nitrogen partitioning after loss of squares and bolls could account for most of the plant responses to insects, irrespective of the species involved. Considering the main organs attacked by cotton's major pests, Matthews (1994a) grouped quite diverse arthropod herbivores into eight categories.

The phytocentric focus of our chapter justifies the approach of dealing with groups of pests rather than with individual species. Boote *et al.* (1983) classified pest effects on plant growth into seven groups. The categories in this classification are not mutually exclusive; spider mites, for instance, are both photosynthetic rate reducers and leaf senescence accelerators (Sadras and Wilson, 1997a). Johnson (1987) grouped pests into two larger groups: those affecting radiation interception and those affecting radiation-use efficiency. Johnson's (1987) approach is particularly useful for models based on the resource capture concept (Rossing *et al.*, 1992; van Emden and Hadley, 1994).

The classifications of Boote *et al.* (1983) and Johnson (1987) provide (i) an interface to link pests and crop simulation models, and (ii) a scheme to analyse the main effects of pests on crop growth and yield. Importantly, both classifications are inappropriate to account for two major types of damage caused by common cotton pests: induction of shedding of reproductive organs, and reduction in lint quality. Two additional categories are proposed to account for these types of damage. Damage to seed is discussed together with lint quality (section 3.2.8), while effects of pests on oil and protein content of seeds (*e.g.* Roussel *et al.*, 1951; Wilson, 1993; Sadras and Wilson, 1996) are not considered explicitly.

For its greater detail, the classification of Boote *et al.* (1983) with our two additional categories has been used as a framework for this section; references to Johnson's (1987) classification will be made for comparative purposes when relevant.

3.2.1 Tissue Consumers

This section deals with tissue consumers that affect vegetative meristems and leaves. Pests that damage stems and roots are briefly considered in the group of turgor reducers (section 3.2.7), and pests that feed on square and young bolls in the group of abscission inducers (section 3.2.2). Pests that feed on sown-seed are included in the stand reducers group (section 4.2). Pests feeding on old bolls and developing seed are discussed in section 3.2.8.

Vegetative Meristems. Early in the season, thrips, mirids, and lepidopteran pests feed on cotton vegetative meristems causing, in many cases, the death of the growing apex. Yield response to vegetative bud damage in cotton ranges from considerable loss to moderate increase (Lane, 1959; Brook *et al.*, 1992b, Da Nóbrega *et al.* 1993; Evenson, 1969; Bishop *et al.*, 1977; Heilman *et al.*, 1981; Sadras, 1996a). A similar range of yield responses to the loss of the apical bud has been reported for many other species (Keep, 1969; Aarssen and Irwin, 1991). Interestingly, much of the debate about whether herbivores may have beneficial effects on plants (section 2.1) has been stimulated by studies dealing with apical damage (*e.g.* Paige and Whitham, 1987; van der Meijden, 1990; Aarssen and Irwin, 1991; Aarssen, 1995).

Dale and Coaker (1958) quantified the effects of feeding by *Lygus vosseleri* on the number and size of cells in cotton apices, separated mechanical and chemical (*i.e.* mediated by the saliva of the bug) effects of *Lygus* feeding, and assessed the insect pressure necessary to kill the meristem. The main recovery mechanism after loss of vegetative buds involves release of apical dominance (or "primigenic dominance", Bangerth, 1989) and activation of axillary buds. Aarsen (1995) presented a general discussion of the importance of apical dominance as a trait for recovery after vegetative bud loss, while ecologists at Lund University (Tuomi *et al.*, 1994, Nilsson *et al.*, 1996) developed a mathematical model to quantify plant responses to the loss of vegetative buds that could be modified for use in cotton studies. Using this model, they showed that selection will favour intermediate phenotypes having both dormant and active meristems in environments where risk of herbivory varies from year to year (Nilsson *et al.*, 1996). This agrees with preliminary experiments showing that intermediate degrees of apical dominance may maximise resistance to insects in cotton (Sadras and Fitt, 1997b).

Changes in the structure of the cotton plant induced by loss of vegetative buds have been described by Evenson (1969, his Table 3) and Heilman *et al.* (1981, their Fig. 4). Recovery of plants that are damaged during the reproductive stage, according to Lane (1959), relies more on greater elongation of existing fruiting limbs rather than on the growth of lateral branches. Thus, the great ability of cotton plants to recover after the loss of vegetative buds is the reflection of a substantial structural plasticity (*sensu* Rosenthal and Kotanen, 1994) that results from a large number of secondary meristems which are easily activated after damage of the dominant apices (*cf.* Tuomi *et al.*, 1994). The concepts of branch autonomy and modular growth, that regard plant growth as the iteration of basic units with varying degrees of physiological integration, are also potentially useful to understand cotton structural changes after loss of vegetative buds (White, 1979; Franco, 1986; Hardwick, 1986; Spruegel *et al.*, 1991; Sachs *et al.*, 1993; Room *et al.*, 1994; Farnsworth and Niklas, 1995). Using these concepts, Room and colleagues developed a model of the cotton plant that can be used to investigate plant-herbivore interactions (Room *et al.*, 1994, 1996).

Some delay in maturity may occur in bud damaged cotton (*e.g.* Bishop *et al.*, 1977). If so, interactions between early (vegetative) and late (reproductive) damage can be important. For instance, Watts (1937) proposed that in "average and severe boll weevil years the delay in fruiting caused by thrips injury becomes of particular importance because much of the later fruit that otherwise would mature can be destroyed by the boll weevil."

In addition to the responses of individual plants to vegetative bud damage, population-level mechanisms may contribute to crop recovery (section 4).

Leaf. Lepidopterous larvae, Orthoptera, thrips, beetles, and other insects can reduce cotton leaf area at different crop stages (Gutierrez *et al.*, 1975; Harp and Turner, 1976; Bishop *et al.*, 1978; Forrester and Wilson, 1988; Quisenberry and Rummel, 1979; Rummel and Quisenberry, 1979; Russell *et al.*, 1993; Matthews, 1994a; Sadras and Wilson, 1998). Growth reduction due to this type of damage can be explained in terms of reduction in light interception.

The ability of the cotton crop to tolerate leaf area loss was well demonstrated by Lane (1959) who found almost no yield reduction after leaf losses up to 20% of controls. Depending on the stage of the crop, losses up to 75% of the total leaf area did not affect yield. Very extreme treatments that affect seedling survival, *i.e.* complete defoliation shortly after emergence, are required to severely reduce yield of cotton crops (Longer and Oosterhuis, 1995). Many studies confirmed Lane's early finding that cotton can indeed tolerate relatively severe defoliation with little yield reduction (Gutierrez *et al.*, 1975; Harp and Turner, 1976; Ferino *et al.*, 1982; Kerby and Keely, 1987; Russell *et al.*, 1993; Wilson *et al.*, 1994). Since changes in leaf area do not necessarily translate into changes in growth, relative leaf damage is probably not a useful measure of genetic resistance to thrips in cotton (Quisenberry and Rummel, 1979; Rummel and Quisenberry, 1979).

The mechanisms of cotton tolerance to leaf area loss remain speculative due to the fragmentary characterisation of the dynamics of plant recovery after damage (Kerby and Keely, 1987; Longer *et al.*, 1993; Gutierrez *et al.*, 1975; Russell *et al.*, 1993; Longer and Oosterhuis, 1995). In well-developed crops (leaf area index >3) moderate reductions in leaf area may have negligible effects on the amount of light intercepted by the canopy, and therefore growth and yield should not be affected. The spatial pattern of leaf damage, however, may have an important effect on the actual crop response, as discussed below. In cases of early damage and/or severe defoliation that significantly reduces light interception with respect to undamaged crops, several mechanisms can contribute to attenuate the effects of defoliators. First, changes in partitioning, *viz*. increase in leaf area/leaf weight ratio and increase in leaf weight/shoot weight ratio may contribute to leaf area recovery. Second, new leaf addition can compensate, at least partially, for leaf loss due to insects and other agents such as hail (Lane, 1959; Bishop *et al.*, 1978). Third, if leaves are involved in apical dominance (Töpperwein, 1993; McIntyre, 1997), then enhanced branching following defoliation might also be a factor in the recovery of damaged crops. Importantly, enhanced branching after the release of apical dominance could contribute not only to the recovery of leaf area but also to a faster production of squares (Sadras and Fitt, 1997a). Fourth, there may be an increase in the photosynthetic rate of undamaged leaves in a damaged plant and/or in undamaged areas of damaged leaves, *i.e.* compensatory photosynthesis (Trumble *et al.*, 1993). Compensatory photosynthesis is further discussed in section 3.2.6.

For a given amount of leaf loss, the pattern of insect distribution within the plant and the pattern of feeding within the leaf both may affect the plant's photosynthetic response. The pattern of damage *among* leaves in a plant is important because leaf position influences the relative contribution of individual leaves to total plant photosynthesis (Constable and Oosterhuis, Chapter 7 this volume). Marquis (1988) showed in *Acer pennsylvanicum* that removal of 25% of the area from leaves subtending infrutescences reduced seed production of those infrutescences, while removal of area from leaves close, but not subtending, the infrutescence had no influence on seed production. To account for this kind of effect, the pattern of distribution of insects and of damage within the plant needs to be known (*e.g.*, Bishop *et al.*, 1978). The pattern of damage *within* the leaf, *e.g.* notches in leaves by weevils, perforations by borers, skeletonising by beetles, may also affect the photosynthetic rate of the remaining leaf tissue, probably because of variations in the proportion of wounded tissue (Morrison and Reekie, 1995). For a given insect, changes in the pattern of within-leaf damage with ontogeny could also be an important source of variation in whole leaf and plant responses (Zangerl and Bazzaz, 1992, their Fig. 16.4).

But leaves are more than sources of organic carbon. They are also the main site of nitrogen assimilation and a large reservoir of organic nitrogen in the cotton plant. Leaf properties (Bondada *et al.*, 1996) and leaf area may also affect the water economy of the crop. Leaf loss, according to McNaughton (1983a), may improve the water relations of remaining tissue and tissue newly synthetised due to a greater root/shoot ratio. For crops relying on stored soil water, early leaf loss may reduce transpiration and increase the proportion of soil available water during the fruit-growth period affecting therefore the crop's harvest index (Passioura, 1977; Richards and Townley-Smith, 1987; Sadras and Connor, 1991). A full analysis of the effects of defoliators on cotton growth and yield should, therefore, take into account their effects on the carbon, nitrogen, and water economies of the crop.

Some ecologists concerned with plant-herbivore relationships have proposed that, in some cases, defoliation may increase plant growth and fitness (Verkaar, 1988). More conservatively, McNaughton (1983a) stated that "tissue destruction is rarely, if ever, translated monotonically into a proportional reduction of final yield". The previous discussion showed that McNaughton's general statement is also valid for cotton crops, and highlighted the importance of the largely unknown mechanisms underlying the capacity of cotton plants to recover after leaf loss.

3.2.2 Abscission Inducers

Key cotton pests feed preferentially on reproductive structures, which usually shed after damage (Hearn and Fitt, 1992). Plant and crop responses to reproductive damage have been recently reviewed (Sadras, 1995). Briefly, yield responses of crops that suffered reproductive damage, in comparison to protected controls, range from moderate gains to severe losses (Sadras, 1995, his Table 1). Loss of reproductive organs induces dramatic changes in the partitioning of plant resources, and in the structure and phenology of the crop. Damaged crops usually have, in relation to undamaged controls: (i) more carbon and nitrogen stores in vegetative organs, which are the primary result of increased vegetative growth (*i.e.* more dry matter in roots, stems, and leaves); greater concentrations of labile carbohydrates and organic nitrogen could also contribute to the greater stores in damaged plants; (ii) a potential to maintain greater radiation-use efficiency, due to changes in plant morphology that improve the distribution of light in the canopy (Sadras, 1996b), and (iii) a potential to intercept more light due to an extended period of leaf expansion (Brook *et al.*, 1992c; Sadras, 1996a).

Altogether, these changes suggest that damaged crops could have a larger yield potential than undamaged ones. The extent to which this potential is achieved depends on (a) the time available for recovery, and (b) the growing conditions. Different combinations of yield potential, as affected by reproductive damage, time for recovery, and growing conditions explain the wide range of yield responses of crops subjected to reproductive damage (Sadras, 1995, his Fig. 2; Sadras, 1996a).

Importantly, reproductive damage may affect not only the yield but also the earliness, harvestability and quality (see section 3.2.8) of cotton crops. The primary benefits sought in short-season cropping systems could therefore be lost by this type of damage. Interactions between plant responses to arthropod damage and growing conditions are further discussed in section 5.

3.2.3 Photosynthetic Rate Reducers

Photosynthesis of pest damaged cotton has received little attention in comparison to the many studies dealing with photosynthesis of healthy plants. Two recent studies investigated the effects of spider mites (*Tetranychus* spp.) on cotton photosynthesis at the cytological and leaf levels (Bondada *et al.*, 1995) and at the crop level (Sadras and Wilson, 1997a). Bondada *et al.* (1995) showed that spider mites disrupt leaf photosynthesis by reducing both stomatal and mesophyll conductance. At the crop level, these effects are reflected in reduced radiation-use efficiency, increased canopy temperature and reduced leaf nitrogen content due to mites (Sadras and Wilson, 1997a). Negligible responses of radiation-use efficiency to mites until a threshold of mite damage was achieved suggests some degree of compensatory photosynthesis that needs further evaluation (Sadras and Wilson, 1997a). Quantitative relationships between radiation-use efficiency and an index of mite damage have been developed that could be used to incorporate the effects of spider mites into cotton simulation models (Sadras and Wilson, 1997a). Further information on the general effects of arthropods herbivores on leaf gas exchange can be found in the review by Welter (1989).

3.2.4 Leaf Senescence Accelerators

Heavy infestations of *Tetranychus urticae* (Sadras and Wilson, 1997a) and *Bemisia tabaci* (Baluch, 1988) can accelerate leaf senescence. Faster leaf senescence implies reductions in leaf area duration (Watson, 1947), and potential reductions in light interception, growth, and yield (Monteith, 1977).

The effects of mites on crop growth are primarily related to reductions in photosynthesis but accelerated leaf senescence could further reduce growth by reducing light interception (Sadras and Wilson, 1997a). Mites have the potential to induce senescence. The mechanisms by which mites and other pests induce fast senescence and the existence of any tolerance mechanism are both unknown. We can speculate that new leaf addition and compensatory photosynthesis could partially compensate for this type of damage. However, given the high levels of infestation necessary for significant defoliation to occur, it might be too late for any compensation to be relevant, at least in the case of crops severely infested with mites.

Important changes in shoot nitrogen distribution can follow mite-induced leaf senescence. First, the process of nitrogen depletion typical of senescing leaves is accelerated in mite infested plants, with the consequent decline in leaf nitrogen concentration (Sadras and Wilson, 1997a, c). This reduction in leaf nitrogen concentration can be regarded as a negative feed-back on mite colonies, whose rapid decline in field crops coincided with leaf nitrogen concentrations dropping below 3.5-4.2% (Sadras and Wilson, 1997c). This agrees with independent laboratory tests showing that fecundity and developmental rate of *T. urtichae* are negatively affected when mites are fed cotton leaves with nitrogen concetration below *c.* 4% (Wilson, 1994). Reduced leaf nitrogen concentration, along with the red discolouration, may make mite infested plants less attractive to other herbivores. In parallel with the rapid reduction of leaf nitrogen, stems and fruits of mite infested cotton had greater nitrogen concentrations than uninfested controls (Sadras and Wilson, 1997c). This could may make mite-infested plants more suitable for a range of Lepidoptera, Coleoptera, and Hemiptera that feed preferentially on reproductive structures. A more detailed discussion of the many possible influences of biotic and abiotic factors on cotton responses to herbivores is presented in section 5.

3.2.5 Light Stealers

Homoptera (*e.g. Aphis gossypii* and *Bemisia tabaci*) produce honeydew and spider mites produce webs. Both honeydew with its fungal colonies and mite webs may reduce the light available for leaf photosynthesis. The importance of these barriers for light transmission has not been assessed in cotton and the mechanisms for tolerance, if any, are unknown. To separate the effects of honeydew from those related directly with the feeding activity of insects, experiments using artificial honeydew have been done with other species. The results of these experiments are ambiguous, probably reflecting the dependence of responses to honeydew on growing conditions and plant species. Hurej and van der Werf (1993) found no effects of artificial honeydew on sugar beet (*Beta vulgaris* L.) growth while Rossing and van de Wiel (1990) reported that wheat (*Triticuum aestivum* L.) dark respiration and mesophile resistance both increased in treated plants with respect to controls under hot-dry conditions but not under moderate temperature and humidity. It could also be that part of the differences between these experiments are related to variation in the chemical composition of honeydew, which depends on both the insect and plant species (Hendrix *et al.*, 1992). Measurements of light transmission by Wood *et al.* (1988) showed that sooty mould fungus grown on aphid honeydew could block up to 98% of incident PAR. Direct assessment of the effects of honeydew on cotton photosynthesis are necessary. Compensatory photosynthesis, we speculate, could be a relevant mechanism of tolerance to this type of damage (section 3.2.6).

3.2.6 Assimilate Sappers

Sucking pests absorb phloem or xylem contents from different organs. In the case of insects that feed preferentially on reproductive structures, the induction of shedding has probably more important effects on crop growth and yield than the actual loss of assimilates (section 3.2.2, cf. also Prokof'ev and Igamberdieva, 1971). This section concentrates on sucking pests that feed on vegetative organs.

Pollard (1973) described the damage caused by aphids at the tissue and cellular levels. At the plant and crop levels, sucking animals that feed on vegetative structures can be considered as additional "sinks" for carbohydrates and as such they are likely to affect source/sink relationships in the host plant (Crawley, 1983). The effect of sucking insects on cotton source/sink relationships has not been investigated. The notion that sucking insects are additional sinks to the plant implies that they have the potential to reduce vegetative and reproductive growth by diverting plant assimilates. Assuming (i) a crop growth rate of 15 g dry matter m^{-2} d^{-1} (Hearn and Constable, 1984), (ii) the energetic requirements for the synthesis of cotton dry matter given by Wall *et al.* (1994), and (iii) an intake of 50-400 mg sugar $aphid^{-1}$ day^{-1} (Hurej and van der Werf, 1993) we calculated that a reduction in growth rate of 10% would require at least 5000 aphids m^{-2}. Despite the many assumptions involved in this estimate, it suggests that a significant drain of carbohydrates in a well developed cotton crop could only occur at very high aphid densities and this is consistent with Smith (1992) who pointed out that "economic damage caused by the cotton aphid today is in dispute; yield losses are rarely definable". In addition, increased photosynthetic rate due to the sink activity of sucking pests might attenuate to some extent the losses due to sucking pests (Crawley, 1983). Evans (1993) summarized a number of studies showing that increased rate of carbon fixation may follow enhanced sink activity. The experiments of Quisenberry *et al.* (1994) suggest that photosynthesis of cotton leaves is responsive to source/sink ratios but direct evaluation is needed. Meyer (1993) and Meyer and Whitlow (1992) found in goldenrod (*Soldago* spp.) that plant growth and photosynthesis of leaves produced after insect removal were unaffected by a phloem-sap feeding aphid, but were severely reduced by a xylem-sap feeding spittlebug. Studies similar to the ones by Meyer and Whitlow (1992) are necessary in cotton.

In addition to sugars, sucking pests remove other plant nutrients, and they may also disrupt phloem-sap transport. Changes in C/N ratios in leaves infested with *Bemisia tabaci* (Baluch, 1988) indicate differential effects on the rate of synthesis, turnover and/or transport of carbohydrate and N-compounds in damaged cotton plants. Changes in C/N ratios, in turn, may have dramatic effects on important physiological processes from regulation of gene expression (Stock *et al.*, 1990) to phenological development of whole plants (Trewavas, 1985).

Importantly, indirect damage caused by succivorous insects, *i.e.* damage associated with (i) insect toxins, hormones and pathogens carried in the watery saliva (Bell, Chapter 18, this volume), and (ii) honeydew that potentially affects lint quality (section 3.2.8) can be comparatively more important than the damage caused by the actual drain of sugars and minerals. This is reflected in current recommendations for management of aphids in Australia: while 90% of infested plants is suggested as a threshold before boll opening, it drops to 10% during boll opening due to the potential for severe downgrading of the lint value (Pyke and Brown, 1996).

In contrast with the previous discussion, in which effects of sucking insects has been implicitly considered deleterious to the plant, Owen (1980) has proposed some beneficial effect associated with the feeding activity of aphids (section 2.1). He suggested the following sequence to explain how plants may benefit from their association with aphids: (i) plants release "surplus" sugar by enlisting the "help" of aphids, (ii) free-living nitrogen-fixing bacteria develop beneath the aphid-infested plant, and (iii) more nitrogen is available for the infested plant. Owen's proposal is consistent with the hypotheses that (a) photosynthesis rarely limits growth (Went, 1974) and (b) that terrestrial plants have evolved a wide range strategies to dispose of excess carbohydrate (Thomas, 1994).

3.2.7 Turgor Reducers

In comparison with other crops, cotton suffers little from root-feeding animals (Matthews, 1994a). The cotton stem weevil (*Apion soleatum*), whose larvae feed on vascular tissues of main-stems and branches, can potentially reduce the growth and yield of cotton in the eastern producing regions of South Africa (Bennett, 1993). Vascular diseases that disrupt cotton water and nutrient economies are much more widespread and have the potential to cause severe yield reductions (*e.g. Rhizoctonia* spp., *Fusarium* spp., *Verticillium* spp.). For details of cotton responses to altered functioning of its root and vasular systems readers are referred to chapters in this book dealing with diseases (Bell *et al.*, Chapter 18) and several aspects of root growth (McMichael *et al.*, Chapter 6), mineral nutrition (Mullins and Burmester; Chapter 9; Hodges and Constable, Chapter 14), and water relations (Hake and Grimes, Chapter 23) in healthy plants exposed to stresses.

3.2.8 Lint Quality Reducers and Seed Consumers

This section deals with pests that typically affect cotton crops late in the season affecting, therefore, lint quality, seeds, and boll opening. Indirect effects of pests on lint quality are also considered.

Lint quality can be affected by pests that (i) affect plant growth and development, and/or (ii) stain or otherwise damage cotton fibres. Fibre quality depends on plant and environmental factors, as discussed by Turley and Chapman (Chapter 29), Haigler (Chapter 4), and Bradow and Bauer (Chapter 5) (this volume). In general, arthropods that reduce crop photosynthesis have the potential to affect lint quality, as illustrated by studies with spider mites (Roussel *et al.*, 1951; Canerday and Arant, 1964a, b; Leigh *et al.*, 1968; Duncombe, 1977; Wilson, 1993). Developmental delays, such as those caused by early-season vegetative damage (section 3.2.1) and loss of reproductive structures (section

3.2.2) could also affect lint quality due to larger proportions of bolls growing under less favourable environmental conditions. Reductions in fibre quality due to damage by *Heliothis* spp. that delays fruit growth (Wilson, 1981) illustrate this point.

Whiteflies and other sucking insects that excrete large amounts of honeydew are responsible for sticky cotton, characterised by little drops of honeydew - often crystallised - that are not eliminated during ginning. Saprophytic fungi that grow on honeydew further reduce lint quality. Details about sticky cotton can be found in Hector and Hodkinson (1989), Butler and Henneberry (1994), and Leclant and Deguine (1994). Lint quality can also be affected by cotton stainers *e.g. Dysdercus* spp. (Broodryk and Matthews, 1994) and by *Pectinophora* spp. (Ingram, 1994).

According to Matthews (1994a) the common stainer bugs and the cotton seed bugs, *Oxycarenus* spp., are able to feed on undamaged cotton seed, whilst scavengers of minor importance can often be found after primary damaged has occurred. Late seed damage is unlikely to affect yield seriously, but reductions in lint quality associated with these insects could be severe.

Whilst squares and young bolls usually shed after damaged (section 3.2.8), older bolls damaged by lepidopteran and other pests are normally retained in the plant. Damage to older bolls is rather localised and yield losses could be limited to the damaged locules which may remain closed at maturity. More often, however, the boll cavity is invaded by secondary fungi and the whole boll could be lost due to rotting (Matthews, 1994b).

Reduced seed number and/or viability is obviously important for plant fitness. We speculate, therefore, that cotton plants might have evolved some tolerance mechanisms for this type of damage. Irrespective of whether such recovery mechanisms exist, the limited time available for recovery (Sadras, 1995) makes them of restricted value from the agronomic viewpoint.

3.2.9 Summary

Crop yield reduction due to pest damage can be associated with reduction in growth, reduction in harvest index, or both. Reductions in growth, in turn, may be the result of less light interception and/or lower radiation-use efficiency. Many of the pests examined above affect growth by reducing radiation interception (tissue consumers, leaf senescence accelerators, light stealers, turgor reducers) or by reducing radiation-use efficiency (assimilate sappers, photosynthetic rate reducers, turgor reducers). In contrast, abscission inducers normally affect yield, despite increases in shoot growth in some cases, due to reductions in harvest index.

Mechanisms of tolerance related to damage that reduces growth include production of new leaves and compensatory photosynthesis. Increased harvest index can also be potentially important. Studies dealing with changes in dry matter partitioning after damage by different pests are scarce. Cotton crops severely damaged by spider mites had a significantly lower harvest index than undamaged controls but allometric analyses showed that reduction in harvest index was associated with small plant size rather than with true changes in partitioning (Sadras and Wilson, 1997b). Overall, the cotton crop seems to have a considerable ability to tolerate damage by herbivores but the actual mechanisms involved are largely unknown. Compensatory photosynthesis and changes in dry matter partitioning after damage can be indicated as two aspects of cotton physiological responses to pests that deserve closer attention.

3.3 Interactions Between Avoidance and Tolerance

Our aim in this section is not to review the research and achievements of breeding for improved cotton resistance to herbivores; this has been done recently by a number of authors (see Introduction). Instead, we will concentrate on traits and interactions between traits that, we believe, have been neglected.

Most research and breeding efforts on cotton resistance to pests have concentrated on avoidance traits. Thomson (1987) pointed out that besides these attributes, “it seems to be almost universally overlooked that increasing yield itself constitutes a form of breeding for host plant resistance”. To highlight this point, Thomson (1987) compared two hypothetical cultivars, A and B, of different yielding ability but otherwise similar in their sensitivity to insects. The higher-yielding cultivar B can absorb nearly twice the insect damage as A can before it yields less than A. With the exception of Thomson’s concept of “yield as a resistance factor”, no consideration has been made of traits related to plant growth (or regrowth after damage) as factors in cotton resistance to pests. Only recently, studies have been designed to assess the importance of tolerance traits in cotton (Sadras and Fitt, 1997a, b). Preliminary experiments suggest that (i) considerable variability exists among *Gossypium* genotypes in their recovery capacity, and (ii) recovery capacity may be an important component of overall resistance to insect pests in the field.

The putative trade-off between allocation of resources to growth and defenses was investigated in many ways: theoretically (Bazzaz *et al.*, 1987; Tilman, 1990; Herms and Mattson, 1992), using simulation models (Basey and Jenkins, 1993; Yamamura and Tsuji, 1995) and in empirical studies including both intra- and inter-specific comparisons (*e.g.* van der Meijden *et al.*, 1988; Coley, 1988; Bryant *et al.*, 1989; Jing and Coley, 1990; McCanny *et al.*, 1990). Negative relationships, as predicted by theory, have been found in many studies whereby plants with high level of defenses had a limited capacity for growth (*e.g.*, Coley, 1988) or regrowth after damage (van der Meijden et al, 1988). Nevertheless, positive association (Bryant *et al.*, 1989) and no association (McCanny *et al.*, 1990) between growth and defenses have also been reported. Further references to relationships between defense and tolerance can be found in a recent review by Zangerl and Bazzaz (1992).

Cotton breeders are, of course, aware of the yield "penalties" that could be associated with enhanced plant resistance to pests (Thomson, 1987) and this was illustrated in the work by Wilson (1987). Cotton lines with enhanced resistance to insects yielded more than a "susceptible" control under high insect pressure but, in general yielded less than the control under low insect pressure. This suggests a "cost", in terms of yield, associated with enhanced resistance to herbivory. Moreover, for the range of resistance traits from 0 to 3, the number of resistance traits accounted for 74% of the variation in yield under low insect pressure. In contrast to the work by Wilson (1987), no association was found between chemical defenses and regrowth capacity in a collection of 25 *Gossypium* genotypes (Sadras and Fitt, 1997b). Furthermore, okra-leaf varieties combine avoidance characteristics with a very good recovery capacity derived, in part, from a high squaring rate (Thomson, 1994). Altogether, the information available for cotton suggests that (i) negative linkages may exist between tolerance and avoidance traits, but (ii) breakdown of the putative links seem feasible and genotypes could be bred that combine both kinds of traits.

Combination of tolerance and avoidance strategies could offer broader and ecologically more stable solutions to cotton's pest problems. On the one hand, the capacity of the crop for yield compensation can be severely limited in extreme environments, *i.e.* in sites with very high (Brook *et al.*, 1992a, b, c) or very low yield potential (Sadras, 1995, 1996c). Compensation is also of limited value for damage that occurs very late in the season (section 3.2.8).Thus, provided avoidance traits are effective over a wide range of conditions, cropping systems relying on both tolerance and avoidance could have advantages over those emphasising tolerance strategies. On the other hand, chemical defenses are, by definition, negative to the fitness of target pests. The negative effect of defenses on pests has the potential for the selection of resistant individuals that, eventually, could restrict the effectiveness of such defenses (see 3.1.2: *"Biotechnology and plant resistance"*). Since morphological defenses and phenological escape have the potential to affect the fitness of target pests, they could also trigger selective processes similar to those described for chemical defenses. To the best of our knowledge, development of resistance to morphological traits or escape strategies have not been reported. The case of the adaptation of rootworm populations to rotations the U.S.A. cornbelt discussed before, however, illustrates how pests could develop resistance to this kind of strategy (Section 3.1.1). Combination of tolerance and avoidance strategies would therefore be a more stable option than strategies relying solely on avoidance.

In summary, while avoidance traits are likely to remain a central component of plant resistance to herbivory, explicit consideration of recovery capacity could be a worthwhile aim for breeding programs. Importantly, a better understanding of the mechanisms of cotton resistance to herbivory are also essential for the development of improved pest management practices. In addition to ongoing research on avoidance traits, research is needed to: (i) fully assess the degree of intraspecific variability in recovery capacity in response to different intensities, types and times of damage, (ii) determine the inheritance of these traits, (iii) develop screening techniques suitable for breeding purposes, and (iv) investigate the link/s between tolerance and other traits relevant for resistance to herbivory and overall agronomic performance.

4. RESISTANCE TO HERBIVORY: AT THE POPULATION LEVEL

4.1 Avoidance

Injured plants may release volatile substances that play defensive roles. These include both elicitors of plant defenses and chemicals that attract natural enemies, as discussed before (section 3.1.2 *"Induced Defenses"*). In this section, we want to briefly emphasise that, due to the volatile nature of these "infochemicals", they could be regarded as defenses at the population level. This is because the benefits of such compounds are not restricted to the injured plant that has produced them, but could also be extended to undamaged neighbours.

The study of Bruin *et al.* (1992) showed that undamaged cotton plants can gain protection against mite herbivory by exposure to compounds released by mite-injured plants. They found that spider mites had oviposition rates on leaves previously exposed to volatiles from infested plants were 10% lower than on untreated controls ($P = 0.008$), and that (ii) predatory mites had a preference for volatiles related to uninfested plants or leaves that had been exposed to volatiles from mite-infested plants, compared to controls ($P < 0.001$).

The fact that volatile chemical signals operate at the population level is important in the consideration of the putative costs associated with their production. This was highlighted in a study of communication between the first (plants) and third ("beneficial") trophic levels by Godfray (1995), who pointed out that any signalling system in which there exists the possibility of a conflict of interest between signaller and receiver will require significant costs for evolutionary stability. Certainly more research is needed in this area.

In addition to plant traits involved in "attracting" predators and parasitoids, a number of morphological traits (*e.g.* domatia, leaf dispersion, petiole length, branching pattern) can influence (i) the ability of the plant to *retain* beneficials and (ii) the *accessibility* of herbivores on the plant to beneficials (Marquis and Whelan, 1996). Agrawal and Karban (1997) showed that the presence of leaf domatia may increase predator numbers, reduce populations of herbivorous mites, and enhance cotton yield. Thus, the ability of plants to attract beneficials should not be considered in isolation of such morphological traits that are likely to influence the overall effectiveness of herbivore control by beneficials.

4.2 Tolerance

Stand reductions can result from the activity of soil-dwelling arthropods but also from seedling diseases, or severe defoliation and meristem damage by early-season pests or hail. Interactions between these factors can be important, as illustrated by the work of Colyer *et al.* (1991) who showed that thrips infestations may increase both the severity of cotton seedling disease and stand reduction.

Tolerance to stand reduction depends on the capacity of the surviving plants to fill the gaps left by dead neighbours (*e.g.* Bardner and Fletcher, 1974). This response fits, in a broad sense, the definition of population-level compensation of Crawley (1983) (section 2.3). The detailed study of Hearn (1972) serves to illustrate the capacity of cotton for this type of compensation. For crops grown under extreme conditions of yield potential, a 10% reduction in maximum yield required (even) stand reductions of more than 70% with respect to the optimal density.

Matthews (1994b) indicated that, as a general rule, seedling pests are not important in Africa and pointed out that some compensatory growth often occurs if the plants are closely spaced (cf. also Pearson, 1958). When stand reduction occurs late in the season, as described by Tiben *et al.* (1990) for cotton crops attacked by the termite *Microtermres najdensis*, crop recovery is much more limited. Timing and heterogeneity of damage are therefore important factors influencing the capacity of cotton crops to compensate for stand reduction.

Significant compensation at the population level can be expected not only after death of plants but also when selective damage affects the competitive relationship between neighbouring plants. This form of compensation was investigated in cotton crops subjected to three treatments: (i) undisturbed controls, (ii) uniformly damaged, in which all plants were damaged, and (iii) non-uniformly damaged, in which every second plant was damaged (Sadras, 1996c). Damaged plants had their vegetative buds manually removed to simulate damage by early-season pests. Removal of vegetative buds did not reduce yield per unit ground area. In uniformly damaged crops, compensation was essentially the result of profuse branching after release of bud dormancy (section 3.2.1). In non-uniformly damaged crops, population level mechanisms acted that involved strong plant-plant interactions. Undamaged plants grown alongside damaged neighbours accumulated more shoot and tap root biomass and produced more seedcotton than undamaged plants in uniform crops. Changes in competitive relationships (Crawley, 1983) as well as early detection of and response to neighbour status (Aphalo and Ballaré, 1995) were likely involved in these responses (Sadras, 1996c; cf. also Watts, 1937). Similarly, Hurej and van der Werf (1993) reported that neighbouring plants of aphid-infested sugar beet plants were heavier than neighbouring plants of healthy controls.

Interactions between neighbours after non-uniform reproductive damage could also be expected. In cotton, as in other indeterminate plant species, fruit loss often counteracts the slowing down of vegetative growth that usually occurs during the stage of active reproductive growth (Section 3.2.2). Due to the relative increase in vegetative biomass, leaf area and plant height after fruit loss, plants that have suffered reproductive damage could be better able to intercept light and acquire soil resources than undamaged plants. If so, plants with damaged neighbours may grow less than their counterparts with smaller, undamaged neighbours (Sadras, 1997b). A study designed to test this hypothesis showed that : (i) as expected, damaged target plants had greater leaf area and more vegetative dry matter than undamaged targets; (ii) neighbour status did not affect vegetative growth; (iii) neighbour status had a substantial, asymmetric effect on the reproductive growth of target plants: while neighbour status did not affect the productivity of damaged targets, it had a significant effect on the production of mature fruit of undamaged targets; (iv) undamaged targets with damaged neighbours had 34% (low density) and 56% (high density) less open boll dry matter than their counterparts with undamaged neighbours; (v) the asymmetric response of target plants to neighbour status determined a reduction in the yield of non-uniformly damaged crops that was greater than expected from the additive effects of damage.

In summary, population-level compensation seems to be an important mechanism of tolerance to stand reduction and early-season bud damage. A substantial phenotypic plasticity (Bradshaw, 1965) and the modular organisation of the cotton plant enables damage to be repaired and differentiation to be adjusted to the availability of resources (Hardwick, 1986, see also section 3.2.1.). In contrast, non-uniform reproductive damage may have a two-fold effect in yield: yield may be reduced in the damaged plants and also in undamaged plants flanked by neighbours that are bigger, taller, and leafier after fruit loss. The impact of plant-plant interactions on yield losses due to insects in commercial crops will depend on the spatial distribution of insects and damage. Interactions between neighbouring plants that suffered different types, timings, and/or intensities of damage deserve further research.

5. INTERACTIONS BETWEEN ARTHROPOD PESTS AND OTHER STRESSES

The previous section outlined the main effects of pests on the physiology and morphology of the cotton plant and described the main avoidance and tolerance mechanisms involved at the molecular, organ, plant, and crop levels. For analytical purposes, those mechanism were mostly considered in isolation of other factors. Plant-pest relationships in the field, however, are strongly influenced by other biotic (*e.g.* weeds, diseases, mycorrhiza, predators, and parasitoids) and abiotic (*e.g.* water and nutrient availability, temperature) factors. These influences are the subject of this section. Our aim is: (i) to illustrate, using selected examples, some of the many possible interactions between these factors, (ii) to discuss, briefly, approaches to investigate these interactions.

5.1 Some Examples

Baumgärtner *et al.* (1986) used a simulation model to investigate interactions between cotton and two pests, *Heliothis* spp and *Bemisia tabacci*. Their simulation experiments indicated that damage caused by *Heliothis* larvae to fruiting structures may increase whitefly numbers at the time of boll opening. This was related to model assumptions, justified by empirical evidence, that (i) reproductive damage extends the period of leaf growth, (ii) a leaf's nutritional value depends on its age, (iii) and host plant quality has an important effect on the population dynamics of whiteflies (Baumgärtner *et al.*, 1986). Other simulation studies on interactions between arthropods and cotton include Gutierrez *et al.* (1975, 1977, 1979ab), Wang *et al.* (1977), Room (1979b), Hearn and Room (1979), Hearn *et al.* (1981), Ives *et al.* (1984), Hearn and DaRoza (1985), Legaspi *et al.* (1989), and Baker *et al.* (1993).

In an interesting study, Simpson and Batra (1983) showed the interactions between air temperature, leaf-feeding insects, sucking insects, scavenger beetles, pink bollworm, and cotton boll rot caused by *Aspergillus flavus*. They showed that *A. flavus* develops better at moderate to high temperatures and that leaf-damaging insect deposits and honeydew promote the fungi's growth. Its transport to bolls is facilitated by scavenger beetles while actual boll penetration and infestation require wounds, such as those caused by pink bollworm. This study illustrates how yield losses due to, say sucking insects, will be influenced by the presence of other living organisms (bollworms, beetles, *A. flavus*) and environmental conditions (temperature) that could contribute to indirect yield losses due to boll rot. Another factor that adds complexity to these interactions is that gossypol can be induced by volatile constituents from leaves infected with *A. flavus* (Zeringue, 1987).

There are two main ways in which weeds and arthropod pests can interact with the crop. The first, and more widely investigated, is through the role of weeds as alternative hosts for, and sources of, pathogens, arthropod pests and beneficials. For instance, the importance of weeds as sources of spider mites has been demonstrated by Brandenburg and Kennedy (1981) for cropping systems in the U.S.A. and by Wilson (1995) for cotton crops in Australia. The second interaction between weeds and pests is related to the changes in cotton competitive ability after damage by herbivores (Sadras, 1997a). As discussed before (Section 3.2.1), early-season loss of vegetative buds transiently delays cotton growth and development and has the potential to reduce its competitive ability. Yield reductions due to weed interference and insect damage, therefore, could be greater than expected from the additive effects of weeds and damage acting separately. A preliminary experiment combining two levels of weed infestation (with and without weeds) and two levels of simulated insect damage (intact plants and plants with vegetative buds removed before squaring) showed a non-additive effect of weeds and damage that accounted for yield losses equivalent to 16% of the yield of control crops.

Interactions between aboveground herbivores and the mycorrhizal mutualists of plants have received little attention but the available data suggest: (i) that severe herbivory reduces root colonization by vesicular-arbuscular (VAM) and ectomycorrhyzal fungi, and that (ii) mycorrhizal fungi could deter herbivores, and interact with fungal endophytes influencing herbivores (Gehring and Whitham, 1994). For instance, larvae of *Helicoverpa zea* and *Spodoptera frugiperda* fed leaves from VAM-infected soybean grew more slowly, took longer to pupate, and had a greater mortality rate than larvae fed on non-mycorrhizal controls (Rabin and Pacovsky, 1985). This kind of interaction deserves to be investigated in cotton.

Hedin and McCarty (1991) showed that the concentration of secondary metabolites, such as gossypol, tannins, anthocyanin, and flavonoids in cotton leaves and squares, can be changed by exogenous plant growth regulators including commercially used cytokinins and mepiquat chloride. The direction, *viz.* decrease or increase in concentration, and magnitude of the change are largely unpredictable, as are most plant responses to exogenous applications of plant growth regulators. The report of Hedin and McCarty, however, is important in that analysis of crop responses to plant regulators in the field should take into account potential changes in plant-animal interactions mediated by changes in concentrations of plant secondary metabolites.

Interactions between insects, water availability and soil fertility have been widely investigated in cotton. In general, conditions that favour crop growth, including frequent irrigation and heavy fertilization, increase the abundance of both herbivorous and predacious arthropods (Joyce, 1958; McGarr, 1942; Mistric 1968; Leigh *et al.* 1970, 1974; Flint *et al.* 1994, 1995; Skinner and Cohen 1994). The overall response of the crop to different combinations of water supply, nutrient availability and pests is, however, difficult to predict due to the complexity of interactions involved. Interactions between the carbon, nitrogen, and water economies of cotton crops after reproductive damage have been outlined in Sadras (1995). Mistric (1968) with boll weevils and Sharma *et al.* (1989) with pink bollworms showed that heavily fertilised cotton: (i) attracted more insects, (ii) had more bolls and squares damaged by insects, but (iii) yielded more than poorly fertilised crops due to increased boll production. Joyce (1958) investigated the interactions between rainfall before sowing, soil and leaf nitrogen and development of jassids, thrips, and whiteflies in cotton crops in Sudan. Leaf nitrogen content and pre-sowing rains were negatively correlated, presumably due to leaching of soil nitrogen. This, together with a positive association between leaf nitrogen and rate of development of insects, resulted in a significant, negative association between rate of insect development and pre-sowing rainfall (Joyce, 1958). McGarr (1942) reported that nitrogen fertilisation increased aphid numbers when cotton was dusted with calcium arsenate but not in the absence of this treatment. Leggett (1992) found that the abundance of cotton insects, both pests and beneficials, was significantly affected by complex interactions between cultivar (Pima vs Upland), irrigation method (drip vs furrow) and sites in Arizona. Sadras *et al.* (1998) found that water deficit enhanced cotton resistance to spider mites in a comparison with well-watered crops. Other studies dealing with water availability-pest interactions include Ogborn and Proctor (1962), Kittock *et al.* (1983), Watson *et al.* (1978), and Ungar *et al.* (1992). Ungar *et al.* (1992) concluded after a five-year experiment that "irrigation scheduling and the control of pests that damage fruiting organs cannot be optimized independently". Leigh and colleagues conclusion after intensive studies (Leigh *et al.*, 1970, 1974) is that "where insect populations are not controlled, a highly complex relationship was found to exist between cotton lint production, vegetative growth, insect numbers, and water and nutritional management".

In addition to studies dealing with cotton, Waring and Cobb (1992) reviewed the general effects of nutrient (N, P, and K) and/or water stress on herbivore population dynamics and Kytö *et al.* (1996) reviewed the effects of soil fertilisation on phytophagous insects and mites on trees. More than 75% of the 450 studies reviewed by Waring and Cobb (1992) showed significant herbivore responses (positive, negative, or non-linear) to plant water and/or nutrient deficits. In general, they concluded, these stresses render plants poor resources for herbivores. However, quantitative and qualitative changes in plant defenses, changes in canopy temperature and effects on the populations of parasitoids and predators, are among the many factors that could be affected by nutrients and water stresses and could, in turn, affect the responses of herbivores to stressed plants, and *vice versa*. In fact, Kytö *et al.* (1996) proposed that enhanced nitrogen availability (i) usually benefits individual herbivores by improving nutritional quality of the host plants, but (ii) it often has non-significant or negative effects on insects at the population level because it also affects higher trophic levels, *i.e.* parasitoids and predators. Changes in community structure, they suggest, override the effects of nutrients mediated by the improved quality of the host plant. These conclusions may not necessarily apply, however, to cropping systems in which the community of parasitoids and predators is significantly disturbed by the use of insecticides.

5.2 Approaches to Investigate Cotton Responses to Herbivory as Affected by Other Biotic and Abiotic Factors

The "limiting factor" concept is often used in agronomic studies (*e.g.* Paris, 1994) as well as in plant physiological research (Trewavas, 1986). This concept is obviously inappropriate to deal with the kind of interactions illustrated in the previous section. Parallel to the recognition of the restricted value of the "limiting factor" approach to analyse plant growth and development in most field situations (Körner, 1991; Gifford, 1992; Sincalir and Park, 1993; Sadras, 1995) the concept of "multiple-stresses" has been formally developed (Chapin *et al.*, 1987; Mooney *et al.* 1991).

It is tempting, in principle, to think of simulation models as a means to investigate the complex interactions involved in crop-pest relationships. Such models, we believe, could be useful as tools to assist in crop management, but they should be taken very cautiously in relation to their value as tools for understanding. Entomologists (Berryman, 1991; Liebhold, 1994) as well as plant scientists (Passioura, 1973, 1996; Sadras and Trápani, 1997) have discussed the main limitations of complex simulation models as tools for understanding. Furthermore, crop simulation models are often taken as a substitute for more appropriate frameworks, namely a suitable theory and, in some cases, models could be an obstacle rather than an aid for understanding biological processes (Sadras and Trápani, 1997). Simple rather than complex, fully testable models (Passioura, 1996) that are "transparent" because their simplicity allows the user to see how they work and what causes their outcomes (Berryman, 1991) are likely to be valuable tools for understanding the biological processes involved in crop-herbivore interactions. This is well illustrated by the models of Tuomi *et al.* (1994) and Nilsson *et al.* (1996) (section 3.2.1).

In summary, we propose that crop-herbivore relationships could be better understood by: (i) adopting a "multiple-stress" approach, (ii) incorporating current concepts of the biology of plant responses to stress, arthropod responses to stressed plants, and ecological theories on plant-herbivores relationships as a general framework (*e.g.* Jones and Coleman, 1991), (iii) developing simple, *ad hoc* models to suit specific research purposes, (iv) using complex crop-pest models with extreme caution, and (v) developing novel analytical methods. All these elements are required to overcome the problems summarised by Leigh *et al.* (1970) who, after intensive research concluded that “direct cause-and-effect relationships between lint production, plant growth, insect populations, and water and plant nutrition management were found difficult to identify.”

6. CONCLUSIONS AND DIRECTIONS FOR FURTHER RESEARCH

Despite the widespread view that cotton is highly susceptible to pests, we have shown that plants are not passive victims of herbivores and that, in some cases, cotton yield could be unaffected or even increased by mild, timely damage.

At the plant level, plant resistance to herbivores has two components: avoidance and tolerance. Avoidance strategies have been used widely in many breeding programs. Earliness in some regions of the U.S.A. and Brazil, okra-leaf genotypes in Australia, and transgenic cottons expressing *Bacillus thuringhensis* insecticidal proteins are some striking examples of the success achieved by breeders in improving cotton resistance to pests. Further biotechnological developments, including the continued identification of genes encoding insecticidal proteins, and manipulation of induced defenses, will certainly play a major role in breeding for improved cotton resistance to arthropod pests.

Not surprisingly, breeders have been more keen to include avoidance, rather than tolerance, traits in their programs of plant resistance. This is because: (i) we have a poorer understanding of tolerance traits than of avoidance traits, and (ii) avoidance traits are, in general, genetically simpler than tolerance traits. It is doubtful, however, whether a plant can be fully protected by its defenses against herbivores (Mc Naughton, 1983a). This, together with the ecological instability of chemical defenses, suggests that more attention should be paid to tolerance traits. Combination of tolerance and avoidance traits could offer broader and ecologically more stable solutions to cotton’s pest problems.

At the population level, avoidance and tolerance mechanisms could also operate that can strongly affect the behaviour of the crop-herbivore-beneficial system, but they are poorly understood in comparison with mechanisms at lower levels of organisation. Widespread speculation, and some experimental evidence indicates that plants injured by herbivores may release chemicals that attract natural enemies of their herbivores (Godfray, 1995). These compounds, as well as volatile elicitors of plant chemical defenses, need to be investigated in conjunction with morphological traits that affect both the ability of the plant to *retain* beneficials and the *accessibility* of herbivores to beneficials (Marquis and Whelan, 1996). Changes in competitive relationships between neighbouring plants brought about by damage that is uneven in space and/or time is an important determinant of the capacity of the crop to compensate for pest damage. Indirect evidence from plant density trials and recent studies with simulated damage support this view. Both positive and negative interactions between damaged and undamaged neighbours have been described, the direction of the response being dependent on the type of damage. Research is needed in which (i) the pattern of plant damage is assessed against the pattern of arthropod distribution and feeding in cotton fields, and (ii) crop yield is interpreted in terms of growth, development and yield of individual plants that have been exposed to different timings and/or intensities of damage.

A cautious, critical use of modelling tools, the consideration of ecological theories on plant-herbivore relationships, and novel conceptual frameworks (Jones and Coleman, 1991) are needed in the research of the relationships between cotton and its pests under varying environmental conditions and management practices. Better understanding of the cotton/pest system is important not only for breeding and selection of improved varieties but also for the development of more effective management practices.

Substantial improvement in cotton resistance to herbivores during the 21st century is likely with programmes fostering multi-disciplinary, basic and applied research. The multi-disciplinary team approach involving plant scientists and entomologists with a backgrounds ranging from molecular biology to agronomy, breeding, and ecology has proven to be a useful model for balancing the reductionist approach inherent to research in molecular biology, and for rapidly shortening the period of time between initial discovery and commercial application.

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