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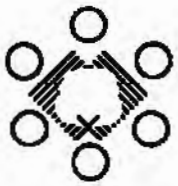

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Host plant resistance in cotton to spider mites

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Abstract
Resistance to spider mites has been found in a number of Gossypium species, including *G. barbadense*, *G. arboreum*, *G. herbaceum* and *G. australe*. Among the cultivated cottons, *G. hirsutum* has several morphological and biochemical traits which confer partial resistance, while *G. barbadense* varieties show high antibiosis to *T. urticae*. Within *G. hirsutum* both constitutive and induced components of plant resistance have been identified. Genotypes with lower sugar and starch content are generally poorer hosts for spider mites. Genotypes with elevated levels of condensed tannins are often, but not always, more resistant to spider mites. *G. hirsutum* also shows induced resistance in response to prior mite feeding or mechanical damage. Morphological traits associated with resistance include thicker spongy parenchyma, layer, which reduces mite stylet penetration of the palisade, and a more lobed leaf shape or glabrous leaf surface, which provide less protection for mite eggs. Genotypes with very hairy leaf surfaces are more resistant to spider mites because they interfere with movement. It is important to consider that some plant resistance traits for mites may conflict with resistance to other pests, with the needs of beneficial insects, with the development of acaricide resistance and with the needs of cotton processors.

Introduction

Mites of the family Tetranychidae, commonly known as spider mites, are pests of a wide range of orchard, vegetable, greenhouse and field crops world-wide (Jeppson *et al.*, 1975). At least 33 species of Tetranychidae are pests of cotton (*Gossypium* spp.) throughout the world, of which the most serious are *T. urticae* Koch, *T. ludeni* Zacher, *T. turkestani* (Ugarov and Nikolski) and *T. cinnabarinus* (Boisduval) (Leigh, 1985). In this review we firstly outline the cotton production system, consider the life history traits of Tetranychids that contribute to their pest status, focusing on *T. urticae,* which is the most cosmopolitan species, and describe the main effects of mite feeding on cotton physiology, growth and yield. Finally, we discuss the value and disadvantages of putative plant resistance traits that could be exploited in breeding cotton varieties with enhanced resistance to spider mites.

Cotton production systems

Most of the cotton grown throughout the world is the upland cotton type of the species *Gossypium hirsutum.* Other cultivated species are *G. barbadense* and *G. herbaceum* but these constitute a small proportion of the total. Cotton is typically grown in tropical or subtropical regions characterised by hot summers. It is normally grown as an annual, though rattoon cotton is grown in a few regions. Sowing usually occurs in late spring with the onset of warmer weather. Squaring (flower bud production) begins after about eight weeks and the first flowers appear in about 10 weeks. Most fruit (boll) is set and begins maturation about three to four months after planting with boll burst (opening of cotton fruits to reveal the cotton lint with seed) usually beginning after about five months. In cropping systems relying on mechanical harvesting, crops are chemically defoliated after about five and a half months and picking begins shortly after.

Production systems range from high input, high yield, highly mechanised systems, typified by the Australian and Californian regions, to low input, low yield, low mechanisation systems, typified by small scale production in regions of Zimbabwe and China. In high input systems cotton is fertilised, irrigated and arthropod pests controlled with pesticides, many of which are broad spectrum, controlling not only the target pests but also reducing the abundance of natural enemies. Control of outbreaks of spider mites relies heavily on use of acaricides, ranging from older broad-spectrum organophosphates (i.e. monocrotophos or profenofos) and older selective compounds such as dicofol or propargite to newer compounds such as avermectin, diafenthiuron or chlorfenapyr.

Life history attributes which pre-adapt mites to become pests

Life cycle

Spider mites on cotton live mainly on the underside of leaves (Jeppson *et al.*, 1975). They are green or red (carmine). Adult females are less than 0.5 mm in length, hard to see and often go unnoticed in crops until visual symptoms of damage appear, by which time they are often too numerous to control effectively with acaricides. Females are normally mated as soon as they emerge from the teliochrysalis (Helle, 1967). Sex ratios vary widely (Wrensch and Young, 1983) but are generally female biased with a ratio of approximately 3:1 (Mitchell, 1981). Reproduction is by arrhenotokous parthenogenesis; unfertilised eggs are laid by virgin and mated females and yield haploid males. Fertilised eggs always yield diploid females. Population development in *T. urticae* typically follows a cycle of initial colonisation of plants by mated female mites followed by rapid population growth, exploitation, and subsequent migration to a new host plant (Smitley and Kennedy, 1985). Adult females are the main migrants (Mitchell, 1973), migrating using wind currents

(longer distances, up to several km) or by crawling (short distance, plant to plant) (McEnroe and Dronka, 1971; Margolies and Kennedy, 1985; Brandenburg and Kennedy, 1987).

Pre-adaptations

Modern agro-ecosystems are ideally suited for development of spider mite populations - crops are often irrigated, fertilised and treated with pesticides to control pests and diseases. These production system characteristics combined with three key life history attributes contributes to the pest status of spider mites (Brandenburg and Kennedy, 1987):

High intrinsic rate of increase (r_m). High reproductive rate and short generation time contributes to high r_m in spider mites (Carey and Bradley, 1982). In natural ecosystems spider mites rapidly exploit newly colonised hosts, producing many dispersers before host quality declines. Under the hot conditions of most cotton growing regions, developmental time of spider mites is short (e. g. at 30 °C egg to oviposition takes 6 d). Combined with high host quality, derived from fertilisation and irrigation, mite populations can develop exponentially, especially if numbers of natural enemies are reduced by insecticides (i.e. mites are induced or secondary pests) (McMurtry *et al.*, 1970). Short generation time also means that several generations per season may be exposed to selection by acaricides, increasing the likelihood of resistance developing. In fact, resistance in spider mites to acaricides has been documented repeatedly (Helle, 1984; Herron *et al.*, 1998; Sabelis, 1985).

Polyphagy. *T. urticae*, like many Tetranychids, is polyphagous and a wide range of cultivated and non-cultivated plant species are hosts. Spider mites migrating using air movement have no directional or altitudinal control. Polyphagy therefore increases the probability of migrating mites encountering a suitable host (Brandenburg and Kennedy, 1987). In situations where association with a particular host species extends over many generations, populations of *T. urticae* may adapt physiologically to that host. When individuals from such populations are placed on a new host r_m may be reduced for several generations until adaptation to the new host occurs (Gould, 1979; Jesiotr, 1979; Fry, 1988).

Adult Diapause. *T. urticae* can survive winter as diapausing adult females or as actively reproducing populations (Jeppson *et al.*, 1975; Veerman, 1985). Diapause facilitates survival in regions where winters are harsh and active forms would probably perish and/or where winter hosts are scarce. The diapausing form is bright orange, non-feeding, non-reproductive and spends winter in sheltered locations such as crevices in bark and soil at the base of trees (Veerman, 1985). Diapause is induced in response to short days though temperature, and plant quality, may also modify the response (Helle, 1962; Veerman, 1985). In areas with mild winters mites can remain in the actively reproducing summer form provided suitable hosts are available (Brandenburg and Kennedy, 1981; Margolies and Kennedy, 1985). In such situations spider mites can use a succession of cultivated and weed hosts, and the abundance of winter hosts can have a strong influence on pest potential in the subsequent summer crop (Wilson, 1994a).

Effect of mites on cotton

Spider mites use their piercing mouthparts to puncture the leaf epidermis and feed on the underlying mesophyll and palisade cells (Jeppson *et al.*, 1975). A bronzed colour is seen on the upper surface of cotton leaves corresponding to the damaged areas on the underside. The damage caused by individual mites is small but when accumulated over time and combined with rapid population increase it can have devastating effects on cotton development, growth, yield and quality.

As mites feed they damage the chloroplasts and impair stomatal functioning, reducing leaf photosynthesis (Bondada and Tugwell, 1995). At the crop level, feeding damage reduces both radiation use efficiency and transpirational cooling, with a consequent increase in canopy temperature (Sadras and Wilson, 1997a). As mite damage increases, leaf senescence is accelerated (Sadras and Wilson, 1997ac). Reduction in yield of mite-infested crops is therefore the consequence of (i) growth reduction resulting from impaired photosynthetic capacity, (ii) low harvest index typical of smaller plants, and in cases of severe damage, (iii) rapid defoliation that reduces light interception (Sadras and Wilson, 1997ab).

The development of cotton lint has two phases; firstly, elongation of cells on the epidermis of seeds (these become cotton fibres), and secondly, the secondary thickening of the elongated cell wall with cellulose (Hearn and Constable, 1984). A reduction in the photosynthetic capacity of the plant, caused by mites, reduces the amount of cellulose produced resulting in less secondary thickening. A higher proportion of lighter, finer and weaker, 'immature fibres' results, reducing the weight of lint in bolls and the fibre quality. Further flow-on effects of severe mite damage include reduced germination and oil content of seeds, resulting in reduced seedling vigour (Wilson, 1993; Sadras and Wilson, 1996).

The extent to which spider mites affect the yield or quality of cotton depends on the interaction between timing of population increase and the rate of increase. The earlier the time of infestation increase and the faster the rate of increase the greater the effect on yield and other economic parameters (Wilson, 1993).

Principles of plant resistance to pests

Plant resistance has been used as a means of protecting plants from herbivores for several hundred years (Smith, 1989) and is an appealing means of managing herbivorous pests for several reasons. It is specific, has cumulative effectiveness over several pest generations, is persistent, environmentally compatible, easy to use and is generally compatible with other pest management tactics (Kogan, 1982). On the other hand, to the extent that plant resistance traits affect the fitness of target populations of herbivores, there is a risk of those populations further developing "resistance" to the barriers build up by the plant, leading to an "arms race". This view of the co-evolution of herbivores and host plants is currently the subject of an interesting debate that includes an alternative, mutualistic rather than antagonistic, viewpoint of the relationship between herbivores and host plants (Owen, 1980; Belsky, 1986; Verkaar, 1986, 1988; Mathews, 1994).

Herbivores respond to a number of cues when selecting host plants, including morphological features, such as trichomes, leaf surface waxes and tissue hardness, and chemical features such as primary (nutrient) and secondary (non-nutrient) phytochemicals. The secondary plant chemicals or allelochemicals, have been divided into two general groups, allomones and kairomones (Smith, 1989). Allomones benefit the producing

organism, such as a resistant plant, and include repellents, locomotor excitants, suppressants, deterrents, antibiotics and antixenotics. Kairomones benefit the receiving organism, such as an insect, and include attractants, arrestants and feeding or oviposition excitants (Kogan, 1982). The definitions of chemicals as either kairomones or allomones are context dependent, i.e. a chemical that is a kairomone to one herbivore may be an allomone to another. Interestingly, proponents of the mutualistic view of plant/herbivore relationships consider allomones as "regulators of consumption" more than "defences".

Painter (1952) defined three main mechanisms of plant resistance to herbivores:

antibiosis, in which the pest is adversely affected by a physical or chemical feature that reduces survival,

non-preference, in which the plant affects pest behaviour so that it avoids the plant and chooses another, such as a plant which contains a repellent, and

tolerance, in which the plant has the ability to withstand a level of herbivore damage and still yield productively.

Another form of resistance, called pseudo-resistance by Painter (1952), occurs when plants evade herbivore attack because their development is out of phase with herbivore activity. These definitions have come under some criticism and Kogan (1982) has proposed a more complete framework for describing plant resistance. He separates mechanisms into those under the primary control of environmental factors, even though they may be genetic in origin, termed 'ecological resistance' and those under the primary control of genetic factors, termed 'genetic resistance'. Ecological resistance includes phenological asynchrony, which is essentially similar to Painter's pseudo-resistance, and induced resistance (Karban and Carey, 1984), while genetic resistance includes antixenosis, which is analogous to Painter's non-preference, antibiosis and tolerance (Kogan and Ortman, 1978). Although these mechanisms may operate independently, in practice they are frequently interrelated (Painter, 1952; Kogan and Ortman, 1978; Smith, 1989). Other recent classifications of mechanisms of resistance to herbivory include those of Belsky *et al.* (1986) and Rosenthal and Kotanen (1994).

Plant resistance in cotton - definitions

Breeding for plant resistance in cotton has mainly targeted the primary pests in the system, most commonly *Heliothis* spp. and *Helicoverpa* spp. but also pests such as jassids (*Empoasca* spp.). Reducing the need to control such pests with broad-spectrum synthetic insecticides helps to maintain beneficial populations, decreasing the likelihood of outbreaks of spider mites. In some systems, breeding for plant resistance in cotton has been extremely successful, such as the development of hairy varieties for resistance to jassids throughout much of Africa and the Indian sub-continent (e. g. Parnell *et al.*, 1949). Due to their status as secondary pests, research into plant resistance to spider mites has generally been of secondary importance. Nevertheless, a number of biochemical and morphological traits have been identified that confer a degree of resistance to spider mites. Plant resistance to mites does not have to be complete for it to be effective in cotton. For instance, a factor that slows or delays the development of mite populations will reduce the potential effect of mites on profitability and reduce the need for intervention with an acaricide.

Throughout this review we have followed a modified version of the classification of degrees of resistance outlined in Wiseman (1994);

- Immunity, the pest will not damage the host.
- High resistance, the pest will only cause minor, non-economic damage to the host;
- Moderate resistance, the pest will cause an intermediate level of damage, less than a susceptible genotype but may still be economically significant;
- Low resistance, the pest will cause slightly less damage to these hosts than to a susceptible crop;
- Susceptibility, a host that is highly suitable for the pest to develop on and on which the pest will cause a high economic loss.

Plant resistance in cotton - across the genus Gossypium

Resistance to spider mites, of varying degrees, has been found in a number of Gossypium species, including *G. barbadense*, *G. arboreum*, *G. herbaceum*, *G. lobatum* and *G. australe* (Schuster *et al.*, 1972b; Zhang *et al.*, 1993). Within *G. hirsutum* a range of morphological and biochemical factors have been identified which confer a range of resistance levels to spider mites, discussed below, although no immune genotypes have been reported. In a survey of 686 wild races of *G. hirsutum* Schuster *et al.* (1972c) and Schuster and Maxwell (1976) found 86 strains that were highly resistant, as reflected by low damage scores in their seedling screening technique (discussed below). Most of these races were from the Oaxaca and Yucatan regions of Mexico. However, of the 36 *G. hirsutum* varieties tested from around the world (i.e. genotypes which have been domesticated and used in breeding programs) most were of low resistance. Jenkins (1994) also reported several wild *G. hirsutum* types that were highly resistant to spider mites, most of which would however require considerable development before they could be useful commercially. In contrast wild and domesticated *G. barbadense* genotypes have repeatedly been found to be highly resistant to spider mites (Leigh and Hyer, 1963; Schuster *et al.*, 1972c; Schuster and Maxwell, 1976) with life history traits such as developmental time and fecundity adversely affected (Schuster *et al.*, 1972a; Trichilo and Leigh, 1985a).

Plant resistance in cotton - within *G. hirsutum* and *G. barbadense*

G. hirsutum and *G. barbadense* are the most widely grown cotton species and throughout the rest of this review we will focus on research to identify mechanisms of plant resistance to spider mites in these species. Within *G. hirsutum* a range of authors (Table 1) has identified both constitutive and induced antibiotic components of resistance. Constitutive traits associated with plant resistance include chemical composition (nutritional and antibiosis) and leaf morphology (discussed below).

Antibiosis - constitutive components - biochemical

A major group of allelochemicals found in cotton are the terpenoids, including the terpenoid aldehydes such as gossypol, and sesquiterpenoid quinones such as hemigosspolone and the sesterterpenoids known as the heliocides (see review by Bell and Stipanovic, 1977). These are contained in black pigmented glands found on the leaves, stems, roots and parts of the fruits of cotton. The density, size and distribution of these glands vary considerably between genotypes. The glands are a spherical 'sac' surrounded by a layer of flattened cells (Bell and Stipanovic, 1977). *G. barbadense* lines generally have more glands than *G. hirsutum* and their glands contain methoxylated terpenoids that are not found in the latter.

Growth studies have shown that the terpenoids, in particular gossypol, have detrimental effects on *Heliothis virescens*, *Helicoverpa zea* (Boddie), *H. armigera* (Hübner), *H. punctigera* Wallengren, boll weevil (*Anthonomus grandis* Boheman), lygus bug (*Lygus hesperus* Knight), cotton flea hopper (*Pseudatomoscelis seriatus* (Reuter), cotton leafworm (*Alabama argillacea*), beet armyworm (*Spodoptera exigua* (Hübner)) and mites (*Tetranychus urticae* Koch) (Bottger and Patana, 1966; Bell and Stipanovic, 1977; Kay *et al.*, 1979; Hedin *et al.*, 1983; Jenkins *et al.*, 1983; Zummo *et al.*, 1984; Mulrooney *et al.*, 1985; Parrot, 1990; Fitt *et al.*, 1995). In general cotton genotypes with higher densities of glands, particularly on the fruiting structures or with elevated levels of terpenoids show higher levels of resistance to *Helicoverpa / Heliothis* spp.

However, comparisons of glanded on non-glanded cotton genotypes and or of genotypes with high or low gossypol levels have shown no correlation between presence of glands or elevated terpenoid levels and resistance to spider mites for either *G. hirsutum* or *G. barbadense* (Schuster *et al.*, 1972b). Significantly, glanded and non-glanded lines of the *G. barbadense* genotype 'Pima S4' were both resistant to mites indicating that terpenoids do not explain the high mite resistance of this species. This is probably because the small size of spider mites allows them to avoid feeding on the glands. Similarly, the small size of neonate *Heliothis / Helicoverpa* allows them to avoid feeding on leaf tissues between glands or to preferentially feed on components of the primordial tissue within the flower buds in which glands have yet to form (Chan and Mahoney, 1988). Increasing the density of glands particularly in the calyx crown has been shown to increase resistance to these pests (Hedin *et al.*, 1992).

A range of flavonoids is also found in cotton, including the condensed tannins, which are contained intra-cellularly in the vacuoles or plastids (Chan and Mahoney, 1988). They adversely affect development of *H. virescens* and *H. zea*, although results are inconsistent (Chan *et al.*, 1978; Klocke and Chan, 1982; Hedin *et al.*, 1983; Zummo *et al.*, 1984; Mulrooney *et al.*, 1985). High levels of condensed tannins may also confer resistance to mites, by inhibiting digestive enzymes (Wu *et al.*, 1996). Lane(1981) found that the leaf tissue of *G. hirsutum* races resistant to spider mites (see above) had elevated levels of condensed tannins, among other things. Some of these races had tannin contents equivalent to 20% of their dry weight (Lane and Schuster, 1981). Similarly the mite resistance of *G. barbadense* genotypes, such as the cultivar Pima S-6, may in part be due to high levels of condensed tannins (Altamarino *et al.*, 1988; Wayne-Smith *et al.*, 1992).

However, the relationship between tannin content and spider mite resistance is not simple. Lane (1981) found one genotype, 'St 7A(GN)', which was susceptible to spider mites despite having condensed tannin content in leaves in excess of 20% of dry weight. The condensed tannin content of young cotton leaves increases progressively with plant growth and is higher than that of older leaves (Zummo *et al.*, 1984; Wilson, 1994b). In Australia, Wilson (1994b), using commercial cotton varieties, showed that spider mites prefer younger, higher tannin, higher nitrogen leaf tissue for feeding and oviposition. Furthermore, in the field, spider mite populations tended to increase in the mid-late season when condensed tannins were at their highest, suggesting that in commercial cotton cultivars tannin levels had little impact on spider mite population growth. Life-history studies and field assessments of spider mite abundance also showed no differences in resistance between several lines with elevated condensed tannin levels and commercial,

mite susceptible varieties (Wilson unpub. data.). Further research into the range of condensed tannins in cotton and their effect on spider mite life history traits is required before their role in plant resistance to mites can be clarified. Simply breeding for enhanced tannin levels may not be effective.

Antibiosis - nutritional components

The levels of chemicals regarded as nutrients for insect growth can also affect plant resistance to spider mites. Genotypes with reduced sugar or starch content appear to be more resistant to spider mites, though the underlying mechanisms are unknown (Schuster and Kent, 1978; Nel, 1989). Wilson (1994b) also showed that *T. urticae* had reduced fecundity and increased developmental time on cotton leaf tissue with lower N content. Sadras and Wilson (1997c) found that spider mite damage causes a sharp decline in leaf nitrogen content, as nitrogen is translocated to stems and bolls. They postulated that this results in a negative feedback on mite population development, possibly contributing to the eventual 'crash' in mite populations on heavily damaged cotton

Antibiosis - induced components

Karban and English-Loeb (1988) defined 'induced' resistance as "a change in the host plant in response to an extrinsic stimulus that results in the plant being a less suitable host for the population growth of spider mites". From an evolutionary perspective, induced defence is seen as a strategy that adjusts the defence level to the prevailing risk of herbivory, in contrast to constitutive, invariant defence level (Astrom and Lundberg, 1994). Karban and Carey (1984) who showed that *T. urticae* populations grew more slowly on the new growth of cotton seedlings that had previously been damaged by another mite species, *T. turkestani*, than on seedling that had not been damaged. This induced response was systemic as tissues that were not themselves damaged were also resistant.

The response reported by Karban and Carey (1984) was non-specific, and mechanical damage, caused by abrading cotton cotyledons with carborundum powder, elicited a similar induced resistance to spider mites (Karban, 1985). Furthermore, Karban *et al.*, (1987) and Karban and English-Loeb (1988) showed that damage caused by one pest could induce resistance responses that affected other organisms. For instance, prior exposure of plants to spider mite damage made them less susceptible to the fungal pathogen *Verticillium dahliae* and more resistant to beet armyworm (*Spodoptera exigua*). Behavioural studies have shown that adult female spider mites (*T. urticae*) can discriminate between plants that have been previously damaged and those that have not, suggesting an olfactory response to the chemical substances involved in the resistance. The induced response appears to be an active reaction of the plant to damage, rather than simply a decline in plant quality as a result of feeding damage. Metabolism of cellular constituents released into the plant during herbivore feeding appears to be the trigger for the production of toxins or protoxins, or may act as a signal to turn on defence genes which result in the production of toxins.

Karban (1986) showed that induced responses were effective in the field. Prior mite or manual mechanical damage on young cotton caused significant reductions in spider mite abundance later in the cotton season. Induced resistance could therefore potentially be manipulated as a component of a pest management system either by damaging plants mechanically or biologically, using a non-economic pest (see English-Loeb *et al.*, 1993), or by applying compounds that elicit an induced response. Hildebrand (1986) showed that

induced resistance in bean seedlings, *Phaseolus vulgaris* L., to *T. urticae* was associated with an increase in the activity of lipoxygenase. Kasu (1990) proposed that lipoxygenase is normally segregated from free fatty acids (FFA's), and it is the availability of the FFA's to the lipoxygenase, brought about by mite feeding damage, that initiates the mechanism whereby FFA's are peroxidated into toxins such as aldehydes. Mite feeding liberate FFA's by (1) damaging cell membranes and exposing lipids are which converted into free fatty acids (FFA's), possibly by way of a lipase reaction or (2) releasing of them from intracellular pools. Application of FFA's to intact bean seedlings caused similar reduction in fecundity of mites raised on these seedlings to that induced by wounding or prior mite feeding (Kasu, 1994). Jiang *et al.* (1996) have similarly shown 1-octen-3-one, a volatile compound arising from lipid peroxidation following damage of subterranean clover cotyledons, *Trifolium subterraneum*, is implicated in antibiotic resistance in this species to redlegged earth mite, *Halotydeus destructor* Tucker.

Almost nothing is known of the pathways by which mite feeding induces defences in cotton, though limited information is available for some lepidopterous pests. Bi *et al.* (1997) found that prior feeding on cotton by *Helicoverpa zea* or application of methyl jasmonate induced resistance to this pest. McAuslane and Alborn (1998) however noted that damaged glanded cotton had higher levels of lipoxygenase products, volatiles such as mono- and sesquiterpenes and terpenoid aldehydes compared with undamaged plants, and that larvae of *S. exigua* showed a 33 fold preference for undamaged tissue. In contrast, damaged glandless plants only had elevated lipoxygenase products and *S. exigua* only showed a 2.6 fold preference for undamaged over damaged glandless tissue, suggesting an unclear role of volatiles and terpenoid aldehydes in induced feeding deterrence to this pest.

The mechanisms underlying the induced responses found in cotton following damage by mites are still unknown. Investigation of these mechanisms may allow identification of 'elicitor' compounds that, according to some authors, could be sprayed onto crops to increase levels of resistance to mites or other pests in a strategic manner. However extrapolation of results from the laboratory to the field should be viewed with caution. In many systems seedling cotton is subject to heavy damage from abiotic factors, such as severe defoliation or abrasion of leaves by wind-borne soil particles or hail (Lane, 1959), and/or from biotic factors such as leaf or terminal damage due to feeding by thrips (Sadras and Wilson, 1998) or jassids (Parnell *et al.*, 1949). Such damage may render the plant less suitable as a host and may also induce high levels of resistance, with both factors contributing to a decline in overall host suitability for spider mites or other pests. Under such circumstances it is unlikely that further resistance could be induced either by more damage or by application of elicitors, limiting the potential to manipulate induced resistance in the field. Another consideration is that cotton is able to compensate for severe damage caused by phytophagous thrips (Sadras and Wilson, 1998), which are also facultative predators of spider mite eggs (Trichilo and Leigh, 1986b; Wilson *et al.*, 1996; Sadras and Wilson, 1998). Using such compensation in pest management would take advantage of both predation on mites by thrips and the systemic induced defences of plants in response to thrips feeding.

Non-preference - constitutive - morphological traits

A number of morphological traits have been identified in cotton which have been associated with plant resistance to various pests (Thomson, 1987; Jenkins, 1994). The most notable among these are the traits for leaf shape, leaf / plant hairiness (trichome

density), presence of extrafloral nectaries and bract shape. An important caveat on use of such morphological features in pest management is that other aspects of the pest / predator complex may be affected, and such issues are discussed later, but also mentioned where relevant below.

Bracts on cotton fruits can encompass the fruit or can be twisted away from the fruit leaving it exposed (frego bract) (Thomson, 1987). Frego bract has been found to increase resistance to the boll weevils (Jones *et al.*, 1978), through reduced oviposition (non-preference), but to increase susceptibility to damage from plant bugs (Maredia *et al.*, 1993) probably because the calyx is more exposed. No effect of frego bract has been found on spider mite populations (Fitt and Wilson, unpublished data).

Cotton produces nectar from nectaries located on the mid-veins on the undersides of leaves and around the base of flower buds (Thomson, 1987). Nectariless mutants are available which do not possess nectaries. The nectariless trait has been associated with resistance to the Helicoverpa / Heliothis complex (Adjeu-Maafo *et al.*, 1983), to plant bugs (Schuster *et al.*, 1976), leaf perforators (Henneberry *et al.*, 1977) and pink bollworm (Wilson and Flint, 1988) but has also been associated with reduced abundance of beneficial insects which may use the nectaries as a supplemental food source (Treacy *et al.*, 1985). However, no effect of the nectariless trait has been found on abundance of mites (Bailey, 1984).

A range of leaf shapes occur in *G. hirsutum*, including the normal broad leaf, sub-okra, where the leaves are moderately lobed, okra leaf, where the leaves are deeply lobed, and super-okra where the leaves are reduced to one to three thin straps. The okra leaf shape (Fig. 1) in particular has received considerable attention and has been shown to confer a degree of resistance to whitefly and the *Helicoverpa / Heliothis* complex (Thomson, 1987; Jenkins, 1994). A number of authors have also reported that okra leaf genotypes afford moderate resistance to spider mites compared with isogenic normal leaf genotypes (Bailey and Meredith, 1983; Wilson, 1994c).

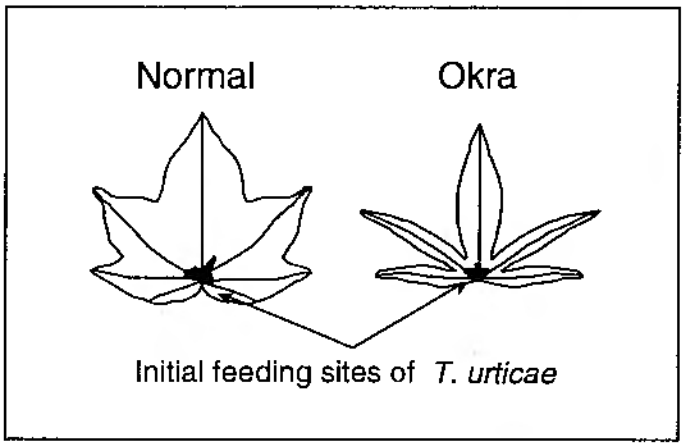

Figure 1. Normal and okra shaped cotton leaves, showing areas of initial feeding by spider mites (*Tetranychus urticae*).

Wilson (1993, 1994c) compared several aspects of mite/plant interactions in okra and normal leaf cottons in Australia. He showed that mite colonies developed more slowly and cotton yield was less reduced in okra than in normal leaf types. Differences between

varieties with contrasting leaf morphology were not related to plant allelochemicals or nutrition, to reduced leaf area of the okra leaf per se, or to differences in the abundance of predators. Spider mites eggs are particularly sensitive to desiccation (Ferro and Chapman, 1979). As mites are small (adults ≅ 0.5 mm and eggs ≅ 0.1 mm) the environment they mostly experience is that of the boundary layer of air trapped close to the leaf surface. The humidity of the boundary layer is influenced by the degree of transpiration and by ambient conditions and can be disrupted by air turbulence or buffered by morphological features that create regions of reduced turbulence such as high hair density, leaf folds, prominent leaf veins and leaf shape. Wilson (1994c) proposed therefore that resistance to mites in okra-leaf cotton was due to the shallower, more disrupted boundary layer of okra leaves (Baker and Myhre, 1969), which would result in fewer high humidity sites suitable for oviposition and egg survival on okra shaped leaves than on normal leaves. This mechanism was defined as ovipositional non-preference. In support of this hypothesis, super-okra genotypes have been found to offer slightly higher resistance to spider mites than okra leaf genotypes (Wilson unpub data).

The difference between boundary layer humidity and ambient humidity and the interaction with temperature are key factors in this resistance mechanism. In cotton regions such as those of Australia, ambient humidity is often low (<40 % RH) and temperature high (often > 35 °C). Disruption of the boundary layer by wind could expose mite eggs to dryness and consequently high mortality, around 40% (Ferro and Chapman, 1979; Wilson, 1994c). In dry, hot environments a thinner boundary layer typical of lobed leaves could be less favourable for mite colonies. Conversely, in more humid regions the exposure of mite eggs to desiccating conditions will be far less and the magnitude of resistance afforded by the okra leaf shape could be expected to diminish.

A limitation of this mode of resistance however is that it is not evident until mites on okra leaves exploit the suitable areas for oviposition and begin to 'run out' of favourable oviposition sites (Fig. 1). Initially mites exploit the sheltered area at the base of the leaf blade, where it joins the petiole. Here large veins form deep sheltered areas favoured by mites. Wilson (1994c) demonstrated that mite populations increased at similar rates on okra and normal leaf genotypes until these areas were exploited then began to diverge with significant slower population development on the okra leaf genotypes.

Wilson (1993) reported that the difference in rate of increase of spider mite populations has highly significant effects on yield and fibre quality, with okra genotypes suffering about half the yield loss of normal leaf genotypes and a shorter period of susceptibility to loss. The amount of leaf area damaged per mite was the same for both leaf shapes and Sadras and Wilson (1997a) showed that there was no intrinsic difference between leaf shapes in their capacity to maintain photosynthesis under mite damage. Differences in yield were therefore due to differences in the abundance of mites (Sadras and Wilson, 1997a) and, secondarily to the higher harvest index commonly found in comparisons of okra leaf and their normal-leaf counterparts (Sadras and Wilson, 1997b). In commercial practice okra leaf cultivars have been recognised by consultants and cotton growers in Australia as being more resistant to *T. urticae* and requiring fewer acaricide applications (Thomson, 1994). A significant side benefit of lobed leaves is that the more open canopy of okra leaf crops allows greater penetration of insecticides and improved control of Helicoverpa / Heliothis spp compared with normal leaf crops (Jones *et al.*, 1986). A further benefit of both okra

and super-okra genotypes is that the more open canopy reduced the degree of boll-rot in lower bolls (Andries *et al.*, 1996).

The potential role of boundary layer humidity in plant resistance to spider mites is supported by the observation that glabrous genotypes (completely hairless leaf) also show moderate resistance to spider mites. Additionally, mite population increase is slower on genotypes with the combination of okra and glabrous traits than the okra trait alone (Fitt and Wilson unpub. data). The glabrous trait probably reduces the degree of protection on the leaf surface resulting in a more disturbed boundary layer. Observation on moderately hairy genotypes support this assertion: increasing density of leaf hairs could be expected to act as an 'insulation' against turbulence, thereby making more of the leaf surface suitable for oviposition by mites. Similarly, Elden (1997) found that glabrous soybean genotypes were more resistant to mites than pubescent isogenic lines, and noted that adult mites often walked off glabrous leaf tissue rather than settling indicating non-preference.

Experiments with hairy and smooth lines show that on smooth genotypes mites tend to colonise the suitable parts of the leaf only, with the result that colonies tend to be sharply defined and show intense leaf damage. On hairy genotypes mites tended to spread further over the leaf surface for both feeding and oviposition, resulting in more of the leaf surface being damaged less intensively, until mites reach high densities after which intense damage results (Wilson unpub. data.). In the field, mite population increase was faster on a moderately hairy genotype than on its sparsely hairy isoline (Wilson unpub. data). Hair density and the number of hair branches originating from each hair point probably interact strongly in relation to mite resistance. Botha *et al.* (1989) found that the genotype BS 80/129 which had an average of 365 hairs cm^2 with an average of about 4 branches per hair site was susceptible to spider mites whereas Kamel and Elkassaby (1965) found that the genotype Bahtim 101 with an average of 804 hair cm^2 and an average of 9.8 branches per hair site was highly resistant. If the density of leaf hairs per unit area and /or the number of hair branches per hair point is increased beyond an as yet undefined density the closeness of the hairs probably physically interferes with mite movement and feeding (e. g. Kamel and Elkassaby, 1965). A conceptual relationship between increasing hair density and resistance to spider mites can be hypothesised and is shown in Fig. 2. The type of hairs may also be important as genotypes with dense tomentose (matted) hairs, which probably impede mite movement, are generally resistant to mites (i. e. Pavlova and Egamberdiev, 1990).

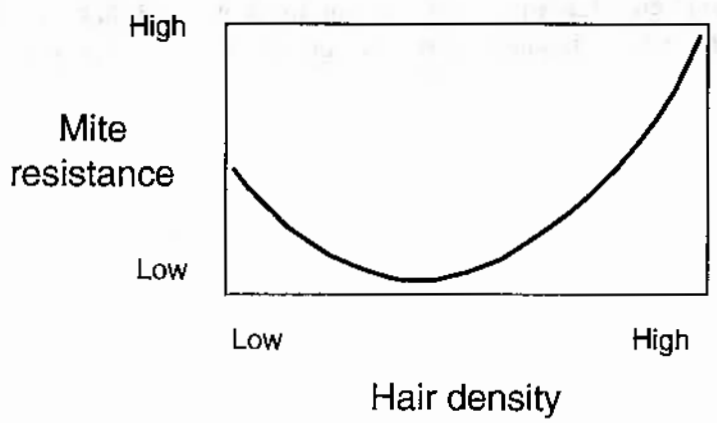

Figure 2. Conceptual relationship between hair density on the undersides of cotton leaves and resistance to spider mites.

Leaf hardness or thickness of the epidermis are additional and often overlooked morphological traits that have been shown to provide resistance to spider mites in cotton and other plants. Pavlova (1981) found that *G. hirsutum* lines with a thick lower leaf epidermis were more resistant to spider mites. Simongulyan (1988) found that leaf thickness and leaf epidermal thickness (barrier layer) were highly correlated and that thicker epidermis conferred resistance to spider mites. Schuster (1978) similarly reported that a thicker spongy parenchymal layer was associated with resistance to spider mites in highly resistant wild *G. hirsutum* race stocks, reducing penetration of the mite stylets into the palisade tissue where feeding normally occurs. Sadras *et al.* (1998) showed that water stress caused in increase in hardness of cotton leaves which was associated with enhanced resistance to spider mites. In other mite / host systems, leaf hardness or penetration resistance has also been associated with resistance to mites. For instance, Jiang *et al* (1996) found that increased mechanical strength of cotyledons of subterranean clover was associated with antixenotic resistance to the redlegged earth mite.

Phenological resistance

Phenological resistance is essentially escaping herbivores in time, by selecting plants that have a different phenology, and is therefore equivalent to the pseudo-resistance of Painter (1952) or phenological asynchrony of Kogan (1982). Breeding cotton for a shorter growing period may enable evasion of some pests in time. For instance use of short-season cultivars to avoid the late season build up of boll weevils (Waddle, 1966). Wilson (1982) similarly employed selection for short season production as a means of resistance to pink bollworm, *Pectinophora gossypiella* (Saunders).

A number of authors have observed in comparisons of short and longer season cultivars that short season cultivars often suffer less damage from spider mites relative to longer season cultivars(Botha, *et al.*, 1989; Pavlova and Egamberdiev, 1990). Wilson (1993) quantified yield loss due to mites in cotton as a function of rate of population increase and time remaining in the growing season for the population to develop. As the crop ages and matures it become less sensitive to spider mite damage. Short season cultivars would mature earlier, allowing less time for mite populations to cause damage compared with a full season cultivar. This type of resistance is illustrated conceptually in Fig. 3 and has been clearly demonstrated in Australia in soybeans where normally lower yielding short season varieties often out-yield normally higher yielding long season varieties under conditions of high mite infestation (Rose, 1996). This occurs because crops with a shorter maturation time are more phenologically advanced than those with a longer maturation time, and hence avoid the heavy damage from mites during the critical pod filling period (Rose, 1996).

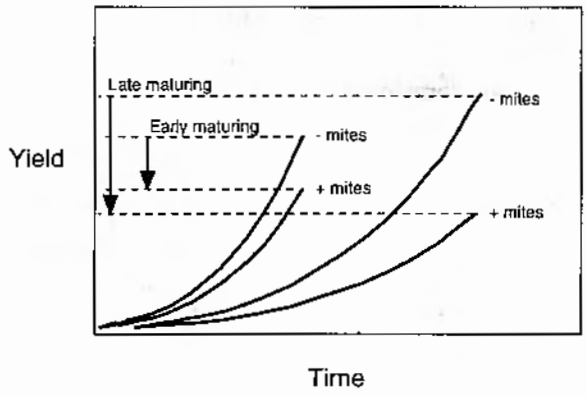

Figure 3. Conceptual relationship between crop growth period and resistance to spider mites (phenological resistance).

Environmental effects on plant resistance

Environmental factors can substantially impact on the effectiveness of plant resistance traits. Interactions between arthropod herbivorous, water availability and soil fertility have been widely investigated in cotton (e.g. Leigh *et al.*, 1974; Flint *et al.*, 1994). In general, conditions that favour crop growth increase the abundance of both herbivorous and predacious arthropods. The actual response of the crop is, however, difficult to predict and non-linear responses to multiple stresses have often been found (English-Loeb, 1990).

Karban *et al.*, (1989) found that plant density influenced the strength of induced resistance to spider mites. Resistance was highest under relatively uncrowded conditions and diminished when plants were crowded. Water stress can also modify leaf properties and hence modulate resistance to spider mites (Sadras *et al.*, 1998). The value of morphological traits such okra leaf shape may also be affected. Hesketh *et al.* (1975) showed that the degree of lobing of okra leaf genotypes was affected by temperature, with the combination of high day and night temperatures (32 °C day / 29 °C night) causing a very diminished okra leaf with only slight lobing compared with a normal leaf genotype, whereas reduced night temperatures (32 °C day / 23 °C night) resulted in a more typical deeply lobed okra leaf. This could affect the degree of resistance that could be expected against spider mites. Additionally, as described above the ambient relative humidity is also likely to interact with the resistance mechanism proposed for okra leaf genotypes.

Ability of mites to overcome plant resistance

Reliance on single plant attributes to cause high mortality in the target insect, such as an allelochemical acting analogously to a synthetic pesticide, is likely to lead to relatively rapid evolution of resistance in the pest to the attribute (Slansky, 1990). This is particularly relevant to a polyphagous pest with a short generation time like spider mites. For instance, Fry (1989) showed that, within ten generations, *T. urticae* was able to adapt to a new host on which they initially had high juvenile mortality. In contrast, morphological characteristics such as leaf shape are likely to be acting on a range of aspects of both mite physiology (susceptibility of eggs to desiccation) and behaviour (avoid laying eggs in 'exposed' sites) and this mechanism of resistance would presumably be more difficult for mites to overcome. However, in principle any plant trait that affects the fitness of target

herbivore populations implies a selection pressure and the potential for adaptation. Continuous exposure to lobed leaves, for instance, might select for smaller mites and eggs, better adjusted to thinner boundary layers.

Assay technique

In investigatiug plant resistance to spider mites the techniques used can have a large bearing on the outcomes and on whether types of resistance may be overlooked. This is well illustrated in the case of the seedling screening technique developed by Schuster *et al* (1972c) where seedling cotton plants are infested with mites and damage scored 20 days later according to a five step damage scale. Such a technique has shown good correlation between rankings of resistance measured in greenhouse and field conditions. Such correlation should not be assumed however, as others have found poor correlation between greenhouse and field measures of resistance (e.g. Quisenberry, 1990). Nevertheless, this technique offers a means of rapidly assessing the resistance of a range of genotypes without the cost and complexity of large-scale field experiments. However, because cotton does not express differences in leaf shape until about 7 th-leaf stage and because humidity levels in greenhouses are typically high this technique is likely to overlook resistance associated with leaf shape or leaf hairiness (or lack of). Furthermore, interactions between environmental factors and plant resistance (see above) should be considered in extrapolating from controlled conditions to the field.

Greenhouse experimentation should therefore be combined with field experiments in the environmental conditions under which the resistance must be effective. Varietal selection on the basis of yield under sprayed conditions has probably often masked any host plant resistance to key pests due to the high efficacy of insecticides (resistance to insecticides not withstanding) (De Ponti, 1977). Prior to the advent of synthetic insecticides mites were only occasionally considered a significant problem in cotton, probably because natural enemies kept populations at sub-economic levels. In any case, given the lack of options with which to effectively control mites, in regions where they were present there would have been a natural selection for tolerant varieties on the basis of yield (De Ponti, 1977).

Investigation of plant resistance to mites should therefore include comparisons of both mite population increase and crop damage under conditions where the cotton is (i) protected against all pests including mites, (ii) protected against all pests except mites and (iii) unprotected. In each of these treatments mites, other pests and predators should be assessed at regular intervals. This allows discrimination of (a) suitability of genotypes for mite population development (b) varieties which may be particularly tolerant or sensitive to mite damage, through comparison of yields under different spray regimes and (c) interactions between varieties and natural enemy populations. Artificial infestation of field plots with mass-reared mites from a glasshouse may assist with such experiments, ensuring equal infestation levels but care must taken with the selection of strains to avoid those that may have been selected on a particular genotype of cotton for a prolonged period (see Fry, 1988).

Where possible detailed assessments of key morphological variables should also be made at intervals through the cotton season, including leaf area, leaf shape (e.g. area/perimeter ratio), leaf hardness, leaf epidermis thickness, hair density and range of hair branching types. Samples should also be taken for analysis of key nutritional components such as starch, sugars and nitrogen and for secondary compounds such as terpenoids and

flavonoids. Once resistant genotypes have been identified a range of techniques, including life history studies and choice tests can be used to identify which aspects of mite development or behaviour are affected (Trichilo and Leigh, 1985b). If resistance is associated with a particular biochemical trait then extraction and bioassay techniques may be used to confirm the activity of the compound (see for instance (Ridsdill-Smith *et al.*, 1995).

Interaction of plant resistance against spider mites with other pests

A wide range of plant resistance mechanisms can be exploited for pest management in cotton. However, factors that increase resistance to one pest may increase susceptibility to another, as indicated above. Such is the case with hairiness, which although conferring resistance to jassids, increases susceptibility to aphids, whitefly and bollworm (Baht *et al.*, 1982). Jenkins (1994) summarised a number of plant traits that clearly reflects their multiple, and often contrasting, effects on different pests.

Interaction with the requirements of cotton processors

Another consideration is the interaction between plant resistance traits and the requirements of cotton processors. For instance, increasing the hairiness of cottons for resistance to spider mites is a viable option in situations where cotton is handpicked while still the plant is green. In mechanically harvested cotton, which is chemically defoliated before harvest, leaf hairs promote adherence of leaf particles to the stem, which ends up contaminating the lint during picking, resulting in 'trashy' seed cotton and price penalties.

Plant resistance and predation

Studies of plant resistance to pests often focus on plant / herbivore interactions (bi-trophic) whereas it is increasingly apparent that inclusion of the next level in the system, predation / parasitism (tri-trophic) is important in understanding outcomes of selection for particular resistance traits (Norlund *et al.*, 1988; Williams *et al.*, 1988). The compatibility of plant resistance with biological control in particular has received considerable attention. Plant resistance may increase the efficiency of natural enemies (Treacy *et al.*, 1985). However, plant resistance traits may also impact negatively on natural enemies, via consumption of prey containing plant toxins or incompatibility of the predator with the mechanism of resistance (Bergman and Tingey, 1979; Campbell and Duffey, 1979). Some traits, however, such as the presence of nectaries are generally associated with an increase in predator numbers, compared with nectariless genotypes and nectaries are very important for survival of hymenopterous parasitoids (Schuster and Calderon, 1986).

Interactions between plant damage, herbivores and predators need also to consider the effects of plant damage on foraging of predators. Dicke *et al.* (1990) discuss how mite predators such as *Phytoseiulus persimilis* are attracted to volatiles, mostly terpenoids, released from Lima bean plants (*Phaseolus lunatus*) following damage by *T. urticae*. Undamaged leaves on plants on which other leaves had been damaged by spider mites also released these volatiles, i.e. an induced indirect defence in uninfested leaves (Takabayashi *et al.*, 1991). Emission of volatiles by a damaged plant may therefore aid foraging predators in locating prey patches, to the benefit of the plant. Bruin *et al.* (1992) later showed that when infested with *T. urticae*, cotton plants also produce volatile cues for predators and furthermore that these volatiles could affect plants downwind, making them also more attractive to predators. Such interaction between plant, herbivore, and predator is potentially important in using plant resistance to spider mites (or other pests) because

cotton genotypes vary in their production of volatiles in response to damage (see for instance Elzen *et al.*, 1985; Williams *et al.*, 1988). However, the nature and role of these "infochemicals" are topics of debate notwithstanding the question of whether these same volatiles may attract not only predators but also herbivores (Sadras and Felton, unpublished).

Plant resistance and resistance to insecticides

Besides their direct effect on the target pest an additional benefit of high levels of antibiotic chemicals in plants is that they may enhance the efficacy of chemical controls. For instance, Trichilo and Leigh (1986a) found that dicofol remained effective longer on a mite resistant cotton cultivar than on a susceptible cultivar, because the slower growth rate of mites on the resistant cultivar did not allow mite densities to become high enough to escape the acaricidal effect. However the reverse may also occur. For instance, Gould *et al.* (1982) found that a population of *T. urticae* selected for survival on a resistant cucumber variety had higher levels of resistance to several organophosphate pesticides than did the control population from which it was derived. The potential for such interactions between plant allelochemicals and development of resistance to insecticides in target pests has been reviewed by Brattsten (1988).

The future; transgenics, new insecticides, direct and indirect effects

The development of molecular techniques, such a random amplified polymorphic DNA (RAPD) offers the potential to screen a wide range of mite resistant and susceptible genotypes and isolate primers that amplify DNA fragments that separate resistant from susceptible genotypes. Such primers could be used to assist in plant breeding by allowing assessment that progeny of crosses of between susceptible and resistant genotypes do carry the mite resistance genetic material (Geng *et al.*, 1995). Genetic engineering offers the prospects to include into the cotton genome genes from other plants or animals that are associated with production of substances that provide resistance to spider mites, problems of resistance not withstanding. However, in most high input cotton systems where mites are a problem, the most effective use of genetic engineering may be to help reduce insecticide inputs for control of primary pests. This would reduce the detrimental effects of insecticides on predators and hence reduce the likelihood of outbreaks of secondary pests, including spider mites (Wilson *et al.*, 1998).

Breeding for plant resistance vs yield and fibre quality

Yield and fibre quality are the primary determinants of profitability in cotton. Varieties selected for plant resistance to spider mites must therefore at least equal commercial varieties or they are unlikely to be taken up by cotton producers. Yield is in itself a form of plant resistance, as pointed out by Thomson (1987), e.g. a variety with a higher yield potential will still produce more after suffering a given intensity of pest damage than a variety with a lower yield potential. This is, in fact, the value of high harvest index as a (minor) component of resistance to mites in okra leaf cottons (Sadras and Wilson, 1997b). While this observation is true up to a point, with a pest such as spider mites, which attacks the 'factory' of the plant, yield losses are likely to be economically unacceptable unless enhanced yield is also supported by plant resistance, biological control or use of acaricides.

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Table 1. Effects of putative plant resistance traits on spider mites. Some side effects of these traits are also shown (see text for sources of information).

Trait	Effect on spider mites	Other effects
Terpenoids (e.g. gossypol)	• no effects to slight effect via reduced fecundity	• resistance to other pests (e.g. *Heliothis / Helicoverpa* spp.)
Flavonoids (e.g. cond. tannins)	• ambigous, probably antibiotic under some circumstances	• possibly increases resistance to other pests (e.g. *Heliothis / Helicoverpa* spp.)
Volatiles (e.g. terpenes)	• unknown	• unknown effect on other pests (may increase resistance to *Heliothis / Helicoverpa* spp.) • may serve as cues for predators
Lower sugar / starch content	• partial resistance	• unknown
Lower leaf nitrogen content	• reduced fecundity and increased developmental time	• unknown, probably less suitable for developments of other pests as well
Glabrous leaf	• probably reduces rate of population increase because of thinner boundary layer (Fig. 3)	• increased susceptibility to pests (jassids) • decreased susceptibility to some pests (Heliothis / Helicoverpa spp., • delayed maturity, lower yield
Hairy leaf	• non-linear (Fig.3)	• trashy cotton • increases susceptibility to other pests (e.g. whitefly, *Heliothis / Helicoverpa* spp., Aphids) • reduces susceptibility to other pests (jassids)
Lobed leaf shape (e.g. okra leaf)	• reduces rate of population increase because of thinner boundary layer	• higher harvest index • better distribution of pesticides within the canopy • improved resistance to some pests (e.g. whitefly, boll weevil *Heliothis / Helicoverpa* spp.) • reduced boll rot
Harder leaves and/or thicker epidermis	• increased resistance	• unknown, probably increased resistance to some pests

Frego bract	• no effect	• increases resistance to some pests (*Heliothis* / *Helicoverpa* spp.) • increases susceptibility to some pests (e.g. Lygus bugs, mirids)
Nectariless	• no effect	• may interact with abundance of predators • increased resistance to some pests (*Heliothis* / *Helicoverpa* spp.)