Leaf hairiness and plant resistance to herbivory: smooth-leaved cottons have fewer mites (Acari: Tetranychidae) but suffer more intense damage.

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Abstract

In agricultural systems, plant resistance has been exploited to minimize losses to pests and/or reduce control costs. In cotton, okra leaf-shape provides partial resistance to spider mites because eggs are exposed to greater risk from desiccation as the humid leaf boundary layer is shallower and more disrupted than on normal-shaped leaves. Extrapolating, we predict moderately hairy cotton leaves should create a deeper, more stable boundary layer, favouring mite development while the boundary layer of smooth leaves should be shallower, providing some resistance to mites. We tested this hypotheses by assessing the dynamics of mite populations and leaf damage, leaf gas exchange and crop yield in a factorial field experiment with eight treatments resulting from two mite treatments (+ mites, - mites), and two leaf types (smooth vs hairy) in two genetic backgrounds (Stoneville 213-4 and Delcott 120238). Mite colonies developed faster on the hairy leaf cultivars, and were unaffected by genetic background or the interaction between genetic background and hairiness. In contrast, leaf damage per mite was higher in smooth leafed cultivars. At the base of the leaf, where mites establish colonies, 50% reduction in photosynthesis required 1.8 times as many mites in hairy leaves than in smooth leaves. The yield of cotton was reduced in +M treatments, but the magnitude of reduction was similar for hairy and smooth isolines indicating no benefit due to fewer mites. Our results supported the link between leaf hairiness and mite colony growth but do not support the putative consequences in terms of photosynthesis or yield. Paradoxically, the relative inhospitality of smooth leaves may have induced mites to concentrate in smaller, relatively protected leaf sections causing more localised and more severe damage. We therefore show an example of plant resistance where the leaf is less suitable for mite development, but more prone to severe damage that reduces leaf performance, consequently negating the potential yield benefits from fewer mites. These results may have implications for other instances of plant resistance.
**Introduction**

Plant resistance to herbivory is an important factor influencing the population dynamics of both plants and herbivores. Resistant plants will generally harbour fewer herbivores, thereby reducing losses of leaf area, assimilates or seeds. However, production of defences, whether physical or chemical, often incurs a metabolic cost, which in turn can reduce the potential fitness of resistant plants compared with non-resistant plants in the absence of herbivores. Nevertheless, under conditions of herbivory, plant resistance, as indicated by fewer herbivores should result in greater fitness. This feature has been exploited in many agricultural and horticultural systems to reduce losses of productivity to pest species, especially insects, mites and pathogens (Wilde et al. 1991; Heinrichs 1992; Wiseman 1994; Chu et al. 2002; Frei et al. 2003). In this study we consider plant resistance, due to reduced leaf hairiness, in cotton to spider mites, and ask the question ‘is pest abundance a good indicator of resistance between cotton genotypes?’

Intra-specific variability in cotton morphological, chemical and physiological traits can affect its suitability as host for a range of arthropod herbivores (Bailey et al. 1978; Bailey and Meredith 1983; Gimenez-Ferrer et al. 1994; MacFarlane and Hepworth 1994; Wilson 1994b; Karban and Niho 1995). Wilson and Sadras (2001) reviewed cotton traits with putative value for resistance to spider mites (Acari: Tetranychidae) and reported several morphological traits that could influence the development of mite populations, such as leaf shape (Wilson 1994b), hardness (Schuster and Kent 1978; Pavlova et al. 1981) or hairiness (Botha et al. 1989). Such traits are of interest because they may be of value in reducing the risk of economic loss from mites, are often simply inherited and easily identified (compared with allelochemicals for instance) making selection in breeding
programs more straightforward and may be more difficult for pests to overcome as they do not rely on a toxin.

Okra-leaf cotton cultivars, in particular have been shown to provide partial resistance to spider mites. In the field, *T. urticae* populations establish faster and cause more damage on normal-leaf shape cultivars than on the deeply lobed, okra-leaf shape cultivars (Wilson 1993). On cotton leaves, colonies of the two-spotted spider mite (*Tetranychus urticae* Koch) establish on the underside of the leaf, in the area where the petiole joins the lamina, and progress preferentially in this area and alongside the larger leaf veins and within leaf folds (Wilson 1994b). This spatial pattern has been interpreted in terms of (a) the size of *T. urticae*, i.e. adults \( \approx 0.5 \) mm, eggs \( \approx 0.1 \) mm, (b) the susceptibility of their eggs to desiccation (Ferro and Southwick 1984), and (c) the protective effect of the high humidity within the leaf boundary layer, particularly around large leaf veins (Wilson 1994b; see also Willmer 1986). This differential response is accounted for by the thicker boundary layer of the leaves of normal-leaf shape cultivars compared to their okra-leaf shape counterparts (Baker and Myhre 1969). This is presumably because the narrow leaf lobes of okra-leaf cultivars make the boundary layer more easily disrupted and/or potentially shallower than on the normal leaf shape, thereby exposing mites or their eggs to lower ambient humidity, rather than to chemical, nutritional or mechanical factors (Wilson 1994b; Wilson 1993). The mechanism of resistance was thus defined as non-preference caused by less suitable feeding and oviposition sites in okra-leaf cottons (Wilson 1994b). The influence of leaf morphology on the suitability of the hosts has also been demonstrated for other pest species in cotton including reduced populations of *Bemisia tabaci* B-biotype on okra leaf compared with normal leaf cottons (Chu *et al.* 2002) and reduced populations of jassids on hairy leafed compared with smooth leafed cottons (Bhat *et al.* 1982). It has also been
demonstrated in other arthropod-plant systems including predators e.g. phytoseiid mites
(Typhlodromus caudiglans) in grapes (Karban et al. 1995).

Building on this explanation, we hypothesised that leaf hairiness may also affect the leaf boundary layer and hence the provision of suitably protected habitats for mites. Leaves with smooth, hairless surfaces may be more prone to having the boundary layer disrupted by wind currents than hairier leaves, thereby making them less suitable for development of spider mites. Hairy leaves, in contrast, are likely to have a thicker boundary layer, because the hairs physically reduce the influence of wind currents that could disrupt or reduce the thickness of the boundary layer (Burrage 1971; Willmer 1986). The presence of hairs, providing they are not at such high densities that they physically impede mite movement or feeding, may therefore provide a microenvironment, in terms of temperature, humidity and air movement, more suitable for the development of spider mite populations e.g. (Holtzer et al. 1988). This may result in more rapid mite population growth and greater mite damage occurring on hairy leafed cotton cultivars compared to smooth leafed cultivars. Leaf hairiness could also influence the distribution of mites on the leaf surface, especially if more of the leaf surface is suitable for mite feeding and oviposition on hairy leaves and less on smooth leaves.

It is usual in studies of host plant resistance to herbivores to assess pest abundance and some measure of plant productivity/fitness, such as seed, fruit or fibre production. In such studies it is common to assume that fewer pests equals less loss of productivity/fitness. This assumption has proven true for resistance of okra-leaf cultivars, which had fewer mites and less yield loss than normal leaf shaped cultivars. However, the potentially more complex relationship between mite population growth, distribution and damage intensity
suggests that the simple relationship between pest abundance and resistance may not always hold.

This paper explores the interaction between leaf hairiness, mite population growth, damage, leaf function (photosynthesis) and yield. Specifically we test the hypotheses that (i) leaf hairiness favours development of two-spotted mite populations while smooth leaf has the opposite effect (ii) leaf hairs influence mite distribution and intensity of damage on the leaf surface (iii) this in turn influences the effect of mites on photosynthesis and (iv) mite abundance and effect on photosynthesis interact to influence yield. We discuss the outcomes in terms of evaluation of plant cultivars for resistance to herbivory.

**Methods**

*Treatments and experimental design*

A field experiment was established at Narrabri, New South Wales (30° S, 150° E) in the 1997-98 cotton season. The experiment consisted of eight treatments resulting from the factorial combination of two mite treatments and two leaf types in two genetic backgrounds. The mite treatments were: control, no mites (-M) and crops artificially infested with mites (+M). Leaf types were near-isogenic lines with smooth or hairy leaf within the genetic backgrounds of Stoneville 213-4 and Delcott 120238, hereafter referred to as Stoneville hairy, Stoneville smooth, Delcott hairy and Delcott smooth. Treatments included four replicates arranged in a split-plot design with mite treatments assigned to main plots, and cotton lines to subplots, each comprising four 15-m long rows spaced at 1 m. This design allowed for the use of miticide to control mites in the –M field section.

*Crop management*
The experiment was sown on October 17, 1997 and the established crop had 10 ± 3 plants per metre row (mean ± SE). It was fertilised with 100 kg N ha\(^{-1}\) two months before sowing. After emergence, the crop was furrow irrigated each time a soil water deficit exceeded 50% (Hearn and Constable 1984). Weeds were controlled with pre-emergence herbicides, hand chipping and inter-row cultivation as required. Once the slowest maturing plot had approximately 60% of bolls opened, the crop was defoliated in preparation for harvest.

**Mite and insect management**

This study used the procedures for experimental manipulation of mites developed by Wilson (1993; 1994a). These included (i) spraying the experimental plots with a broad-spectrum insecticide (thiodicarb, 750 g ai ha\(^{-1}\)) before mite infestation to eliminate mite predators (Wilson *et al.* 1998) and encourage establishment of mite colonies, (ii) infestation of +M plots with mite-infested cotton seedlings that were grown in a glasshouse, and (iii) control of mites in -M plots with selective acaricides (propargite, 1500 g ai ha\(^{-1}\); abamectin, 5.4 g ai ha\(^{-1}\)) whenever populations exceeded 1 adult female mite/leaf. Granular aldicarb (450 g ai ha\(^{-1}\)) was applied in the seed furrow at sowing to reduce the risk of confounding effects due to damage by thrips and other sucking pests. Through the season, insect pests were monitored twice weekly and controlled with insecticides, which did not control mites, when necessary according to published thresholds (Shaw 1996). Insecticides and acaricides were applied using a high clearance ground sprayer.

**Leaf gas exchange, chlorophyll and mite dynamics**

Weekly measurements of gas exchange, leaf chlorophyll content and mite density, began on the week prior to the establishment of +M treatments (91 days after sowing, DAS). To avoid possible effects of miticides (see above) on photosynthesis, measurements were not
taken within 48 h of an application. Measurements were done on the first fully expanded leaf from the top of the canopy, which was usually four nodes below the terminal; this is also the node most likely to contain the highest mite density within the cotton plant (Wilson and Morton 1993). This means that the position of the leaf measured remained constant relative to the plant terminal but that it was at a progressively higher node position in relation to the cotyledons as the season progressed. Because the leaf that occupied this position changed from week to week, the fate of particular leaves over time was not studied. Each week, two measurements were taken on one leaf on a previously tagged plant in the centre row of each plot, one measurement at the basal and one at the distal portion (see below). A new plant was tagged in each plot each week (i.e. four leaves were measured per mite treatment per week, four new leaves the following week and so on).

Leaf physiological variables and mite abundance were measured as described by Reddall et al. (2004). Briefly, photosynthesis, stomatal conductance, transpiration and intercellular CO₂ content were measured with a LI-6400 (Lincoln, Nebraska, USA) portable photosynthesis system, with a clear leaf chamber covering an area of 6 cm². Measurements were made around midday on clear, sunny days and leaves were held perpendicular to the sun. Chamber conditions included (i) ambient CO₂ concentration, (ii) photosynthetic photon flux density, PPFD > 1600 μmol m⁻²s⁻¹, (iii) temperature set to 2 °C below ambient to allow for slight heating when the chamber is clamped on the leaf (usually between 25°C and 35 °C), and (iv) relative humidity controlled to 60-70 % using air flow rate and moisture scrubbers. For gas exchange variables and PPFD, each measurement was the average of five consecutive readings, taken sequentially at 2 s intervals. Leaf chlorophyll content was measured with a SPAD 501 (Minolta, Osaka, Japan) which has been tested in a number of plant species, including cotton (Wood et al. 1992). Data was analysed and presented in SPAD units. Basal (near the junction with the petiole) and distal (near the leaf
edge farthest from the petiole junction) leaf positions were distinguished for gas exchange and chlorophyll measurements to allow for differences in mite distribution between smooth and hairy varieties as described in Reddall et al (2004). Adult female mites per leaf were counted and damage assessed on the same leaves used for gas exchange measurements. Percentage leaf area damaged by mites was scored using the method of Wilson and Morton (1993b) as adapted by Reddall et al (2004) to account for low or ‘light’ damage, where the leaf showed the pale yellow mottling typical of a short period of mite feeding and extreme or ‘heavy’ damage, where the leaf showed the dark red-brown scarred areas typical of prolonged mite feeding.

**Leaf hardness and hairiness**

We measured leaf hardness (penetration resistance) and quantified leaf hairiness to better understand differences between leaf types. Penetration resistance was measured on attached leaves with a dial tension gauge (Sands and Brancatini 1991; Sadras et al. 1998). Ten leaves of each variety across the –M plots and three positions per leaf near the insertion of the petiole, where mites prefer to feed (Wilson 1994b), were measured on February 17, 1997.

Leaf hairiness was assessed by counting the number of trichomes on a 6mm diameter circle of leaf on each of 10 leaves from the –M section for each variety. Trichomes were scored as having one, two, three, four or more hairs (almost always 5) originating from each trichome base. The number of each hair type was multiplied by the number of trichomes to yield an average hair density per mm².

**Yield**

Yield of mature crops (all bolls open) was assessed by machine harvesting one of the central two rows of each plot with a single row spindle cotton picker. A sample of seed
cotton for each plot was weighed then ginned in a small saw gin to separate seed from lint and the lint weighed.

**Analysis**

Leaf hardness and hairiness were analysed using a two way ANOVA with cultivar (Delcott, Stoneville) and hairiness (smooth, hairy) as treatments using Genstat 8 (Payne et al. 2005). Mite density, gas exchange, chlorophyll content and yield were analysed using a two way ANOVA and yield with a split plot design with +M and –M as main plots and cultivar and hairiness as subplots using Genstat 8.

The response of gas exchange to mites was described by an exponential decay curve in basal leaf sections (Sances et al. 1979) and by a negative logistic curve with a distinct lag-phase in the distal section (Sadras and Wilson 1997). Curves were fitted using (SigmaPlot 2000, SPSS Science, Chicago, IL, USA). Photosynthesis, transpiration and stomatal conductance in +M treatments was normalised as percent of controls to account for effects of crop age.

**Results**

*Mite infestations and leaf damage*

The procedure to establish mite colonies in +M plots while maintaining negligible mite numbers in nearby –M plots was effective, except for a single episode of propargite drift from a nearby field which caused a transient decline of mites in +M plots (Fig. 1). Mite colonies grew faster in the hairy leaf cultivars, with statistically significant differences detected at 123 DAS (F = 8.87; d.f. = 1, 5; P = 0.032) and 139 DAS (F = 10.19; d.f. = 1, 5; P = 0.020). There was no significant effect of genetic background (Stoneville vs Delcott) or interaction between genetic background and hairiness on mite populations.
As the crop aged and mite colonies developed, leaf damage increased and was substantially greater in hairy than in smooth lines (Fig. 2), both for heavy and light damage. Leaf area was not affected by cultivars ($F = 0.11$; d.f. = 1, 9; $P = 0.75$), leaf hairiness ($F = 3.74$; d.f. = 1, 9; $P = 0.085$) or their interaction ($F = 0.51$; d.f. = 1, 9; $P = 0.49$). There was a significant linear relationship between the total percent leaf area damaged and the number of adult female mites per leaf for both smooth and hairy lines in both genotypes (Figure 3). For both genotypes, the slope was greater in the smooth than in the hairy leaves, indicating greater damage per mite, though this difference was only significant for Delcott ($t = 3.8$, d.f. = 7; $P = 0.0018$; hairy; 0.91 % leaf area damaged mite$^{-1}$, smooth; 1.87 % leaf area damaged mite$^{-1}$).

**Leaf hardness and hairiness**

There was no significant difference between cultivars or hairiness for leaf hardness ($P > 0.07$ in both cases, mean hardness = 4.01 kPa). However, the interaction was significant ($F = 5.26.1$; d.f. = 1, 27; $P = 0.03$, LSD = 0.26) for Stoneville where the smooth isoline had slightly harder leaves (4.19 kPa) than the hairy isoline (3.81 kPa).

Leaf hairiness differed between the two cultivars ($F = 4.37$; d.f. = 1, 36; $P = 0.044$) with Delcott (4.4 hairs mm$^{-2}$) slightly hairier than Stoneville (3.1 hairs mm$^{-2}$). There was also a significant difference between smooth and hairy cultivars ($F = 109.3$; d.f. = 1, 36; $P < 0.001$; smooth; 0.4 hairs mm$^{-2}$, hairy; 7.1 hairs mm$^{-2}$) but the interaction was not significant indicating the difference between hairy and smooth isolines was similar for both varieties.

**Leaf physiological responses to mites**

As crops aged and mite colonies developed, photosynthesis (Fig. 4) transpiration (not shown), stomatal conductance (not shown) and leaf chlorophyll content (Fig. 5 – Delcott
only shown) all declined faster in mite-infested crops than in uninfested controls. To summarise the effects of hairiness on these physiological responses, non-linear functions were fitted as illustrated in Fig. 6. The number of mites required to reduce response variables to 50% of controls was obtained from the fitted functions (Table 1). At the base of the leaf, where mites first establish their colonies, 50% reduction in gas exchange and stomatal conductance required 1.8 to 5.9 times more mites in hairy leaves than in smooth leaves. At the distal leaf position, at least 4 times as many mites were necessary to bring about a similar 50% reduction in hairy leaves than in smooth leaves.

Crop yield

The hairy isolines of both cultivars had higher yields than the smooth isolines ($F = 10.5$; d.f. = 1, 18; $P = 0.005$) (hairy isolines; 1625 kg lint ha$^{-1}$, smooth isolines; 1413 kg lint ha$^{-1}$). Mites reduced yield of both cultivars ($F = 619.1$; d.f. = 1, 18; $P < 0.001$) (-M; 1837 kg lint ha$^{-1}$; +M; 1201 kg lint ha$^{-1}$). None of the possible interactions were significant ($P > 0.3$ in all cases). This indicates that the effect of mites on yield was similar for the two cultivars and for smooth and hairy isolines of each cultivar.

Discussion

Effect of leaf hairiness on mite population and leaf damage

Mite populations developed faster on hairy leafed cottons than on their smooth-leafed counterparts, consistent with the hypothesis (i) that moderately hairy cotton types may be more suitable for mite population development. Such a difference could possibly due to the provision of a more suitable microenvironment for feeding and oviposition (Wilson and Sadras 2001). This is also in agreement with Karban et al. (1995) who found that numbers of phytoseiid mites were positively associated with the density of vein hairs and the density of bristles in leaf axils of grape leaves (Vitis spp.). Karban et al. 1995 noted that
knowledge of the density and locations of hairs, bristles and domatia (small shelter-like structures) provided considerable information about the number of mites that would be found.

Our data also appear to confirm hypothesis (ii) that the presence of absence of leaf hairs may influence mite distribution and damage intensity. Damage could be less intense but more widespread if mites colonised more of the leaf surface, as occurred with hairier leaves, and more intense and concentrated if they colonised less of the leaf, as occurred with smooth leaves. In both genetic backgrounds (Stoneville and Delcott), the percentage of leaf area damaged per mite was greater in the smooth leaves than in the hairy leaves, indicating more intensive feeding. However, this was only significant in Delcott, probably reflecting in part differences in hairiness, as Delcott was slightly hairier than Stoneville. Leaf hairiness may have affected the mite distribution over the leaves. From direct observations, the mites were more evenly distributed over the leaf surface in the hairy leaf types, whereas they were more aggregated in the protected areas near veins and leaf folds in the smooth leaf types; this is partially indicated by the higher percentage of light damage on hairy cultivars than smooth cultivars on some dates.

*Effects of mites on leaf gas exchange and yield of hairy and smooth leafed cottons*

The more intensive damage on smooth leaves resulted in greater reductions in photosynthesis per mite than on hairy leaves and supported hypothesis (iii) that mite distribution and damage intensity influenced the effect of mites on photosynthesis. Our results also therefore support hypothesis (iv) that mite abundance and effects on photosynthesis interact to affect yield, but not in the direction we expected. Paradoxically, the relative inhospitality of smooth leaves may have induced mites to concentrate in smaller, relatively protected leaf sections causing more severe damage and greater reductions in photosynthesis. Overall, gas exchange and related variables were more
strongly affected by mites on the smooth than in the hairy leaf types, as indicated by the rapidity and magnitude of effects in the basal leaf area and the dramatic difference in mites numbers required to halve photosynthesis and stomatal conductance between leaf types (Table 1). This may be because more intense damage near the base of the leaf blade on smooth leaves reduces movement of water into and assimilates out of the leaf, thereby explaining the rapid decline in photosynthesis in the basal area and, not long after, the distal area of smooth leaves (Delcott). The results with Stoneville show a similar trend though less clear, probably partially reflecting the lower hair density, and hence smaller differences between smooth and hairy leaves in mite numbers (Figure 1) and damage intensity.

The putative benefit of inhospitable micro-environments for mites in smooth leaves was therefore negated by the behaviour of mites seeking protected leaf sections. Importantly, we showed that mite abundance alone is not necessarily a good indicator of resistance in terms of yield. Changes in plant morphology, e.g. leaf shape, may strongly influence pest abundance, and also pest distribution and feeding intensity. Our results suggest that for mechanisms of plant resistance where the physical environment is altered to make the leaf or plant less suitable, such changes may alter pest behaviour which may in turn influence potential productivity (e.g. yield) outcomes in unpredictable ways.

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References


**Table 1.** Sensitivity of responses to mite damage in near-isolines of Stoneville and Delcott cottons with hairy and smooth leaves. Values are numbers of adult female mites per leaf necessary to reduce the response variable to 50% of uninfested controls.

<table>
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*∞* mite populations did not reach sufficient numbers to reduce response to 50% of controls.
Captions to Figures

1. Dynamics of mite populations on infested (+M) and uninfested (-M) plots of near-isolines of Stoneville and Delcott cottons with hairy and smooth leaves. Values are means, error bars are two standard errors. The arrow indicates the date when spray drift may have affected mites in +M plots.

2. Dynamics of leaf damaged caused by mites in near-isolines of Stoneville and Delcott cottons with hairy and smooth leaves. Error bars are two standard errors. *p<0.05, **p<0.01, ***p<0.001 indicate significance of the ANOVA comparing hairy and smooth leaf damage.

3. Relationship between leaf damage and number of adult female *T. urticae* per leaf mites in near-isolines of Stoneville and Delcott cottons with hairy and smooth leaves. Fitted equations are: Stoneville hairy: y = 1.30*x, Stoneville smooth: y = 1.64*x; Delcott hairy: y = 0.91*x; Delcott smooth: y =1.87*x; for all regressions R² > 0.67, p<0.0001.

4. Dynamics of leaf photosynthesis as affected by mites in near-isolines of Stoneville and Delcott cottons with hairy and smooth leaves. Measurements included basal and distal leaf sections. Error bars are two standard errors. *p<0.05, **p<0.01, ***p<0.001 indicate significance of the ANOVA comparing infested and control crops.

5. Dynamics of leaf chlorophyll (SPAD units) as affected by mites in near-isolines of Delcott cottons with hairy and smooth leaves. Measurements included basal and distal leaf sections. Error bars are two standard errors. *p<0.05, **p<0.01, ***p<0.001 indicate significance of the ANOVA comparing infested and control crops.

6. Example of functional relationship between leaf physiological variables and mite numbers. Functions were fitted for each variable, leaf type and position, and
genetic background, and fitted functions were used to derive a mite threshold required to reduce response variable by 50% (Table 1). Relationships between % photosynthesis of the +M hairy and smooth leafed Stoneville and Delcott genotypes and number of adult *T. urticae* / leaf;

Exponential decay equations for basal leaf portions:

Stoneville:  
- Hairy: $y = 2.48 + 112.29 \times \exp(-0.06 \times x)$, $R^2 = 0.89$; df=19, $F=67.43$, $p<0.0001$
- Smooth: $y = 24.79 + 63.83 \times \exp(-0.10 \times x)$, $R^2 = 0.60$; df=19, $F=12.56$, $p=0.0004$

Delcott:  
- Hairy: $y = -3.86 + 106.76 \times \exp(-0.03 \times x)$, $R^2 = 0.80$; df=19, $F=32.88$, $p<0.0001$
- Smooth: $y = -62.88 + 171.03 \times \exp(-0.07 \times x)$, $R^2 = 0.79$; df=19, $F=31.30$, $p<0.0001$

Negative logistic equations for distal leaf portions:

Stoneville:  
- Hairy: $y = \frac{107.17}{1 + (x/50.99)^{0.90}}$, $R^2 = 0.73$; df=19, $F=23.20$, $p<0.0001$
- Smooth: $y = \frac{95.16}{1 + (x/118.87)^{0.13}}$, $R^2 = 0.19$; df=19, $F=2.01$, $p=0.1651$

Delcott:  
- Hairy: $y = \frac{101.42}{1 + (x/55.33)^{2.02}}$, $R^2 = 0.76$; df=19, $F=27.35$, $p<0.0001$
- Smooth: $y = \frac{111.97}{1 + (x/12.18)^{1.39}}$, $R^2 = 0.75$; df=19, $F=25.40$, $p<0.0001$
Figure 2

![Graphs showing % leaf area damaged for Stoneville and Delcott varieties over days after sowing.]

- **Stoneville**: % leaf area lightly damaged increases with days after sowing. % leaf area heavily damaged also increases but at a faster rate than lightly damaged. % total leaf area damaged increases significantly with days after sowing.
- **Delcott**: Similar trends observed but at a slightly lower rate compared to Stoneville.

* * * * • Hairy • Smooth
Figure 3

![Graphs showing the relationship between the number of adult female mites per leaf and the percentage of total leaf area damaged for 'Hairy' and 'Smooth' varieties of cotton, with data points for 'Stoneville' and 'Delcott'.]
Figure 6

![Graphs showing the relationship between photosynthesis and the number of adult female mites on hairy and smooth leaves.](image-url)