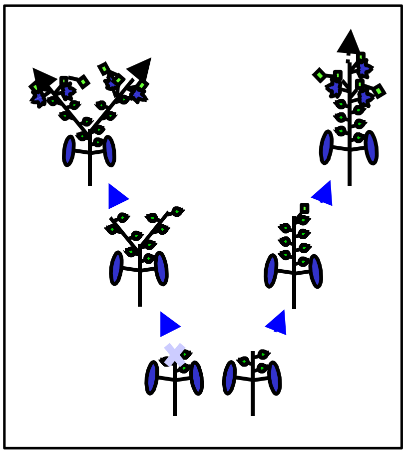
Predicting and enhancing cotton compensation following pest damage

Project CSP124C

Final Report
October 2003



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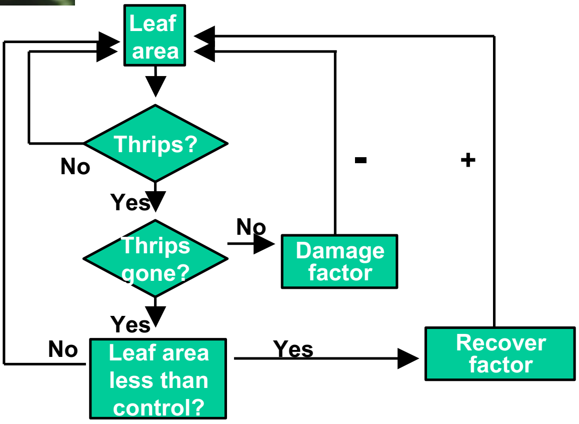

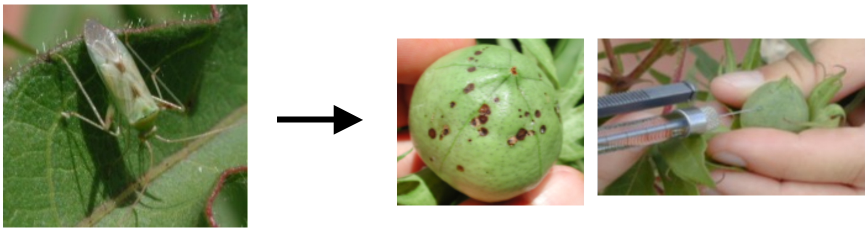

Part 1 - Summary Details

REPORTS

Please use your TAB key to complete part 1 & 2.

CRDC Project Number:		**CSP124C**
Annual Report:	☐	Due 30-Sep-03
Progress Report:	☐	Due 29-Jan-03
Final Report:	☒	Due 30-Sep-03 (or within 3 months of completion of project)

Project Title: **Predicting and enhancing cotton compensation following pest damage**

Project Commencement Date: 1/07/2000

Project Completion Date: 30/06/2003

Research Program: Insect Management

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Outline the background to the project.

This project continues an ongoing investigation on the ability of cotton to recovery from major pests in Australia. Previous studies (i.e. CSP39C/68C) have shown that cotton plants could compensate for pest damage but the degree of compensation varied with a large number of factors including pest type and the timing and level of damage and agronomic factors such as cropping region (i.e. climate), cultivar, soil nitrogen and plant density. This study explored in greater depth the limits of compensation following a variety of damage regimes, in particular, multiple tip and fruit loss to better mimic natural damage encountered in the field. Increased yield resulting from damage is also known but the conditions that enable this response are not obvious. Our team investigated ways by which recovery can be enhanced. We know that cotton often achieves full recovery even when the damage exceeded the current industry thresholds but there is insufficient knowledge about the mechanisms of recovery. Understanding the mechanisms is critical to making robust predictions on plant recovery. Data collected in this project will make yield predictions using OZCOT more robust and reliable, and in the future, produce a better decision support tool for pest management.

List the project objectives and the extent to which these have been achieved.

i. Investigate compensation in cotton resulting from multiple damage of early season tip removal and later season fruit loss of various intensities – multiple trials completed

ii. Quantify the relationship between plant growth (e.g., node and leaf area production) and yield compensation under various soil N levels – achieved

iii. Evaluate the potential for enhancing compensation from multiple damage events by varying cultivar and plant density – achieved

iv. Examine the nature of compensation in cotton grown during the dry winter months in northern Australia – first trial completed (results published in Journal of Economic Entomology), second trial to be completed in 10/2003.

v. Quantify the spatial and temporal patchiness of pest damage caused by natural and manual damage and their effect on yield – multiple trials completed

vi. Incorporate *Helicoverpa* damage and plant recovery in a simulation model (OZCOT) – achieved

vii. Address the emerging threat of green mirids in cotton: can cotton compensate from damage by mirids to squares and bolls? Two seasons of research completed.

Detail the methodology and justify the methodology used.

This project relied primarily on field trials to evaluate compensatory responses in range of cultivars grown under different agronomic and damage conditions. We also conducted similar trials in various locations to assess the effect of climate on compensation. A variety of manual damage was employed including the removal of leaf terminal, leaf area and fruit at various stages of the season. In several trials we used a repeated damage regimen to mimic more realistically seasonal pest occurrence, and to evaluate the interactions between damage events. Cultivar specific responses to damage were assessed by including in the trials cultivars of different leaf types, growth forms and determinacy. Contribution to compensation by agronomic variables such as soil nitrogen, plant density and Pix application was also examined. Trial data collected included the analysis of canopy development, growth and fruiting patterns across seasons in various damage treatments as well as yield and maturity. Regular harvests of plants, which were partitioned into roots, stems, leaves, squares, bolls, seed and lint, allow us to assess allocation of growth and how it was affected by different damage types. Findings derived using this experimental approach allow us to quantify compensation under a wide range of cropping conditions. In addition, the data set accumulated will improve the simulation of pest damage and plant recovery in OZCOT.

In the light of an increasing threat of sucking pests such as green mirids, we have initiated an investigation on the effect of these pests on cotton during the fruiting period. This is the time when mirid feeding has the greatest impact on yield and maturity. To assess the effect of mirid feeding at different times and intensities, we have developed an artificial means of mimicking mirid damage by injecting pectinase using a syringe into squares and bolls. Pectinase is a natural enzyme constituent of the mirid saliva which helps in breaking down plant tissue for resorption. Damage to fruit resulting from injecting pectinase has been found to be similar to actual mirid damage. We have begun a trial evaluation of yield and maturity outcomes of cotton damaged by the injection method at early to late fruiting period and at low to high levels of damage.

1. Detail and discuss the results including the statistical analysis of results.

In the interest of clarity, the findings and the significance of each trial has been presented in the form of a manuscript or published paper. The manuscripts will be submitted to peer-reviewed journal in the near future.

The trial results are presented in the following order:

Thrips Experiment
Cultivar by Plant Density Trial
Nitrogen Trial
Tip Damage Trial
Fruit by Timing Trial
Spatial Configuration of Damage Trial
Patchiness Trial
Mirid Trial
The High Yield Potential Trial
Enhancing and validating OZCOT
Threshold Trial (published paper attached)
Kununurra Damage Trial (published paper attached)

Detail how your research has addressed the Corporation's three Outputs - Economic, Environmental and Social?

Sustainability and profitability

This study aimed at increasing the awareness in growers and consultants of the significance of plant compensation when making pest management decisions. Our results have repeatedly demonstrated that, in the Lower Namoi and in northern Australia, full recovery is still possible even after repeated tip and fruit removal, at levels 2-3 times the industry thresholds (for *Helicoverpa*). Along with the full yield recovery, a modest delay of less than a week is generally observed. These data strongly indicate that current practice in pest management has not taken full advantage of the compensation potential of cotton. In many situations, doing nothing and allowing full recovery from damage sustained is the best IPM option. Sustainability and profitability are the clear benefits of this non-action. While this message has been available to growers and consultants in all cropping regions, more confidence about yield recovery is still needed. To fully implement a strategy of not spraying unless the damage outweighs the economic costs, an effective decision support system is essential. This aspect of the research is ongoing in collaboration with the Decision Support team in ACRI.

People and professional training

During the three years of the project, together with Lewis Wilson, we have been promoting the concept of compensation to a wide range of audiences within and beyond the cotton industry. We have made presentations at field days, cotton conferences, CCA meetings, IPM Short Course, UNE Cotton Production Course residential, and to CSIRO Plant Industry. I have taken part in training and advising technical staff, university and post-graduate students in the physiological aspects of cotton research. As a co-supervisor of David Kelley, I participated in advising him on the formulation, interpretation and write up of his Masters thesis on the effects of tip damage on cotton grown in central Queensland. Sara Winston-Smith (University of Sydney) was appointed as the CRC Summer Scholarship student to carry out a mirid damage experiment at ACRI. I supervised her research and she has successfully completed a number of key experiments. Training of technical staff including Simone Heimoana, Kylie Borchardt, Tanya Smith, Jane Caton, Kellie Baguley and Deon Cameron in the use of physiological instruments. The technical skills they have acquired are benefiting the ongoing project on compensation and other research projects at ACRI. I also provided input into the supervision of a CRC Honours student (Kylie Borchardt) looking at effects of jassid on photosynthesis. Taking part in supervising the PhD research of Simone Heimoana, providing technical advice and the development of physiological experiments.

Detail a plan for the activities or other steps that may be taken:

During the three years of this project, it became clear that there was a major shift in the pest complex in cotton crop underway. Transgenic cotton will increasingly reduce the need for *Helicoverpa* control, and in so doing, foster the general increase in the numbers of sucking pests. Of a great concern is the build up of green mirids and GVB, which are not well controlled by natural predators, later in the season. As growers and consultants are still uncertain about the amount of damage by sucking pests cotton can tolerate, inappropriate management of these pests at mid-season could undermine some of the IPM benefits gained by transgenic cotton. We have initiated research to address this issue (see findings in Mirid Trial) and will continue with a new project funded by the CRDC (2003-2006).

Because mirid damage to cotton fruit differs significantly from that by *Helicoverpa*, a new approach to defining the impact of damage on yield and maturity is needed. The new study will address the issue of defining tolerance of cotton to mirid damage by using a suite of experimental approaches including trials with natural infestation, simulated damage, and cage experiments. It is designed to achieve these key objectives:

- Define the economic threshold and compensation of mirid damage to cotton fruit
- Calibrate external and internal boll damage to total feeding pressure (in terms of mirid-day)
- Develop mirid damage and recovery routines in OZCOT as a decision support tool for the industry

Relevant information derived from rigorous experiments will be provided to the cotton industry in the new two-gene cotton era. This information will contribute to managing sucking pests to optimise profit and enhance sustainable cotton cropping. The key outcome for the cotton industry will be recommendations on the best management strategy for mid to late season mirid populations and similar sucking pests.

List the publications arising from the research project and/or a publication plan.

Published journal and conference papers

Lei T.T. 2002. Cotton (*Gossypium hirsutum*) Response to simulated repeated damage by *Helicoverpa* spp. larvae. Journal of Cotton Science 6(4): 119-125

Lei T.T. and N. Gaff. 2003. Recovery from terminal and fruit damage by dry season cotton crops in tropical Australia. Journal of Economic Entomology 96 (3): 730-736

Lei, T. T., M. Khan and L. J. Wilson. 2002. Boll damage by sucking pests: an emerging threat but what do we know about it? The 11th Australian Cotton Conference 2002.

Lei, T. 2000. Cotton makes a comeback after attack. Farming Ahead 97:52-53

Lei, T. Tolerance of cotton to simulated *Helicoverpa* damage. 10th Australian Agronomy Conference, Hobart Jan 29-Feb 1, 2001 [poster]

Submitted manuscripts

Lei TT. Yield recovery following repeated damage to cotton (*Gossypium hirsutum* L.) is not affected by cultivar and plant density. Target journal: Crop Science

Lei TT, Wilson LJ. Recovery of leaf area through accelerated shoot ontogeny in thrips damaged cotton seedlings. Target journal: Annals of Botany

Lei T, Baguley K, Cameron D, Wilson L. Does cotton's capacity to recover from pest damage decline with high yield potential? Target journal: Australian Cottongrower

Provide an assessment of the likely impact of the results and conclusions of the research project for the cotton industry. Where possible include a statement of the costs and potential benefits to the Australian cotton industry or the Australian community.

The development of damage routines (by Lei and Takenaka) to enable OZCOT to simulate compensation in cotton is a significant enhancement of the existing model.

The technique of using pectinase injection to mimic green mirid damage in cotton fruit is a methodological advancement aimed at addressing the issue of damage thresholds of green mirids and other sucking bugs on cotton fruit.

Part 4 – Final Report Executive Summary

General

This project has produced data which confirmed past findings of the robustness of cotton to compensate for levels of insect damage exceeding those of current industry thresholds for *Helicoverpa* and mirids. We have further quantified cotton's ability to recover from damage by compiling a significant database of yield outcomes in a variety of single and multiple damage situations across a wide range of agronomic conditions (i.e. cultivar, plant density, N and Pix application) and in a number of regions from northern Australia to Queensland and NSW (to assess compensation under diverse climatic regimes). To link artificial damage, which is normally implemented evenly within a row of cotton, with the more patchy damage caused by insects, we assessed the effects of various spatial distributions of damage within a stand on growth and yield.

Outcomes in summary

One of the earliest findings of this project showed no yield effect of repeated damage to terminal and fruit simulating that caused by *Helicoverpa* larvae of 2 to 8 per metre (Threshold Trial). This prompted us to ask the question, can tip damage increase the ability cotton tolerates further damage by improving its canopy structure? We addressed this question by examining in detail the process of plant growth following tip damage at different ages (Tip Damage Trial). We found a strong enhancement in lateral branch growth with tip damage prior to first square, indicating that the effect of apical dominance diminished with the onset of reproduction. There appears to be a optimal response when plants were tipped out at node 5-7, which we have incorporated into the simulation of tip damage in OZCOT (Enhancing and Validating OZCOT). Yield increases over the control due to tip damage have been found in some cases (Kununurra Damage Trial, Tip Damage Trial). In one case, damage to tip and fruit combined with high nitrogen (120 kg ha^{-1}) led to a decline in yield which was attributed to branching resulting in excessive vegetative growth and self shading. This prompted research into varying the cultivar, plant density and nitrogen input in assessing whether a right combination of these could enhance compensation. While all of these factors could modify canopy development and interact with damage, in general, we found little evidence for an optimal combination (Cultivar by Plant Density Trial and Nitrogen Trial). This led us to conclude that even though yield may differ between cultivars and nitrogen levels, in a full season area, adjustments in growth after damage did not enhance or depress compensation. Plants responded simply by exploiting the available space or nutrient without interacting with damage. Whether an enhancement might exist in dryland or cool region crops remains to be investigated.

The ability to compensate from damage may also decline with increasing yield potential. Results of Brook, Hearn and Kelly suggested that the margin for full recovery from damage becomes smaller with high yielding crops. Perhaps these crops can "afford" less loss because they are developing at an optimal condition. If so, then we need to factor in the rate of compensation based on the yield potential of the crop. We tested this hypothesis by imposing moderate fruit damage to commercial crops that yielded up to 12 bales ha^{-1} but did not find any decline in compensation (High Yield Potential Trial). This indicates that modern cultivars and management practices posed no further constraints to recovery even when crops were pushed to high yield levels.

In addition to quantify the limits of compensation, we also examined the process of damage and recovery. In a trial testing the hypothesised mechanisms of recovering from loss of leaf area by early season thrips damage, we were able to discount competing theories and conclude that recovery is achieved by an accelerated ontogeny of intact leaves (Thrips Trial). Because of reduced resource demand by the small deformed leaves damaged by thrips, growth of the intact upper node leaves was faster than control plants, allowing affected plants to “catch up” in lost leaf area.

An essential component of pest damage is its variation along the temporal and spatial scales. A question we addressed was does cotton respond in the same way to one large damage as it would to several smaller damages when all treatments received the same total amount of fruit loss. We found the answer to be yes for damage simulating 8 larvae m^{-1} once, 4 larvae m^{-1} twice, and 1 larva m^{-1} eight times (Fruit by Timing Trial). This highlights an interesting point which is even though the yield response was the same, only the 1 larva m^{-1} eight times was below the threshold requiring control measures while the other treatments would have prompted one, two and four sprays! In addressing the patchiness of damage, we conducted two sets of experiments. The first was simply to document the natural level of tip and thrips damage along time and space (Patchiness Trial). In unprotected crops, we found significant variation in the temporal and spatial patterns of damage. This indicates that tip damage during the pre-squaring period is quite likely to be spread evenly across most plants with only a small number (2-3%) of plants being tipping out three times. The second set of experiments varied the degree of patchiness using artificial damage to terminal, to leaves and to fruit (Spatial Configuration of Damage Trial). Yield outcomes over a 6 m^{-2} stand were the same across all patchiness treatments regardless of the type of damage imposed. We conclude that although the response of individual plants may be affected by their neighbours as was found by V. Sadras, the differential effect of single plants evens out over a larger area. This means that compensation depends not on the degree of patchy damage but on the overall proportion of damage in the field.

Given the emerging threat of sucking pests, we have initiated research into recovery from mirid damage to cotton bolls and squares. Our results indicate that damage by mirids differs fundamentally from that by *Helicoverpa* (Mirid Trial). We have developed a novel technique of injecting pectinase (a digestive enzyme) to simulate mirid damage in order to determine the economic threshold of these pests. Preliminary findings indicate some compensation occurring as plants re-allocate resources from the lower demand of damaged bolls to produce larger undamaged bolls. The limit of this type of yield recovery appears to be greater than 1 mirid/m but requiring further research (currently underway in a new CRDC-funded project).

In all of the field trials, we have established that the delay in maturity associated with yield compensation was in general less than 7 days. This indicates that in a warm region like the Lower Namoi, significant delays in earliness are not an important issue. In Kununurra, the increasing heat at the end of the “winter” cropping season further reduces the delay as the rate of boll opening reached >10% per day.

The cotton model OZCOT has been improved by incorporating routines to mimic the damage and recovery process of tip damage, leaf area, and fruit loss (Enhancing and Validating OZCOT). Yield predictions have been validated and are shown to be robust at $R^2=0.78$. There is a tendency for the predicted yield to be under-estimated at higher control yields which indicates that further refinement of the model would be desirable.

Recovery of leaf area through accelerated shoot allometry in thrips damaged cotton seedlings

Tom T Lei and Lewis J Wilson

Target journal: Annals of Botany
Running title: recovery from defoliation through leaf allometry

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Abstract

Leaf area of cotton seedlings (*Gossypium hirsutum* L.) can be reduced by as much as 50% from early season thrips infestations. But it is well documented that plants can regain the difference in leaf area once infestation ceases. While cotton has the ability to recover, the process involved in the recovery has not been identified. Several mechanisms previously proposed include an enhanced photosynthetic rate, more efficient leaf construction (i.e. higher area to mass ratio), and greater branching structure. This 2-yr study examined these potential processes and found that thrips affected plants recovered from a 30% reduction in total leaf area. This, however, was not achieved through the previously proposed mechanisms of enhanced photosynthesis, improved leaf construction or increased branching. The pattern of nodal development indicated that by virtue of completing the expansion of the smaller deformed leaf area sooner, thrips affected plants were able to begin expansion of the healthy upper node leaves 1 to 2.5 nodes in advance of control plants. The proposed process of recovery is evident but weaker in the second year where thrips numbers were higher. It is concluded that thrips affected plants overcame the leaf area disparity through an accelerated developmental allometry of unaffected apical leaves. The generality of this mode of plant resistance to pest damage remains to be determined.

Abbreviations: *Gossypium hirsutum*, cotton, leaf allometry, thrips damage, defoliation, leaf area recovery

Introduction

Recovery from herbivory, or compensation, is an important process in plant herbivore interactions in natural systems. It is also important in many cultivated systems where it can be used in integrated pest management systems (IPM) to reduce insecticide use. Thrips are common pests in many cotton production regions (Hawkins et al., 1966; Quisenberry and Rummel, 1979; Wilson and Bauer, 1993; Atakan et al., 1996). Their numbers frequently build up rapidly early in the cotton season (Watts, 1937) leading to infestations resulting in the visually dramatic deformation of seedling leaves (Quisenberry and Rummel, 1979). The crinkled leaves are significantly smaller than normal leaves. The reduction in leaf area continues until thrips numbers drop, generally within 3-4 weeks following the initial increase (Sadras and Wilson, 1998). Then affected plants resume normal leaf growth but in an accelerated manner whereby leaf area recovers to equal that of unaffected plants within weeks (Hawkins *et al*., 1966; Sadras and Wilson, 1998). It is common for cotton to show full recovery from the effect of early season thrips infestation without any economic consequences (Harp and Turner, 1976; Sadras and Wilson, 1998). There is, however, an increased risk of yield loss and delay in maturity from severe thrips infestation (Watts, 1937), particularly in cooler cotton production regions (Wilson *et al.*, unpublished). The most common means of controlling early season thrips is the application of systemic insecticides, such as aldicarb, at sowing. Since thrips are also effective predators of spider mite eggs, broad-spectrum insecticides applied to the foliage after germination could contribute to outbreaks of spider mites later in the season (Wilson *et al.*, 1996). Given the capacity for cotton to recover from early season thrips damage, many growers have withheld insecticide use or switched from foliar to soil applied insecticides to treat thrips at this stage in accordance with IPM strategies. Here we investigate the mechanism of recovery of cotton following thrips damage. This understanding will enhance field management and IPM programs in general.

While it is well known that cotton seedlings can routinely achieve full recovery after losing as much as 70% of total leaf area (Wilson et al., 2003), the process of recovery has not been identified. Sadras and Wilson (1998) raised four possible mechanisms for leaf area recovery: 1) increased photosynthetic capacity, 2) increased leaf area to mass ratio, 3) improved branching (Watts, 1937), and 4) new leaf addition. Direct tests of these potential mechanisms of recovery have not been made. Identifying the actual process by which plants recover from reduced leaf area will not only improve our understanding of cotton's response to thrips, but could have broader implications for understanding the physiological basis of plant tolerance to herbivory (Belsky et al., 1993).

This study examined the process of leaf area recovery in cotton naturally infested with thrips during the seedling stage. Leaf physiological and morphological characters were measured during the damage and the recovery phase with the aim of identifying the most likely mechanism responsible for the recovery in leaf area lost to thrips.

Materials and Methods

This study was conducted over two seasons (2001-02, 2002-03, to be referred to as year 1 and 2) at the Australian Cotton Research Institute in Narrabri, NSW Australia (30.4°S, 149.8°E). Cotton (cultivar Siokra V-16i, transgenic cotton containing the Monsanto Co. Cry 1Ac gene) was sown on October 17, 2001 (year 1) and on September 30, 2002 (year 2) at 10-12 plants per metre. Two treatments were used: a control where the systemic insecticide aldicarb (Temik, Aventis) was applied at sowing at 450 g ai/ha to protect seedlings against thrips species, and a thrips-damaged treatment where no aldicarb was used, allowing thrips to establish during early season growth. Plots were laid out in a randomised block design with 4 replicates.

Thrips numbers were monitored by regular sampling of control and treatment plants from each plot. On each weekly sampling date, 5 plants were randomly taken from each treatment plot, placed in a ziplock bag and immediately brought back to the lab. The plants were thoroughly washed by adding water to the bags and agitating them vigorously for one minute. The water containing dislodged thrips was poured through a fine mesh sieve. This process was repeated then the thrips retained in the sieve were flushed onto a filter paper, which was placed in a petri dish and stored frozen until counting using a stereomicroscope. Thrips numbers were given as total number per plant which includes adults and larvae of all thrips for year 1, but for year 2 larvae were separated from adults. While there are three common thrips species found on cotton, *Thrips tabaci* Lindeman predominates at this time of the year

(Wilson and Bauer 1993). The mean area of cotyledons and leaves at each node position of the five plants was measured using a leaf area meter (LiCor, Nebraska). Leaves and cotyledons were then placed in separate bags for each node and dried to constant mass at 70°C to determine the mean specific leaf mass. Since leaf area of individual node positions were recorded, it was possible to detect the change in nodal and whole plant leaf area during the damage and recovery phases.

Gas exchange was also measured in the field to test if damaged plants had changed photosynthetic rates during the recovery phase. Four sets of gas exchange data were taken each year at 27, 35, 44 and 56 days after sowing (year 1) and at 31, 38, 46 and 56 days after sowing (year 2). A portable photosynthesis system (Li-Cor 6400) was used, measurements were made with the following settings: photon flux density at 2000 μ mol m^{-2} s^{-1} (Li-Cor light source), chamber block temperature at 30°C, vapour pressure deficit of the leaf was maintained at less than 3 by adjusting the flow through the desiccant, reference CO_2 concentration at 370 μ mol m^{-2} s^{-1} (using a CO_2 mixer). Gas exchange of leaves at individual nodal positions (including cotyledons) was measured for six plants of each treatment (3 plants x 2 reps in year 1 and 2 plants x 3 reps in year 2). If leaf area was less than 6 cm^2 (the leaf chamber opening), then the leaf was labelled and leaf area later determined using a leaf area meter. Gas exchange parameters were then recalculated using the correct leaf area.

Plots were maintained with furrow irrigation as required but no pesticides were applied throughout the season. At the end of the season, all bolls were harvested from four 1-m sections of cotton in each plot. Total boll numbers and seed cotton mass per metre were recorded.

No block effect was detected using ANOVA (SAS Institute, 1988) for any of the measured parameters. Hence differences between treatments were compared using a T-test (SAS Institute, 1988).

Results and Discussion

The loss of leaf area in cotton seedlings began shortly after germination as thrips moved in. In both years, thrips numbers in plots unprotected by aldicarb at sowing began to exceed the controlled plots within 3 weeks after sowing. In year 1, by 33 days after sowing (DAS), the number of thrips in unprotected plants was 10.6 per plant, double those of control plants ($P<0.05$, Fig. 1). In year 2, larvae numbers were significantly higher on unprotected plants from 22 to 52 DAS. Adult numbers did not differ between treatments. The reason for the peak in adult numbers at 38 DAS is not clear but could be due to an influx from an adjacent wheat crop. Nevertheless, the influx did not appear to have a large impact on damage to leaf area. The total number of thrips was about twice as high in year 2. Thrips numbers declined naturally to a similar level in all treatment plots but much more quickly in the first year. We estimate that the duration of infestation was about 20 days for year 1 and 40 days for year 2.

Thrips infested plants produced main stem leaves that were deformed (often circular in shape) and cupped (Fig. 2). Since the infestation occurred after the expansion of the cotyledons and the thrips were concentrated in the shoot meristem, the cotyledons remained largely intact, as has been noted by Sadras and Wilson (1998).

The reduction in leaf area caused by thrips began at about 3 weeks after sowing (Fig. 3), in close correspondence with the increase in thrips number (Fig. 1). By summing all leaves (including the cotyledons), the total reduction in leaf area of thrips-affected plants reached a maximum of 30% relative to the control between 40 and 60 DAS in both years (Fig. 3). The quicker drop in leaf area in year 2 is attributed to the higher number of thrips early in the infestation (Fig. 1). Sadras and Wilson (1998) found comparable degree of leaf area reduction associated with peak thrips counts of 10 to 30 thrips (larvae + adults) per plant. The total duration of leaf area reduction was about 50 days (20 to 70 DAS). This is similar to the 40 days (generally between 20 and 60 DAS) reported by Sadras and Wilson (1998). The recovery in leaf area per plant began at 50-60 DAS, reaching 89 and 83% of the control 68 and 67 DAS for the two years respectively. The subsequent decline (after 70 DAS) in leaf area in year 2 was largely associated with the greater recruitment of non-main stem leaves located on vegetative and fruiting branches (Fig. 4). While Sadras and Wilson (1998) found a full recovery in leaf area after 60-80 days for most trials, some trials showed a similar dip in leaf area about 80 days after sowing.

The progression of leaf area development (Fig. 4) shows that a significant reduction in damaged plants began 23-24 DAS in both years which continued through to node 8 (68 DAS, year 1) and node 9 (67 DAS, year 2). Leaf area recovery began 45 and 50 DAS with leaf size of upper nodes beginning to exceed that of corresponding leaves in control plants. No vegetative branch growth in year 1 was detected in either treatment during the measurement period (up to 68 DAS). Some vegetative branch growth was observed in year 2 with leaf area on these branches contributing 9 and 14% to total leaf area on 59 DAS and 24 and 29% to total leaf area on 74 DAS (insets of Fig. 4b). The latter date also included leaves from fruiting branches.

One of the mechanisms facilitating the leaf area recovery Sadras and Wilson (1996) suggested is an increased photosynthetic rate of the damage leaves. A higher carbon gain should provide the necessary resource to accelerate the development of younger leaves. Photosynthetic rate (A) was measured on individual leaves (including cotyledons) spanning the infestation and recovery phases. Data revealed no significant enhancement in A in thrips-affected leaves (Table 1). While A changed between nodes in accordance with the stage of leaf maturity, the pattern was the same between control and unprotected plants. Given that main stem leaves were smaller in unprotected plants, the similarity in A translates to a reduction in total carbon gain per plant comparable to the leaf area (i.e. by up to 30% between 40 and 60 DAS). Therefore, compensatory photosynthesis is an unlikely factor contributing to recovery. It is, however, possible that damaged plants with their smaller pool of carbon further limited carbon allocation to root growth in favour of aboveground growth. In an environment where soil moisture is maintained at a non-stress level, reduced root growth may have no consequences in plant growth. This assumption requires further confirmation.

Increased branching has also been suggested as a mechanism of recovery from thrips damage (Watts, 1937). Thrips infested plants did not show damage to the apical meristem (tip), which is known to promote vegetative branch growth (Sadras and Fitt, 1997; Jones and Wells, 1998; Lei and Gaff, 2003). Destruction of the apical meristem by thrips only occurs at very high numbers (Wilson, unpublished data) and damage found in the present study caused only deformation of the small unfolding leaves surrounding the meristem. A survey of tip damage conducted in year 1 found very low levels of tip damage between control (2.6%) and thrips-affected plants (4.0%). Therefore branching did not play a role in leaf area recovery because the degree of thrips damage observed in this study resulted in only leaf damage and was insufficient to initiate lateral branch growth.

Wilson et al. (2003) have shown that leaf area recovery from up to 70% leaf area reduction was possible with no effect on lint yield. This indicates that the amount of carbohydrates required to maintain normal shoot growth during the recovery phase is relatively small and the 30% leaf area reduction found in this study may not be sufficient to affect this requirement. Within 1-2 days after leaf unfolding, immature cotton leaves have already reached a positive carbon balance (i.e. carbon assimilation exceeds dark respiration; Constable and Rawson, 1980a, b). This means that the rate of leaf development in control plants was not carbon limited. While an expanding leaf may be self sufficient in carbon, to achieve maximum A at 75-90% final leaf area (Constable and Rawson, 1980a) would require continuing nitrogen import associated with the maturation of chloroplasts. Since the time required to reach physiological maturity is greater for control plants, this could contribute to the accelerated leaf development in damaged plants.

Decreased leaf mass to area ratio (LMA) has also been suggested as a mechanism of recovery where leaves on damaged plants in the recovery period with a smaller LMA would enable them to intercept more light with thinner leaves. To support this mechanism, it would be necessary to find significantly lower LMA in thrips-affected leaves, especially those produced after the infestation (upper nodes). But Table 2 shows little difference in LMA in corresponding upper node leaves between treatments. Instead we found that some affected leaves (lower nodes) have a significantly higher LMA than the control, more so in year 2 than in year 1. This is consistent with their tougher texture (Table 2). If LMA of affected leaves was higher, then it may be associated with increased photosynthetic potential with greater mesophyll cell packing, higher leaf nitrogen, and more chloroplasts (Evans 1986; Reich et. al. 1991). While some lower deformed leaves were higher in LMA, they showed no corresponding increase in photosynthetic rate (Table 1). The hypothesis that improvement in leaf construction facilitates leaf area recovery in thrips affected plants is rejected. Wilson *et al*. (2003) similarly found no effect of leaf removal of 50% at nodes 2 + 4 on LMA, but did find a lower LMA in damaged plants at higher levels of damage.

Having found no evidence that thrips-affected plants were able to increase carbon assimilation, to economize on leaf construction (i.e. produce more leaf area per unit dry matter) or to increase branching, we propose that leaf area recovery is achieved simply through a more rapid leaf developmental allometry. While Sadras and Wilson (1998) suggested that the addition of new leaves can “partially compensate” for the loss of leaf area, we offer a mechanism by which this occurs. Since the lower thrips-affected leaves are smaller, leaf expansion can be completed sooner, thus making resources available for the development of younger upper leaves. This is evident in Fig. 4a where by 50 DAS in year 1, all damaged leaves up to node 6 had reached full expansion (open arrow) while nodes 4-6 of control plants (solid arrow) were still expanding. By 58 DAS, thrips-affected node 7 had expanded fully compared to node 4 in control plants. A similar pattern was seen in year 2 where, on 67 DAS, node 6 and 7 were the uppermost fully expanded leaves for thrips-affected and control plants, respectively. By reaching full expansion sooner than control plants, resources can be channelled to accelerate the growth of upper leaves (above node 9). Together with a more rapid upper leaf expansion, node development may also be marginally higher in damaged plants. The pattern of leaf expansion between nodes is nearly identical between control and damage plants when the latter was shifted 2.5 nodes to the left (Fig. 4a, 68 DAS). This suggests that by compressing the allometric progression of lower node leaves, damaged plants are able to regain total leaf area simply by advancing normal leaf expansion of the larger upper nodes leaves 2-3 nodes earlier. A similar process was demonstrated in soybean by Thrower (1962) where leaves less than 50% fully expanded are significant importers of assimilates. Upon reaching 50%, export of assimilates begins, adding to the assimilate pool which is translocated towards the plant apex.

Together with the recovery in leaf area, we found no residual effect of the early season damage on yield. Harvest conducted when all plots reached greater than 80% open bolls showed no significant difference (P>0.05) between control and unprotected plants in total number of bolls and in seed cotton mass in both years (Fig. 5). There was, however, a trend for a lower yield in thrips infested plants in the second year when the infestation was higher and the recovery in leaf area was delayed. Sadras and Wilson (1998) found only one in 10 thrips trials with a significant yield loss. Interestingly, the affected trial also showed a relapse in leaf area recovery after 60 days from sowing, shortly after fruiting begins. We therefore suggest that if the allometric recovery in leaf area is not completed before the establishment of fruiting branches (with their additional leaf area), the smaller assimilation capacity of damage plants could result in a loss of yield.

Conclusions

Within a very short time period (<3 wks), thrips feeding on leaf primordia can lead to a significant loss of leaf area in main stem node 1 to 8. Since the residency time of thrips is generally short, affected cotton plants were able to recover completely. Evidence indicates that the transient loss and the subsequent recovery of leaf area resulting from thrips feeding, at the densities experienced, was not achieved through active responses such as an improved carbon assimilation or better biomass allocation to leaf construction, but through an altered allometric process. This process involves the rapid completion of expansion of lower, thrips-affected main stem leaves which shortened the duration of these leaves compete for resources (Constable and Rawson, 1980b) making them available for the accelerated emergence of upper, undamaged leaves.

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Table 1. Photosynthetic rate (measured at PFD=2000 µmol m^{-2} s^{-1}) of cotyledons (leaf node=0) and main stem leaves (µ mol m^{-2} s^{-1}) measured during thrips infestation and at the subsequent recovery phase. Significant differences between treatments are indicated by numbers in bold type.

Year 1

Leaf node	27 DAS		35 DAS		44 DAS		56 DAS	
	Control	thrips	Control	thrips	Control	thrips	Control	thrips
6							30.4	30.3
5							27.4	29.1
4					16.6	13.0	26.5	23.1
3			13.1		15.0	16.0	24.8	18.8
2	11.6	13.4	17.2	18.0	16.4	17.6	19.9	19.8
1	14.8	14.3	17.3	15.8	12.0	16.4	20.5	23.9
0	10.7	9.3	13.3	11.7	10.5	10.3	15.0	13.9

Year 2

Leaf node	31 DAS		38 DAS		46 DAS		56 DAS	
	Control	thrips	Control	thrips	Control	thrips	Control	thrips
8							30.7	35.3
7							35.8	35.1
6					37.1	39.3	36.4	33.5
5					39.2	36.2	34.7	31.7
4			15.9	20.5	**40.2**	**31.8**	32.1	26.1
3			28.7	28.9	36.3	31.3	26.2	26.2
2	20.2	16.2	30.9	34.1	**31.9**	**25.9**	24.3	20.0
1	26.2	25.6	33.6	28.6	**32.5**	**24.5**	**22.9**	**17.0**
0	20.7	22.9	26.1	20.5	**27.0**	**22.9**	18.9	17.6

Table 2. Leaf mass to area ratio (mg cm^{-2}) of cotyledons (leaf node=0) and main stem leaves measured during thrips infestation and at the subsequent recovery phase. Significant differences between treatments are indicated by numbers in bold type.

Year 1

Leaf node	27 DAS		35 DAS		44 DAS		56 DAS		68 DAS*	
	Control	thrips	Control	thrips	Control	thrips	Control	thrips	Control	thrips
14									-	12.4
13									-	8.5
12									11.3	8.6
11									9.0	8.9
10									**7.9**	**9.2**
9									8.7	9.6
8									9.2	8.9
7									**9.1**	**10.6**
6							9.4	9.5	8.7	10.2
5							9.0	9.3	9.9	11.5
4					8.2	8.0	9.2	9.5	9.9	11.5
3			7.4	-	9.7	9.0	9.8	10.3	10.3	13.1
2	6.7	6.6	**8.7**	**9.9**	10.1	10.3	9.2	11.4	10.5	12.9
1	8.0	7.8	9.5	9.8	10.1	10.5	**9.7**	**11.5**	10.7	14.7
0	8.9	8.2	10.2	10.1	10.5	10.9	10.6	11.3	20.2	16.7

Year 2

Node	24 DAS		31 DAS		38 DAS		45 DAS		52 DAS		59 DAS		67 DAS		74 DAS	
	control	thrips	control	thrips	control	thrips	control	thrips	control	thrips	control	thrips	control	thrips	control	thrips
VB									6.1	6.8	5.6	5.7	6.1	6.3	6.5	6.8
16															-	8.8
15															10.5	12.5
14											-	9.0	11.4	7.6	7.5	7.8
13											-	6.5	8.5	7.1	7.6	7.3
12											7.3	9.1	7.1	7.2	7.8	7.9
11											6.0	6.7	6.8	7.4	8.2	8.8
10									10.6	7.7	7.1	6.4	7.2	7.9	8.7	9.0
9									7.9	7.1	6.3	7.0	7.5	8.4	9.1	9.3
8									6.8	7.4	6.8	7.6	8.0	8.9	9.5	9.2
7							8.0	5.7	7.0	7.4	7.3	8.1	8.5	9.1	10.0	9.6
6							6.9	7.5	7.8	8.6	8.0	8.6	9.2	9.4	9.6	10.0
5					12.9	10.4	**7.1**	**8.2**	8.5	8.9	8.1	8.6	9.4	9.4	10.0	10.1
4					8.7	8.8	**8.4**	**10.1**	9.0	9.4	8.6	9.8	**9.8**	**10.9**	10.7	11.2
3			10.7	15.2	8.2	9.4	**9.0**	**10.9**	**9.2**	**10.6**	**9.0**	**10.9**	10.6	11.4	11.3	13.1
2	**6.8**	**11.2**	**9.9**	**14.5**	8.9	11.1	**9.4**	**12.3**	**9.5**	**12.5**	**9.1**	**12.9**	**10.1**	**14.9**	11.3	12.5
1	**7.5**	**11.8**	**9.8**	**13.1**	11.0	12.6	**10.0**	**12.3**	**10.6**	**13.5**	**9.3**	**12.8**	10.8	16.4	12.4	15.6
0	8.6	8.8	10.2	10.1	**10.8**	**10.3**	10.6	11.2	10.9	11.5	**10.2**	**11.7**	12.1	13.1	12.8	13.3

Figure captions

Figure 1. Average thrips number per plant for the two years between control (aldicarb-protected) and thrips infested plants. Year 1 shows the total numbers of adult and larvae. Asterisks indicate significant difference at $P<0.05$.

Figure 2. An example of the difference in leaf development between control (undamaged) and thrips damaged plants. The photo was taken at the 4-node stage showing the four main stem leaves (numbers identify the node position) and the terminal at centre. The coin is 19 mm in diameter.

Figure 3. Proportional leaf area per plant between thrips infested and control plants during the damage and recovery period for the two years (year 1= circles, year 2=triangles). Total leaf area was calculated by summing the average leaf area of all nodes (including cotyledons).

Figure 4. Leaf area development at individual main stem nodes (cotyledon = node 0) through the thrips infestation and recovery period between aldicarb-protected control (solid circle) and thrips infested (open circle) plants in year 1 (a) and year 2 (b). Values represent mean of four plots at 5 plants per plot; * indicates significant difference ($P<0.05$) in leaf area between control and infested plants. Arrows indicate the uppermost fully expanded leaf in control (solid) and infested (open) plants. The line formed by the gray circles in Fig. 4a at 68 DAS shows the correspondence between treatments when leaf area of infested plants was shifted 2.5 nodes to the left. Insets in Fig. 4b represent the total area of non-main stem leaves per plant of control (solid bar) and infested (open bar) plants. There was no significant difference in non-main stem leaf area between treatments at all dates.

Figure 5. Yield parameters between control and thrips affected plants. The difference between treatments was not significant ($P>0.05$) in both years for boll number and seed cotton mass.

Figure 1.

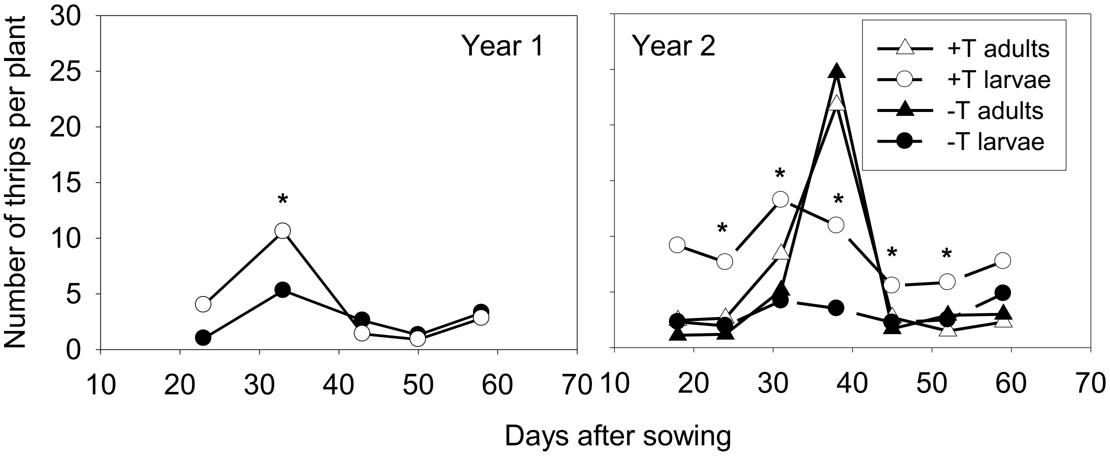


Figure 2.

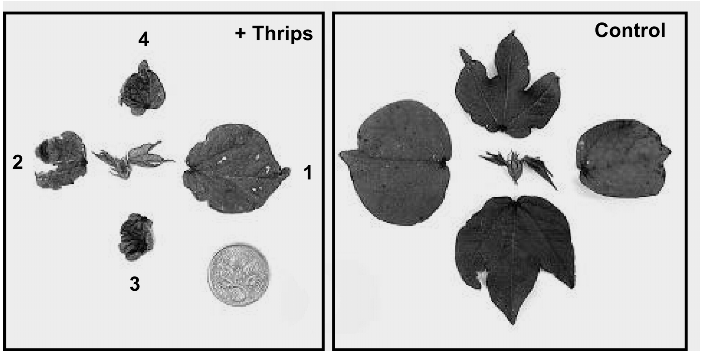


Figure 3.

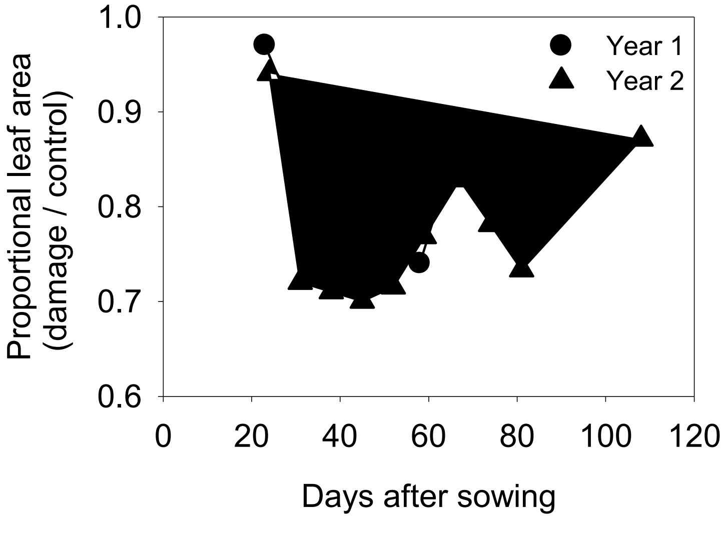


Figure 4a.

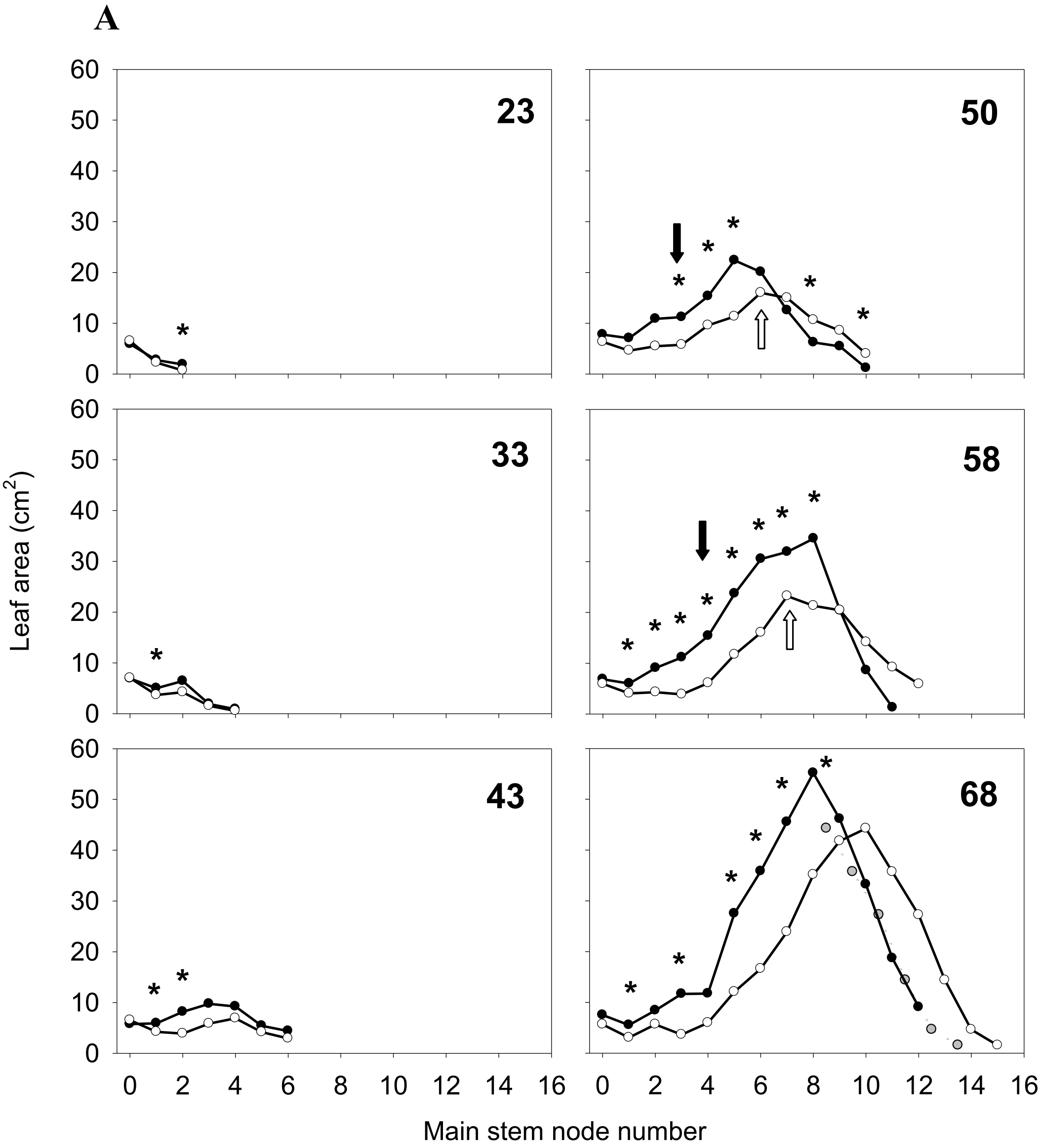

A
23
33
43
50
58
68
Leaf area (cm^2)
Main stem node number
0
10
20
30
40
50
60
0
2
4
6
8
10
12
14
16
*

Figure 4b.

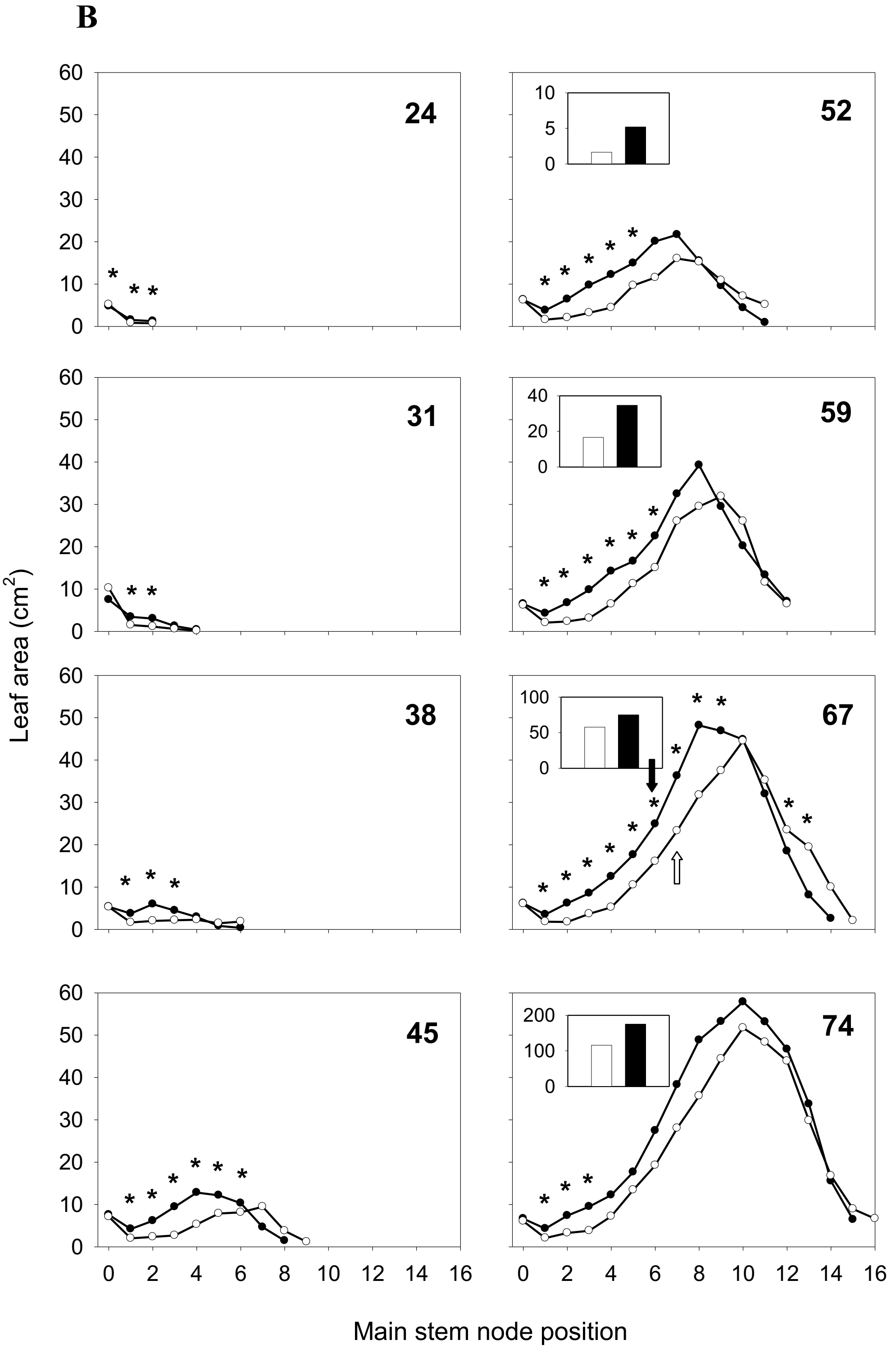
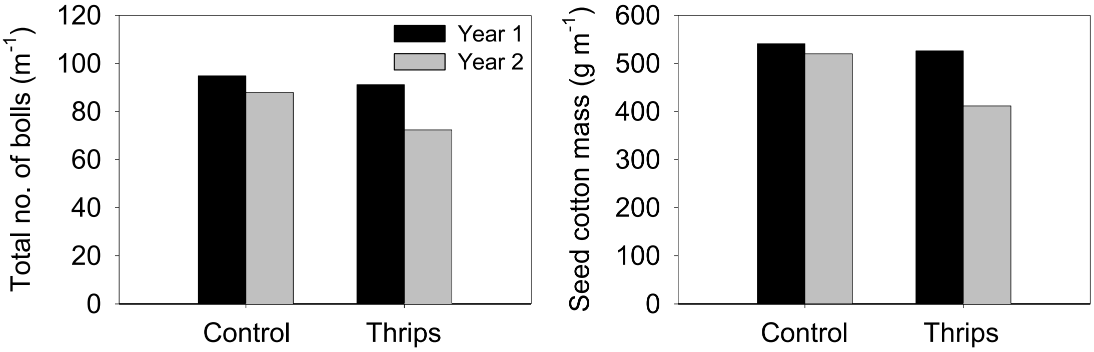

B
24
31
38
45
52
59
67
74
Leaf area (cm^2)
Main stem node position
0
10
20
30
40
50
60
0
2
4
6
8
10
12
14
16
*

Figure 5.


Total no. of bolls (m^{-1})
120
100
80
60
40
20
0
Year 1
Year 2
Control
Thrips
Seed cotton mass ($g\ m^{-1}$)
600
500
400
300
200
100
0
Control
Thrips

Yield recovery following repeated damage to cotton (*Gossypium hirsutum* L.) is not affected by cultivar and plant density

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Abstract

Yield of cotton (*Gossypium hirsutum* L.) can be correlated with plant size and leaf area production. Variations in these growth properties depend on many factors including cultivar, plant density and insect damage. Plant response to plant terminal and fruit damage may result in a canopy modified by increased branching and leaf production. It is, therefore, possible that the plant density sown for optimal yield may be altered by pest damage lowering its yield potential. This offers the scope for improving compensation from pest damage by selecting cultivars and planting densities that optimize the canopy response. This study examined growth and yield responses of eight (year 1) and four (year 2) cultivars planted in a range of plant densities (5 to 25 m^{-2}) and subjected to repeated damage to plant terminal (twice at pre-squaring) and fruit (twice, simulating 6 *Helicoverpa* larvae m^{-1}). Results show that while there were significant increases in vegetative branch growth following damage, they showed no consistent pattern associated with plant densities. Fruit development was delayed by damage where, at 120 days after planting, square production was higher and bolls younger compared to the control. The mean delay in crop maturity was 6 days with lint yield of damaged plants significantly lower (by 12%) in year 1 but no difference in year 2. The lack of a clear pattern in the interactions among cultivar, plant density and damage on yield indicates that developmental plasticity in a full season high yielding production system makes it unnecessary to select cultivars and plant density to maximize recovery from multiple damage events.

Introduction

Cotton (*Gossypium hirsutum* L.) is well known to have the capacity to recover from pest damage, particularly in the pre-squaring and early fruiting stages (Brook et al., 1992; Sadras, 1995; Jones et al., 1996; Lei, 2002; Lei and Gaff, 2003). However, the extent of recovery may be affected by a number of variables including climate, nutrition, cultivars and planting density. Variations in morphology (i.e. normal and okra leaves) and stature (compact or tall) of cultivars could interact with different plant densities to affect plant response to injuries (Brook et al., 1992; Mann et al., 1997). For example, damage to apical meristem (tip) has the same effect as low plant density by increasing vegetative branch development, but the degree of branching may be different among cultivars. Low plant densities permit more vegetative branch growth and higher fruit production later into the season (Jones and Wells, 1998). In contrast, high plant densities (such as those in narrow row configurations) enable a more rapid establishment of canopy cover (Constable, 1977a; Jost and Cothren, 2001) and, in some cases, earlier fruit maturation (Heitholt et al. 1993; Jost and Cothren, 2001) Plant density can also have a strong effect on leaf expansion rate, light attenuation through the canopy (Constable, 1986; Heitholt, 1994; Sadras, 1996), leaf area index (Kerby et al., 1990b; Heitholt, 1994), number of monopodia, plant height

(Jones and Wells, 1997), final main stem node number (Kerby et al., 1990a), boll size (Bridge et al., 1973; Constable, 1977b) and maturity (Jones and Wells, 1998).

Cotton densities between 7 and 22 plants m^{-2} had no effect on yield (Buxton et al., 1979; Jones and Wells, 1998). This was attributed to the density–dependent growth habit of cotton where the occupation of available space under low densities is achieved through a greater production of vegetative branches. Variation in yield was found as a product of the interaction between plant density and cultivars (i.e. okra versus normal leaves; Heitholt, 1994). This suggests that there is scope for improving yield when a cultivar is matched with an appropriate plant density.

When cotton plants experience damage to plant terminals and fruit, significant modifications in growth can occur. For example, tip damage stimulated an increase in vegetative branch development and light interception (Lei and Gaff, 2003). By increasing vegetative branching, there will also be a greater number of fruit bearing stems per unit land area, which effectively mimics a higher plant density. Such growth response could interact with existing plant density to enhance or impede the compensation ability of cotton. Changes in canopy structure can also occur through loss of fruit, resulting from shifting assimilates from fruit to vegetative growth. This will alter the ability of the canopy to intercept light and can affect whole plant carbon gain (Sadras, 1996). Therefore, fruit loss could produce plants that are larger but with a delay in fruiting, the effect of which on yield may be cultivar and density specific.

In a production system with high insect pressure such as in Australia, management factors to take advantage of crop compensation can be an important contribution to Integrated Pest Management. The question being addressed here is whether yield recovery following damage can be enhanced when subsequent growth response results in an optimum canopy structure (Hearn, 1972; Basinski et al., 1975; Heitholt, 1994). Given that both insufficient or excessive leaf area will hinder compensation, the potential exists for maximizing growth and yield when cultivars are grown in specific plant densities. This study explored the potential for enhanced recovery from repeated terminal and fruit damage through the interaction between cotton cultivars with different leaf types, growth and transgenic characteristics (Table 1) and plant densities ranging from 5 to 25 plants m^{-1}.

Materials and Methods

A two-year field study (1999-2000) was conducted at the Australian Cotton Research Institute in Narrabri, Australia (30.4°S, 149.8°E). Cotton cultivars were sown in gray-clay field plots on 13 October 1999, and on 28 October 2000. Seedlings were thinned to desired densities in early November (Nov 5-11). Anhydrous ammonia fertilizer was applied to the field at 120 kg ha^{-1} N prior to sowing. The fields were furrow irrigated when moisture deficit reached ca. 90mm. Weeds and pests were controlled using standard management practices which was applied uniformly to all treatment plots. Treatment plots were 3 rows by 3 m in size and established using a randomised block design with cultivar, plant density and damage as main effects. In the first year, normal leaf cultivars were thinned to 5, 10 and 15 plants per meter, and okra leaf cultivars to 10, 15 and 20 plants per meter. These densities were selected because the okra leaf form allows for greater light penetration (Wells and Meredith, 1986) and appears to have a higher optimal leaf area index than normal leaf cultivars (Heitholt, 1994). In the second year, the number of plant densities was expanded to between 5 and 25 plants m^{-1} for two cultivars (Table 1). Eight cultivars of various morphological and transgenic characteristics were used in the first year and a subset of four with more density treatments was used in the second year (Table 1).

Table 1. Cultivars used in the study with a range of growth habits and earliness. There were eight cultivars the first year, 4 normal leaves and 4 okra leaves. They also represent 4 INGARD (Monsanto Cry 1Ac Bt transgenic- indicated by the "i" suffix) and 4 conventional cultivars.

Cultivar	Symbol	Plant density (m^{-1})		Plant characteristics		
		Year 1	Year 2	Leaf type	Stature	Season
Sicala V-2	⊞	5, 10, 15	-	Normal	Normal	Med-late
Sicala V-2i	□	5, 10, 15	5, 10, 15, 20	Normal	Normal	Med-late
Siokra V-16	◈	10, 15, 20	-	Okra	Normal	Medium
Siokra V-15i	◇	10, 15, 20	10, 15, 20, 25	Okra	Normal	Medium
Sicala 40	△	5, 10, 15	5, 10, 15	Normal	Compact	Early
Sicot 189i	⊕	5, 10, 15	-	Normal	Tall	Late
Siokra S-101	○	10, 15, 20	10, 15, 20	Okra	Compact	Early
Siokra L-23i	◬	10, 15, 20	-	Okra	Tall	Late

The damage imposed on each cultivar x plant density treatment involved two terminal damage followed by two fruit removal events. The damage regime and timing are given in Table 2. Terminal (tip) was removed from all plants using tweezers, fruit were removed by hand within each meter. The fruit numbers taken simulate the damage caused by a cohort of 6 larvae m^{-1} over a 2-week period and are dependent on available fruit classes on the plants. The numbers were derived using a feeding model for *Helicoverpa* larvae developed by Wilson and Waite (1982). Details of the damage regime are given in Table 2.

Table 2. The multiple damage regime used in the study. Timing of the four damage events (days after planting) and the number of various fruiting classes removed per meter (based on the development stage of the crop) are given.

Treatment	Time (DAP)		Fruit removed†	
	1999	2000	1999	2000
Tip damage 1	42	41		
Tip damage 2	62	53		
Fruit damage 1	86	73	MS=3, LS=11, FL=31§	MS=12, LS=31
Fruit damage 2	126	101	MS=2, LS=17, FL=4, SB=9, MB=2	MS=10, LS=11, FL=12, SB=7

† Number of fruit types removed were derived from a *Helicoverpa* feeding model (Wilson and Waite 1982)

§ MS=medium squares 0.5-1 cm, LS=large squares >1 cm, FL=flowers, SB=small bolls <2.5 cm, MB=soft bolls >2.5 cm.

In year 1, light interception through canopy was measured using a ceptometer (AccuPAR, Decagon Devices, Inc. Pullman, Washington) 97-98 days after planting. Light interception was determined during solar noon at two canopy depths: mid-canopy (1/2 canopy depth) and at ground level. The 80-cm ceptometer was centered at the plant row and oriented at a right angle to the plant row.

All plants within a 0.5 m row of each plot were destructively sampled at peak fruiting (corresponding to maximum LAI, also reported by Kerby et al. 1990b) 117 DAP (1999) and 109-112 DAP (2000). Plants were sorted to taproot, leaves, stems and fruit (squares and bolls). Leaf area index (LAI) was calculated from the leaf area of a ca. 10 g dry mass sub-sample and the proportional dry mass of the sub-sample to the total. Plant components were dried at 70°C for 48 h and mass recorded. Weekly hand picking of open bolls from 2 m in the center row began when 20% of bolls were open. Crop maturity was defined as the date when 60% of the bolls were open. Seed cotton was ginned to yield the dry mass of lint.

Data analysis was performed in two ways. First, LAI, and yield parameters were analyzed (ANOVA, SAS Institute, 1985) for the effect of cultivar, plant density and damage on eight cultivars at 2 common plant densities (10 and 15 plants m^{-2}) for year 1 and on four cultivars at 3 common plant densities (10, 15 and 20 plants m^{-2}) for year 2. Since Sicala 40 was not grown at the 20 plants m^{-2} in year 2, the orthogonal requirement for the ANOVA was met by providing missing values at this density. Second, to examine the interaction between plant density and damage on lint yield and maturity date across the full density range, ANOVA was applied to each individual cultivar and year.

Results and Discussion

Canopy development and light interception

There was a significant overall increase in branch development (P<0.001 in both years) in plants with repeated tip and fruit damage compared to the intact control (Fig. 1). The deviation away from 1:1 was greater in year 2 than in year 1. There was also an apparent cultivar difference (P=0.003) in the first year with Siokra V-16 being the highest and Siokra L-23i the lowest but the cultivar effect was not significant in the second year (P=0.14). Jones and Wells (1998) reported that, in some cases, vegetative branching increased at lower plant densities. While this will be the case on a single plant basis, I found no evidence of a density effect when branch length was summed over a meter. Within cultivars, density effect on branch growth was significant only in the first year (P<0.001), but the pattern was not consistent across cultivars. A cultivar with a compact stature (Siokra S-101) generally produced greater branch lengths per meter over the two years than a taller cultivar (Siokra V-2i).

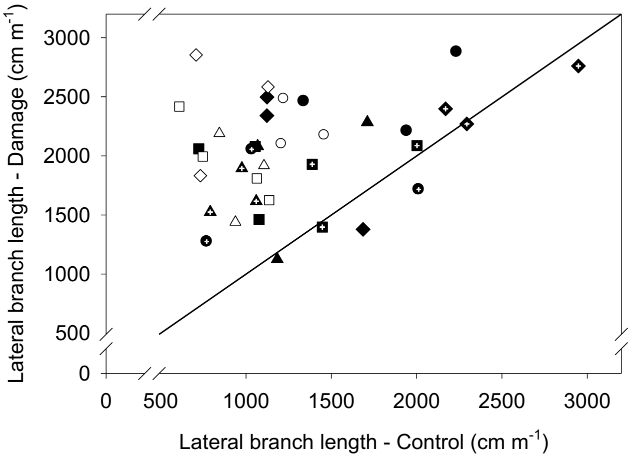

Figure 1. Total length of lateral branches per meter cotton in control and damaged treatments. Eight cultivars were measured in year 1(closed symbols) and four in year 2 (open symbols). Cultivars corresponding to symbols are given in Table 1. The 1:1 line is shown.

The increased branching in tip-damaged plants could be associated with greater foliar coverage and better light interception (Lei and Gaff, 2003). Leaf area index (LAI) was measured at peak fruiting (approximating the time of maximum LAI). Similar to branch growth, significant cultivar and density effects were observed in year 1 (Table 2). The same two cultivars (Siokra V-16 and Siokra L-23i) with the highest and lowest branch growth ranked similarly for LAI. The overall mean LAI was 2.35 and 2.75 for year 1 and 2, respectively. These LAI values are substantially lower than the 3.9 (Kerby et al., 1990b) and the 4-5 (Heitholt, 1994) associated with maximum dry matter production. Light interception measured in year 1 using a ceptometer showed an average of 75-80% of full sunlight intercepted by the upper half of the canopy, and 81-85% intercepted by the entire canopy layer (i.e. lower canopy leaves contribute to about 5% of the total light interception). There was no significant effect of cultivar or plant density (all P>0.05) on light interception, which is consistent with the lack of distinct patterns in LAI across cultivars and plant densities. This is in contrast to the improved light interception by a given leaf area at low (2 plants m^{-2}) than at high populations (15 plants m^{-2}; Heitholt et al. 1992). It is possible that even the lowest density of 5 plants m^{-2} in this study (year 1) had sufficient growth to prevent a detectable difference in light interception over the higher density treatments. No significant variations in LAI were found in year 2 (Table 2).

Table 2. ANOVA for leaf and fruiting characteristics of cotton cultivars grown at different plant densities and subjected to multiple tip and fruit damage. No interaction terms were significant (P>0.05). Comparisons made with 2 and 3 common plant densities for all cultivars in year 1 and 2, respectively.

Main effect	Cultivar		Plant density		Damage	
Year	1	2	1	2	1	2
LAI	<0.001	NS	NS	NS	NS	NS
Lint yield	<0.001	NS	NS	NS	<0.001	NS
Boll number	<0.001	0.001	NS	NS	<0.001	NS
Maturity	<0.001	0.030	NS	NS	<0.001	<0.001

Repeated damage did not have an effect on LAI that was significantly different from the control in both years (P>0.05). These results differ from Heitholt et al. (1992) where, at LAI=3 reducing row spacing from 1 to 0.5 m improved light interception from 82 to 93% in both normal and okra leaf cultivars.

Fruit production

While damage did not affect LAI (or total leaf dry mass), it clearly delayed fruiting, as results from year 2 demonstrate (Fig. 2). Across a similar range of leaf mass between control and damage treatments, the latter showed little variation in fruit production while in the control, fruit production was positively correlated with leaf mass (i.e. plant size). This relationship indicates a similar degree of delay in fruiting following damage with little differentiation between cultivars and plant densities.

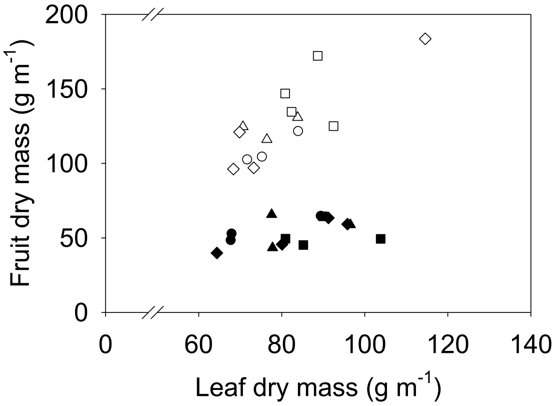

Figure 2. Relationship between leaf and fruit production at 117 DAP (year 2) in the undamaged control (solid symbols) and the repeated damage treatment (open symbols). Data shown are from year 2. See Table 1 for symbols of cultivars.

A delay in attaining full boll load can also occur under low plant density (2 m^{-1}) because of a slower rate of fruiting site development (Jones and Wells, 1997). This delay is attributable to the fact that additional fruiting branches must be borne on multiple vegetative branches that are produced sequentially from main stem nodes, rather than on similarly aged main stems under higher plant densities. Therefore, we would expect, under low plant densities, an association between higher lateral branching and higher fruit production later in the season (Jones and Wells, 1998). In this study, a similar outcome was observed due not to low plant density but to damage where plants responded to the loss of terminals by initiating multiple vegetative branches (Fig. 1). The effect of damage on fruiting dynamics is clearly evident as a delay in the peak of square production (Fig. 3a) while maintaining a similar boll count (Fig. 3b). But bolls of damaged plants were younger and smaller in dry mass at the same date (Fig. 3c). These data, collected nearly 4 months from planting, indicate that there was still good potential for full yield recovery if the bolls can be maintained to maturity.

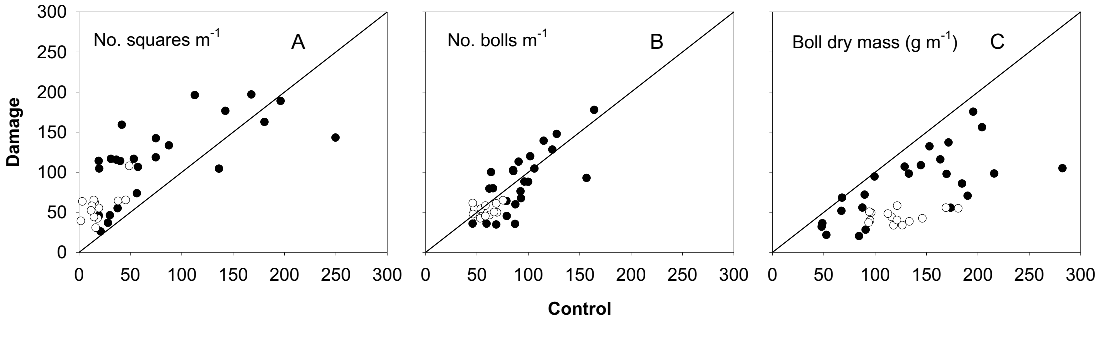

Figure 3. Fruit numbers and dry mass between control and damage treatments at about 115 DAP in the two years: year 1 (closed) and year 2 (open) circles.

Yield and maturity

Full recovery was achieved in year 2 where boll numbers and yield were not statistically different between damage treatments (Table 2). In year 1, the average lint yield was significantly different ($P<0.001$) at 159±3 g m^{-1} for control and 140±3 g m^{-1}

for damage. It is likely that the later dates (ca. 2 weeks) of both fruit damage events in year 1 compared to year 2 contributed to the lack of full recovery. Environmental factors also affected the overall yield potential in year 1 as indicated by the higher lint yield of control plants in year 2 (196±4 g m^{-1}, Fig. 4). This may have further contributed to curtailing the full recovery of damaged plants in year 1 as the season cooled during boll maturation. Fig. 4. also illustrates the lack of distinct patterns in yield resulting from the interaction between cultivars and plant densities. In year 2, the significant difference in the number of harvested bolls among cultivar with similar lint yield indicates cultivars such as Siokra S-101 with the highest boll number (107 m^{-2} averaged across all treatments) had smaller bolls than Sicala 40 with 90 bolls m^{-2}. These findings contrast with the significant cultivar by density interactions reported by Heitholt (1994). One possible reason for the difference may be the comparatively shorter growing season in Mississippi is (i.e. average maturity date of 140-150 days, Heitholt et.al., 1993) compared with Narrabri (160-180 days, Fig. 5). It is likely that the longer growing season here has allowed sufficient time for cultivar by density treatments with slower boll development to fully mature whereas a shorter season might halt that development earlier resulting in a significant interaction effect.

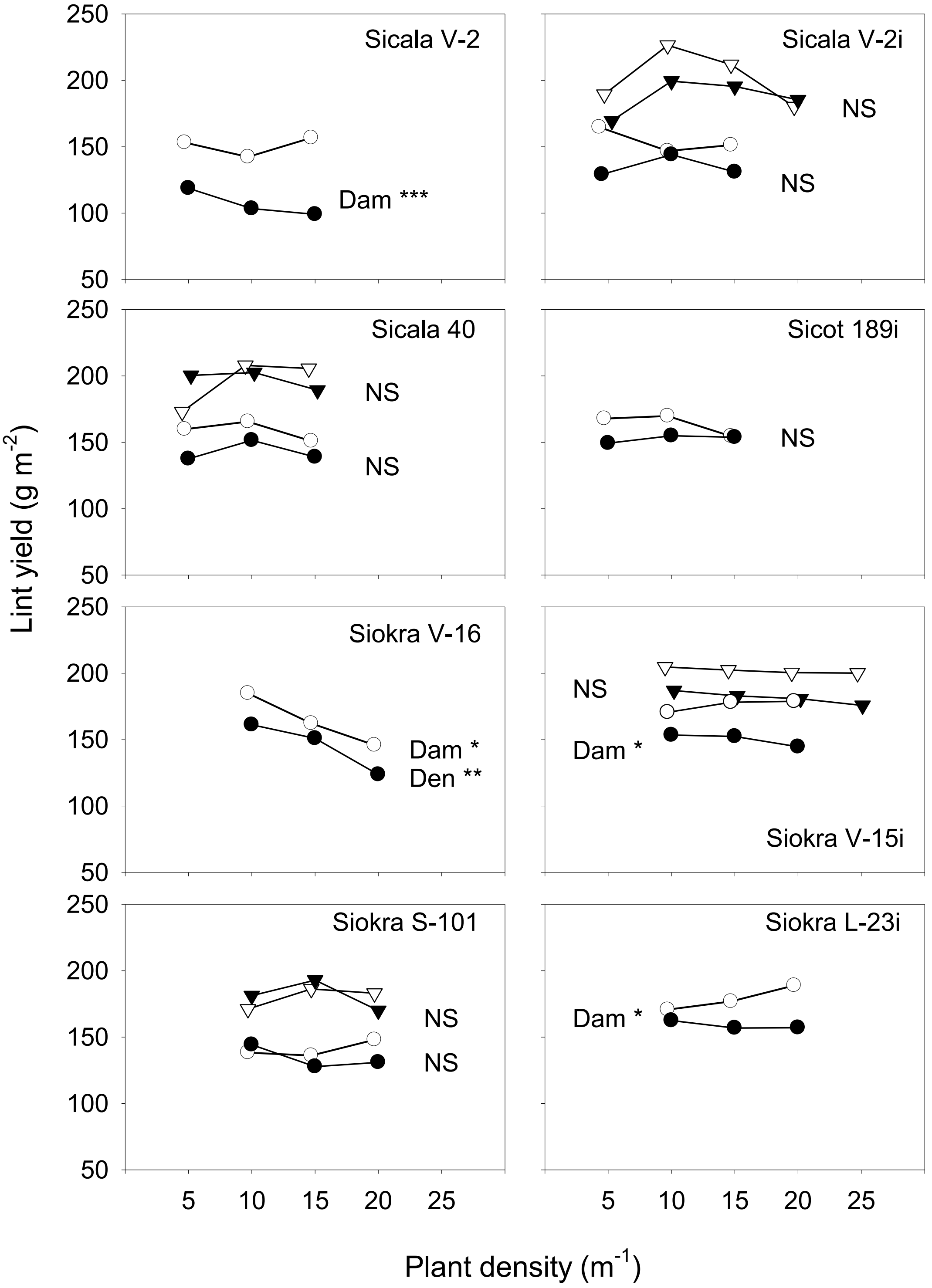

Figure 4. Lint yield of eight cultivars grown in a range of plant densities. Year 1 results were shown in circles and year 2 in triangles, solid symbols indicate damage treatment and open symbols the control. Significant effects of damage and plant density for each cultivar and year are indicated. No interaction terms are significant. NS, *P*>0.05; *, *P*=0.01, **, *P*=0.001.

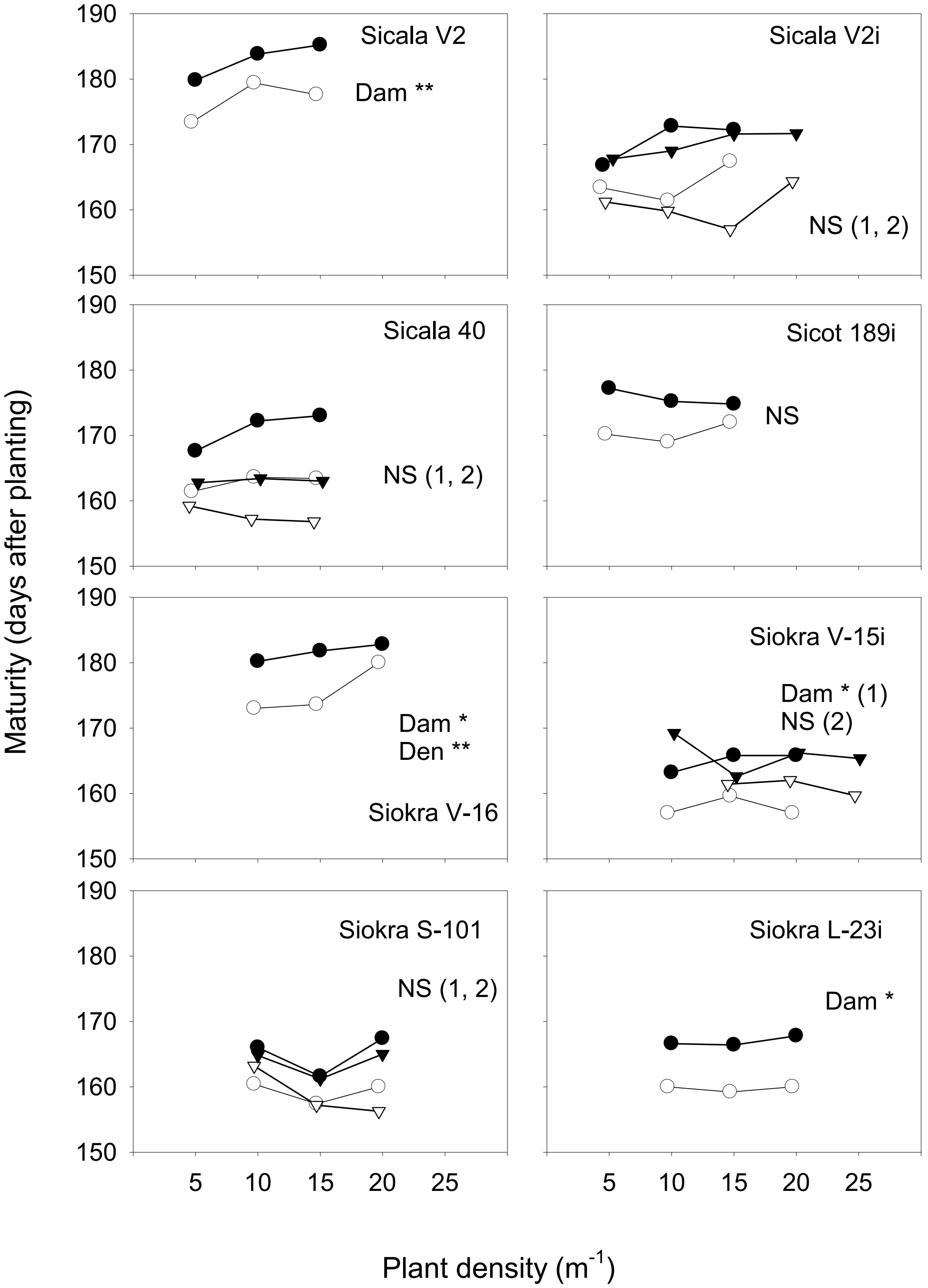

Figure 5. Maturity (i.e. 60% open bolls) of eight cultivars grown in a range of plant densities. Year 1 results were shown in circles and year 2 in triangles, solid symbols indicate damage treatment and open symbols the control. (1, 2) denotes the effect of the two year. Significant effects of damage and plant density for each cultivar and year are indicated. No interaction terms are significant. NS, *P*>0.05; *, *P*=0.01, **, *P*=0.001.

The lower boll mass of damaged plants (Fig. 3c) implied a delay in boll filling and later crop maturity (i.e. date of 60% open bolls). This was confirmed by the significantly later maturity of damage treatments in both years (Table 2). The delay ranged from 1 to 11 days with a mean of 6.4 (year 1) and 5.7 days (year 2). Time of maturity was significantly different among cultivars of different leaf forms and growth habits (Table 2). The difference was greater in year 1 (157 to 176 DAS, among control plants) than in year 2 (159 to 161 DAS, among control plants). Using a subset of plant densities common to all cultivars, I found no significant effect plant density on crop maturity (Table 2). Further analysis on individual cultivars using the full range of damage by density treatments revealed a significant effect of damage in some cultivars (Fig. 5). The only significant density effect was in Siokra V-16 in year 1. Kerby et al. (1990a) found a significant interaction between cultivars and plant density where maturity was delayed in indeterminant genotypes at high plant density but not in determinant ones. However, no significant interaction between cultivar and plant density was found in this study. The ranking in maturity date of control plants in year 1 (with its larger range) was Sicala V-15i<Siokra S-101<Siokra L-23i<Sicala 40<Sicala V-2i<Sicot 189i<Siokra V-16<Sicala V-2 (Fig. 5). The earlier maturing of the INGARD cultivars over the near isogenic conventional lines is attributed to the improved, in-built insect control of the former. Using stature and season length in Table 2 as a guide of determinacy, no correspondence between determinacy and maturity date was evident.

Conclusions

Even at the high level of repeated damage at both the pre-squaring and the fruiting period (mimicking 6 larvae m^{-1}), yield was reduced by 12% in year 1 and not affected in year 2. Damaged plants developed significantly more vegetative branches, which can be attributed to plant response to the two tip damage events. But the enhanced branching did not produce significantly higher LAI at peak fruiting. Recovery was the result of higher fruit production that extended later in the season; delay in maturity due to damage was about 6 days and not affected by plant densities. Overall, variations in canopy development attributable to cultivar and plant density (from 5 to 25 m^{-1}) did not reveal patterns of optima where yield recovery from damage can be maximized. These results indicate that the natural plasticity in canopy and fruit development in this long season and high yielding production system made it unnecessary for cultivar and density selection as crop management options to enhance recovery. In regions where the length of the growing season is shorter, or in situations where management or weather significantly shortened the season, an interaction between cultivars and density may be evident and offer scope for optimizing yield through the selection of cultivar and plant density.

Acknowledgments

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Effect of nitrogen levels on growth and yield recovery of cotton with repeated simulated pest damage

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Introduction

Cotton has demonstrated the capacity to produce greater leaf area and more fruiting sites after early and mid-season pest damage (Sadras 1996). This has resulted in full or over-compensation (i.e. higher than a control) in yield as reported by Brook, Hearn and Kelly (1992a, b) and Sadras (1996). For example, in 13 out of 14 trials conducted by Brook et al. (1992b) where the control crop yield was between 5 and 7 bales ha^{-1}, the yield of the corresponding damaged crop was 97 - 112% that of the control. They have also shown a high recovery potential under intermediate resource availability (i.e. soil nitrogen) but the ability to fully recover declined at high and low resource levels. The mechanism for the observed patterns of recovery remains unclear. However, it is suspected that adjustments in canopy structure and photosynthesis associated with resource availability are important. It is possible that greater levels of available N will allow for higher photosynthetic capacity therefore greater carbon supply. Milroy and Bange (2003) have also showed that varying N application significantly altered the development of canopy (LAI) and the radiation use efficiency (RUE) of the canopy. This implies that higher N with its greater carbon supply would enable greater fruit retention and facilitate better recovery from pest damage than lower N. To examine the potential for enhancing compensation under an appropriate level of N, a field trial was conducted where plant response in growth and yield were monitored after shoot terminals, squares and bolls were manually removed.

This 3-yr study examined the interaction between cultivars, applied N (3 levels) and two pest damage levels (i.e. an undamaged control and the repeated removal of plant terminals and fruit). Two cultivars were used in the last two seasons to examine the responses to the N and damage treatments of different genotypes (i.e. normal versus okra leaved cultivars).

Materials and Methods

The field trial was conducted at the Australian Cotton Research Institute in Narrabri, NSW Australia (30.4°S, 149.8°E) over 3 seasons: 1998-99 (year 1), 1999-2000 (year 2), and 2000-01 (year 3). The cotton cultivars Sicala V-2i (transgenic cotton containing the Monsanto Co. Cry 1Ac gene) was used in year 1 and in years 2 and 3 Sicala V-2i and Siokra V-15i were compared. Three N levels (0, 60, and 120 kg ha^{-1}) and two damage treatments (control and damage) were applied. Each treatment combination was replicated four times in a complete randomised block design. Sowing dates for the three years were October 16 (year 1), October 13 (year 2), and October 23 (year 3). The fields were irrigated 2-3 wks prior to sowing. A systemic insecticide aldicarb (Temik, Aventis at 450 g ai/ha) was applied at sowing to protect seedlings against early season pests such as thrips (*Thrips tabaci* Lindeman and *Frankliniella schultzei* (Trybom)).

N application and irrigation

In year 1, anhydrous ammonia (15 cm from plant line) was applied as side dressing after sowing on 20 November at 0, 60, and 120 kg ha^{-1}. In years 2 and 3, the same three levels of anhydrous ammonia were applied in the field approximately one month before sowing. Plant density was thinned to 10 m^{-1}. Furrow irrigation was applied 6 times in year 1: 13, 31 December, 11, 19 January, 25 February, and 19 March; 5 times in year 2: 14 December, 10 January, 25 January, 8 February, and 1 March); and four times in year 3: 4 January, 19 January, 20 February, and 8 March. Standard pest management was applied to minimise extraneous pest damage.

Damage

The damage treatment involved four damage events: terminal removal (1) in late November – early December, terminal removal (2) mid- December (both before first square), fruit damage (1) late December - early January, fruit damage (2) early to mid-February. The first terminal removal was made using forceps to break off all terminals of all plants and the second terminal removal only the terminal of the dominant lateral branch (i.e. 1 tip per plant). Pre-squaring tipping out has significant physiological consequences on canopy development through the initiation of lateral vegetative branch growth. Fruit damage was imposed twice to cotton plants during the first 8 wks of the reproductive stages (Fig. 1). The damage was equivalent to that made by 6 small larvae m^{-1} using a feeding model developed by Hassan and Wilson (1993) where the number of fruit sizes removed was based on actual feeding preference and feeding rates of *Helicoverpa* over a 2-week period (which simulates the completion of development for a cohort of larvae). Note in Fig. 1 that the amount of damage to the larger plants grown in high N was relatively small as a proportion of the total number of fruit present when compared with those in moderate and low N. These values were taken from the second fruit damage event. Both terminal and fruit damage was done on 3 rows of cotton with the centre row used for developmental and yield measurements.

The responses in growth and yield were monitored throughout the season where the biomass of plant parts, number and length of vegetative branches, and number of fruiting structures were recorded for each treatment combination. All tissue mass were weighed after drying at 70°C for 48 h. Leaf area of plants sampled from a 0.5m-row was measured using a LiCor Area meter (Li-3100, Lincoln, NE) and leaf area index (LAI) determined. Light interception below the canopy was measured using a ceptometer (AccuPAR, Decagon Devices, Inc. Pullman, Washington) at ±1.5 hr around solar noon. Light inteception was determined at 50% canopy height with the 80-cm ceptometer centred at the plant row and oriented at a right angle to the plant row. Light interception is expressed as a proportion of radiation above the canopy (which was ca. 2000 $\mu mol\ m^{-2}\ s^{-1}$ on a typical sunny day). Cotton yield was determined by sequentially hand picking open bolls in 1m of the centre row in each plot each week from the time that open bolls were first observed until all bolls were harvested. The date corresponding to 60% open bolls (defined as the maturity date) was derived from a regression of 3 or more harvest dates spanning the point of 60% open bolls.

Results

Leaf N

The patterns of mean leaf nitrogen content across the season for the three levels of pre-sowing N application is seen in Fig. 2 (data from year 1). There was a general decline in leaf N as the season progressed but the patterns diverged between treatments at the start of fruiting (Fig. 2). The decline in HN was significantly more gradual than the two lower N treatments. The greatest difference in leaf N occurred around peak fruiting (90 DAS) before the reconvergence of leaf N at the end of the season.

Plant development

In our experiment, damaged plants of all three nitrogen treatments had significantly more lateral branch growth than the control (Fig. 3). Branch length increased in proportion to greater branch numbers but the relationship was different between control and damage treatments where the slope for damage plants was significantly greater than that for the control. The relationships between branch length (BL, cm m^{-1}) and branch number (BN, m^{-1}) for the two treatments are:

damage plants: BL=-88.8+28.4 * BN (n=24, R^2=0.86)
control plants: BL=-636.7+67.5 * BN (n=24, R^2=0.94)

While there was an increase in lateral branches following damage, light interception was improved only at one date (122 DAS, Figure 4). There was, however, a strong influence of N treatment on % light intercepted at mid-canopy where higher N produced canopies that intercepted more light throughout the season.

When measured at peak fruiting (90-110 DAS), yield for the 3 years showed a strong association with leaf area (Fig. 5). LAI reached its maximum at this stage of growth. There is evidence of an optimal LAI at ca. 2.8 where lint yield declined at higher or lower values. No significant effect of damage or N on the relationships was detected. Fruit production (square and boll dry mass) across season for the 3 yrs is shown in Fig. 6. As the ANOVA indicates, there was generally higher production at higher N, while in some cases, production was higher in damaged plants compared to the control within each N level (e.g. square mass in year 3). There was no significant interaction between N and damage treatments. Fruit production between the cultivars was only significantly different in year 2 (data not shown).

Yield and fibre quality outcomes

Both boll number and lint yield were marginally higher in year 2 for Siokra V-15i than Sicala V-2i (Fig. 7, Table 1). Damage only affected yield in year 2 with years 1 and 3 showing no difference from the control. High N generally produced the highest yield but there was little interaction between N and damage. Crop maturity was slightly later in Sicala V-2i compared with Siokra V-15i (Fig. 7). Damage significantly delayed maturity in both cultivars but N only affected maturity in Sicala V-2i (year 1 and 2). Notably, in year 2, the yield of Siokra V-15i was consistently higher than Sicala V-2i yet matured earlier than Sicala V-2i (Fig. 7). Fibre quality was examined for year 1 and no significant differences in all indices were found except for micronaire where the effect of was significant (P=0.003; High N=3.81^b, Medium N=4.31^a, Low N=4.29^a). In year 3,
micronaire showed no difference between the two cultivars and were pooled for the analysis of other effects. When micronaire of three sequential hand picks were compared, it was found that micronaire declined with later opening bolls and that it was consistently lower in the damage treatment (Fig. 8). As the amount of lint taken from the three sequential picks for both treatments was similar and approximately evenly divided (Fig. 8 inset), the overall lint quality of each treatment should equal the mean micronaire of the three picks.

Discussion

This study examined the assumption that resource availability represented by soil N has a strong influence on the degree of compensation following repeated pest damage. The results show a clear effect of soil N on yield but a weaker influence on relative degrees of compensation. Only in year 1 was there an indication that yield responded to N differently between damage and control. Compensation was the greatest (exceeding that of the undamaged control) in intermediate N (MN, Fig. 7). This was found to be associated with canopy development and maximum LAI where MN Damage was in the optimal range between 2 and 3 while MN Control was less than 2. The reduced yield in HN Damage was related to excessive vegetative growth where LAI was 3.5 while that of HN Control was 2.8 (Fig. 5). I attribute the yield loss to the high N and weather conditions that accelerated the response to tip and fruit loss resulting to excessive leaf area production and severe self shading. Under MN, lateral branching induced by tip damage appears to have improved canopy development to a range where light interception was optimal. A similar pattern is evident in year 3 between damage and control of Sicala V-2i (Fig. 5). Greater yields associated with greater branching following tip damage have also been found in Kununurra (Lei and Gaff, 2003). Compensation under low N appears in general to be comparable to the control, suggesting that compensation was inhibited by low resources in this region.

Results from this and previous studies suggest that the response of cotton to early season tip damage can play an important role in the compensation capacity later in the season. The increase in lateral branch growth and leaf area can also be associated with greater fruit production (Fig. 6) which would increase the tolerance of cotton to additional fruit damage later in the season.

If yield response was depressed by damage under high N due to excessive canopy growth, would we be able to enhance compensation using lower plant densities to shift LAI into the optimal range? Experiments testing these ideas have been done and is presented in the “Variety by plant density” study.

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Sadras, V.O., 1996. Cotton responses to simulated insect damage: radiation-use efficiency, canopy architecture and leaf nitrogen content as affected by loss of reproductive organs. Field Crops Res. 48, 199-208.

Table 1. ANOVA table of yield parameters for the 3-yr field trial varying applied N and simulated damage in two cotton cultivars. Graphical representation of these results are shown in Fig. 7. Abbreviations: CV, cultivar; D and C are damage and control treatments; H, M and L are 120, 60 and 0 kg ha-1 N applied. Significance level is indicated by the *P* values, and differences ($P<0.05$) between treatments are shown by different letters.

	Year	CV	V2i			V15i		
			Damage	Applied N	Damage x N	Damage	Applied N	Damage x N
Boll no. m^{-1}	1	-	NS	H^a M^b L^b	NS	-		
	2	0.038	D^b C^a	H^a M^b L^b	NS	D^b C^a	H^a M^{ab} L^b	NS
	3	NS	NS	H^a M^a L^b	NS		H^a M^b L^b	NS
Lint yield (g m^{-1})	1	-	NS	H^a M^b L^b	0.034	-		
	2	0.026	D^b C^a	H^a M^b L^b	NS	D^b C^a	H^a M^b L^b	NS
	3	NS	NS	H^a M^b L^c	NS	NS	H^a M^b L^b	NS
Maturity (DAS)	1	-	D^a C^b	H^a M^b L^b	NS	-		
	2	<0.001	D^a C^b	H^a M^b L^b	0.013	D^a C^b	NS	0.015
	3	0.010	D^a C^b	NS	NS	D^a C^b	NS	NS

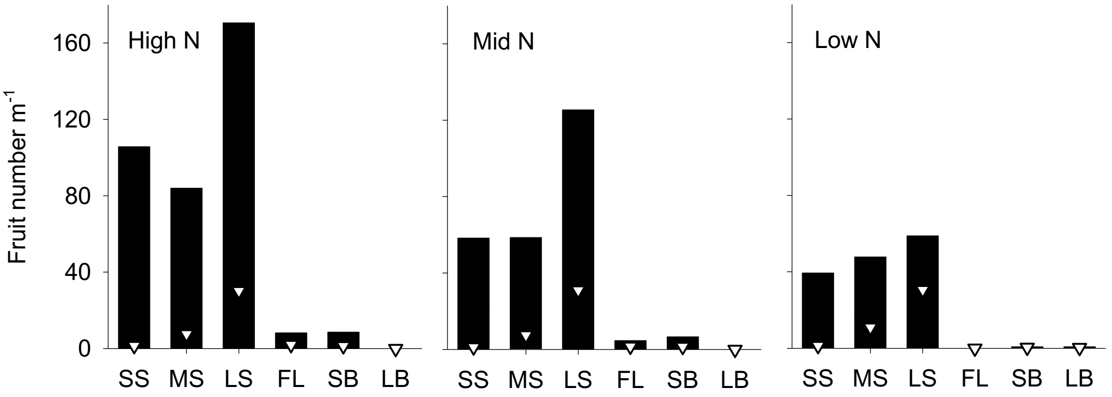

Figure 1. An example of fruit removed in relation to that available on the plants in the three N levels. The numbers of fruit in the various classes are shown in solid bars and the number removed from each class simulating 6 *Helicoverpa* larvae m^{-1} in triangles. Data taken from the second fruit damage in year 1.Abbreviations: SS– small squares (<0.5 cm), MS– medium squares (0.5-1.0 cm), LS– large squares (>1.0 cm), FL– flowers, SB– small bolls (<2.5 cm), and LB– large bolls (>2.5 cm, soft).

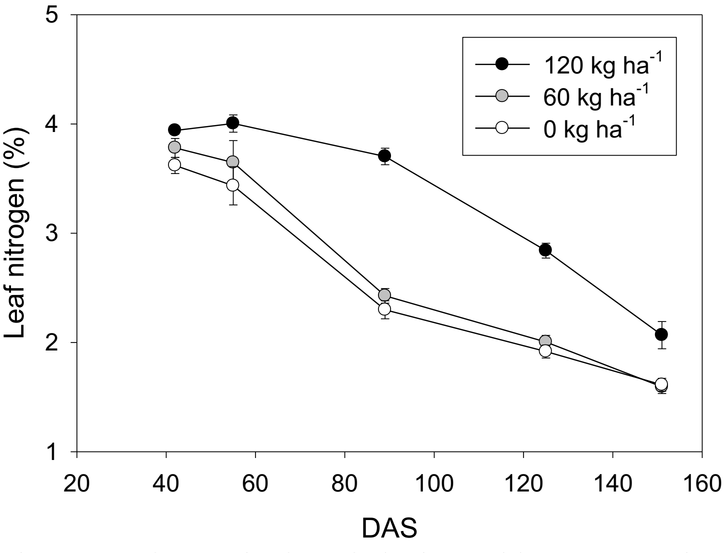

Figure 2. Seasonal pattern of mean leaf N of Sicala V-2i in year 1. Values were based on 4 replicate samples per treatment for each sampling date.

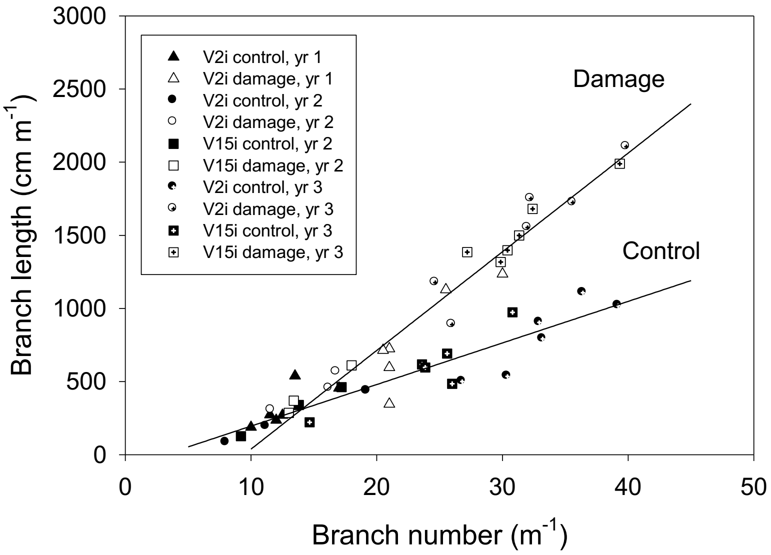

Figure 3. Relationship between branch length and branch number. Branch length increases in proportion to increasing branch number but the rate of increase was significantly different between control and damaged plants.

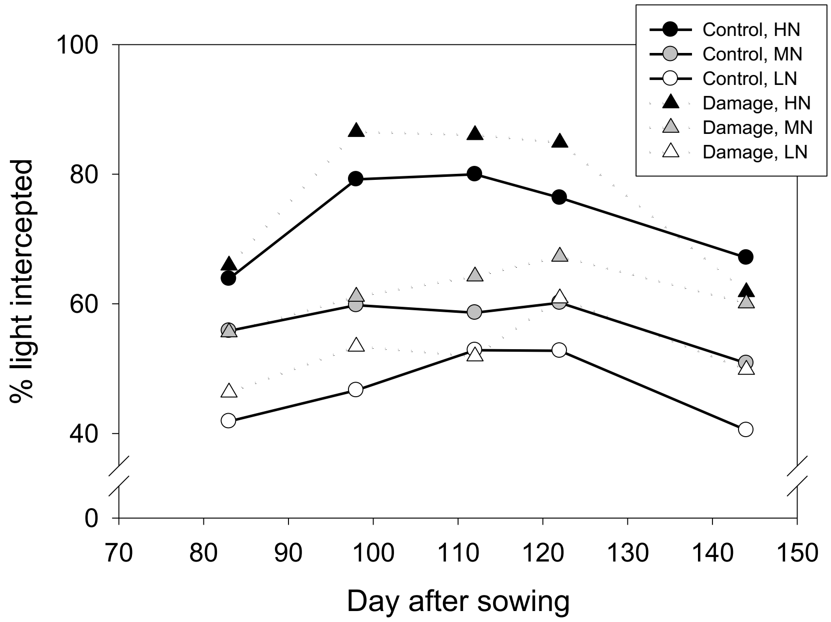

Figure 4. Light interception (% above canopy) patterns during the growing season as affected by damage and N treatments. Measurements were taken at mid canopy (i.e. at 50% plant height) around solar noon. Data shown were taken in year 1.

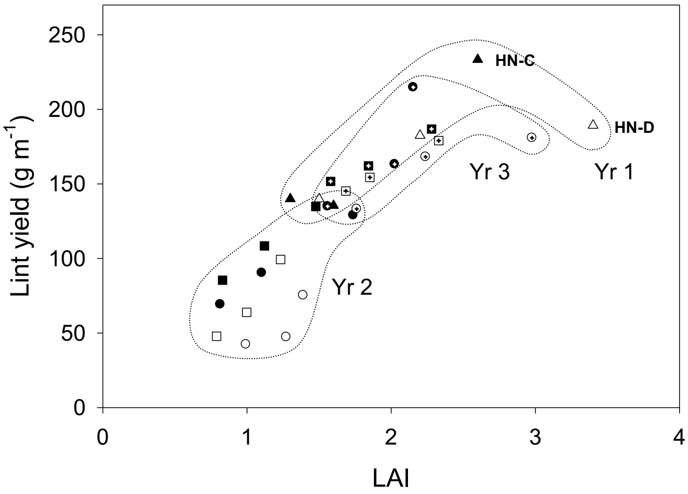

Figure 5. Relationship between lint yield and leaf area index for the 3 years (defined by dashed lines). Data points represent Values are the means of four replicates of each damage by N treatment. HN-C and HN-D are the control and damage treatments under high N in year 1.

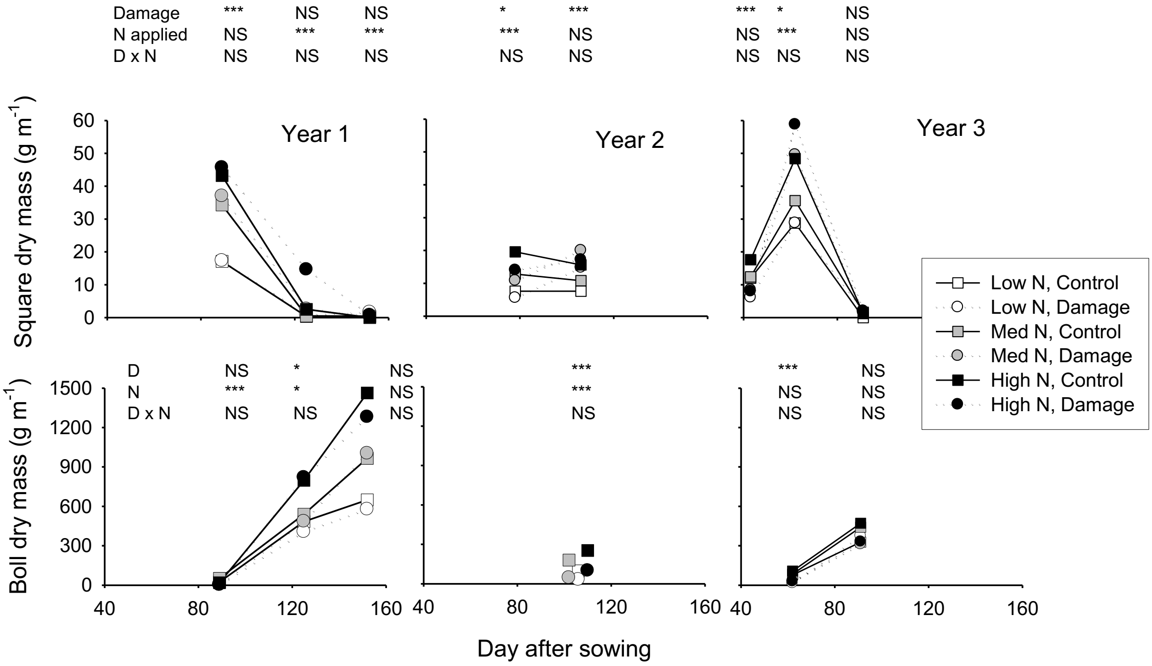

Figure 6. Square and boll dry mass during the three seasons. Above the graphs are ANOVA for damage, N and interaction terms corresponding to each sampling date.

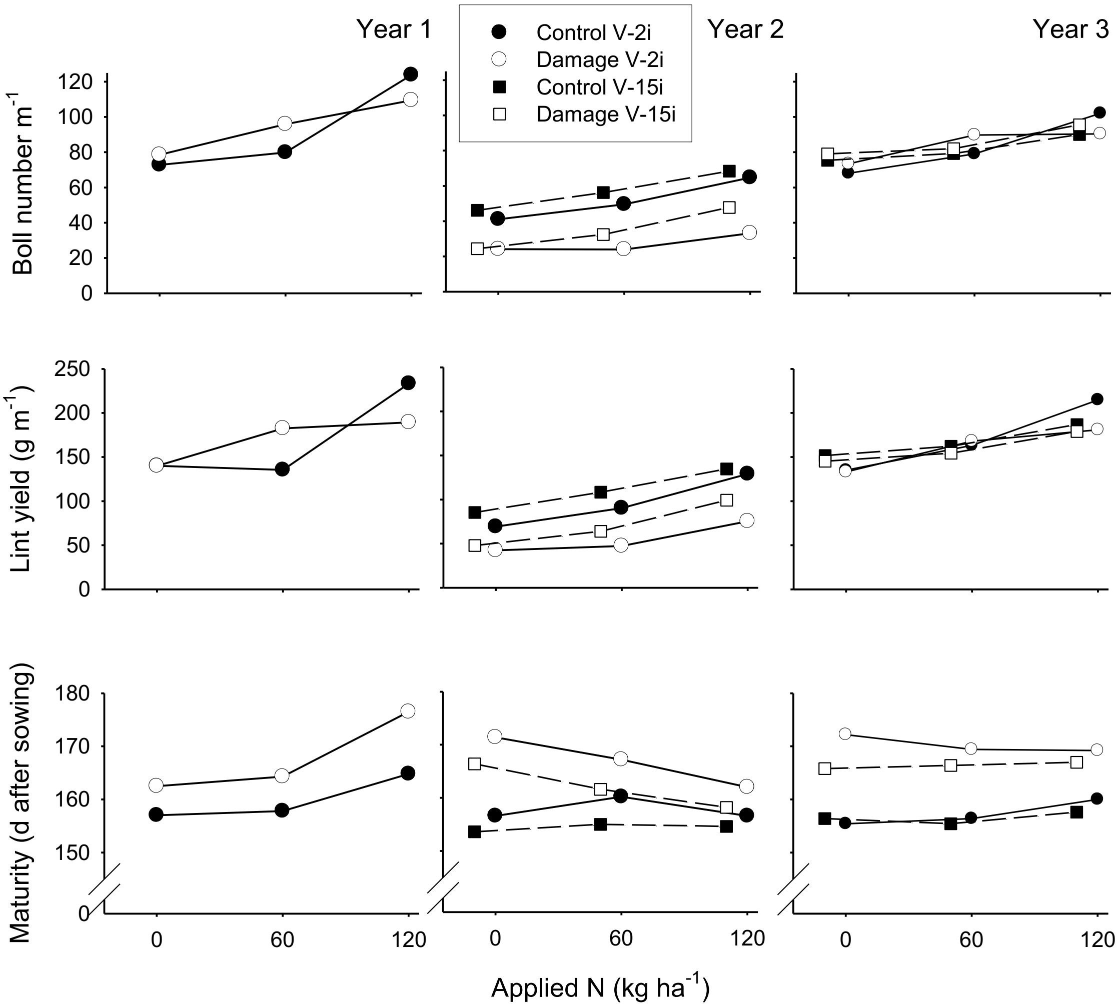

Figure 7. Final yield and maturity parameters for the two cultivars and two damage treatments over 3 years, represented by boll number, lint yield and maturity date.

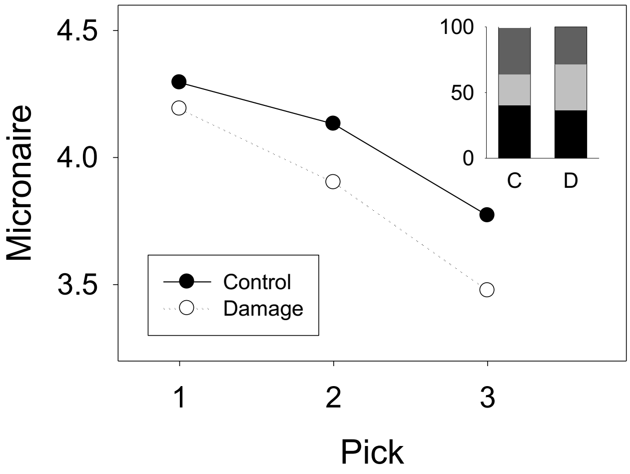

Figure 8. Fibre micronaire values of three sequential picks (i.e. early, mid and late opening bolls) for yr 3 showing the effect of damage. Data for the two cultivars have been pooled after determining a lack of cultivar and nitrogen effects. The inset bars show the percentage of total lint taken from each of the three pick for the control (C) and damage (D) treatments.

Consequences of early season tip damage in cotton shoot development and yield

Introduction

Early season tip damage is common in cotton seedlings but their structural response to such damage is not well known. Terminal damage at this stage will promote the development of lateral vegetative branches and alter the shape of the cotton canopy (Lei and Gaff 2003). Previous studies have shown that the ability of cotton to recover from fruit damage later in the season is closely related to its canopy structure. Key plant parameters associated with growth and yield such as leaf area index (LAI), light interception and fruit production are affected by tip damage (Lei and Gaff 2003). An integral part of our current effort to model compensation in cotton is quantifying how cotton responds to early season tip damage and how subsequent canopy development is altered. The rate of lateral branch release of some cotton cultivars has already been assessed by Sadras and Fitt (1997) but we have no data on the delay to time of first square, and the position, number and rate of bud release. This study addressed these issues as they relate to the ability of cotton to compensate from later season pest damage and to the development of OZCOT to simulate the process of terminal damage. Tip damage is common in Australian cotton crops early in the season. Tip damage could lead to significant changes in crop development including delay to first square, increased branching and higher fruit production. We have been working on describing these processes to better predict the consequences of tip damage. The following are some results on delays to first square. Since a delay is added each time a plant is tipped out, we can also use Table _ to estimate the cumulative delay of multiple tip events in cases where early season pressure from *Helicoverpa*, tip worm or mirids is high.

Materials and Methods

This field trial was conducted at the Australian Cotton Research Institute in Narrabri, NSW Australia (30.4^{o}S, 149.8^{o}E) over 3 seasons: 1998-99 (year 1), 1999-2000 (year 2), and 2000-01 (year 3). To assess the effect of tip damage among cultivars, several cultivars of different leaf type, growth form, phenological and transgenic status were examined (Table 1). To focus on obtaining more detailed data on growth response to tip damage, fewer cultivars were used in years 2 and 3. The INGARD cotton cultivars (with subscript "i" were transgenic cotton containing the Monsanto Co. Cry 1Ac gene. The field was fertilised with anhydrous ammonium at 120 kg ha^{-1} about one month before sowing. Sowing dates for the three years were October 16 (year 1), October 13 (year 2), and October 23 (year 3). The fields were irrigated 2-3 wks prior to sowing. A systemic insecticide aldicarb (Temik, Aventis at 450 g ai/ha) was applied at sowing to protect seedlings against early season pests such as thrips (*Thrips tabaci* Lindeman and *Frankliniella schultzei* (Trybom)). Plant density after establishment was ca. 10 plants per metre.

Terminal damage were imposed manually at five different node ages (i.e., at 2, 4, 6, 8, and 10 node stages plus a no damage control) and the subsequent number and rate of lateral bud development were recorded. Each tip treatment was replicated three to five times in a complete randomised block design with each plot being 3 rows by 3-m. Plots were managed using standard agronomic practice. Tip damage was imposed by removing the terminal using fine forceps without damaging the partially expanded leaves. Node age corresponds to the node where the uppermost expanding main stem leaf was 1 cm in length. Immediately following tip damage, the rate and number of lateral bud development of randomly selected plants in the centre row were monitored on a weekly basis for several weeks. Plots were harvested at the end of the season to obtain yield and maturity date as well as total branch growth.

Table 1. Cultivars used in the study with a range of growth habits and earliness. There were eight cultivars the first year, 4 normal leaves and 4 okra leaves. They also represent 4 INGARD (Monsanto Cry 1Ac Bt transgenic- indicated by the "i" suffix) and 4 conventional cultivars.

Cultivar	Symbol	Plant characteristics		
		Leaf type	Stature	Season
Sicala V-2	⊞	Normal	Normal	Med-late
Sicala V-2i	□	Normal	Normal	Med-late
Siokra V-16	◈	Okra	Normal	Medium
Siokra V-15i	◇	Okra	Normal	Medium
Sicala 40	△	Normal	Compact	Early
Sicot 189i	⊕	Normal	Tall	Late
Siokra S-101	○	Okra	Compact	Early
Siokra L-23i	◬	Okra	Tall	Late

Results and Discussion

Removing the plant terminal to simulate early season *Helicoverpa* (and light mirid) damage is known to cause a delay in growth (Sadras and Fitt 1997). Here we have quantified the delay based on timing of damage in two cultivars. The delay in days is given in Table 2. Tipping out at most nodes caused a delay to 1st square of up to 9 days. Tipping out at node 6 appears to cause little delay. The delay can be converted to degree days using the calibration curve given in Fig. 1. For example, a delay of 5 days from 56 to 60 DAS is equivalent to 65 DD. By converting delays to DD, we are able to implement age- and cultivar-specific effects due to tip damage in OZCOT.

Treatment	Control	Node 2	Node 4	Node 6	Node 8	Node 10
Tipped (DAS)		30	37	44	52	58
Sicala V-2i	54.2	63.5	61.0	54.9	57.8	60.2
Siokra V-15i	56.7	60.5	62.0	56.4	60.3	61.2

Table 2. Average date of first square in the undamaged control and two cultivars tip damaged at 5 node ages. Experiment conducted in 2001-02 at ACRI.

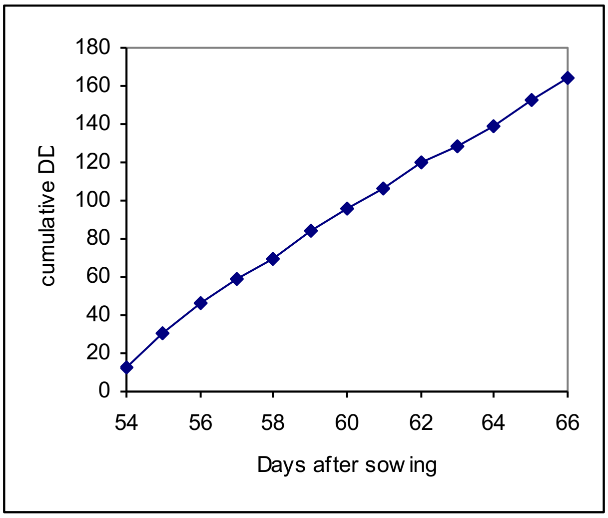

Figure 1. Calibration curve used to convert the amount of delayed to 1st square in days (in Table 1) to day degree. Cumulative DD was derived using a base temperature of 12°C and Narrabri Airport weather data for the same dates (i.e. Dec. 2 -14, 2001).

While the pattern of branch growth is variable among cultivars and timing of damage in year 1 (Fig. 2), there was a significant effect of tip damage in producing greater branch length than the control (orthogonal contrast: tipped vs control P=0.001). There was also a significant difference among cultivars (P=0.011) where Siokra S-101 and Siokra V-16 had the highest branch lengths while Sicala V-2i was the lowest. The effect of tip damage on the number of open bolls and lint yield (as seed cotton wt) was also variable with the damage treatments not significantly different from the untipped control (P>0.05, Fig. 2). Both boll number and seed cotton wt were significantly different among cultivars (P=0.019 and 0.017, respectively) with Siokra S-101 producing the greatest number of bolls but Siokra V-15i the most seed cotton wt. Interestingly, there was a significant relationship between yield and branch growth among cultivars. Using the difference between control and the average response of five tip treatments (among cultivars, tipped plants increased yield but only at low to moderate levels, there was a negative linear relationship between increased branch development and higher yield (Fig. 3). It may be possible that excessive branch growth has a negative impact on the partitioning of resources to bolls which includes both yield and date of maturity. We will use these data as part of the compensation model under development.

In year 2, branch growth was also significantly different between the untipped control and all tip treatments (orthogonal contrast, P<0.001). It is also appears that enhancement of branch growth were at its greatest when plants were tipped out at node 6 or 8 (Fig. 4). Tip damage had no effect on lint yield (P>0.05), but delayed maturity significantly but only in comparison to tip damage at nodes 6 to 10 (orthogonal contrast, P=0.008). Both lint yield and maturity were different among cultivars (P<0.001) with Siokra V-15i yielding the highest and Sicala V-2i the latest in maturity.

In year 3, the number of harvested bolls was no different among tip treatments and between cultivars (Fig. 5). Lint yield, however, was marginally lower for Siokra V-15i than Sicala V-2i (P=0.04). Together with the higher yield, Siokra V-15i also matured a few days later than Sicala V-2i (*P*<0.001). There was a significant delay of 2 to 6 days in maturity due to tip damage but only in the 6-8 node treatments (orthogonal contrast, *P*=0.015).

The process of shoot growth in tip-damaged plants was monitored in year 3 where an enhancement in total shoot length was evident in all tipped treatments (Fig. 6). The relative ranking and temporal patterns of the tip damage treatments is similar in the two cultivars but Siokra V-15i responded more strongly to damage, particularly when tipped out at 6, 8 and 10 nodes. Despite its greater shoot growth, Siokra V-15i yielded lower than Sicala V-2i. Clearly, there are other mediating factors obscuring the linkage between branch development and lint production. An initial examination of branch growth after the initial tip damage (i.e. between 20 and 60 DAS) indicates a general delay (tipped treatment curves below the control, Fig. 6) but a subsequent recovery. The timing of delay in branch development and the associated degree day is still being analysed. Once the delay has been calibrated, we will be able to, together with the delay to 1st square, refine OZCOT in simulating the process of tip damage.

Reference

Sadras VO, Fitt GP. 1997. Apical dominance - variability among cotton genotypes and its association with resistance to insect herbivory. Environmental and Experimental Botany 38: 145-153.

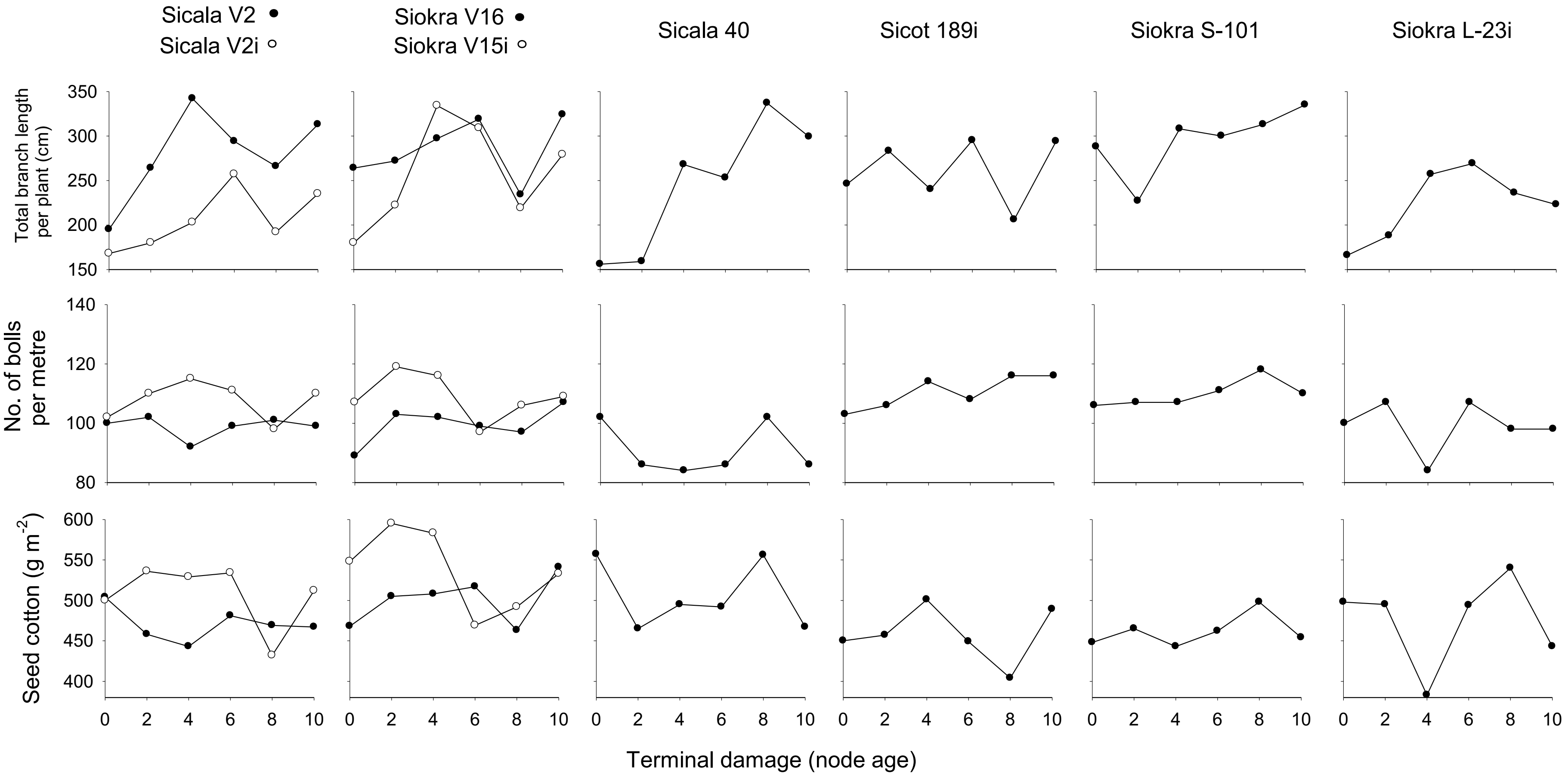

Figure 2. This graph shows the effect of tip damage on the development of vegetative branches for the 8 cotton cultivars in year 1 (Table 1). Tip damage was made at 5 different node ages when plants reached 2, 4, 6, 8 and 10 main stem nodes. The values at node age=0 are the undamaged control. Branch development was measured at peak fruiting (120 DAS). Yield outcomes are given as number of open bolls and seed cotton weight for the eight cultivars and the 6 tip damage treatments. Year 1 results are shown.

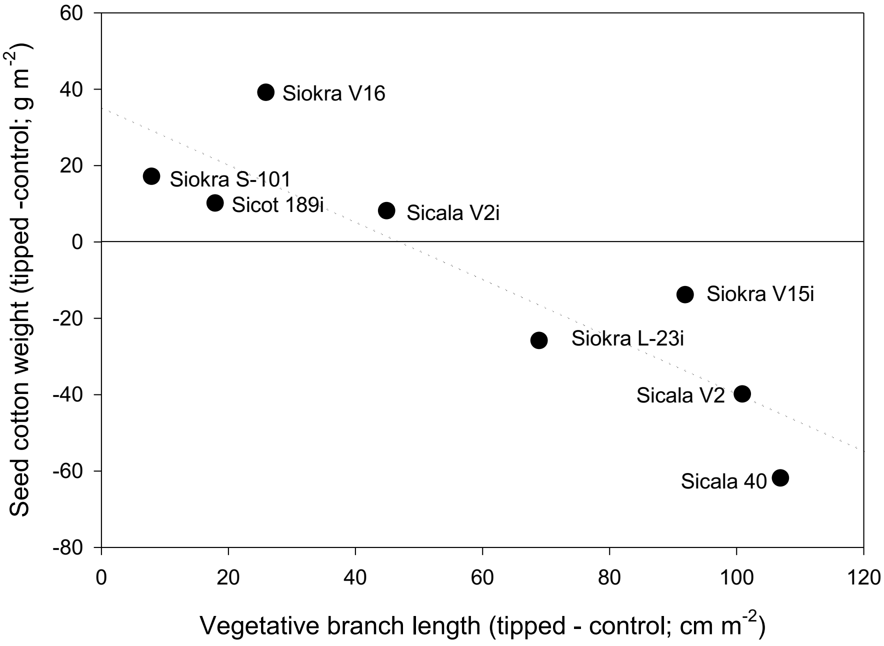

Figure 3. Cultivar specific responses in yield (in seed cotton wt) to the effect of tip damage in branch growth. The plot shows the difference between control and the mean value of the five tip damage treatments in yield and branch length. The regression line, SCWt =35.1-0.75*VBL, is significant with R^2=0.78.

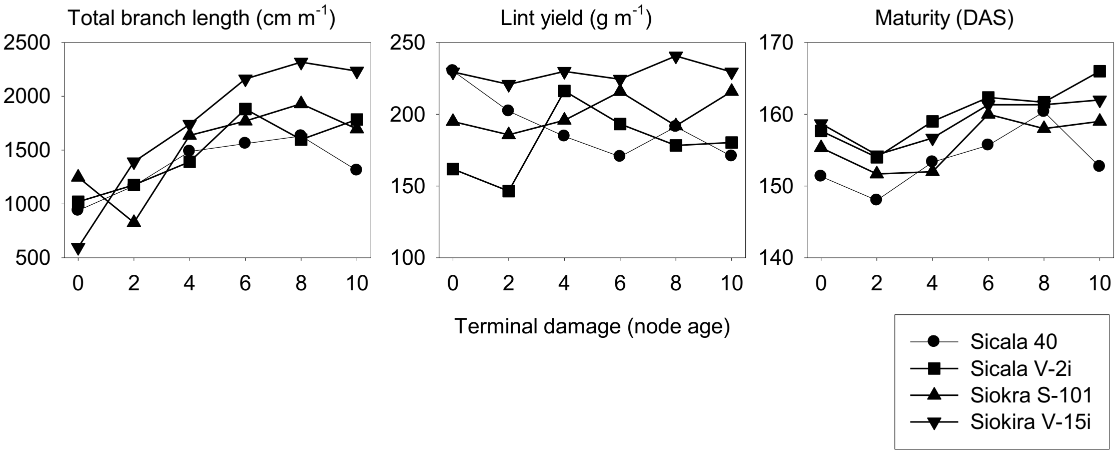

Figure 4. Year 2 results of branch growth, yield and maturity of four cotton cultivars after terminal damage carried out at 5 node ages (2, 4, 6, 8, and 10). 0 represent the untipped control.

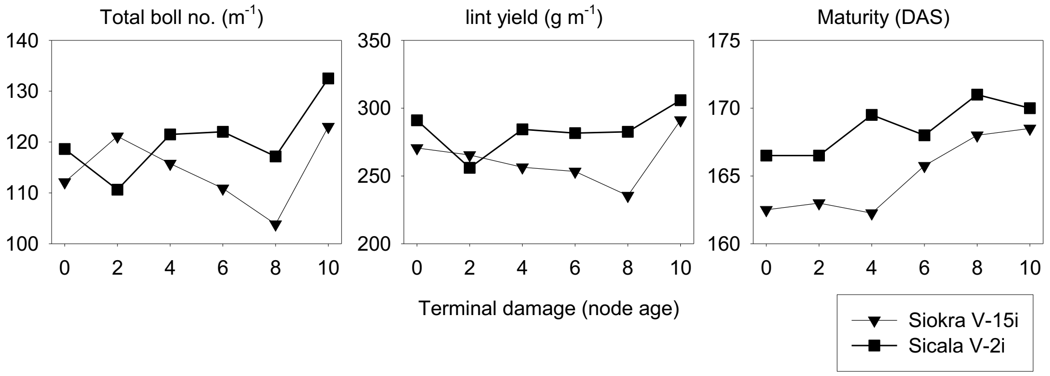

Figure 5. Yield parameters from year 3 showing total numbers of open bolls, lint yield and maturity date.

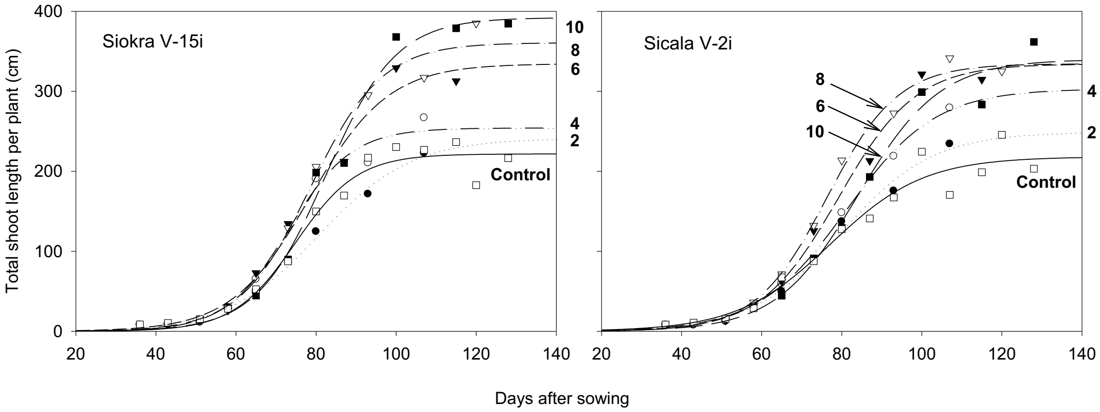

Figure 6. Patterns of total shoot development (main stem + lateral branches) over the season following tip damage at various node ages. Data shows the two cultivars grown in year 3.

Applying a similar cumulative *Helicoverpa* pressure over various time spans: from subthreshold grazing to Big Bang

Aim

A multitude of experiments have examined the growth and yield effects of pest damage imposed at different times of the season and at different intensity levels. These studies, however, do not address the question of what is the effect of the same total amount of cumulative damage applied over different time intervals? Is it the case that a cotton plant will respond similarly to a single event of heavy damage (equivalent to 8 small larvae per metre) as it would to eight damage events at one larva per metre? While the total amount of fruit lost by these two scenarios is similar, they are hugely different in terms of economic thresholds the industry uses to manage the pest. Small damages spread over a wider time span may allow plants to recover more will readily because the "stress level" at individual events is mild. Whereas a large dose of damage at one time may shock the system which will take much longer to recover. In this study, we tested the idea using a control and four damage treatments: l larva 8 times, 2 larvae 4 times, 4 larvae 2 times, and 8 larvae once.

Methods and Materials

This study was carried out at ACRI over two seasons. In both years, Sicala V-3i and Siokra V-16i were sown in early October. Nitrogen fertiliser at 120 kg/ha of anhydrous ammonia was applied about 1 month prior to sowing. Plant density after establishment was ca. 10 plants per metre. The experimental design consisted of five treatments each replicated five times. The size of each replicate plot was 3 rows x 5 m. Damage commenced ca. 9 weeks after sowing or 2 weeks after 1st square. The five damage treatments were:

1. Control – no damage
2. One damage event x 8 larvae per metre
3. Two damage events x 4 larvae per metre
4. Four damage events x 2 larvae per metre
5. Eight damage events x 1 larva per metre

Damage was imposed on the centre row x 5 m by removing by hand specified number of fruit spread evenly across each metre. The timing of the damage events are given in Fig. 1 and the numbers of fruit removed at each damage event are given in Table 1. Damage was Keep 2 m for maturity picks where yield and maturity (60% open bolls) will be determined.

Results and Discussion

We found no significant different in boll numbers harvested and lint yield among treatments in either year (Fig. 2). Both yield parameters were similar in year 1 between cultivars, but in year 2, Sicala V-3i was significantly higher than Siokra V-16i. There was also a large between year difference where year 1 was significantly higher than year 2 where the overall mean lint yield was 307.4 and 238.0 g m^{-1}, respectively. In terms of crop maturity, the 163 DAS achieved by the control in year 1 was significantly earlier than all damage treatments (i.e. 166.5-167.6 DAS). In year 2, no treatment effects were found but the 152.1 DAS of Sicala V-3i was significantly later than Siokra V-16i (150.4). Overall the difference in maturity was less than 5 days between all treatments.

Conclusions

Even at a level where a total of ca. 50 fruit were removed simulating the feeding damage caused by a total of 8 small larvae per metre, there was little or no effect on yield and maturity. More importantly for this study, there was no difference among treatments where the total damage was concentrated in one event or spread weekly over 8 weeks. This has significant indications on the current pest management practice where the 8Lx1, 4Lx2 and the 2Lx4 scenarios would have warranted one, two and four sprays to control the pests while the 1Lx8 would have been tolerated in many cropping regions. These results also demonstrated that a one larva sub-threshold grazing over 2 months would have little effect on production.

Tables and Figures

Table 1. Fruit removal regime used in this study. For the damage treatments, the number of fruit taken from each size class was based on the available fruit at the time of damage and calculated using the *Helicoverpa* feeding model of Hassan and Wilson 1993). Abbreviations: ms- medium squares (0.5-1.0 cm), ls- large squares (>1.0 cm), flr- flowers, sb- small bolls (<2.5 cm), and lb- large bolls (>2.5 cm, soft).

Treatment	Event	Fruit class				
		ms	ls	flr	sb	lb
Control		0	0	0	0	0
8Lx1	1	11	12	12	7	4
4Lx2	1	6	7	8	5	
	2	5	6	6	4	2
2Lx4	1	5	10			
	2	3	4	3	2	1
	3	3	3	3	2	1
	4	3	3	3	2	1
1Lx8	1	3	5			
	2	3	5			
	3	3	5			
	4	1	2	1	1	1
	5	1	2	1	1	1
	6	1	2	1	1	1
	7				2	1
	8				2	1

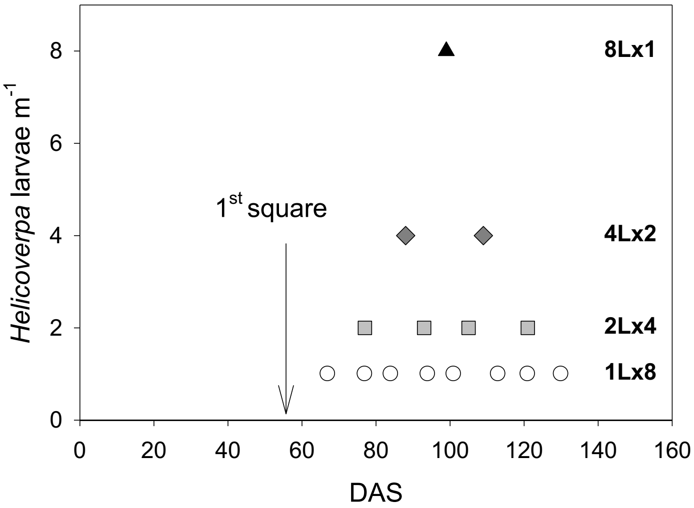

Figure 1. Damage regimen used in the study. The total damage caused by 8 small larvae m^{-1} was distributed in 4 different temporal patterns ranging from one damage event by 8 larvae m^{-1} to eight events by 1 larva m^{-1}. The timing of damage centred ca. 100 DAS with the earliest fruit damage (1Lx8) beginning ca. 12 days after the appearance of first square.

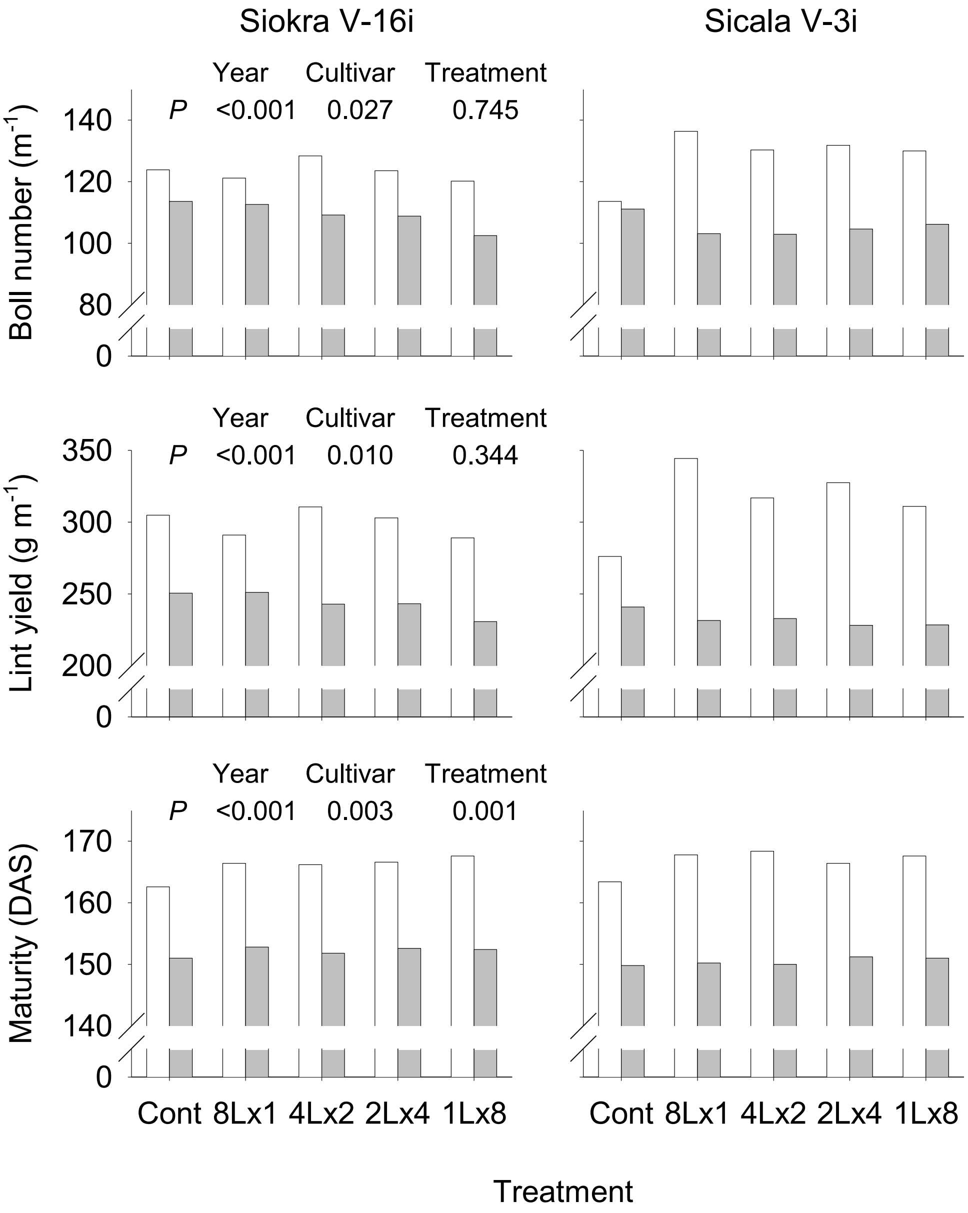

Figure 2. Yield consequences of two cotton cultivars subjected to a similar high level of total damage (i.e. 8 larvae m^{-1}) distributed in four different temporal regimes (see Fig. 1). Two years results are shown represented by the open and the shaded bars.

Yield consequences of patchy damage to cotton terminal, leaves and fruit: does what happened to your neighbours matter?

Background and Aim

Findings by Sadras (1995, 1997) indicated that the recovery to damage by an individual plant can differ quite dramatically depending on two factors: one, the type of damage (i.e. tip or fruit loss), and two, whether its neighbours were also damaged. If one uses these results and scale up to a stand of cotton, the implication is that the overall compensation achieved will vary depending on the distribution of damage and on the type of damage neighbouring plants have. If a plant experienced fruit damage while its neighbours remained intact, it will grow larger and yield higher than if its neighbours are also damaged (Sadras 1997). Therefore, if 50% of the plants were damaged but in one instance these were all separated by undamaged plants (i.e. xoxoxoxo where x is damage and o is undamaged) and in another instance they were grouped together (i.e. xxxxoooo), the total amount of compensation will be larger in the first case. If this is true, then it is no longer sufficient to know only the total damage caused by pests, the degree of compensation will also depend on the spatial distribution of the damage. The latter is not accounted for in the current determination of pest pressure in cotton cropping. Yet, it is well know that pest occurrence and their damage in the field tend to be patchy (Wilson and Room 1983, Wilson et al. 1983), creating variable spatial distribution of damage.

The aim of this study was to examine the yield outcomes of damage imposed on a variety of spatial distributions based on artificial and natural patchiness. We imposed three types of damage: tipping out, leaf area reduction and fruit loss to assess the possible interaction between spatial distribution and damage type.

Methods and Materials

Sicala V-3i was sown in early October in 2001 and 2002 at ACRI. Temik was applied at sowing at 5kg/ha to protect from thrips and other sucking pests early in the season. There were six treatments replicated five times set in a complete randomised block design. Experimental plots were 3 rows x 2 m with a 2 row or 2 m buffer between plots. The field was irrigated and managed for pest and weeds using standard practices.

Damage scheme

All damage trials used plots 3 rows of 2 metres. This represents a 6m^2 stand of cotton within which a variety of spatially distributed damage, as specified below, were imposed. The final harvest was also made on the whole plots to ensure that the overall yield of the stand is properly determined.

Tip damage was imposed by removing the plant terminal between the top two expanding leaves using a curved forceps at the 5 true leaves stage. Damage treatments consisted of tipping out 50% of the plants in five spatial distributions plus an untipped control. The treatments are:

1. Control (C), no tip damage
2. Uniform (U), tipping out every other plant
3. Clustered (K), tipping out the first half of the plants in each metre
4. Random (R), tip out half of the plants using a random number generator

5. All (A), tip out all plants
6. Negbin (N), tip out half of the plants selected using a negative binomial distribution model (Wilson et al. 1983)

Figure 1 gives an example of the different spatial distributions of damage. By applying the designated damage configurations, we generated a range of patchiness from very small (i.e. U treatment) to large patches (i.e. K treatment) with intermediate patchiness represented by the other treatments. Tip damage of all treatments was carried out in one day.

Leaf area reduction was imposed by removing all leaves (excluding the cotyledons) of 50% of all plants on three successive weeks beginning when seedlings reached the 3 node age. The spatial scheme used is as follows:

1. Control (C), no leaf damage
2. Uniform (U), damage every other plant
3. Clustered (K), damage first half of the plants in each metre
4. Random space (Rs), damage half of the plants using a random number generator, the same plants were damaged 3 times
5. Random time (Rt), damage half of the plants using a random number generator, three different sets of randomly selected plants were damaged for each event
6. Negbin (N), damage half of the plants selected using a negative binomial distribution model (Wilson et al. 1983)

Fruit damage began when the crop reached the stage of 2 flowers per plant (mid to late Jan.). The simulated damage was imposed on the $6m^2$ stand (i.e. 3 rows x 2 metres) where each 2m was divided into 10 equal 20-cm segments. Fruit were removed from five out of the ten segments. The spatial arrangement of damaged segments were determined using the same procedure as that for the leaf area reduction, except that the damage was imposed not on a per plant but on a per 20-cm segment basis. Fruit damage was imposed removing 120 fruit over 2 metres spread over three dates during a two-week period. This was to simulate the feeding done by a cohort of 9 larvae from emergence to pupation (Hassan and Wilson 1993). The number and size classes of fruit removed at each damage date were: ms=2, ls=2, fl=1, sb=2, lb=1.

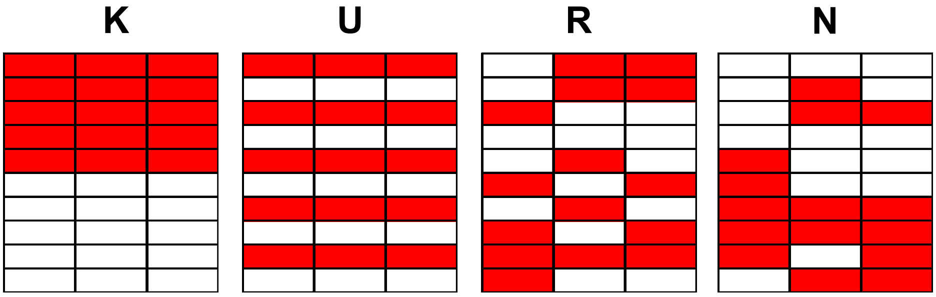

Figure 1. Schematic diagrams of the various spatial configurations used in this study. Each cell in the plots represents one plant in the tip and leaf damage experiments and one 20-cm segment of row in the fruit damage experiment. Codes for the spatial distributions are: K=cluster, U=uniform, R=random (space), and N=negative binomial. See Methods and Materials for more detail. In random time, the R pattern is different for each of the three damage events.

Results and Discussion

While detailed analysis of results is still in progress, here we show an overview of some key outcomes from the experiments. In Fig. 2, the relative lint yield of damage treatments to the control shows some year-to-year variation but little difference among damage treatments. In some years, full yield recovery was evident in tip and fruit damage while others show a general decline in yield relative to the control. Regardless of their relative yield to the undamaged control, in all cases, the yield among damage treatments varied by only ±4% from the mean. The main conclusion at this stage is that, while tip, leaf or fruit damage to 50% of the plants may cause some yield reduction, the relative effect is similar among treatments. Therefore, even though the distribution of damage status among neighbouring plants differed widely among treatment configurations, this had no effect on the overall yield of a $6m^2$ stand. The implications are that while individual plants may respond differentially to damage to itself and its neighbours, the overall production of a stand was the same because the utilisation of the available resources was adjusted between plants.

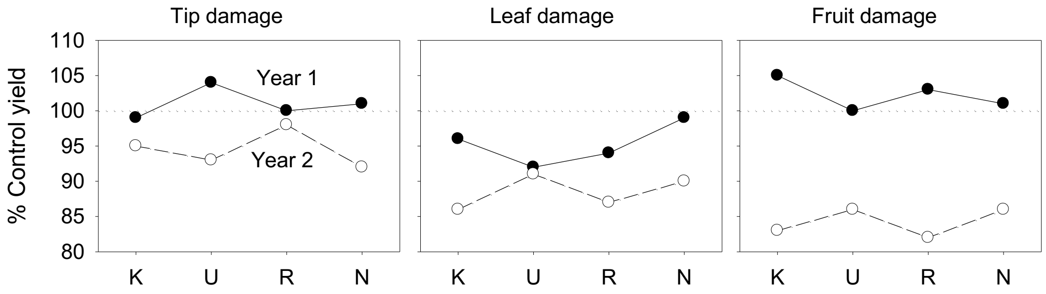

Figure 2. A summary of yield consequences of spatially variable damage to plant terminal, leaf area and fruit. Two years results are shown. In all cases, the damage imposed was to 50% of the plants arranged in the spatial configurations illustrated in Fig. 1. The dotted line indicates the 100% line. this comparison, for R, only the random space treatment which is common to all damage trials is shown.

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Natural patchiness in tip damage and thrips infestation

Introduction

This is a companion study to the artificial patchy damage presented in the previous section. It was initiated to assess the nature of patchy damage (to terminal and leaf area) in naturally pest infested cotton. Patchy damage leads to unevenly damaged neighbours which could confound the degree of growth and yield recovery of individual plants (Sadras 1995, 1997). He also found differences in growth and yield responses in cotton plants depending on the type of tissue that was damaged. However, his studies were based on individual plants either receiving very heavy damage or no damage at all. Because we know that the distribution of pests in a stand of cotton is patchy (Wilson and Room 1983), to assess plant responses using static spatial arrangements may not be realistic in the field as pests move amongst the plants. Therefore, if damage in nature occurred in patches that shift in size, location and time, the difference in damage among neighbours may be much less distinct than that Sadras applied. Therefore, it is imperative that we quantify spatial patchiness at both the spatial and temporal scale. In this study we made detailed observations on the patterns of natural tip damage for 3 years and natural thrips damage for 1 year.

Methods and Materials

To assess the pattern of early season natural infestation, we planted Siokra V-16 and Siokra V-16i in unsprayed fields at ACRI. The selection of the two near isogenic cultivars with (V-16i) and without (V-16) transgenic Bt (INGARD) which allowed the comparison of plants with and without protected against *Helicoverpa* early in the season. To provide a control to natural sucking pest infestation, the systemic insecticide aldicarb (Temik, Aventis) was applied at sowing at 450 g ai/ha to some plots. This treatment protects seedlings from early season sucking pests. Plots were laid out in a complete randomised block where the four treatments: V16 – Temik, V16+Temik, V16i – Temik and V16i+Temik were replicated four times. Each plot was 6 rows x 10m. The field was fertilised with anhydrous ammonia at 120 kg/ha about one month prior to sowing. Fields were furrow irrigated based on standard management practices. Plant stand following establishment was ca.10-12 m^{-1}.

In each plot, 15 one-metre subplots were established in the following manner: on 3 rows each separated by a buffer row, the five subplots were marked with a 1m buffer separating the subplots. The number of plants in each subplot was recorded. The distribution of tip damage was assessed three times each year during November and early January. The census dates were separated by ca. 3 wks. At each census, each plant within the subplots was checked for tip damage. Damaged plants were identified with a skewer and a date specific marker. If a plant was tipped out a second time, an additional marker was placed on the skewer. Following the census period, the history of tip damage for every plant was recorded. For the assessment of the spatial distribution of natural thrips damage, the criterion for assigning damage is given in Fig. 1. As thrips only affected young seedlings, damage (identified with a marker different to tip damage) was recorded only on the first census.

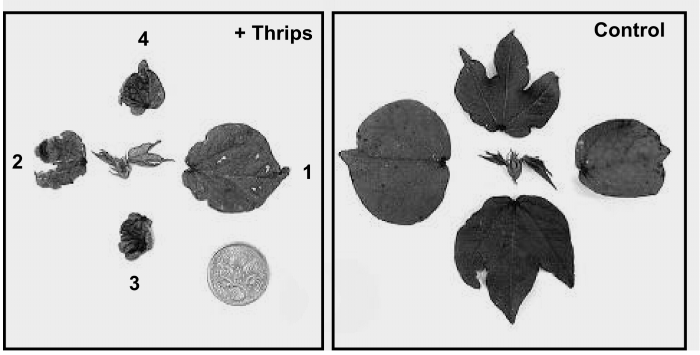

Figure 1. The criterion used to determine whether a plant was tagged as severely affected by thrips. A plant is only deemed severely damaged when 3 of the first four main stem leaves showed leaf area reduction >50% of the corresponding control leaf. An example of the difference in leaf development between control (undamaged) and thrips damaged plants. The photo was taken at the 4-node stage showing the four main stem leaves (numbers identify the node position) and the terminal at centre. The coin is 19 mm in diameter.

In the last two years of the study, yield of the treatments was determined by harvesting the open bolls from three 1m subplots (centre row) from each treatment rep.

Results and Discussion

Results from all three years indicate that the spatial and temporal distributions of tip and thrips damage are not static. Patterns of patchiness shifted between census dates indicating that damage was dispersed through time and space. This is illustrated by the year 3 results shown in Figure 2. Conventional V-16 without Temik suffered the greatest damage from both thrips and tip damage. Tip damage became progressively more widespread later in the census period. It is clear that INGARD plus Temik offered the best protection against both tipping out and loss of leaf area from thrips. Temik alone offered significant protection to the conventional Siokra V-16 but did not prevent early tip damage (49 DAS). This indicates that tipping out is caused by predominantly *Helicoverpa* and not by thrips except in very severe cases.

Among years, the patterns of tip damage were remarkably similar (Fig. 3). Year 1 with only one treatment (Siokra V-16-Temik) showed a similar rise in % tipped plants with time. In year 2, a similar low (10%) tipping out was found in all treatments at 41 DAS (INGARD no protection). There was little tip damage in INGARD on the 2nd and 3rd census dates. The high tipping out in conventional suggests a weak protection conferred by Temik against *Helicoverpa*. INGARD offered effective protection against tip damage by *Helicoverpa* until at least 79 DAS in both years 2 and 3. We assessed the yield outcomes among treatments and found that the conventional V-16 without Temik suffered an 18% yield reduction compared to its counterpart with Temik (Fig. 3). There was an additive effect of high tip damage and high thrips damage (in V16 without Temik) in significantly reducing yield. In the case of V16i without Temik, while a third of plants were damaged by thrips, only 10% were tipped out, the latter equates with 1/3 of all thrips damaged plants experiencing tipping out. In this treatment, despite the heavy leaf area loss (inset of 2001-02, Fig. 3) early in the season did not affect the final yield.

If we compare the INGARD cotton with and without Temik, it is clear that 8-10% of plants are still tipped out regardless of the level of thrips damage. This point to the possibility that the tipping out was caused by mirids and not by *Helicoverpa* or thrips.

Damage details	Siokra V-16		Siokra V-16i	
	- Temik	+ Temik	- Temik	+ Temik
Total plant number	694	753	710	774
Total tip events	675	850	88	61
% of all plants tipped	74.5	84.1	9.9	7.6
% of plants tipped twice	23.7	28.4	4.5	2.5
% of plants tipped three times	2.3	3.2	1.8	0.0
Number of plant with thrips damage	231	19	204	6
% of plants thrips damaged	33.3	2.5	28.7	0.8
% of tipped plants with thrips damage	33.3	2.9	34.8	1.2

Table 1. A summary of the properties of tip and thrips damage in year 3.

To further evaluate the level of damage an individual plant can experience, we found that a plant may experience multiple tip damage, with two tip events quite common (25-30% of tipped plants), it is less common to have three tip events (<3%, Table 1). Using our thrips damage criterion, 1/3 of the plants unprotected by Temik suffered significant leaf area loss. Interestingly, regardless of the total number of tip damaged plants, without Temik protection, about 1/3 of them will also suffer severe leaf area loss.

These findings lead us to conclude that the effect of uneven damage among neighbours may be less distinct that derived from controlled experiments by Sadras. We are currently analysing the data to determine whether the observed distribution conforms to that described by the negative binomial equation developed for *Helicoverpa* and thrips (Wilson and Room 1983). We are also assessing the frequency of uneven neighbours to answer the question "how many instances of asymmetric tip damage occurred in the field?" These field observations will permit us to scale up the yield consequences of uneven tip damage from the immediate neighbours to the entire field.

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Figure 2. Natural occurrence of tip damage in an unsprayed field. The numbers above the contour maps indicate distribution of thrips damage (measured on 49 DAS) and tip damage on three dates (DAS). The contour maps of damage show a range between 0 and 80% tipped plants (per subplot).

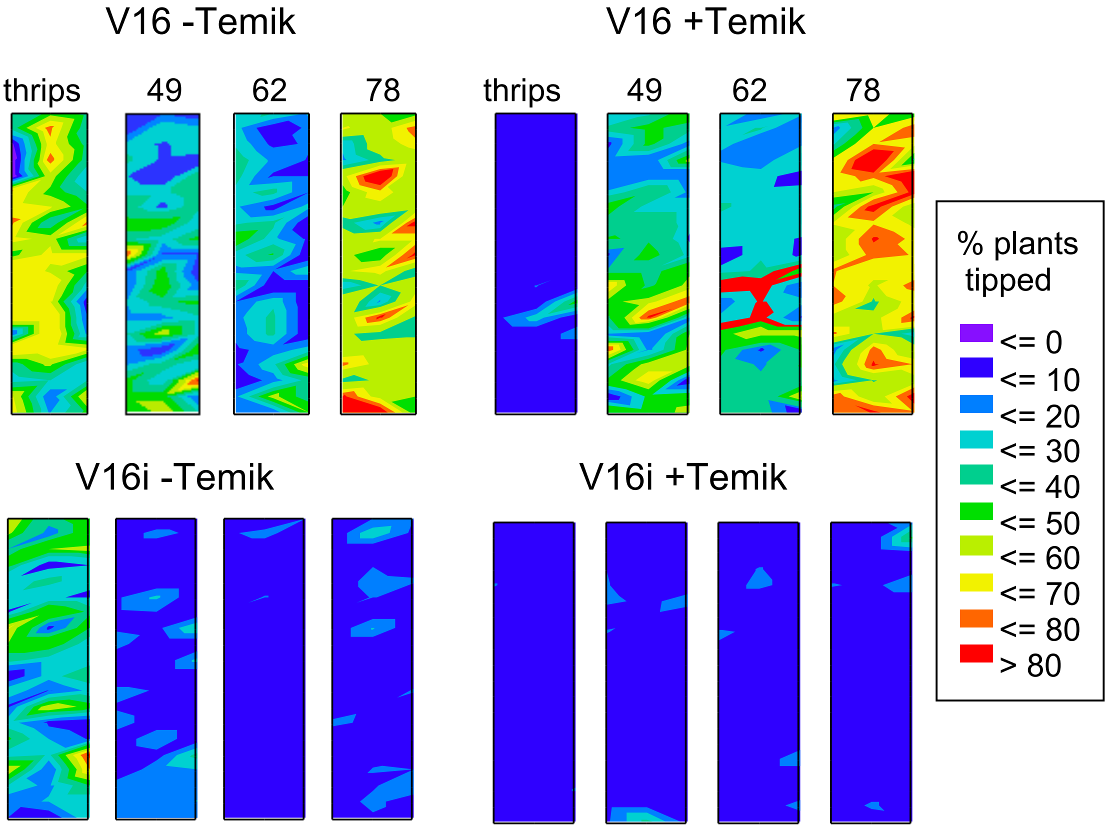
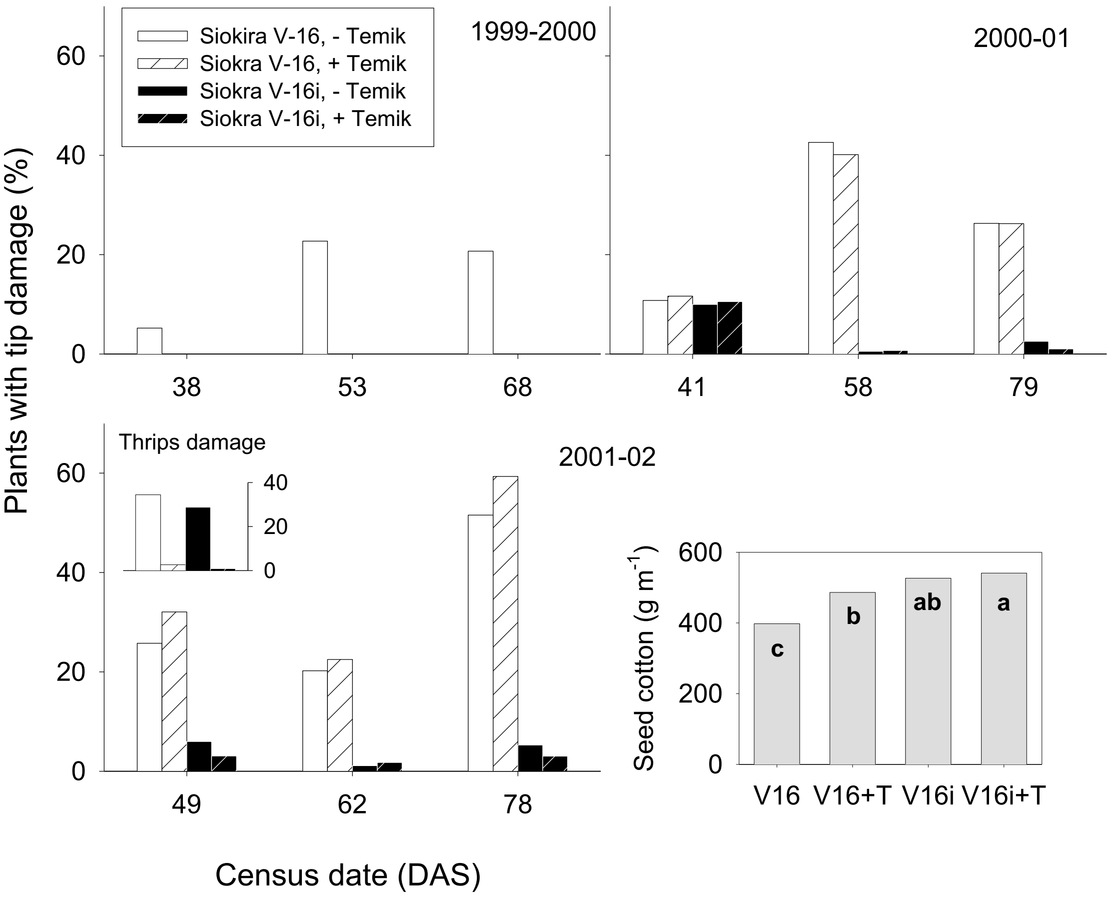


Figure 3. Percent of plants with natural tip and thrips damage in 1-m rows. Variations in damage was examined by using an INGARD cotton cultivar and its near isogenic conventional counterpart. Each of these cultivars was also sown with or without aldicarb (Temik) to confer early season protection against sucking pests.



Investigating green mirid damage on cotton squares and bolls

The mirid study was initiated in the last 2 seasons of the project in response to the emerging threat of sucking pests in general in INGARD and BOLLGARD II cotton. There are two reports of this work. The first one "Boll damage by sucking pests: An emerging threat but what do we know about it?" was a paper published in the 10th Australian Cotton Conference and presented at the 3rd World Cotton Conference (by Dr L. Wilson). The second part is "Defining thresholds for mirids during the fruiting period" with data collected from Narrabri (by CRC summer scholarship student Sara Winston- Smith) and from Katherine NT (by Andrew Ward)

Part 1- Boll damage by sucking pests: An emerging threat but what do we know about it?

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Introduction

Historically, green mirids are common pests of seedling cotton but not during fruit set and green vegetable bugs (GVB) are rarely a problem. This is because broad-spectrum pesticides applied against Helicoverpa larvae usually control mirids and GVB through the mid- and late season. With the introduction of Bt-cotton however, the number of Helicoverpa sprays used has declined allowing green mirids and GVB to build to potentially damaging levels in some instances. Spraying for Helicoverpa is expected to drop even further with two-gene cotton (Bollgard II), raising the concern that sucking pests may become a significant problem during the fruiting period. The effect on yield and fibre quality by the increased feeding of mirids and GVB on bolls is not well understood. In one of the few studies to date, Khan and Bauer (2001) found that damage to young bolls (<10 days old) often causes shedding. Damage to older bolls (10-20 days old) usually does not cause shedding but the damaged locules may not develop properly. This has implications for the capacity of the crop to compensate for daamge by producing more bolls, making undamaged bolls larger or making undamaged locules in damaged bolls larger.

An understanding of the effect of mirids and GVB on cotton yield and fibre quality is therefore crucial to development of rational thresholds and IPM strategies. To accurately predict the yield consequences of boll damage by sucking pests, we first need to understand the process of the damage and the response of cotton to the damage. When bolls are fed upon by sucking pests, the causes of lint damage is unclear: was it physical piercing of the immature seed, or the injection of enzymes breaking down the developing fibres or seed, or a combination of these and other factors? We are developing techniques to answer these questions by mimicking mirid damage artificially. This provides a way to precisely quantify the relationship between a given level of damage and its effect on yield parameters. For growers, the impact of sucking pests on yield and fibre quality and whether cotton can compensate from this type of damage is clearly a priority.

Here we report on the first phase of an on-going investigation with the aim of quantifying the ability of cotton to tolerate this type of boll damage, and the mechanism by which this is achieved. In the end, we hope to provide growers and consultants with the necessary knowledge to make better decisions on the management of sucking pests in the age of the two-gene cotton.

Methods and Materials

Mimicking mirid boll damage using injection of the pectinase enzyme

Experiment 1. Sicala V-3i was grown in 50 litre bins that were watered regularly. Bolls when they reach 25 cm in diameter, which corresponds to 10 days after white flower, were damaged. Damage was imposed by injecting 2 locules in each boll with pectinase (an enzyme in the saliva of mirids that breaks down complex carbohydrates including cellulose). The pectinase we used was a commercial extract from Aspergillus niger (Sigma-Aldrich Pty Ltd, Sydney Australia). We diluted the pectinase (in 40% glycerol) with water at 1:4. A 1ml syringe was used to inject 20 µl of the pectinase solution in each locule to be damaged. Out of the 30 plants were used for this experiment, 20 received damage and 10 were kept as undamaged control. Plants assigned to receive the damage were treated on 2 consecutive weeks where all bolls within the target size were injected with pectinase. This method allowed us to produce a range in the number of bolls damaged, i.e. from 1 to 9 damaged bolls per plant. Plants were grown to maturity when open bolls were harvested. The number and mass of undamaged and damaged bolls were recorded for each plant.

Experiment 2. In this experiment we tested lower volumes and concentrations of pectinase that may be closer to that injected by mirids. Two cotton varieties (Sicala V-2 and Siokra V-16) were grown in a glasshouse in 42L pots at 2 plants per pot. When plants reached sufficient boll number (about 8 per plant), randomly selected bolls about 10 days in age were injected with pectinase at 1 µl or 3 µl of two dilutions (1:4 and 1:10 pectinase to water). Some bolls were also injected with 1 µl or 3 µl of water as controls for the injection process. Two locules were injected in each damaged boll with a Hamilton repeating dispenser and a 50 µl Microlitre syringe (Hamilton Co. Reno, USA). An average of 3 bolls per plant were injected, with each boll receiving a randomly assigned treatments. There was a total of 6 bolls per treatment. Plants were grown to maturity and harvested. Damaged bolls were weighed individually. The number of all undamaged bolls per plant was recorded and weighed as a pooled sample.

Natural boll damage by mirids

In the 2001-02 cotton season, we did experiments at two location in southeast Queensland where mirid numbers were high to establish the effect of mirids on boll size, damage, yield and fibre quality. The first field was located at Byee in the South Burnett. This field was sown with Siokra V16i at 5-6 plants / m. Plots were established with low mirid density where they were controlled with Folimat (100 mL/ha) or Rogor (250 mL/ha), or with high mirid density where they were left uncontrolled. In the high mirid treatment, mirid numbers increased from 1.5 / m at first square (52 DAS) to a peak of 6.25 / m (105 DAS). In the low mirid treatment, numbers were 1.66 and 1.16 / m at 52 and 105 DAS, respectively. GVB was also present at low numbers during late fruiting season, but their effect on boll damage was considered minor. At the end of the season, all open bolls were collected from 20 plants (i.e. 10 plants from each of 2 replicate plots) in each treatment. Bolls were individually scored for their degree of damage of individual locules), mapped and harvested.

The second field was located at the QDPI Sir Joh Bjelke-Petersen Research Station (JBP) in Kingaroy. Siokra V16i was established in this field at 10-12 plants / m and was left unsprayed to allow mirid damage to accumulate. Mirid numbers increased from 1.3 / m at the seedling stage (36 DAS) to a peak of 1.8 / m at boll stage (113 DAS). At JBP, we randomly selected 10 pairs of plants comprising of a high and a low damage plant based on the extent of boll damage determined visually. We assigned a categorical score of 0 to 4 (i.e. 0 = no damage to 4 = severely damaged) to each locule on each boll on each plant. Figure 1 shows the range of damage. Numbers of undamaged and damaged bolls and their weights were recorded for each plant. Seed cotton of all bolls (damaged and undamaged) was combined for ginning and fibre quality test (HVI) to produce a final yield and quality value for each plant.

Figure 1. The five classes of locule damage (the bottom locule of each boll) by mirids. The severity of damage increases from right (no damage, damage score =0) to left (damage score =1, 2, 3 and 4, respectively). This picture also illustrates how common it is to have locules of a single boll having different levels of damage.

Results and Discussion

Artificial damage

In a preliminary study, we found that puncturing the outer boll wall always resulted in a visible scar whether it is produced by a needle or the stylet of a sucking pest (Figure 2 left). Penetrating the inner boll wall always resulted in the formation of warts (Figure 2 right). This is probably a form of defence to seal off the wound against infection.

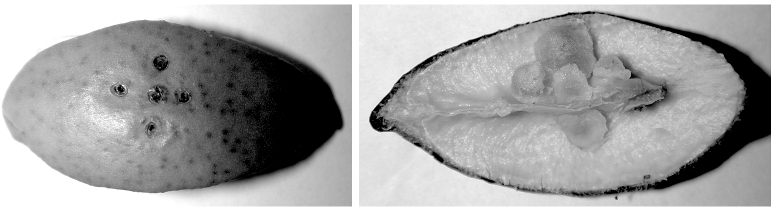


Figure 2. Piercing of the boll wall with a pin led to the development of internal warts.

But the formation of warts does not always mean that there will be lint damage. Our results suggest that if the puncture has pierced a seed, this could cause the seed to die and terminate its fibre development resulting in lint damage. We found light to moderate locule damage simply from puncturing a seed with a pin. But if the puncture misses a seed and only pierce developing lint, no damage results. Since we have no direct means of determining if a pin had penetrated a seed during its entry, these inferences require further validations.

Experiment 1. The injection of pectinase clearly exacerbated the piercing damage resulting in varying degrees of locule damage and lint discolouration (Figure 3). Compared to undamaged bolls, the seed cotton mass of individual damaged bolls was reduced by 38% (Experiment 1, Table 1). Despite the formation of warts, wounding with pectinase injection led to secondary fungal infection and boll rot in 31% of the bolls damaged.

Figure 3. Boll damage caused by injecting a locule with 20 µl of pectinase (1:3 dilution).

Table 1. The effect of simulated and natural mirid damage on seed cotton mass.

	Average mass (g) of seed cotton per boll		% reduction in boll mass
	Undamaged bolls	Damaged bolls	
Experiment 1	4.2	2.6	38
JBP	5.6	4.3	23
Byee (low mirids)	6.3	2.9	54
Byee (high mirids)	6.6	3.5	47

Plants responded to boll damage not by increasing the number of undamaged bolls, but by increasing their size (Table 2). We conclude that cotton plants could partially compensate for boll damage by allocating more resources to healthy bolls.

	Control plants	Damaged plants
Number of undamaged bolls / plant	21.7±5.5	15.6±4.1
Mass of undamaged bolls (seed cotton g / boll)	4.2±0.9	4.8±0.8

Table 2. Differences in boll number and seed cotton weight between control plants and those with bolls damaged by pectinase injection. Values are mean ± standard deviation.

Experiment 2. Based on the size of mirids, in this experiment we reduced the volume of pectinase from about 20 µl (Experiment 1) to 1 and 3 µl to mimic more closely the amount of saliva mirids might inject. We also tested a lower pectinase concentration of 1: 10 dilution in addition to the 1:4. The results indicate that our lowest dose of 1 µl of pectinase at 1:10 dilution was still sufficient to cause heavy damage to locules. Table 3 shows an average reduction in boll mass from 41% (1 µl and high dose) to 63% (3 µl and high dose) from the undamaged control. Injection of water alone produced a significant 25% reduction in seed cotton per boll (Table 2). These results support the earlier tests that piercing the boll without pectinase can also cause locule damage but adding pectinase greatly exacerbates the damage. While we do not know how closely our treatments mimicked the actual volume and enzyme content of mirid saliva, it is apparent that the resultant damage was similar to that caused by actual mirid feeding as described below.

Table 3. The effect of varying the dosage of pectinase per locule on seed cotton mass. The values in brackets indicate the % reduction in mass of treatment bolls compared to undamaged bolls.

Treatment	Average mass (g) of seed cotton per boll	
	1 µl of treatment / lock	3 µl of treatment / lock
High pectinase dose (1:4)	2.69 (41%)	1.74 (62%)
Low pectinase dose (1:10)	2.18 (52%)	1.85 (59%)
Water (Control)	3.42 (25%)	3.30 (27%)
Undamaged bolls	4.53	

Natural mirid damage

The percentage of bolls damaged by mirids per plant ranged from 10% (Byee, sprayed to reduce mirid numbers) to 54% (Byee, unsprayed); the mean for JBP was 43%. In all cases, damaged bolls were substantially lower in boll mass (Table 1) than undamaged bolls. For Byee, the high mirid plants returned a yield of 6.4 bales/ha compared to the 13.4 bales/ha for the low mirid plants. It is worth noting that the reduction in average boll mass caused by actual mirids (at 47-54% in Byee, Table 1) was similar to that induced by artificial damage (at 41-62% with pectinase, Table 3).

Natural mirid damage (based on external scars) could occur anywhere on the boll wall but tended to concentrate along the suture region which corresponds to the centre of a locule (i.e. a cracking boll splits down the middle of locules to maximise lint fluffing and seed dispersal). Figure 4 illustrates the typical result of moderate feeding damage. The internal damage of the same boll is localised and is probably the result of mirid damage killing a single seed. Note that the seed adjacent to the wounds has disintegrated while other seeds in the locule remained unaffected.

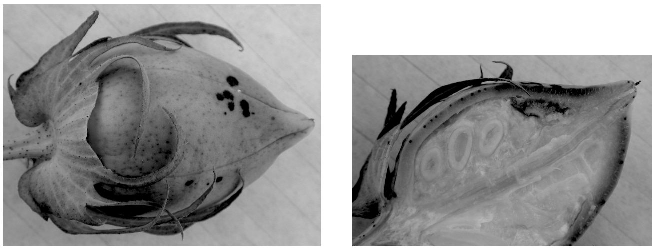


Figure 4. Natural damage caused by mirids showing for the same boll the external scars and the localised internal damage.

There are two major differences in boll damage caused by the chewing action of Helicoverpa and by the sucking action of mirids. Firstly, while very young bolls (<7 days old) are easily shed following any damage, older bolls attacked by Helicoverpa are more likely to be shed soon after damage while those fed by the latter are more likely to remain on the plant until maturity. Secondly, when bolls are fed upon by mirids, not all locules are damaged to the same degree while Helicoverpa larvae tend to cause significant damage to all locules. Mirid damaged bolls may therefore have some locules that still produce harvestable lint.

We examined the extent of locule damage in the two locations and found an interesting, but perhaps not unexpected, trend. We found that indeed a range of locule damage existed (Figure 6). Where mirid damage was high (i.e. JBP and Byee high mirids), more bolls showed ¾ or all locules damaged than when mirid numbers were low. But even under high damage, between 60 and 75% of the bolls had at least one undamaged locule. When mirid numbers were low (Byee low mirids), damage to bolls was limited most to 1 or 2 locules. This suggests that individual mirids tended to feed in one region causing damage to single locules. Bolls with multiple locule damage probably experienced repeated visitation by several mirids. Field confirmation of these inferences is required.

In addition to the distribution of undamaged and damaged locules in damaged bolls, we were also interested in the severity of damage between locules, i.e. were they all damaged to the same extent? Using the scoring system shown in Figure 1, we obtained the results shown in Table 3. When damage by mirids affected more than one locule in a boll, in 70% of the cases the level of damage among locules was different. And there is remarkable consistency in this observation regardless of location or mirid numbers. While the cause of this finding is not clear at this point, it will be useful in future prediction of boll damage by sucking pests.

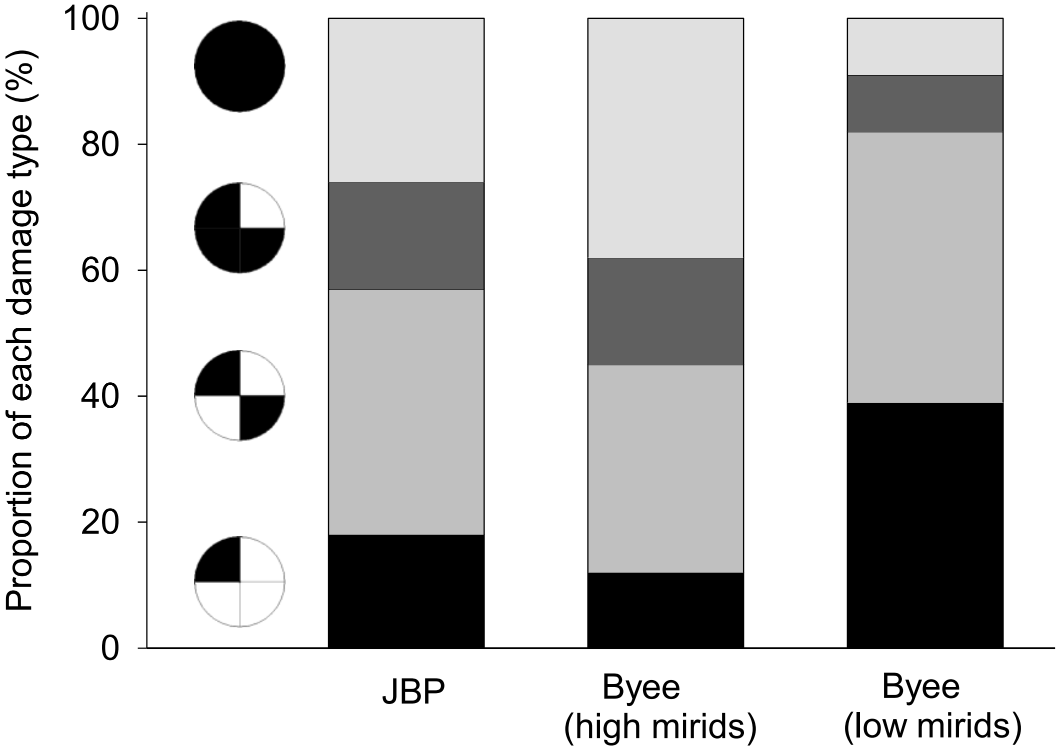


Figure 6. Proportion of locule damage types in damaged bolls at the two Queensland sites that experienced natural mirid infestations. The solid wedges of the pies represent the number of damaged locules in a boll, the four corresponding bar segments are their proportions in all damaged bolls.

Table 3. Data showing the proportion of differential damage among locules in a boll from the two Queensland locations with natural mirid infestations.

	All locules similarly damaged (%)	Locules differently damaged (%)
JBP	27	73
Byee (high mirids)	28	72
Byee (low mirids)	30	70

The relationship between seed cotton mass per plant and total boll number in Byee (Figure 7) showed a reduced seed cotton yield per boll in damaged plants (slopes are significant different at $P<0.05$). Figure 7 also showed an overall reduction in boll number per plant for the high mirid damage treatment which suggests that there was no evidence of compensation for boll damage by increasing boll production. There was, however, a weak but significant positive relationship between the mean seed cotton mass of undamaged bolls and % damaged bolls ($R^2=0.12$, $P=0.015$). This indicates that the reduced resource demand of damaged bolls was able to be distributed to the development of larger undamaged bolls. These results are consistent with those of the artificial damage of Experiment 1. We conclude that there is some potential for compensation in increasing the size of undamaged bolls but not the number of bolls. Whether the inability to increase boll production is related to the fact that damage occurred too late in the season remains to be investigated.

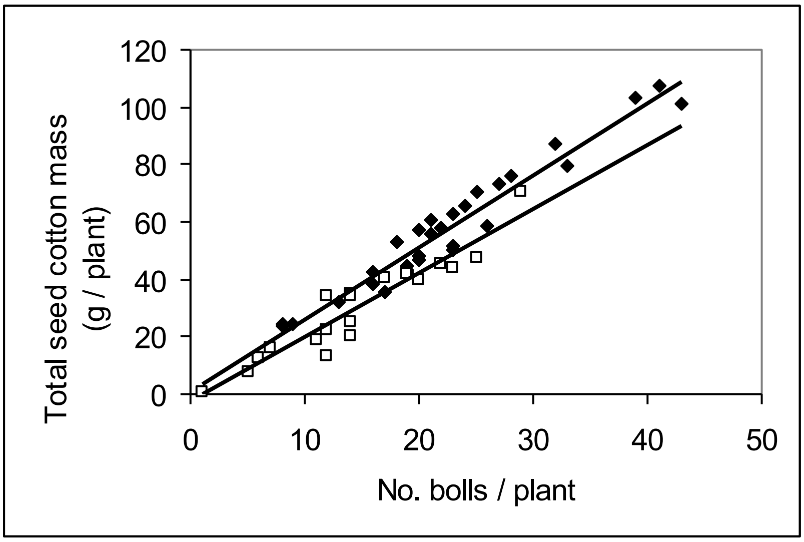


Figure 7. The seed cotton mass to boll number relationship in cotton grown in Byee after low (diamonds) and high (squares) levels of natural boll damage by mirids. The regression lines are for low (upper) and high (lower) levels of damage.

Gin turnout and fibre quality

Another issue of concern with the retention of damaged bolls is the contribution of damaged lint to the final yield. Discoloured and immature lint remaining on damaged bolls could be picked and contaminate clean fibre. Figure 8 shows a clear trend of lower gin turnout with higher damage which indicates that damaged locules have been largely excluded in the ginning process, i.e. they did not gin properly and end up in trash. This interpretation is supported by fibre quality measurements (Table 4). All measures of fibre quality were similar between plants with high and low mirids, except for a modest decline in short fibre index in the high mirid treatment. These findings indicate that mirid damaged locks which often form a “tight lock” where lint does not expand (see Figure 1) has several implications. One, damaged locules may not be picked at all which equates with a yield loss; and / or two, if they are picked, “tight locks” do not go through the gin and are do not contaminate lint.

Table 4. Fibre quality parameters showed little difference between plants with heavy and light boll damage from mirids. * represents values significant (P<0.05) different between treatments.

	Low mirids	High mirids
Staple length (inches)	1.17	1.17
Uniformity index	85.1	85.1
Short fibre index	3.3*	3.9
Fibre strength	31.7	30.4
Elongation	4.0	4.1
Micronaire	4.3	4.7

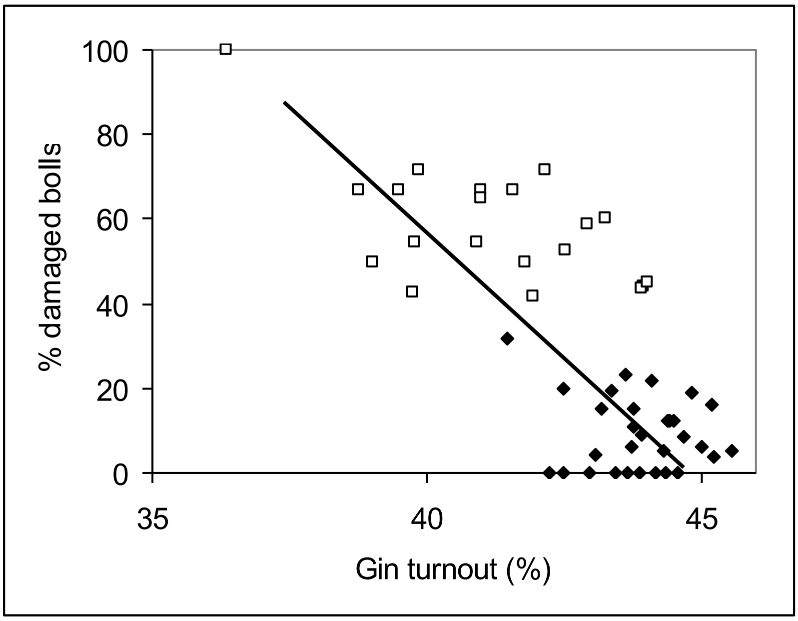


Figure 8. Using data collected from Byee, we show that the higher the damage sustained by a plant, the lower the gin turnout. Symbols: diamonds are low mirids and squares are high mirids.

Conclusions and future directions

This study shows that sucking pests have the potential to affect yield dramatically. For instance, in our experiment a substantial mirid pressure of 1.5 – 6.25 mirids / m over a 50-day period resulted in a yield loss of 52%. Because mirid damage usually does not affect whole bolls, plants tended to retain partially damaged bolls without responding by increased fruit production indicating limited compensation due to this possible mechanism. There is, however, some evidence that damaged plants are able to direct some resources from damaged to undamaged bolls, resulting in increased size of the undamaged bolls as a form of compensation. Our results show that although yield may decline with increasing mirid damage, there may not be an associated degrading of fibre quality since most of the damaged locules are excluded from the final lint. One encouraging result from Byee shows that high yields are still possible at 10% boll damage (or an average of 1.4 mirids / m for 50 days at 55-105 days after sowing). Our next task is to explore the tolerance limits of mirid damage on bolls. This can now be achieved using artificial damage which closely mimics the effect of sucking pests and by further experiments with real mirid damage.

Since there is evidence indicating that external scars do not strongly associate with locule damage, another challenge ahead is to develop techniques where internal damage can be quantified quickly and accurately, preferably through non-destructive means. In this study we have used mirids as a model species to represent a range of sucking pests including green vegetable bug, red-banded shield bug and harlequin bugs. There is a need to define the feeding behaviour of different sucking pests on cotton bolls and some work is underway (see paper by Khan and Bauer in this proceedings).

If we find that cotton has limited ability to recover from boll damage by sucking pests, alternative IPM strategies will become more critical. Controls such as HPR, predators and parasitoids, and softer chemistry should all be earmarked for future research.

Acknowledgements

This study was partly supported by a CRDC grant to TL (CSP124C) and to MK (DAQ 110C). Peter Enkelmann of Byee, Queensland kindly provided the field with spray and unsprayed plots for us to sample plants with natural mirid infestations .We thank Kellie Baguley for her excellent technical assistance. Fibre quality (HVI) was determined at CSIRO Narrabri by Chris Tyson and Kellie Cooper.

References

Khan, M. and Bauer, R. (2001). Comparing damage from green mirid and green vegetable bug. The Australian Cottongrower. 22(4): 16 – 18

Part 2 – Defining thresholds for mirid during the fruiting period

Partly based on the final report for a Cotton CRC Summer Scholarship Project
Conducted by Sara Winston-Smith (University of Sydney)
Supervised by T Lei and L Wilson

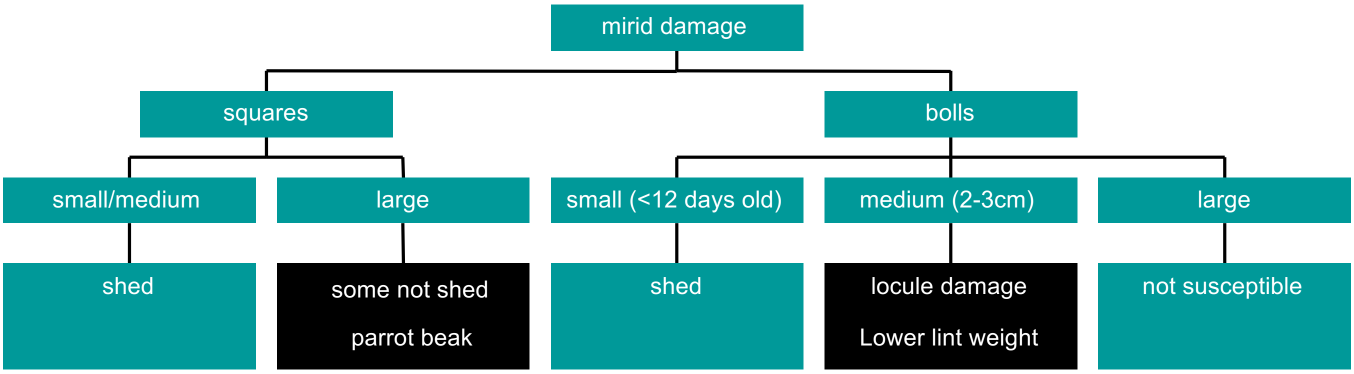
Introduction

The aim of this study was addressed the issue of increasing levels of boll damage by green mirids in transgenic cotton in Australia. There is an expectation that with the increasing planting of INGARD and, in the near future, Bollgard II, fruit damage by mirids will be significant. Since at present there is little information available on the tolerance of cotton to fruit damage by green mirids, there may be a tendency to over-spray to control them. Because mirid damage is very different from that caused by *Helicoverpa* larvae, we need to produce reliable data on damage and recovery for this pest. With data produced in this study, we can begin to develop sound thresholds for mirids that growers can use to make informed decisions on managing these pests.

Methods and Materials

Various field and cage experiments were carried out to explore and evaluate new methodologies to address the mirid question. Since damage to medium sized bolls is most likely to contribute to yield loss (Fig. 1), we conducted a field trial assessing the yield effect of boll damage at low, medium and high levels at early, mid- and late fruiting stages (corresponding to 2, 5 and 8 weeks after first flower respectively). We employed a method of artificial damage where bolls were injected with pectinase enzymes (Fig. 2). Pectinases are constituents of the digestive enzymes in the mirid saliva injected into plant tissue during feeding. Three cotton cultivars were tested in this manner: Sicala V-3i and Siokra V-17i, and Sicot 71. The three levels of boll damage were: 5 (low), 20 (moderate) and 50 (high) bolls per m. Each artificially damaged boll received 1.0 µl pectinase enzyme solution injected into a single lock per boll. Treatment plants were harvested at the end of the season where boll number, lint yield and maturity were recorded.

Figure 1. A summary of the effects of green mirids feeding on fruit of various types. The black boxes indicate the areas related to this project. Damage to medium size bolls was the focus of this study and deformation due to feeding on large squares was also examined in a supplemental experiment.



Three cotton cultivars are used in the artificial damage trial: Sicala V3i and Siokra V16i, and Sicot 71. Sicot 71 is a full season, determinant cultivar with short fruiting branches and is known to be attractive to insects). Seeds were sown on 10 October, 2002. Each plot was 2m by 3 row. Plant density was 10 – 12 plants m^{-1}. Standard management regime used for N application, weed and pest control and irrigation scheduling. There are 9 treatments replicated 4 times in a complete randomised block design. The treatments are given in the table below. The three levels of boll damage were: 5 bolls per m (low) and 20 bolls per m (high). Bolls to be damaged will be randomly chosen but spread roughly evenly across the 2 m row. Damage was imposed on one 2m row only.

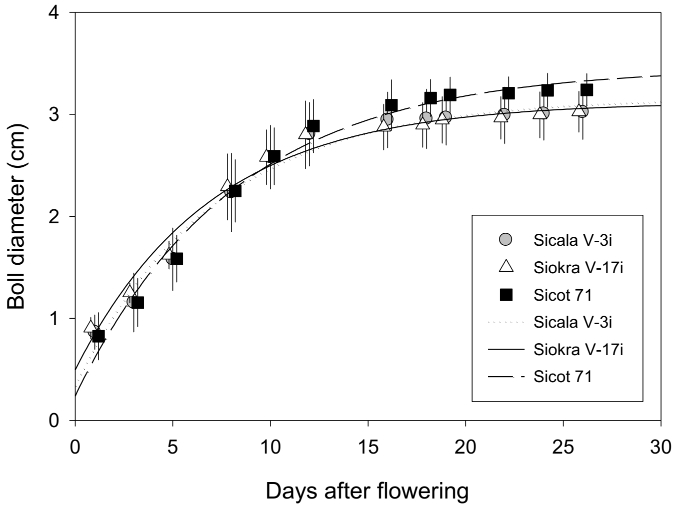


Figure 2. Patterns of boll development in three cotton cultivars. Based on these curves, by selecting bolls at 2.5 cm diameter for inject, we targeted bolls of ca. 10 days old which are most vulnerable to sustain damage and retain that damage to maturity.

Each boll to be damaged received 1.0 µl pectinase enzyme solution injected into one locule. The bolls selected for damage should be 8-12 days old. We have found that this corresponds to a boll diameter of 2-3 (average 2.5) cm. This is shown in Fig. 2 with boll development in three cotton cultivars grown in Myall Vale measured during peak fruiting (i.e . mid-Jan to early Feb) This calibration curve was used to determine the appropriate age based on size for simulated mirid damage. Bolls of Sicot 71 reached a larger final size than the other two cultivars. The solution is prepared by mixing one part pectinase (Sigma-Aldrich P4716 Pectinase from *Aspergillus niger*, solution in 40% glycerol) and 10 parts water. Since this enzyme may degrade in high temperature, the mixture should be freshly prepared on the day of the application and kept in a cooler with ice while in the field. Early damage will take place 2 weeks after first flower (to ensure sufficient number of bolls of the appropriate age), mid and late damage treatments will occur at 3 and 6 weeks following the early damage.

Treatment	No. of bolls damaged per metre		
Control	0 [C]		
Early damage	5 [EL]	20 [EM]	
Mid damage	5 [ML]	20 [MM]	
Late damage	5 [LL]	20 [LM]	50 [LH]

Table 1. Experimental design of the three timings of damage and three intensity levels.

There was a 10-m buffer to head ditch or tail drain to avoid edge effects on maturity. There were two buffer rows between plots and 2-3 m between plots down the row.

At the time of each treatment, collect 10 plants (randomly selected) of each cultivar and measure the following for each plant:

- plant height
- node age
- lateral branch number
- fruiting branch number
- fruit count (no of small, medium and large squares, flowers and small, medium and large bolls)
- leaf area
- dry matter of shoot, leaves, fruit (2 lots – combining all squares in one and all flowers and bolls in the other), and tap root

At harvest, the maturity date was estimated by sequential picks. The entire 2m row was picked. At each pick, note the number of bolls with tightlock (fail to fluff out) and the extent of staining on seedcotton was recorded. Seedcotton was ginned, weighed and fibre quality determined.

Sara also conducted a supplemental experiment on the effect of mirid damage to large squares. It is known that large squares fed upon by green mirids are not shed (Fig. 1). Instead, they develop into flowers with damaged pollen sacs which could lead to deformed bolls with a “parrot beak” appearance (Fig. 3, top). The effect of this type of mirid damage is quite different from that resulting from direct boll feeding (i.e. no wounds on the boll wall and no discoloration of lint). Damaged squares were tagged and assessed for pollen damage and boll deformation

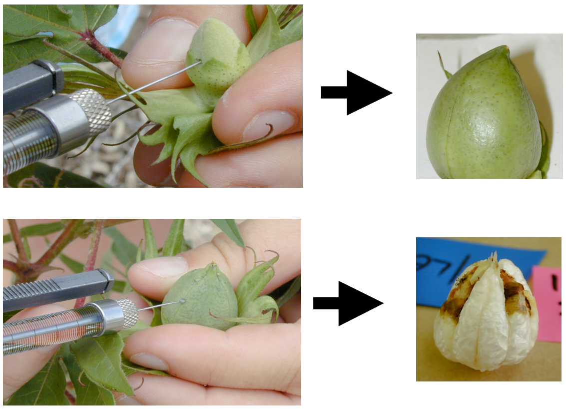


Figure 3. A novel technique was developed to simulate mirid damage. Here Sara demonstrated the injection of pectinase into squares (above) and bolls (below) and the outcome of these treatments in the form of parrot beak bolls and discoloured locules.

Results and Discussion

The outcomes of the boll damage experiment are presented in Figure 3. We found that damage can lead to a reduction in boll numbers and a loss of yield but not a delay in maturity. While treatments produced various degrees of yield reduction, there were no clear trends associated with either the level or the timing of damage. There was, however, a significant overall difference among the three cultivars in all three parameters. Sicala V-3i yielded higher than Sicot 71 and Siokra V-17i. Maturity was similar between Siokra V-17i and Sicala V-3, both were significantly earlier than Sicot 71. While these results are inconclusive, they are important in providing basic data from which more targeted future experiments can be designed and implemented.

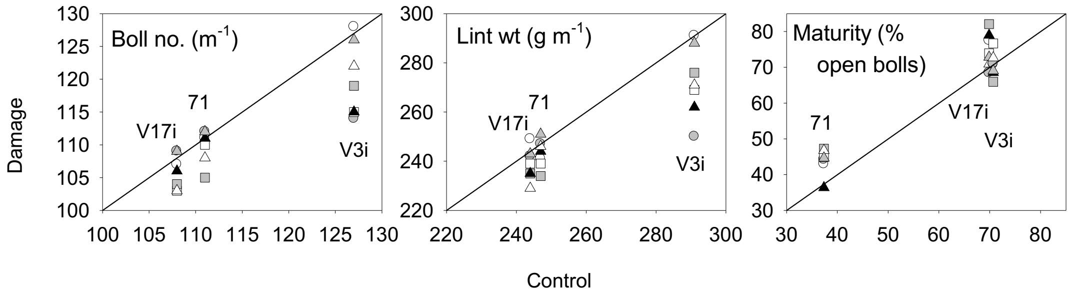


Figure 3. Comparisons of yield and maturity between control and treatments simulating various types of mirid damage in three cotton cultivars (V17i=Siokra V-17i, 71=Sicot 71, and V3i=Sicala V-3i). Damage at low (5), medium (20) and high (50 bolls m^{-1}) levels is represented respectively by open, grey and closed shading, the timing of damage at 2, 5 and 8 wks after first flower is represented by circles, squares and triangles respectively.

In a comparable experiment conducted by Andrew Ward in Katherine NT in 2002, he found no effect of simulated mirid damage on yield (Table 2). It is possible that climatic differences (the NT trial was conducted during the tropical dry winter months) contributed to the variable recovery patterns. The NT results have also produced an interesting outcome suggesting that compensation may be occurring on an individual plant basis. Fig. 4 shows the average lint weight per boll for the treatments imposed (Table 2). When bolls were lightly damaged, its lint wt was similar to the control (close to 1:1). With increasing damage, the lint wt of damaged bolls declined while that of the undamaged bolls increase in wt, forming a strong inverse 1:1 line. This suggests that for every unit of loss in mass in damaged bolls, it was gained by producing larger undamaged bolls. This means of compensation (through re-allocation of resources) is an important aspect of future investigation.

	Timing of damage			
Damage level	Early	Mid	Late	Control
Low (5/m)	167.6	144.6	148.8	154.7
High (50/m)	169.1	148.2	160.9	

Table 2. Yield outcomes in lint wt (g m^{-1}) for the mirid damage trial conducted in Katherine NT in 2002. No significant differences were detected between damage levels and among timing of damage.

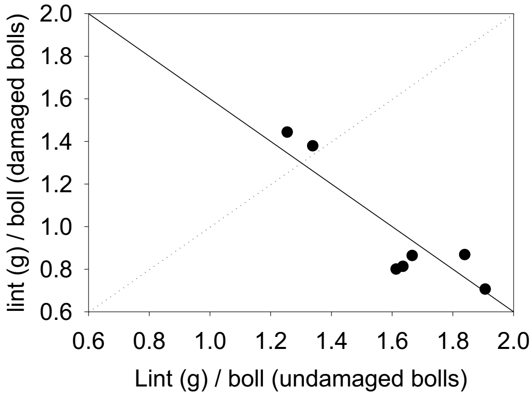


Figure 4. Average mass of lint per boll in damaged and undamaged bolls of various damage treatments (not identified) from a trial conducted in Katherine NT. The dotted line is the 1:1 and the solid line the inverse of the 1:1 line.

In terms of mirid damage to large squares, we hypothesised that feeding (and the effect of digestive enzymes in the mirid saliva) on large squares degrades either the pistil column or the pollen sacs resulting in incomplete fertilisation of seed in discrete locules. This will lead to the development of parrot beaked bolls as normal locules grow around the unfertilised, empty locule. In this experiment, we were able to reproduce the parrot beak (PB) development in 12% to 37% of the “candlewick” squares injected with pectinase. The difference was attributable to the cultivar where Siokra V-16i and Sicala V-3i were low in PB (12-14%) while Sicot 71 produced 37% PB bolls. Further research on genotype differences in susceptibility to mirid damage is warranted. The majority of the remainder of squares that were injected were shed with a few developing normally. At flowering, injected squares showed no signs of discolouration in the pollen sacs. This was unexpected and suggests that the damage was largely occurring in the staminal column or in the ovaries.

In conclusion, the summer scholarship project carried out by Sara Winston-Smith and the trial conducted by Andrew Ward in NT have contributed significantly to our understanding of mirid damage. They will allow us to refine the experimental procedures to simulate mirid damage to cotton fruit. Ultimately, the knowledge acquired here will facilitate the determination of economic thresholds of mirid damage.

Does cotton's capacity to recover from pest damage decline with high yield potential?

Tom Lei, Kellie Baguley, Deon Cameron and Lewis Wilson
CSIRO Cotton Research Unit, Narrabri NSW 2390
In collaboration with managers of 5 commercial farms

Background and Aim

Past research on compensation in cotton has suggested the possibility that at very high yield potentials, even a small amount of damage to fruit will result in a yield loss. The pattern of declining compensation with higher yields was first observed by Dr Brian Hearn and his colleagues in the 1980s as shown in Figure 1. However, this trend has not been tested with the more recently developed higher yielding varieties and management practices. If we find that such a limitation exists, then it is critical to account for it in future development of IPM strategies. If not, then we can use compensation to help reduce insecticide use regardless of the crop's yield potential. We also need to refine the cotton simulation model (OZCOT) in order to make better yield predictions on recovery following pest damage in high yielding cotton crops.

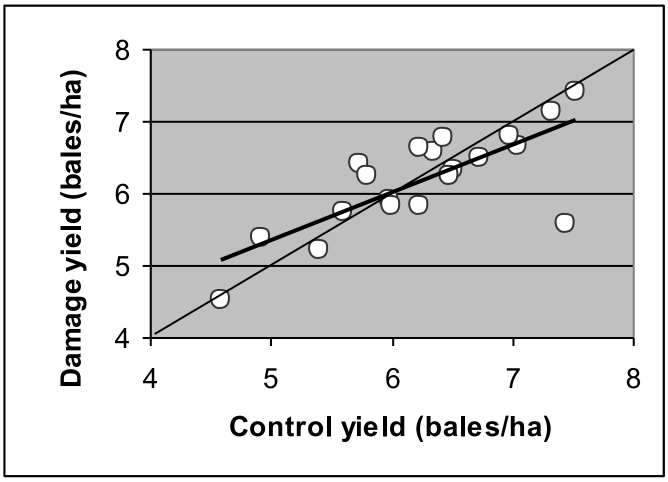


Figure 1. Declining yield recovery (damage yield) with increasing yield potential (control yield). The heavy line represents the regression line for all data points and the light 1:1 line. The crossing over point at about 6 bales ha^{-1} suggests that plants are unable to fully compensate from damage at higher yield potential. Data taken from Brook, Hearn and Kelly (1992).

Methods and Materials

We conducted a field trial replicated at five commercial farms in the Upper and Lower Namoi Valley in 2002-03. The five participating farms were selected because of their track record of producing high yields. The farms, location and the cultivar planted in as follows:

1. "Riverstone" in Baan Baa (Sicot 70)
2. "Merinda" on Spring Plains Rd (Sicot 71)
3. "Waverley" 14 km W of Merah North (Sicot 71)
4. "Greenbah" on Spring Plains Rd (Sicot 71)
5. "Dorren" on Doreen Lane (Sicot 189)

At each farm, we established experimental plots in a field where high yield was expected. Sowing time was late September to early October for all farms. The plots contained three treatments each replicated five times laid out in a complete random block design as shown in Fig. 2. Each plot was 2 metres long by 3 rows wide. The plots were separated with at least 2 m of buffer and two rows between plots.

<table>
<tr><td colspan="3">Head ditch</td></tr>
<tr><td>Control</td><td>Early damage</td><td>Early + Mid damage</td></tr>
<tr><td>Early damage</td><td>Control</td><td>Early + Mid damage</td></tr>
<tr><td>Early + Mid damage</td><td>Early damage</td><td>Control</td></tr>
<tr><td>Early + Mid damage</td><td>Control</td><td>Early damage</td></tr>
<tr><td>Control</td><td>Early + Mid damage</td><td>Early damage</td></tr>
<tr><td colspan="3">Tail drain</td></tr>
</table>

Figure 2. A typical plot layout used at the five farms.

The three treatments applied were:

1) Early damage- damage once at 3 wks after 1st flower
2) Early + Mid damage- damage twice at3 wks and 6 wks after 1st flower
3) Control- no damage

The Early damage was imposed ca. first week of January and the Mid damage last week of January. The two damage treatments involved the removal of fruit which simulates the damage caused by 3 *Helicoverpa* larvae/m once (Early damage treatment) or twice (Early + Mid damage treatment). The total number of fruit removed was about 20 per metre and is consisted of the following fruit sizes for the two damage times:

Early damage - medium squares (ms, 0.5 – 1 cm) =4, large squares (ls, > 1 cm) = 5, flowers (fl) =6; small bolls (sb, < 2.5 cm) = 4
Mid damage - ms =3, ls =5, fl =4, sb =2, medium bolls (mb, > 2.5 cm) = 2

The reason for choosing 3 larvae/m is that evidence suggests that for crops at lower yield potentials, this level of damage will result in no yield loss (i.e. full compensation), even when two damage events were imposed. So, if the assumption that higher yields is associated with reduced recovery, we would expect a proportional decrease in yield in damaged crops with increasing yield of undamaged plants. We would also expect a proportional reduction in yield at two damage events (Early + Mid damage) than at one damage event. The removal of fruit was applied on the 2 m x 3 rows area by haphazardly removing for each metre the assigned number of fruit of different sizes. The fields were managed by the grower as per normal until open bolls.

During harvest, we conducted maturity picks to quantify the amount of delay in maturity, and weighed the total seed cotton yield.

Results and Discussion

Unlike the earlier findings of Brook, Hearn and Kelly (Fig. 1), we found no evidence of reduction in yield following either the early or the early + mid damage treatments (Fig. 3). Yield from all farms fell along the 1:1 line which indicates full yield recovery from the two damage treatments within a range of 7 to 12 bales per hectare in undamaged yield. There was no significant difference in the yield of crops damaged once versus twice. The difference in yield among farms, however, was significantly different (*P*<0.001). The ranking of the farms is as seen in Fig. 1 with Merinda topping the group and Doreen the lowest. Doreen sustained some hail damage on 3/12/02 (about 60 DAS) which affected ca. 30% of plants. Due to the size (6-8 cm diameter) and density (per ground area) of the hail, plants (at 10-11 nodes) were either completely destroyed or little affected. The resulting lower plant density contributed to the yield reduction. The pattern of open bolls per metre at harvest among treatments resembles that of lint yield (Table 1).

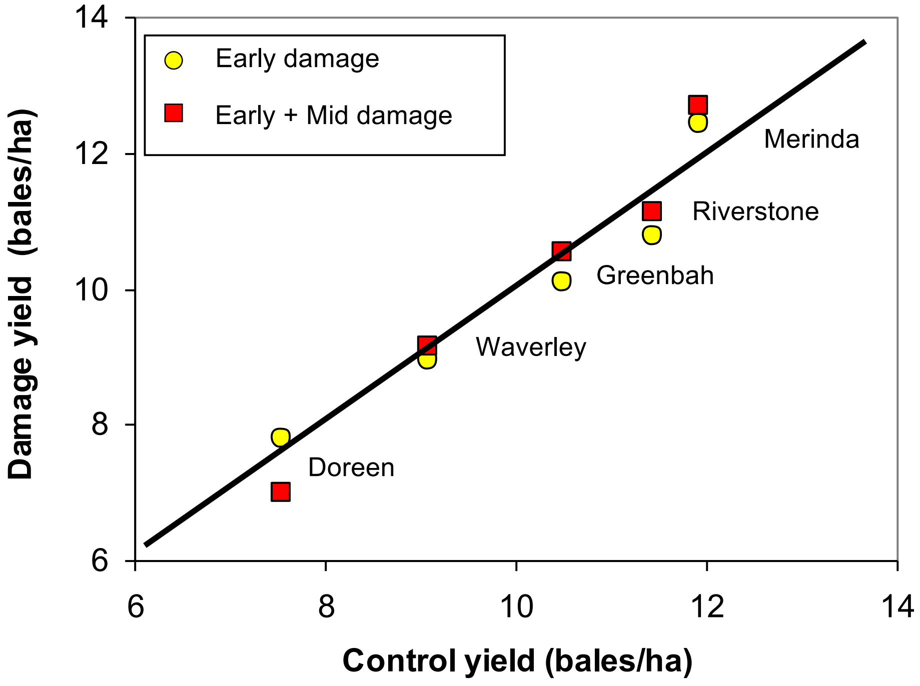


Figure 3. Comparison of control (undamaged) yield against that of the two damage treatments for the five farms. The solid line is the 1:1 line.

There was a 17-day spread in crop maturity (at 60% open bolls; Table 1) between sites. It was different among farms (*P*<0.001, with data available from only four farms) and among treatments (*P*=0.001). The order in increasing date of maturity is Greenbah > Merinda > Waverley > Riverstone. The latest maturity at Riverstone might be associated with the Upper Namoi compared to other farms located in the

Lower Namoi. Among treatments, control is significantly earlier compared with the two damage treatments (no difference between E and EM). Even though the delay in maturity was significant for damage treatments, the delay was a modest 1 to 3 days.

Table 1. Yield and maturity outcomes from simulated *Helicoverpa* damage imposed at five commercial farms. ANOVA table shows the significance level (*P*) of the main effects and their interaction.

Farm	Average boll no.(/m)			Average SC wt (g/m)			60% open bolls (DAS)		
	C	E	EM	C	E	EM	C	E	EM
Merinda	126.9	132.7	132.6	676.5	705.4	720.0	157.4	160.4	158.8
Riverstone	120.8	114.7	115.9	649.2	611.8	631.9	168.2	169.8	169.6
Waverley	96.1	94.4	95.3	514.6	507.9	519.0	164.0	165.6	165.8
Greenbah	108.1	102.5	108.4	595.1	573.1	598.3	153.2	154.4	156.8
Doreen	86.0	86.9	79.8	427.5	442.6	397.7	-	-	-
ANOVA									
Farm	<0.001			<0.001			<0.001		
Treatment	NS			NS			0.001		
Farm x trt	NS			NS			NS		

Conclusion

An examination of the compensation potential in cotton following simulated *Helicoverpa* damage found no evidence of a decline in high yielding crops. The five farms produced a range of yield potentials from 7 to 12 bales per hectare but all recovered completely in yield from either one or two fruit damage events simulating that caused by 3 small larvae per metre. A modest but significant delay (1 to 3 days) in crop maturity of damaged plants should have no real impact on the picking of the crops. We conclude from these findings that recovery from fruit damage remains strong even for high yielding crops. Perhaps improvements in cotton genotypes and management practices in recent years have conferred greater ability to recovery from fruit loss in recent years compared to 15 years ago (Brook, Hearn and Kelly 1992) when the initial concern was raised.

Acknowledgments

We are grateful for the participation and cooperation of the five farms in this trial. The farms and their managers were: Steve Brown at“Riverstone”, Dougall Burke at “Dorren”, Andrew Grest at “Waverley”, Richard Jackman at “Greenbah” and Mike Logan at “Merinda”.

References

Brook KD, Hearn AB, Kelly CF. 1992. Response of cotton, *Gossypium hirsutum* L., to damage by insect pests in Australia: manual simulation of damage. Journal of Economic Entomology 85(4): 1368-1377.

Additions and enhancements to OZCOT: simulating pest damage and recovery

Tom Lei and Akio Takenaka (National Institute for Environmental Studies, Tsukuba Japan)

Summary

The new code linked to the core OZCOT allows the simulation of damage occurring during the vegetative stage (pre-squaring) and the fruiting stage of cotton growth. Model implementation of pre-squaring damage includes **thrips damage** (suppression of leaf area expansion and subsequent recovery), and **tipping out** (can be caused by *Helicoverpa*, tipworms and mirids). Recovery from thrips damage is largely restricted to the pre-squaring period while that from tip out extends from pre-squaring to the end of the growing season. Also implemented in the new code is **fruit loss** simulating *Helicoverpa* larvae feeding on squares, flowers and bolls. Contrary to thrips and tip out damage, there is no explicit enhancement in recovery from fruit loss. Instead, the crop is allowed to increase fruit production based on existing code which detects an improvement in the status of the plant's carbon balance.

Modelling pre-squaring tip damage

Functionality achieved

- accounting for age-dependent increases in branching following tip damage
- branching associated enhancement in leaf area development prior to first square
- the improvement in light interception resulting from the modified canopy geometry following tip out is not explicitly modelled but is captured in the branching factor and applied to the leaf area and fruit production enhancement factors
- branching associated enhancement in square initiation and the corresponding leaf area increase
- delay in branch emergence and in reaching first square implemented
- the enhancements may be in effect through to the end of the season
- input file includes day of tip damage, maximum branching factor, leaf area enhancement factor, site production enhancement factor, and delay in lateral bud emergence and in timing of first square

Thrips damage causing early season leaf area reduction

Functionality achieved

- explicitly defined the duration of thrips infestation and the start time of infestation in terms of plant development stage
- use input value for the amount of daily suppression of leaf area expansion due to infestation
- simulating an enhanced leaf area production (i.e., recovery) due to higher performance of leaves on the thrips affected plants
- scale the enhancement to the amount of leaf area reduction up to a maximum
- as leaf area recovers (checked against an undamaged reference plant), the amount of enhancement declines

- enhancement ceases on day of first square
- delay in plant development and time of first square due to thrips is implemented

Implementation of fruit lost to *Helicoverpa* feeding

Functionality achieved

- new subroutine to execute the removal of specified numbers of fruit of various categories on specified date(s)
- on removal day, the fraction of fruit to be removed to total fruit number in each category is determined
- distributing % fruit removal equally among all cohorts within a fruiting category
- reduced the remaining fruit number in each cohort for continued development
- in a cohort, marked fruit for shedding after fruit loss is not retained to substitute for lost fruit
- allowed a lower boll load (demand) and a larger size of the reserve in carbon carrying capacity (supply) following fruit removal to increase fruit number (fewer marked for shedding) - compensation in the form of greater fruit retention after damage

Future elaborations based on the new damage and recovery code

1. Explore the interactions among tip out, thrips damage and fruit loss on cotton yield. Identify situations such as combining tip out with fruit damage which will result in an yield gain over the undamaged control. Use simulation and field data to argue that an yield benefit may exist when a certain level of fruit loss is preceded by tip out.
2. Detail the model process where fruit production, retention and maturation are driven by the balance between resource supply and demand on a daily cycle. Demonstrate how varying climatic conditions could dramatically alter the balance and the yield outcome by changing the supply function; and how fruit removal could have a similar effect by changing the demand function.
3. Explore the degree of yield recovery as a function of climatic variations. For example, what is the effect on recovery of a warm mid-season followed by hot late season (northern Australia) versus a hot mid-season followed by a warm late season?
4. Explore the degree of yield recovery as a function of variety. For example, what is the effect of different variety-specific leaf expansion rate on compensation?
5. Is there a difference in branching factor , leaf area development and fruit production enhancements between normal leaf and okra leaf varieties? Because the canopy of okra leaf varieties has inherently greater light penetration (due to their more dissected leaves), would the enhancement from branching be smaller if their gain in light interception is smaller compared with normal leaf varieties?

Industry implications

The current advances in enabling OZCOT to simulate damage caused by different pests and to predict yield will become an integral part of the decision support system in the management of Australian cotton crops. The new functionality of OZCOT in predicting compensation will be used to evaluate the justification for spray applications at a given pest number. To convince growers to withhold pesticide application based on a no-yield-loss prediction by the model is considered to be the major achievement of the current collaboration. Further, through iterative simulations, situations where damage may result in an yield gain will be established, validated and the information disseminated to growers.

Acknowledgment
Funding for TL to travel to Tsukuba Japan was provided by Cotton Research and Development Corporation Australia

Appendix

Implementing pest damage and recovery: coding details

Routine	code for new functionality implemented (line number)
CINPUT.FOR	tip out (181-196), thrips (197-213), fruit removal (214-247)
EMERG.FOR	tip out (66-68)
FRUGEN.FOR	tip out (101-107)
FRUIT.FOR	fruit removal (214)
INIT.FOR	tip out (18, 251-260), thrips (18, 261-278), fruit removal (19)
ISTSQ.FOR	tip out (33-38), thrips (39-44)
LAIGEN.FOR	tip out and thrips (23, 40-89, 91-92)
PLTGRW.FOR	tip out (81-105)
FR_REMOV.FOR	New routine developed by Takenaka and Lei
OZCOT.INC	tip out (52, 57, 70-73), thrips (52, 57, 74-77), fruit removal (53, 57, 78-79)

New input files

TIPOUT.INP
THRIP.INP
REMOVE.INP

List of new global variables

IDAY_TIPOUT	! Day of tip damage after sowing,
TIPOUT_DELAY	! Delay of 1st square due to tipout in Deg Day
BRANCH_FCT_MAX	! Maximum branching factor.
FRUGEN_FOR_BR	! enhancement of site production due to branching
RGRLF_FOR_BR	! enhancement of leaf production due to branching before 1st square
IDAY_THRIP_START	! First day of reduced LA prodn due to thrips
IDAY_THRIP_END	! Last day of reduced LA prodn due to thrips -1 for no thrips damage
RGR_REDC_THRIP	! Reduction of LA production due to thrips; 0 for no reduction
THRIP_DELAY	! Delay (in DD) of 1st square due to thrips

COMPENSAT_MAX	! Max rate of growth compensation after thrips; 0 for no compensation
COMPENSAT_FCT	! LA reduction-dependent growth compensation ! compensation=COMPENSAT_FCT * relative LA reduction; ! 0 for no compensation
ALAI_REF	! ALAI of a plant not damaged by thrips calculated only before 1st square

NDAY_FR_REMOVE	!Day (after sowing) of fruit removal
FR_REMOVE (x1, x2)	!Number of fruit removed on IDAY (x1) for each of the 8 fruit categories (x2)

An example of fruit removal

REMOVE.INP

```
89                !fruit removal date
0,5,5,5,5,0,0,0   !remove 5 fruit from each of fruit categories 2, 3, 4 and 5
```

Action taken and output in FRUITCNT.OUT

```
Removal on          89
FRUCAT;CATEGORY          1      11.667070
FRUCAT;CATEGORY          2      20.336850
FRUCAT;CATEGORY          3       5.710421
FRUCAT;CATEGORY          4    0.000000E+00
FRUCAT;CATEGORY          5      18.787010
FRUCAT;CATEGORY          6       6.324003
FRUCAT;CATEGORY          7       5.966648
FRUCAT;CATEGORY          8      11.675740
          61          5    2.186242        2.661413E-01    1.604393
          62          5    2.203371        2.661413E-01    1.616963
          63          5    2.226285        2.661413E-01    1.633778
          64          5    2.195105        2.661413E-01    1.610897
          65          5    3.453518        2.661413E-01    2.534394
          66          5    3.301282        2.661413E-01    2.422675
          67          5    3.221206        2.661413E-01    2.363910
          71          3    0.000000E+00    8.755922E-01    0.000000E+00
          72          3    0.000000E+00    8.755922E-01    0.000000E+00
          73          3    0.000000E+00    8.755922E-01    0.000000E+00
          74          3    0.000000E+00    8.755922E-01    0.000000E+00
          75          3    0.000000E+00    8.755922E-01    0.000000E+00
          76          3    0.000000E+00    8.755922E-01    0.000000E+00
          77          3    1.771599        8.755922E-01    2.204008E-01
          78          3    1.897347        8.755922E-01    2.360448E-01
          79          3    2.041476        8.755922E-01    2.539756E-01
          80          2    2.110029        2.458591E-01    1.591259
          81          2    2.146898        2.458591E-01    1.619064
```

```
      82         2   2.214157          2.458591E-01   1.669786
      83         2   2.284266          2.458591E-01   1.722659
      84         2   3.757258          2.458591E-01   2.833502
      85         2   3.860647          2.458591E-01   2.911472
      86         2   3.963592          2.458591E-01   2.989107
Stop - Program terminated.
```

Further refinements to the damage routines in OZCOT

The initial validation of the damage routines have shown a good correspondence between predicted and observed. This is demonstrated by two examples. First, the mimicking the process of leaf area damage by thrips and the subsequent recovery (Fig. 1) resulted in a similar pattern to the actual pattern. Second, the fit between predicted and observed yield across a large number of damage types was highly signficant at $R^2=0.78$ over a range of yield between 4 and 11 bales ha^{-1} (Fig. 2). Yield predictions made by OZCOT, however, were slightly conservative where, compared to the 1:1 line, predicted yields were 14% lower than the observed values (see regression equation, Fig. 2). The slope and the scatter (i.e. R^2) around the 1:1 line could be improved. Some of the these improvements may be achieved by addressing the following aspects of the damage routines:

- calibrate the enhancement factors used in the thrips and tip damage routines
- calibrate the delay in development (i.e. time to first square) in simulating thrips infestation
- allow gradual leaf area recovery to continue after first square
- link Dr LT Wilson's fruit loss model to OZCOT. This will allow current fruit count to be sent to the predation model and returns larval number-specific fruit loss to the fruit removal routine

As the current fruit damage routines (which are largely based on *Helicoverpa* feeding) are being refined, there is a critical need for the responses of cotton to sucking pest damage (to bolls in particular) to be incorporated in OZCOT. An aim of the new compensation project funded by CRDC is to address the modelling of mirid damage (and possibly of other sucking pests) on cotton fruit and the subsequent recovery process.

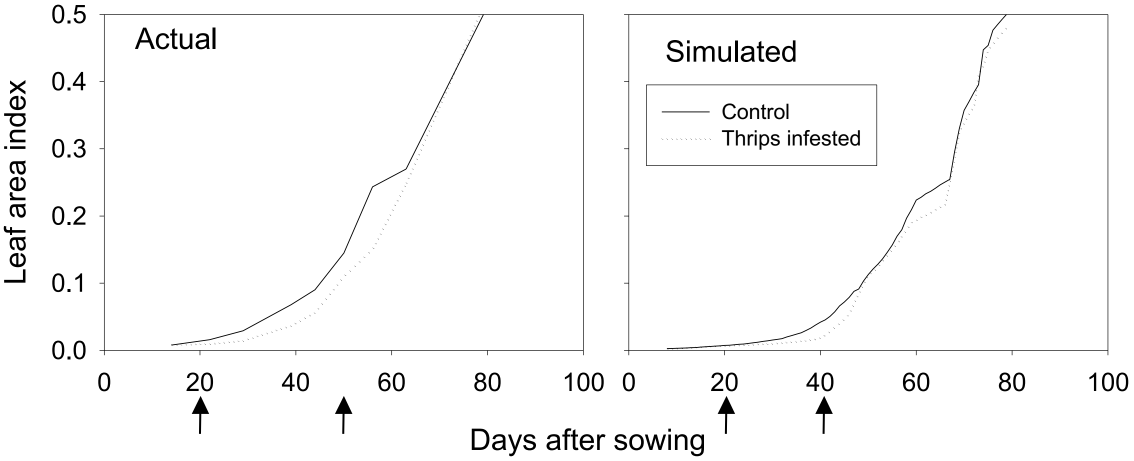


Figure 1. The graphs show the average rate of leaf area development between plots with and without thrips (actual) and simulated patterns with and without infestation (simulated). The arrows represent the start and finish of the infestations.

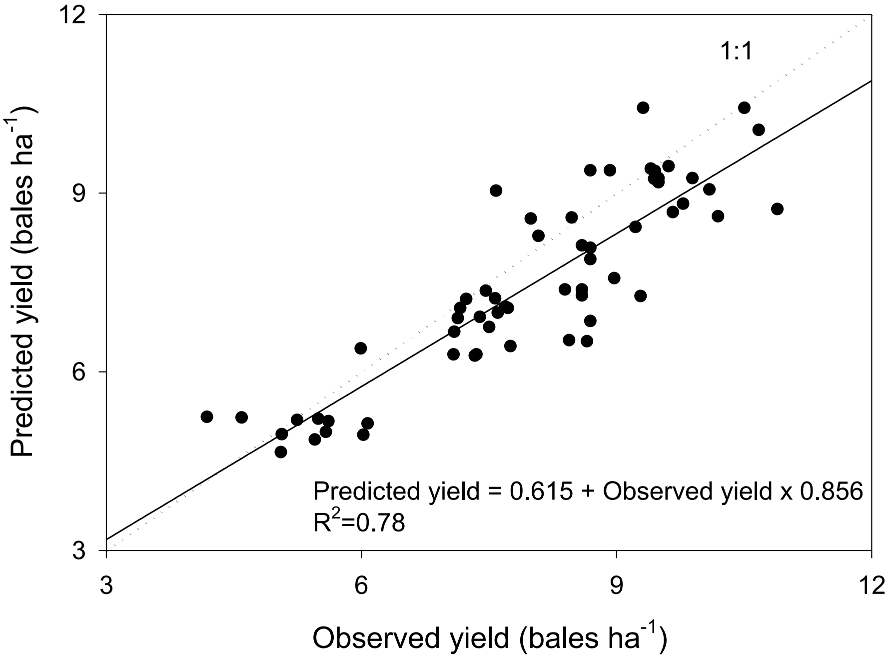


Figure 2. Predicted versus observed yield of 59 treatment-trial outcomes. Data included only yields of treatments with simulate pest damage. Damage included loss of terminal, reduction in leaf area, fruit loss, or a combination of these. The sample size is 59.

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