Library

Part 1 - Summary Project Details

Final Report

Report Due Date: 29-Sep-00

CRDC Project Number: CSP82C

Project Title: (< 15 words) Physiology of crop responses to insect pests

Output: Sustainability

Research Program: Farming systems & agronomy

Part 2 - Project Contact Details

Admin Contact: Mr | Ken | Parker
Title (i.e. Mr/Ms) | First Name | Last Name

Organisation: CSIRO Division of Plant Industry
(Name of organisation that will be administering the funding)

Postal Address: 1600 | Division of Plant Industry
PO Box | Street
Canberra | ACT | 2601
Town | State | Post code
02 6799 1500 | 02 6793 1186 | kenp@mv.pi.csiro.au
Phone | Fax | Email

Primary Research Dr | Tom | Lei
Title (i.e. Mr/Ms) | First Name | Last Name

Organisation: CSIRO Division of Plant Industry
(Name of organisation that will be administering the funding)

Postal Address: 59 | CSIRO Cotton Research Unit
PO Box | Street
Narrabri | NSW | 2390
Town | State | Post code
02 6799 1500 | 02 6793 1186 | toml@mv.pi.csiro.au
Phone | Fax | Email

Supervisor: Dr | Lewis | Wilson
Title (ie Mr/Ms) | First Name | Last Name

Organisation: CSIRO Division of Plant Industry
(Name of organisation that will be administering the funding)

Postal Address: 59 | CSIRO Cotton Research Unit
PO Box | Street
Narrabri | NSW | 2390
Town | State | Post code
02 6799 1500 | 02 6793 1186 | lewisw@mv.pi.csiro.au
Phone | Fax | Email

A plain English summary not exceeding 200 words

Research has shown that damage caused by chewing and sucking pests does not necessarily lead to a yield loss in cotton. The ability to compensate for tissue loss in cotton is attributed to an improved canopy development stimulated by pre-squaring tip damage, and to fruit substitution for damage and increased fruit production during the reproductive stage. However, cotton's ability to compensate for fruit loss declines dramatically as boll development accelerates (3-4 weeks after first square) and as other stress factors appear. But we have also shown that mild drought stress may limit the extent of mite damage possibly by making the canopy less attractive to mite development. Compensation can be enhanced through maintaining a healthy crop canopy but not one with excessive leaf area (which leads to yield loss). We are exploring options to minimise excessive growth response to pest damage such as selecting okra leaf cultivars and appropriate planting density. A well-managed crop may even respond to damage such as early season tipping out with yield gain over an undamaged crop - an area of focus in our on-going research. We are also continuing the effort to incorporate compensation results in a decision support system for pest management.

Background to the project

Previous research has shown that cotton plants could compensate for pest damage but the degree of compensation varied with the yield potential of the crop. Cotton often achieved full or over-compensation if yield potential was moderate but failed to fully compensate when yield potential was high. This pattern has been consistently demonstrated in published studies but is somewhat at odds with expectation (i.e., more resources equals greater recovery) and points to the limitation of our knowledge of the mechanisms of cotton responses to pests.

This project continues research into the physiological responses of cotton plants to pest damage that was developed in two previous projects: CSP39C/68C. The specific aim of this investigation is to enable the prediction of the recovery of cotton following pest damage and to use this information in tactical pest management decisions. It builds on previous work in the following areas:

- effects of resource availability (i.e., soil N and plant density) on compensation
- canopy response to tip and fruit damage (apical dominance and changes in radiation use efficiency)
- consequences of mite infestation
- spatial heterogeneity in pest damage and its effect on compensation

Uniform damage of plant stands to patchy distribution of damage. The patchy distribution is more typical of pest damage and accounts for interactions between neighbouring plants (i.e., a damaged plant next to an undamaged one). We have also demonstrated that (i) undamaged plants had a greater lint yield when grown next to neighbours that suffered early tip damage than when grown alongside undamaged ones, and that (ii) undamaged plants yielded less when they were flanked by neighbours that suffered square damage in comparison to undamaged plants flanked by undamaged neighbours. Such neighbour-to-neighbour interactions are therefore important in understanding compensation.

After taking over this project from Dr. Victor Sadras one year after funding began, I was able to conduct two years' of field work. This report therefore includes both published results completed in the first year by Dr. Sadras and a description of experiments I made since his departure.

The objectives and the extent to which these have been achieved

1. Continuing and completing research into plant compensation for different types of insect damage, focussing on the underlying physiological and morphological mechanisms. Current status: significant amount of new information has been collected.

2. Assessing the likelihood of compensatory responses in relation to major agronomic (i.e., cultivars including INGARD) and environmental factors. Current status: field trials offer an improved understanding of the causal relationship.
3. Simulating more realistic pest damage (mainly *Helicoverpa*) at both the pre-squaring and the fruiting period. Current status: multiple damage events including fruit removal simulating actual larval feeding preferences were imposed for 2 field seasons.
4. Initiating a compensation study in Kununurra to evaluate the effect of cropping in the tropical winter season. Current status: one year of field trial has been completed.
5. Extending research into compensation when damage in cotton crops was uneven and patchy. Current status: field manipulation experiments and an assessment of in-situ spatial patterns of damage have been conducted.
6. To improve the OZCOT simulation model into one which is capable of predicting compensation. Current status: empirical data collected in the last few years are being used to test the capacity of the model to simulate compensation responses.

The methodology and a justification for the methodology used

The main experimental technique employed is the analysis of canopy development and growth patterns across season. This methodology involves the measurement of plant dry mass through periodic harvests and of crop light interception using a ceptometer (light sensors). Light interception and dry matter data are used to estimate crop-level photosynthesis and the effect of insect damage on it. Regular harvests of plants, which are partitioned into roots, stems, leaves, squares, bolls, seed and lint, allow us to assess allocation of growth and how it is affected by pests.

Field trials evaluating the compensatory response under different agronomic conditions involved the comparison of a large range of cultivars (up to 8 cultivars of conventional and INGARD cotton, different leaf types and canopy height), three soil nitrogen levels, four plant densities and several types of manual tip damage. These variables are imposed in a number of discrete field trials over the last 2 years. Damage treatments have been made more realistic - instead of single large damage event per season, I have employed multiple damage events at both the pre-squaring and the fruiting period at levels simulating that of typical field densities of *Helicoverpa*. Findings derived from this protocol reflect more closely the field situation. Also, I have also simulated fruit damage more realistically by using a "feeding model" of *Helicoverpa* developed by Dr. LT Wilson. With this approach, we are more confident of attributing the response by cotton to larval-specific damage levels which in turn will help in limiting pest damage with the cotton model.

Detailed results including the statistical analysis of results

Threshold Trial: This trial was designed to establish the limits of cotton compensation to simulated and repeated damage during the pre-squaring and fruiting periods. This 2-year trial, we imposed tip damage twice prior to squaring and fruit damage twice simulating damage of 0, 2, 4, 6, and 8 *Helicoverpa* larvae per meter. We found no significant loss in yield with increasing pest pressure (Fig. 1). We conclude that cotton can tolerate repeated damage at levels as high as 8 *Helicoverpa* larvae per metre and as late as 130 days after sowing when there is sufficient time for recovery. Even though the yield potential may have differed considerably between the years (i.e., Yr 2 was twice that of Yr 1), the ability to compensate was not strongly affected. Maturity date of damaged treatments were delayed progressively with higher simulated damage: for 0, 2, 4, 6, and 8 *Helicoverpa* larvae per m respectively -176, 180, 181, 182, and 184 DAS (1998-99) and 171, 174, 177, 174, and 179 DAS (1999-00).

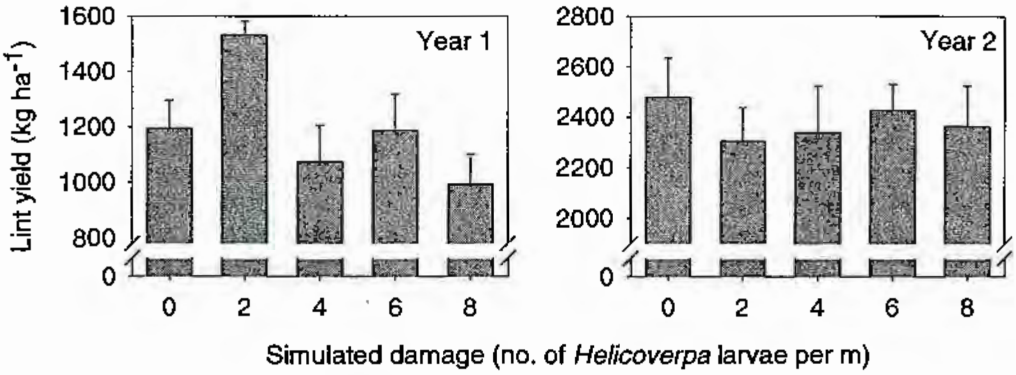


Figure 1. A two-year field trial conducted at Narrabri examining the ability of cotton to compensate from repeated damage simulating 0-8 *Helicoverpa* larvae per metre. The damage imposed consisted of two tip damage events before first square (80% of plants tipped out) and 2 fruit removal events (last event was about 130 DAS). Sicala V-2 (Yr 1) and Sicala V-2i (Yr 2) were grown using standard N and irrigation management and plant stand at 10 plants per metre. The number of fruit removed for each level of simulated larval number was calculated using a feeding model developed by Dr. LT Wilson (Texas A&M University).

Nitrogen Trial: This trial was intended to explore the assumption that resource availability is a key underlying cause of variation in compensation. We tested this by growing cotton with a range of soil nitrogen conditions (from 0 to 120 kg/ha) to produce plants of various sizes and leaf areas. The range of LAI observed at 120 DAS was between 1 and 6.5. Correlating LAI determined on this date with the final yield, we found a strong relationship with an optimal leaf area index (LAI) at about 2.5 (Fig. 2). Furthermore, compensation was clearly affected by soil N supply. Specifically, yield recovery was greatest (exceeding that of the undamaged control) when LAI was between 2 and 3 but was poor (less than the undamaged control) when LAI exceeded 3.

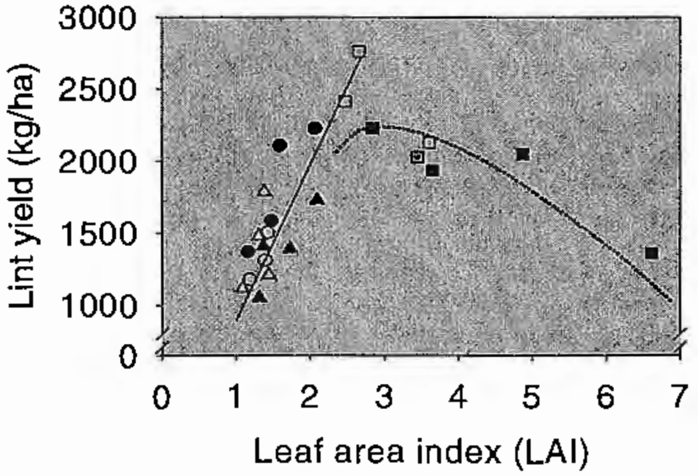


Figure 2. The relationship between leaf area index (total leaf area per ground area) and yield from the N trial conducted in 1998-99. the pattern was produced by growing Sicala V-2i in three soil N levels: 0 (triangles), 60 (circles), and 120 (squares) kg ha^{-1} applied. The filled symbols

represent multiple damaged plants (as described in the text) and the open symbols undamaged plants. LAI was determined at about 120 DAS.

The observed response pattern evoked a mechanism which we believe is the basis for the variation in compensation. Namely, when pests damage the terminal of a young cotton plant, the plant is stimulated to produce lateral branches from dormant buds in the main stem leaf nodes below the terminal. Figure 3 illustrates the significant increase in the number of branches produced from manual tip damage prior to squaring. With the development of lateral branches, the cotton canopy usually becomes more efficient in intercepting light and therefore could accumulate more carbon. More branches also means more potential fruiting sites and a larger square production. Since plants with more fruit can tolerate more damage (through substitution of lost fruit), we believe tip damage could also help cotton to be more resistant to fruit damage later in the season. However, the positive effect of tip damage is lost in a high input system because canopy development following damage led to excessive leaf production. This creates a dense canopy where a greater proportion of the leaves on the plants are shaded, thereby reducing the efficiency of radiation conversion to carbon. Solutions to reducing the excessive leaf growth when a high input crop is damaged are using okra leaf cultivars (its open canopy is more resistant to excessive leaf area) and reducing the planting density (to minimise shading by neighbours). Options to reduce excessive plant growth include:

1. use NutriLogic / NutriPak to determine N requirement
2. assess crop vigour to determine the need for crop growth regulators
3. match appropriate varieties to field and region
4. optimise plant density (8-12 /m irrigated; 5-10 /m dryland)
5. optimise irrigation to avoid waterlogging and water stress which may inhibit leaf size and cause fruit shedding.

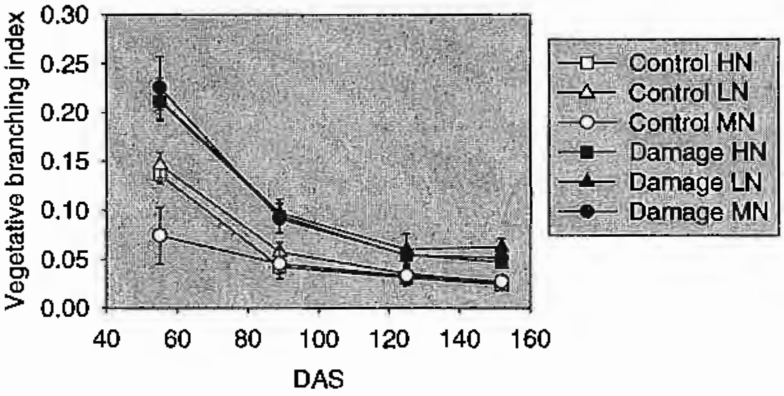


Figure 3. A comparison of the number of lateral branches across season (Das After Sowing) on cotton plants grown under low, medium and high nitrogen levels - LN, MN, and HN respectively (see Fig. 2 for N rates). Damaged plants produced more branches compared to the undamaged plants for all N treatments. The decline in branch number is due to standardising values to plant height.

Variety Trial: With the strong non-linear relationship (Fig. 2) between yield and the amount of leaf area per meter (LAI) and the mechanism we derived to explain such a pattern, this trial was intended to determine whether compensation could be increased through the manipulation of cultivar type and planting density. The goal is to maximise compensation by achieving optimum LAI in a pest damaged crop. Because the okra leaf type offers a higher optimum LAI than normal leaf varieties (Heitholt 1994), we predict that 1) okra leaf cultivars would suffer less yield loss than normal leaf ones under a high resource (N=120 kg ha^{-1}) situation; and 2) excessive LAI may also be controlled by lowering plant density.

Based on one year's (1999-2000) results, we found an overall increase in leaf area index in damaged over undamaged plots and that the increase was generally highest in the medium planting density (i.e., 10 plants per m for okra and 15 plants per m for normal leaf cultivars) (Fig. 4). However, the degree of yield recovery did not consistently match that of the LAI as we have predicted. This may have been due to two reasons, one, the second fruit damage was imposed too later for full compensation to occur, two, the agronomic condition did not force the crop into excessive leaf production (i.e., all LAI less than 3). This trial will be repeated for a second season in 2000-01 with an earlier date of second fruit damage.

Tip Damage Trial: Early season terminal damage to cotton is common in commercial cotton fields, even for well-protected crops. Such damage can promote the development of lateral vegetative branches and alter the shape of the cotton canopy. As we have demonstrated in the Nitrogen Trial, canopy structure has an influence on the ability of cotton to recover from fruit damage later in the season. This trial was intended to further examine the link between canopy development and compensation by directly quantifying the extent of canopy change when tip damage occurred at different times (i.e., plant ages) before squaring began. We assessed the growth and yield consequences of pre-squaring terminal damage in eight modern cultivars with different leaf type, growth form, phenological and transgenic status. As Figure 5 shows, it was more common to see a slight increase in both yield parameters for tip damaged (at nodes 2-10) versus undamaged plants (terminal damage=0). The obvious exception was Sicala 40 where yield was suppressed by tip damage. Also, we found no clear indication of an age-of-damage dependent yield response. Curiously, the relationship between branch development and yield was not one of an increasing slope, in fact, it is a negative slope (Fig. 6). This suggests that a moderate degree of branch increases resulting from tip damage enhances yield (shown by cultivars above the 0 horizontal line). But too much branch growth will inhibit yield. These results will be confirmed by repeating the trial for a second season beginning in Oct. 2000.These findings are consistent with the earlier hypothesis regarding the benefits additional lateral branching confers (see Nitrogen Trial). Specifically, there may be an optimal level of yield stimulation from tip damage which only some cultivars can achieve. The need to select appropriate cultivars to maximise yield gain resulting from tip damage will require further research. The link between responses observed in this trial and apical dominance (Sadras and Fitt 1997) will also be explored.

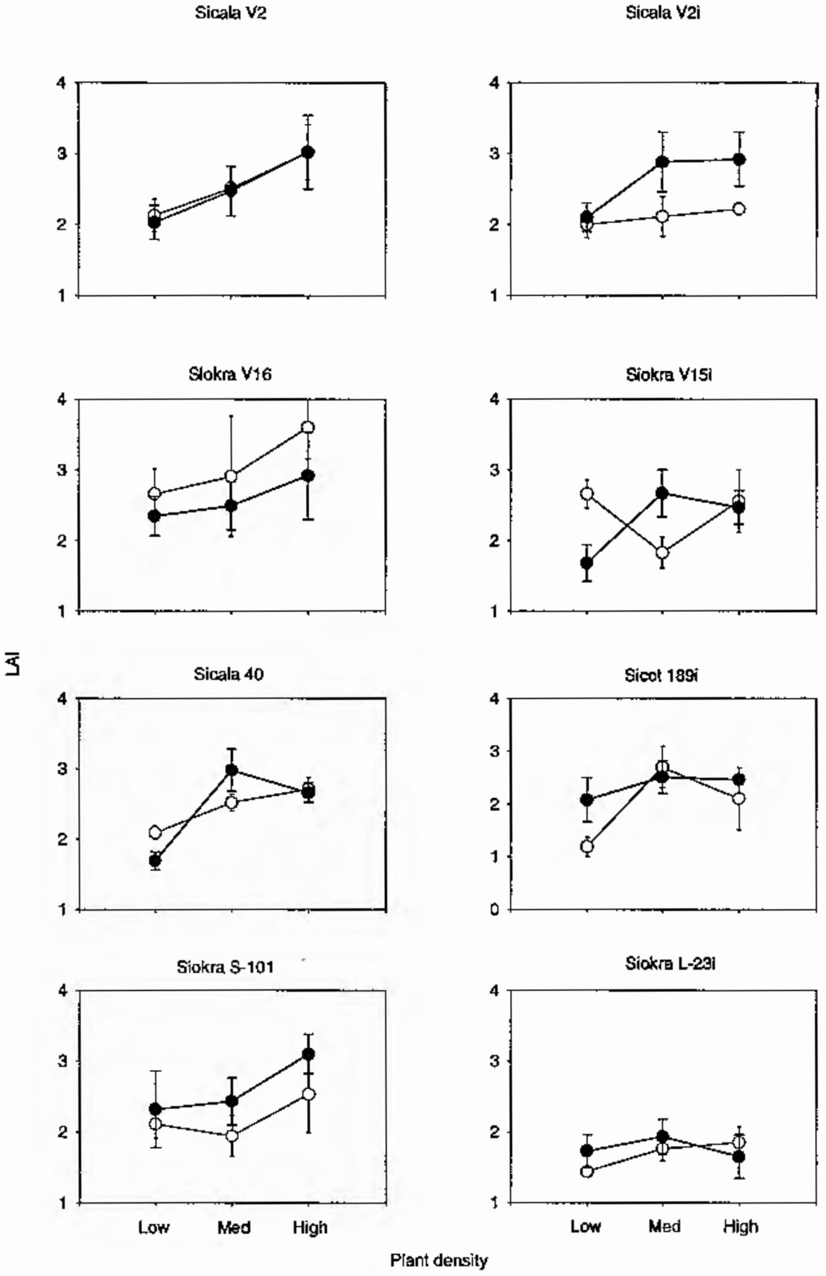


Figure 4. A trial conducted in 1999-2000 using eight cotton cultivars to examine the effect of planting density on leaf production (LAI) in damaged (solid symbols) and undamaged plants (open symbols). Plant density for okra leaf cultivars was set at 10 (low), 15 (med), and 20 (high) plants per meter; for normal leaf cultivars, it was set at 5 (low), 10 (med), and 15 (high) plants per meter. LAI was determined at about 120 DAS.

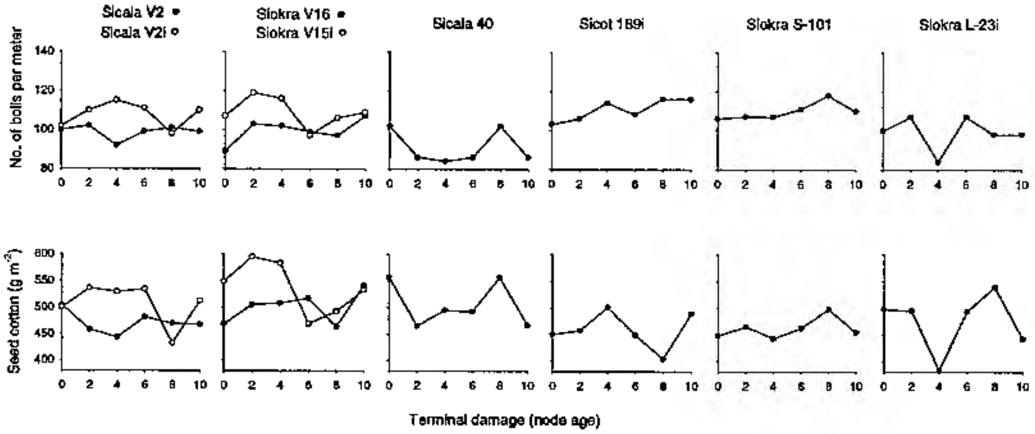


Figure 5. Yield consequences of eight cotton cultivars tipped out at 5 different node ages (at the 2, 4, 6, 8, and 10 true leaf stage). Values for the undamaged control are given as terminal damage (node age) = 0. Plant density was 10 m^{-2}.

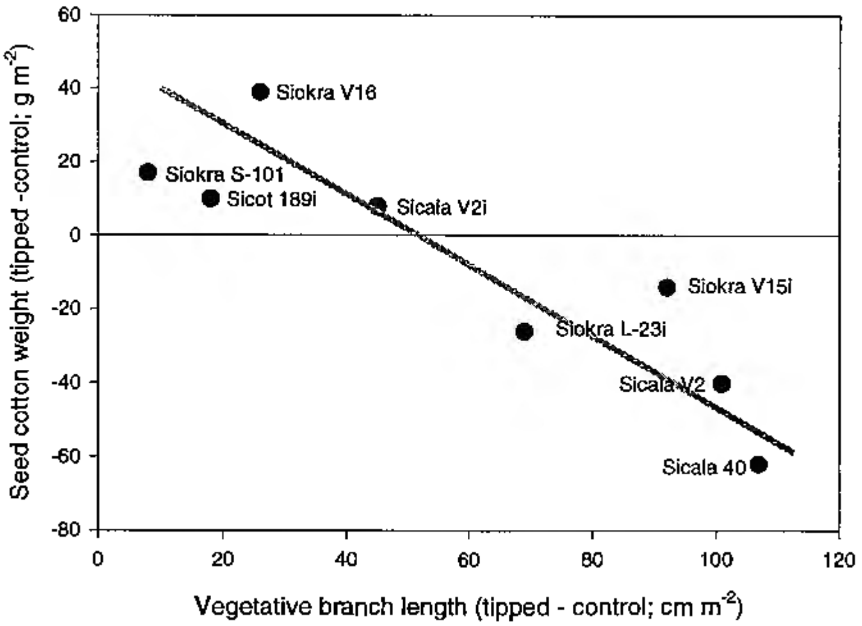


Figure 6. The relationship between increasing lateral branch growth and yield in eight cultivars. The difference in vegetative branch length is between tipped (mean of the 5 node age treatments, see Fig. 5) and the untipped control. Data show tipped plants of all cultivars increased in lateral branch length (tipped-control > 0). However, only cultivars with moderate increases in branch length showed an yield gain over the control (above the horizontal line) while there was an overall

trend of decreasing yield (gray line) below the control with branch length differences greater than 50 cm per meter.

Patchiness Census: The rationale for this study was based on results published by Sadras (1996, 1997; data collected during the previous compensation projects funded by CRDC). He demonstrated changes in growth and yield potential of cotton plants experiencing either direct pest damage to its vegetative or reproductive tissue or an indirect effect as immediate neighbours of damaged plants. In brief, growth and reproduction declined when a plant is damaged (tipped out) at the pre-squaring stage but that of its neighbours were stimulated. If a plant suffered damage to its reproductive structures, an asymmetric response opposite those of pre-squaring results. We know that the distribution of pests in a stand of cotton is patchy (Wilson and Room 1983), therefore could result in a substantial number of unevenly damaged neighbours. However, we do not yet know if the spatial patchiness is static on a temporal scale or do the patches "move" as the season progresses. The two alternatives may affect population level compensation in very different ways - the moving patches will tend to smooth out large neighbouring effect.

With one year's results of the spatial distribution of tip damage on two survey dates (Dec. 14 and 29), we found little evidence for the presence of static patchiness (Fig. 7).

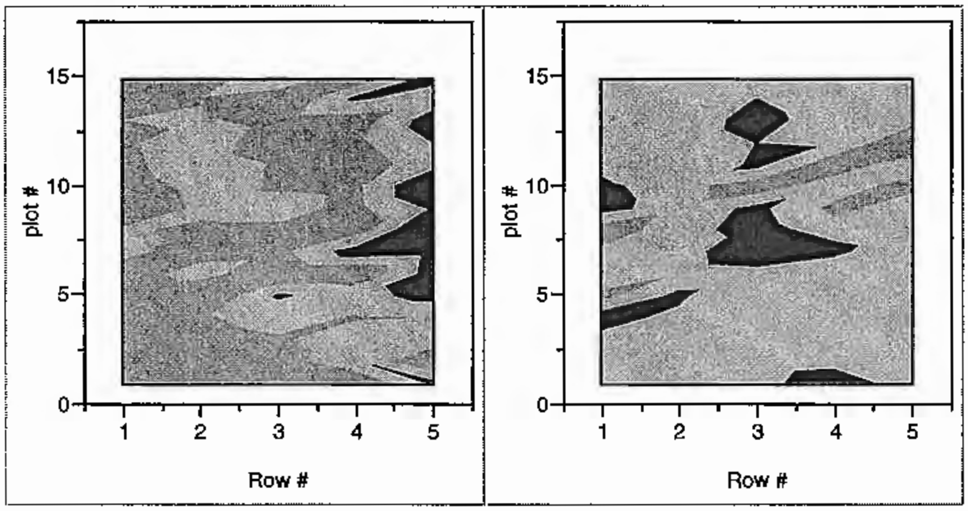


Figure 7. The contour patterns of percent tipped plants in an unsprayed field using conventional cotton (Siokra V-16). Data were collected from an area 20mx30m where individual sampling plots of one meter in length at 1m intervals along a row and 4m between rows. Percent tipped plants was calculated on an individual plot basis at two census times: Dec. 14, 1999 (left panel) and Dec. 29, 1999 (right panel). Values of percent tipped were: light gray (<20%), medium gray (20-40%) , and dark gray (>40%).

Compensation of cotton in the Ord River Irrigation Area: As part of the broader appreciation of compensation in diverse cotton cropping areas, it is crucial to examine cotton grown in Kununurra WA during the tropical "winter" where the seasonal thermal regime is the inverse of that for south-eastern Australia. Plants may recover in quite a different manner to pest damage in WA because the accelerated boll development phase occurs much later in the growing season. As such, it would be useful to know whether fruit loss during early fruiting is less critical to maintaining yield than the southern crop. If that is the case, a different IPM strategy would be warranted. In collaboration with Dr. Jay Singh in Kununurra, we began a field trial in 1999 collecting growth, fruit production and yield data. Analysis of the first year's results is currently underway, and thus far, we have found indications that tip damage and early fruit removal (at 800 day degrees) have a slightly positive effect on yield while the later season fruit removal (at 1200 DD) resulted in some delay and yield loss.

Discussion of results including an analysis of research outcomes compared with objectives

Threshold trial – The lack of a detectable yield effect from repeated damage by 2, 4, 6 and 8 *Helicoverpa* larvae per meter attests to the extent of tolerance in cotton. The associated delay in maturity is up to a maximum of 9 days between control and 8 larvae per m. Although we hypothesised that at zero damage would have a yield lower than those at moderate levels of pest damage, such a stimulatory effect was not evident. Perhaps the recovery pattern was masked by the fact that even at "0" damage, some natural damage occurred. It may be concluded that an increase in yield over the undamaged crop is possible within the range of damage level so long as sufficient time remains in the season for regrowth.

Nitrogen Trial – A clear pattern of over-compensation at moderate levels of yield potential. The interaction between resource availability and the degree of compensation potential reveals an underlying process which may explain why recovery is sometimes poor under high yield potential. The effect of excessive leaf area exacerbated by damage resulting in lower assimilation capacity and lower yield. This physiological process regulating the degree of compensation will be an important component of the modelling of compensation.

Variety trial – From the observation that a high input crop will develop excess leaf area which is exacerbated by tip damage, this trial examined two ways of mitigating this effect. With its more open canopy, we expected higher yield recovery from damage in okra leaf cultivars than normal leaf ones. We also expected that by reducing planting density, it would be possible to prevent excessive shading from lowering yield. The first year's results were inconclusive due to a rather narrow range of LAI among planting densities. We will repeat this trial using a larger range of planting density to generate LAI values greater than 3.

Tip Damage Trial – terminal damage increased vegetative and square production. While it varied among cultivars and timing of damage, there wasn't a consistent pattern of yield gain or loss in tipped plants. Interestingly, tipped plant increase yield but only at low to moderate levels, there was a negative linear relationship between increased branch development and higher yield. 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.

Patchiness Census – The first year's spatial and temporal distribution patterns of tip damage indicates that patches are not static. This leads 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 LT Wilson developed for *Helicoverpa* and thrips. 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.

Compensation in the Ord – The key contribution this trial makes to the compensation study is to elucidate the interaction between fruiting dynamics and pest damage driven by very different thermal regimes between the southeast and northern Australia. Because yield of the Ord region cotton is much more dependent of the late season bolls (in conjunction with the increasing temperature), we suspect that much greater amount of fruit loss can be tolerated without yield reduction. More definitive results are expected from the second season ending in early October 2000.

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 and future research needs

This project aimed to explore ways to reduce the use of insecticides while maintaining the productivity of the current cropping systems by exploiting the natural ability of cotton to recover from pest damage. While we already use compensation in pest management when we assume that no significant yield loss will occur if an insect infestation is below a given threshold, there appears to be room for increasing the threshold. Our results show that under certain conditions, cotton can compensate from substantially higher damages than those set by current thresholds. In fact, in some instances damage such as tip damage combined with moderate fruit loss early in the fruiting season could even increase yield over the well-controlled crops. It is clear that compensation has not been fully exploited as a means to reduce insecticide input (with all of its attendant benefits) or as a management tool to increase yield.

Description of the project technology (e.g. commercially significant developments, patents applied for or granted, licenses, etc)

A technical summary of any other information developed as a part of the research project including discoveries in methodology, equipment design, etc.

Manipulation experiments were carried out with more realism than past compensation trials. The implementation of multiple damage events at both pre-squaring and fruiting periods gives us greater power to interpret plant response. The adoption of the *Helicoverpa* feeding model developmed by Dr. L.T. Wilson gives us an additional level of precision in simulating fruit damage.

Recommendations on the activities or other steps the may be taken to further develop, disseminate, or to Exploit the Project Technology

It is a priority in the progression of compensation research to develop a decision support system capable of predicting yield consequences based on pest damage. We have begun this effort by encoding the existing OZCOT model with damage and compensation subroutines in collaboration with Dr. S. Milroy and Dr. M. Bange (ACRI). Specifically, we are adding components such as architectural changes due to tip damage and the light interception and fruiting consequences of early season tip damage. Further steps to be taken would be making the system user friendly (e.g., as part of CottonLogic) and incorporating economic (including the longer term cost of resistance) and gross margin analysis of spray decisions.

A list of publications arising from the research project

Peer reviewed publications:

Sadras VO. 1998. Herbivory tolerance of cotton expressing insecticidal proteins from *Bacillus thuringiensis*: responses to damage caused by *Helicoverpa* spp. and to manual bud removal. Field Crops Research 56: 287-300.

Sadras VO, Wilson LJ. 1998. Recovery of cotton crops after early season damage by thrips (Thysanoptera). Crop Science 38:399-409.

Sadras VO, Wilson LJ, Lally DA 1998. Water deficit enhanced cotton resistance to spider mite herbivory. Annals of Botany 81: 273-286.

Industry publications:

Sadras VO. 1998. Bt cotton tolerates damage as well as conventional cotton. Proc. Ninth Australian Cotton Conference, Broadbeach, August 12 -14, 1998. pp. 343-349.

Wilson LJ, Sadras VO. 1998. How important is early season damage? Proc. Ninth Australian Cotton Conference, Broadbeach, August 12 -14, 1998, pp. 409-416.

Sadras VO, Wilson LJ, Lally DA. 1998. Dryland cotton tolerated mites better than irrigated cotton. Proc. Ninth Australian Cotton Conference, Broadbeach, August 12 -14, 1998, pp. 423-426.

Redall AA, Sadras VO, Wilson LJ. 1998. Photosynthetic responses of cotton to spider mite damage and water stress. Proc. Ninth Australian Cotton Conference, Broadbeach, August 12 -14, 1998, pp. 427-433

Lei T. 1999. Recovery of cotton in growth and yield after repeated damage. The Cotton CRC Research Conference. 21-22 July, 1999. Narrabri RSL.

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

Lei T. 2000. Compensation in cotton following pest damage: potential and limitations 10th Cotton Conference Proceedings. Aug. 15-18, 2000 Brisbane Convention Centre.

Invited book chapter

Sadras VO, Felton GW. 2001. Mechanisms of cotton resistance to arthropod herbivory. In: Stewart JM, Oosterhuis D, Heitholt JJ (eds) Handbook of Cotton Physiology. Kluwer, in press.

Cited references

Heithold JJ. 1994. Canopy characteristics associated with deficient and excessive cotton plant population densities. Crop Sci 34: 1291-1297.

Sadras VO. 1995. Population-level compensation after loss of vegetative buds: interactions between damaged and undamaged cotton neighbours. Oecologia 106: 417-423.

Sadras VO. 1997. Interference among cotton neighbours after differential reproductive damage. Oecologia 109: 427-432.

Sadras VO and Fitt GP. 1997. Apical dominance - variability among cotton genotypes and its association with resistance to insect herbivory. Environ Exp Bot 38:145-153.

Wilson LT, Room PM. 1983. Clumping patterns of fruit and arthropods in cotton, with implications for binomial sampling. Environmental Entomology 12: 50-54.

Acknowledgments:

We express our thanks to the manager of ACRI, Bruce Reddan, the farm foreman, Des Magann and all the farm staff for their cooperation in establishing and maintaining the experimental fields. Indispensable technical assistance was provided by Leslie Burke, Kelly Scott, Tanya Smith, Jane Caton, Deon Cameron, and Renee Schick. Steven Pirlo was the CRC-funded student who undertook the tip damage trial in 1999-2000. Field trial in Kununurra WA was managed and conducted by Jay Singh, Nerylie Gaff, and Sally Phillips. Steve Milroy, Lewis Wilson, Mike Bange, Brian Hearn, Greg Constable, Jay Singh and Martin Dillon offered valuable information and advice on cotton physiology and agronomy.

Annals of Botany **81**: 273–286, 1998

Water Deficit Enhanced Cotton Resistance to Spider Mite Herbivory

V. O. SADRAS*, L. J. WILSON and D. A. LALLY

CSIRO Plant Industry, Locked Bag 59, Narrabri, New South Wales 2390, Australia

Received: 26 August 1997 Returned for revision: 26 September 1997 Accepted: 6 October 1997

We investigated the responses of cotton (*Gossypium hirsutum* L.) to the combined effects of soil water deficit and two-spotted spider mite (*Tetranychus urticae* Koch) infestation. Two mite treatments (−M: uninfested, +M: artificially infested 83 d after sowing), and two water regimes (+W: well watered, −W: water stressed) were combined factorially in four treatments. Mite colonies developed at similar rates in well-watered and water-stressed crops. Despite the similar intensity of infestation, visual symptoms of mite injury were more marked in well-watered host plants (+M+W) than in their water-stressed counterparts (+M−W). Lint yield of unstressed controls (−M+W) was 175 g m^{-2}. In uninfested crops, water deficit reduced yield by 30%, mites reduced the yield of well-watered crops by 92%, and the combination of mite infestation and water deficit reduced yield by 72% (water effect: $P < 0\cdot01$; mite and interaction effect: $P < 0\cdot0001$). Differences in yield responses to mites between well-watered and water-stressed crops were mostly related to differences in reproductive partitioning. The interaction between mites and water deficit was also significant for other crop variables including canopy temperature, leaf water potential, concentration of nitrogen in reproductive structures and seed oil concentration. The magnitude and consistency of the interaction between both stresses indicates that, under our experimental conditions, mechanisms of adjustment to water deficit may have enhanced cotton resistance to mites. This is further supported by (*a*) an increase in specific leaf weight and a parallel increase in leaf penetration resistance due to water deficit; (*b*) a negative association between macroscopic symptoms of mite injury and leaf penetration resistance; and (*c*) a choice test showing that adult female mites preferred to feed and oviposit on leaves from well-watered plants. © 1998 Annals of Botany Company

Key words: *Gossypium hirsutum* L., *Tetranychus urticae* Koch, leaf water potential, leaf penetration resistance, canopy temperature, multiple stresses, specific leaf weight, radiation use efficiency, nitrogen concentration, reproductive allocation.

INTRODUCTION

The two-spotted spider mite (*Tetranychus urticae* Koch) is a mesophyll feeder whose effects on cotton (*Gossypium hirsutum* L) have been investigated at the cytological, leaf and crop levels. Research at the leaf level demonstrated that *T. urticae* can reduce stomatal conductance, photosynthesis and transpiration rate (Bondada *et al.*, 1995), responses that are consistent with increased foliage temperature and reduced radiation-use efficiency measured in mite-infested crops (Sadras and Wilson, 1997*a*).

However, plants in the field are frequently exposed to multiple stresses (Chapin *et al.*, 1987; Mooney, Winner and Pell, 1991). Water deficit and arthropod herbivory can substantially reduce plant productivity and the interactions between these stresses have received considerable attention (Jones and Coleman, 1991; Waring and Cobb, 1992). Interactions between arthropod pests and water deficit in cotton have been investigated in studies dealing with *Bemisia* spp. (Flint *et al.*, 1994), *Pectinophora gossypiella* (Saunders) (Kittock *et al.*, 1983), *Lygus hesperus* Kingh, *Empoasca* spp., *Geocoris pallens* Stal and *Orius tristicolor* White (Leigh *et al.*, 1970; Leigh *et al.*, 1974; Flint *et al.*, 1994). Only one of these studies considered the interactions between mites, *T. pacificus* McGregor, and crop water regime (Leigh *et al.*, 1970). No attempt has been made, however, to measure the physiological responses of cotton to the combined effects of mites and water stress.

Importantly, maintenance of leaf and canopy temperature within a range from about 23 to 32 °C through stomatal regulation of transpiration seems to be critical for the growth and yield of *Gossypium* spp. (Burke, Mahan and Hatfield, 1988; Radin *et al.*, 1994). Because mites disrupt the functionality of the stomatal apparatus (Bondada *et al.*, 1995) the interactions between mites and water stress in cotton are likely to be important.

This study investigated the responses of field-grown cotton to the combined effects of soil water deficit and *T. urticae* infestation. Our approach involved measurements at the leaf and crop levels in contrast with studies of interactions between mites and water stress in other species that concentrated on leaf-level responses (Youngman and Barnes, 1986; Hare *et al.*, 1989).

MATERIALS AND METHODS

A field experiment was carried out at Narrabri (30° S, 150° E) on a deep uniform grey clay soil (Northcote, 1979). Crops of cultivar NuCotn 37 were sown on 9 Oct. 1996. This cultivar produces *Bacillus thuringiensis* subsp. kurstaki insecticidal proteins (Cry IAc) that reduce the need of chemical control of *Helicoverpa* spp (Lepidoptera: Noctuidae), the main pests of cotton in Australia. Additionally,

---

* For correspondence at: Universidad Nacional de Mar del Plata, Facultad de Ciencias Agrarias, CC276, Balcarce (7620), Argentina.

0305-7364/98/020273+14 $25.00/0 bo970551 © 1998 Annals of Botany Company

1993). Between ten and 20 leaves per subplot were sampled at weekly intervals and these leaves were also kept for damage scoring (see below). Full details and justification of sampling procedures are given in Wilson (1993) and Wilson and Morton (1993).

A preference test was carried out to assess whether adult female mites would, given the choice, discriminate between leaves from well-watered (+W) and water-stressed (−W) plants. We used adult females from a glasshouse culture and third (from the apex) mainstem leaves taken from −W−M and +W−M plots 122 DAS. Leaf discs (2·5 cm in diameter) consisted of two semicircles, one from each treatment, placed in contact with the abaxial side uppermost. These were placed in petri dishes lined with moist cotton wool to maintain turgor, and five adult females were placed on each half-disc. After 24 h in a growth chamber (temperature: 28 ± 0·5 °C, light/dark period: 14/10 h) the number of adult females and eggs on each half disc was counted.

Predator abundance in each treatment was assessed on two dates (97 and 120 DAS) using suction samplers as described by De Barro (1991). On each sample date a complete row was sampled in the centre of each subplot. A zigzag sampling technique, where the suction device was passed along the lower, middle and top strata of the canopy, was adopted to ensure adequate coverage of the canopy. Insects collected were killed using chloroform and the abundance of spider mite predators, as described in Pyke and Brown (1996), was scored.

Crop and soil. Soil water content was measured with a neutron probe at about weekly intervals and, when possible, shortly after irrigation. One access tube was located in the central row of each subplot and measurements were taken at 0·05, 0·15, 0·25, 0·35, 0·45, 0·60, 0·80, 1·0 and 1·2 m depths.

Shoots and tap roots were sampled at fortnightly intervals from 85 DAS (sample size = 0·5 m^2). Plant components were separated and over-dried to constant weight. Green leaf area of at least two whole plants was measured with a leaf area meter (LI-3100, LICOR, Lincoln, NE, USA) to estimate specific leaf weight, and this variable used to estimate leaf area index (LAI) of the crop from green laminae biomass values. Leaves and other abscissed plant parts were collected fortnightly in 1 m^2 trays placed between the rows. Mature fruit ('open bolls') were counted weekly in 2 m^{-2} crop sections. Lint yield was measured in large crop samples (30 m^2) by harvesting the two centre rows of each subplot with a spindle picker 189 DAS. Sub-samples were ginned with small saw gins to estimate lint fraction, i.e. lint/(lint + seed). Oil concentration of delinted seed was measured by the NMR technique using a cotton-oil standard.

Plant organs taken in the fortnightly harvests were milled after drying and nitrogen content was determined using a near-infrared protein analyser (Inframatic 8100, Perten Instruments, Sweden) as described in Rochester, Constable and MacLeod (1993). Small amounts of plant material allowed nitrogen analysis in reproductive structures for some dates only (97 DAS for flowerbuds, 132 and 146 DAS for capsule walls).

At approximately weekly intervals, the fraction of PAR intercepted by the canopy at noon (*Qn*) was calculated from measurements made with a ceptometer. Noon canopy temperature was measured with an infrared thermometer (Everest Interscience, Tustin, CA, USA) on clear days following the procedure described in Idso, Reginato and Farah (1982). Temperature was measured at weekly intervals from 92 to 132 DAS; four readings per subplot were taken and averaged.

Leaf. All leaf variables were measured on the third or fourth mainstem leaf below the apex. Leaf damage was scored immediately after mite counts on ten to 20 leaves per subplot. Leaf damage was scored by visually recording the percentage of the leaf area damaged by mites, irrespective of damage intensity as described in Wilson (1993). Starting at 116 DAS we also recorded the percentage of leaf area severely damaged by mites, i.e. where the effects of cumulative mite feeding caused the abaxial side of the leaf to become brown and desiccated. For samples taken after 104 DAS, leaf area and dry weights were measured and specific leaf weight calculated.

Leaf water potential was measured using the pressure chamber technique following the procedures described by Hsiao (1990). Measurements were taken at around solar noon (±1 h) on clear days; two leaves per replicate were sampled at 107, 124 and 133 DAS. Percent water content, i.e. 100 × (fresh weight − dry weight)/dry weight, was measured on samples (20 leaves per subplot) taken at 133 DAS. Note that this definition of leaf water content, often used in studies of plant/herbivore relationships (Sagers, 1992) is different from the definition of relative water content used in studies of plant water relations (Wright, Morgan and Jessop, 1996).

Penetration resistance was measured on attached leaves with a dial tension gauge (probe diameter 0·73 mm; Chatillon AG50, John Chatillon & Sons, New York, NY, USA) as in Sands and Bracantini (1991). Three leaves per subplot and three positions per leaf near the insertion of the petiole, where mites prefer to feed (Wilson, 1994), were measured and averaged at approximately weekly intervals between 99 and 132 DAS. Mechanical properties of leaves depend on a number of factors, including their turgor pressure (Sands and Bracantini, 1991). Thus, measurements were taken early in the morning (before 0800 h) to minimize the importance of turgor pressure as a source of variation in leaf penetration resistance. This procedure implies that differences caused by treatments were more likely to be structural than turgor-related. This assumption is further supported by visual inspection of −W crops indicating no wilting early in the morning, in contrast to marked wilting often observed in the afternoon.

Calculations and statistical analyses

Mite, soil, crop and leaf variables were analysed by ANOVA with mite treatment, water regime and their interaction as experimental sources of variation. Mite numbers were $\log_e$ transformed and proportions arcsin transformed prior to analysis, but untransformed values are shown in figures for easier interpretation of data. Relationships between some variables that require measurements at the same time of the day, e.g. (noon) canopy temperature but significant interactions developed as the intensity of both stresses increased (Fig. 4). Calculations to estimate the effect of each individual stress as described above indicate that +M − W canopies were 7% (98 DAS) to 44% (132 DAS) cooler than expected from the additive effects of mites and water stress.

At 107 DAS, canopy temperature was closely associated with leaf water potential irrespective of mite treatment (slope = −3·6 °C MPa^{-1}; r^2 = 0·80, P < 0·0001, n = 16, Table 2). For uninfested crops, the relationship was consistent through time with an average rate of change in canopy temperature of −3·4 °C MPa^{-1} (Table 2). Canopy temperature in crops with more than 20 mites per leaf was unrelated to leaf water potential (+M crops at 124 and 133 DAS, Table 2).

Leaf penetration resistance

Penetration resistance was greater in leaves from water-stressed crops than in leaves from well-watered treatments (Fig. 5A). We did not find any consistent effect of mites or mite × water treatment interaction on leaf penetration resistance. Specific leaf weight was also greater in the water-stressed treatment (P < 0·001) and there was a close association between specific leaf weight and leaf penetration resistance (Fig. 5B). Significant negative associations were found between leaf penetration resistance (Fig. 5A) and leaf injury caused by mites (Fig. 2B and C) with leaf penetration resistance accounting for 59 to 74% of the variance in total leaf damage (P < 0·05) and for 66 to 93% of the variance in severe leaf damage (P < 0·01).

LAI, PAR interception, RUE and crop growth

Figure 6 shows the dynamics of LAI, PAR interception and shoot dry matter between 85 and 146 DAS. Average LAI at the beginning of the measurement period was 1·7. In control crops (−M+W), LAI reached a maximum of 2·7 at about 135 DAS. Irrespective of mite treatments, LAI of water-stressed crops (−M−W, +M−W) did not increase during the measurement period. It remained stable until 100 DAS (+M−W) or 132 DAS (−M−W) and declined rapidly thereafter. Well-watered, mite infested crops (+M−W) maintained rates of LAI increase similar to controls (−M+W) until 102 DAS and declined sharply afterwards. Changes in PAR interception reflected, with some delay, changes in LAI (Fig. 6B).

Control crops (−M+W) maintained a stable rate of shoot dry matter accumulation during the 85-146 DAS period (Fig. 6C). There was a clear sequence of the effect of stresses on shoot growth whereby stressed crops maintained growth rates similar to controls until (*a*) 97 DAS in mite-infested, water-stressed crops (+M−W); (*b*) 119 DAS in mite-infested, well-watered (+M+W) crops; and (*c*) 132 DAS in uninfested, water-stressed crops (−M+W). The

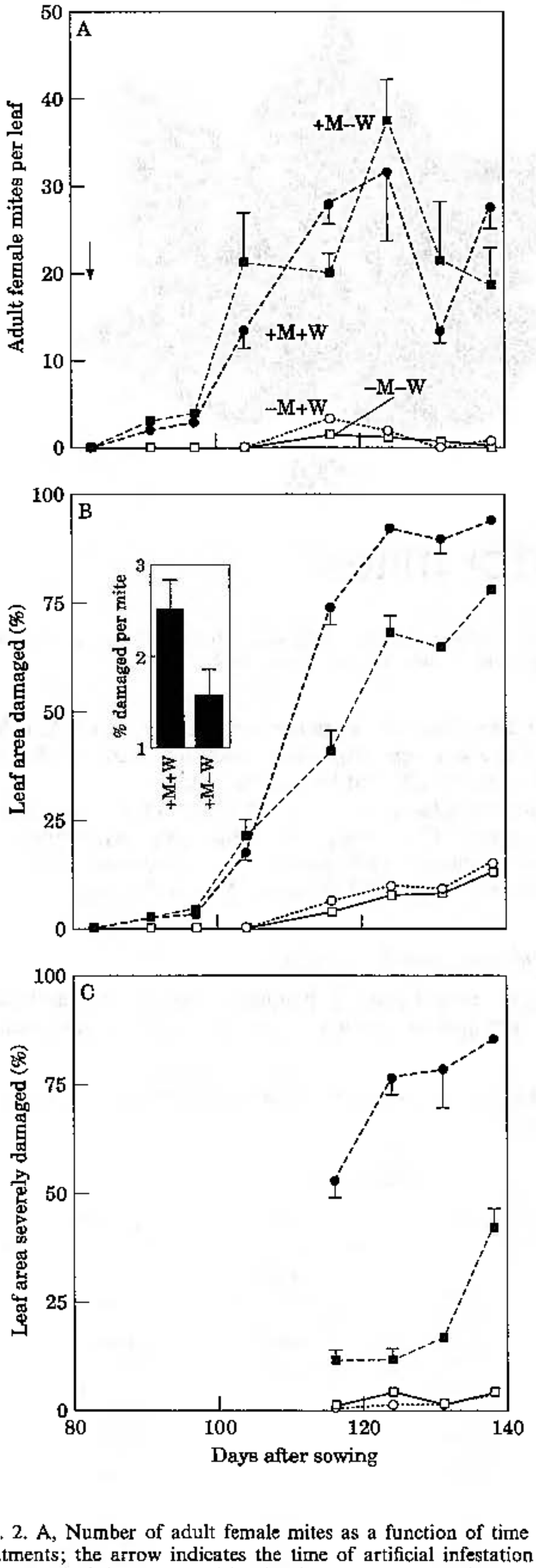


FIG. 2. A, Number of adult female mites as a function of time and treatments; the arrow indicates the time of artificial infestation; B, percentage of leaf area with visual symptoms of mite damage (irrespective of intensity of damage). Inset shows the slope of the regression between mite number and % leaf damage; C, percentage of leaf area with severe symptoms of mite damage. Error bars in A, B and C are one s.e.m. and were not plotted when smaller than symbols; error bars in the inset are s.e. of the regression coefficients.

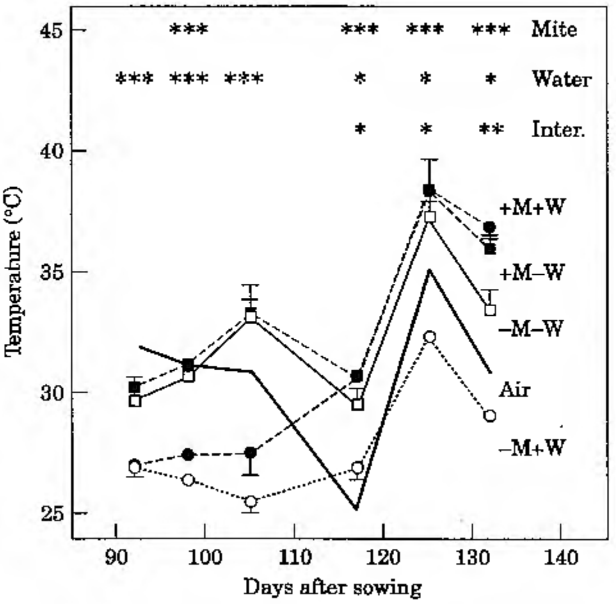


FIG. 4. Canopy temperature as affected by mite infestation and water deficit. Air temperature, measured at a meteorological station 0·5 km from the experimental plot, is shown as a reference. Error bars are one s.e.m. and were not plotted when smaller than symbols. Levels of significance are: $P < 0·05$ (*), $P < 0·01$ (**) and $P < 0·001$ (***).

treatment and water × mite interaction), peak fruit number was reduced from 115 m^{-2} in uninfested crops to 63 m^{-2} in mite infested crops ($P < 0·01$) (Fig. 8, horizontal lines). Fruit matured faster in water-stressed crops than in well-watered ones; for instance, at 145 DAS, −W crops had 31 mature fruit m^{-2} in comparison to +W crops that only had 5. At the end of the season, the proportion of fruit that reached maturity was 0·79±0·09 in uninfested crops irrespective of water regime; mites reduced this fraction to 0·68±0·05 in −W crops and to 0·28±0·03 in +W crops (mite effect significant at $P < 0·01$, interaction significant at $P < 0·05$) (Fig. 8).

Lint yield is a function of dry matter production and partitioning. Relevant partitioning variables in cotton include: fruit/shoot (Fig. 9A), seed cotton per fruit (Fig. 9B) and lint fraction (Fig. 9C). Fruit/shoot partitioning of crops affected by both stresses (+M−W) was 53 % greater than that of control crops (−M+W), while it was unaffected by either mites or water stress acting separately (Fig. 9A). Seed cotton per fruit was reduced by mites ($P < 0·0001$) and unaffected by water deficit ($P > 0·93$) or the interaction between stresses ($P > 0·05$). Irrespective of water regime, lint fraction was 0·41 in uninfested crops; mites reduced lint fraction to 0·37 in −W crops and to 0·33 in +W crops (water effect: $P < 0·001$; mite and interaction effect: $P < 0·0001$). Lint yield of unstressed controls was 175 g m^{-2} (Fig. 9D). In uninfested crops, water deficit reduced yield by 30 %, mites reduced the yield of well-watered crops by 92 %, and the combination of mite infestation and water deficit reduced yield by 72 % (water effect: $P < 0·01$; mite and interaction effect: $P < 0·0001$).

Nitrogen and oil concentration

Figure 10 shows the dynamics of nitrogen concentration in vegetative organs. Leaf nitrogen concentration declined with time in all treatments. The rate of decline was accelerated by mites and unaffected by water deficit or the interaction between them. Stem nitrogen concentration in uninfested, well watered plants (−M+W) declined steadily from 1·2 % at 85 DAS to 0·32 % at 146 DAS. In the same

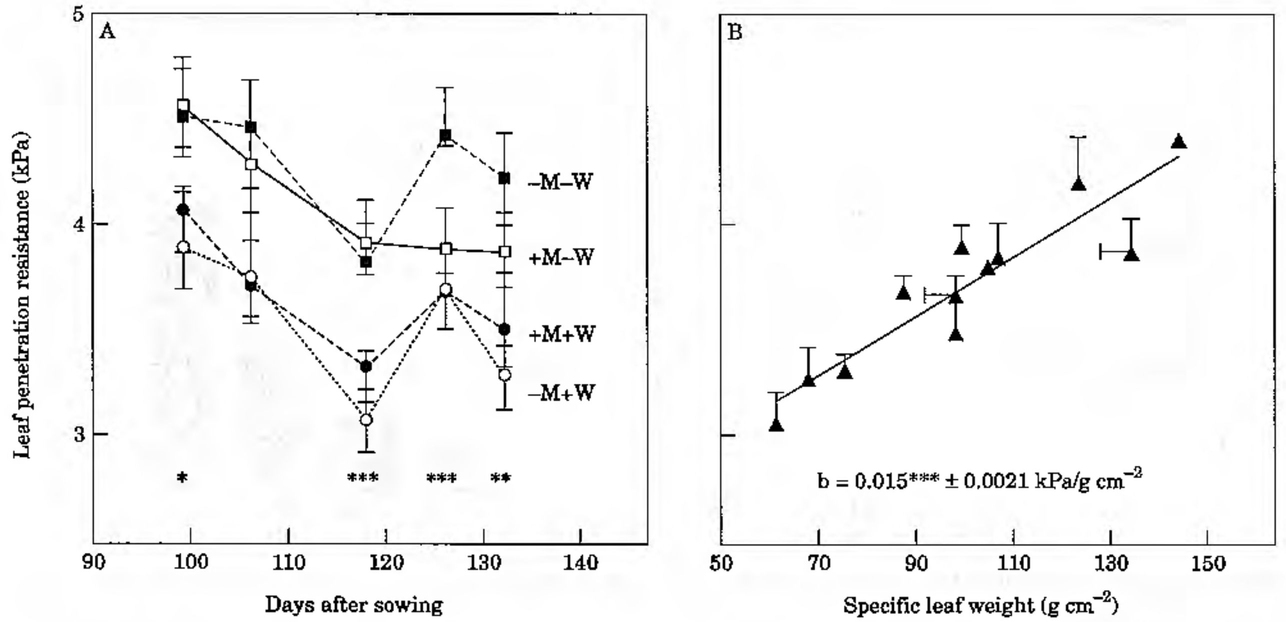


FIG. 5. A, Leaf penetration resistance as affected by mite infestation and water deficit; B, relationship between leaf penetration resistance and specific leaf weight. Error bars are one s.e.m. and were not plotted when smaller than symbols. In A, asterisks indicate effects of water treatment; in A and B, levels of significance are: $P < 0·05$ (*), $P < 0·01$ (**) and $P < 0·001$ (***).

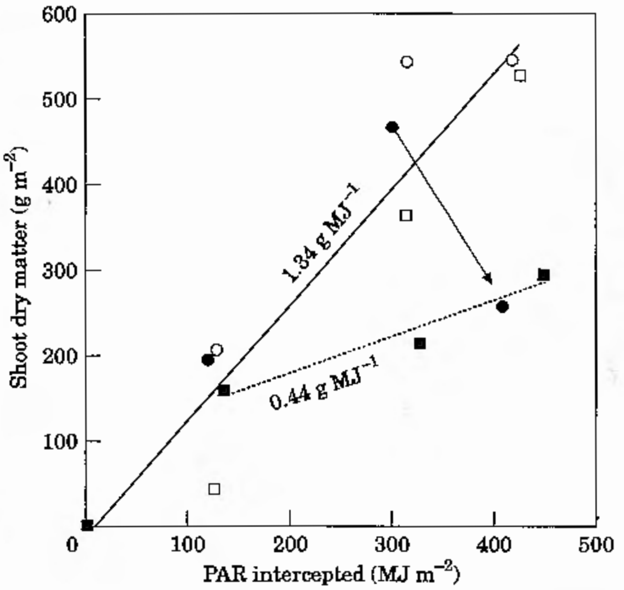


FIG. 7. Relationship between shoot dry matter and cumulative PAR interception as affected by mite infestation and water deficit. The solid line (slope = 1·34 g MJ^{-1}) was fitted to data from uninfested crops (−M−W, −M+W) and the dotted line (slope = 0·44 g MJ^{-1}) was fitted to +M−W data; the arrow indicates the drop in shoot dry matter of +M+W crops between 119 and 132 DAS (cf. Fig. 6C). □, −M−W; ○, −M+W; ■, +M−W; ●, +M+W.

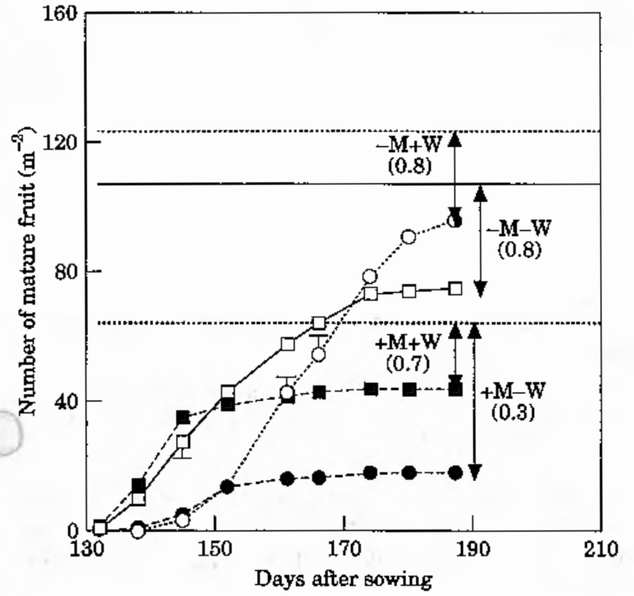


FIG. 8. Dynamics of mature fruit production as affected by mite infestation and water deficit. Horizontal lines show peak number of immature fruit, reached between 132 and 146 DAS. Numbers in parentheses are the ratio between total number of mature fruit at 187 DAS and peak fruit number. Error bars are one s.e.m. and were not plotted when smaller than symbols.

period, well watered, mite-infested plants (+M+W) had a much smaller fall in stem nitrogen concentration (from 1·3 to 0·98 %). Irrespective of mite treatments, stem nitrogen concentration of water-stressed plants (−W) declined sharply between 85 and 97 DAS ($P < 0\cdot 0001$). Thereafter, stem nitrogen concentration remained stable in −M−W plants while it increased in +M−W plants. Changes in nitrogen concentration in tap-roots were comparable to those in stems except for a less clear pattern in −M+W plants. At the end of the measurement period, and irrespective of water treatment, mite-infested plants had significantly ($P < 0\cdot 001$) greater nitrogen concentration in both stems and roots than uninfested plants.

Water deficit significantly reduced the nitrogen concentration of flowerbuds at 97 DAS ($P < 0\cdot 0001$) when the effect of mites was non-significant (Fig. 11A). At 132 DAS, nitrogen concentration of capsule walls was significantly increased by mites ($P < 0\cdot 0001$) and was reduced by water deficit in mite-infested but not uninfested plants (water effect: $P < 0\cdot 05$, interaction: $P < 0\cdot 01$). At 146 DAS, the trend was similar and the magnitude of these effects was more marked (all three factors significant at $P < 0\cdot 0001$) (Fig. 11A).

Seed nitrogen concentration increased from 3·4 % in −M+W controls to 4·2 % in all stressed treatments (Fig. 11B). In comparison to unstressed controls, seed oil concentration was moderately reduced by water deficit. Mites reduced seed oil concentration substantially and their effect was greater in water stressed crops than in well-watered ones. As a result of these changes in seed composition (Fig. 11B), the ratio between oil and N-compounds declined from 1·17 in controls (−M+W) to 0·96 in −M−W, 0·87 in +M−W and 0·76 in +M+W.

DISCUSSION

The aim of this study was to investigate the responses of cotton to the combined effects of mites and water deficit in the field. The methods used in this experiment allowed us to generate contrasting soil water contents in −W and +W plots 90 DAS (Fig. 1D), and substantial mite infestations in +M crops while maintaining negligible mite numbers in −M crops (Fig. 2A).

Effects of water-stressed cotton on mites

In comparison with unstressed host plants, the abundance of spider mites in water-stressed hosts can increase, decrease or remain unchanged (English-Loeb, 1989). Actual mite responses seem to depend on the intensity of water deficit experienced by the host plant (English-Loeb, 1989; 1990). Under our experimental conditions, cotton water status did not affect the abundance of adult female mites.

Further analysis of the effects of water-stressed cotton on mites requires details of life history, population dynamics and behaviour of mites (e.g. Smitley and Kennedy, 1985) that were beyond the scope of this study. Nonetheless, we will discuss three findings related to the growth and activity of mite colonies in water-stressed cotton namely: (*a*) the lack of effect of host-plant water status on the number of adult females (Fig. 2A); (*b*) the greater extent and intensity of injury per mite in well-watered plants (Figs 2B, C and 3); and (*c*) the preference of adult female mites for leaves from

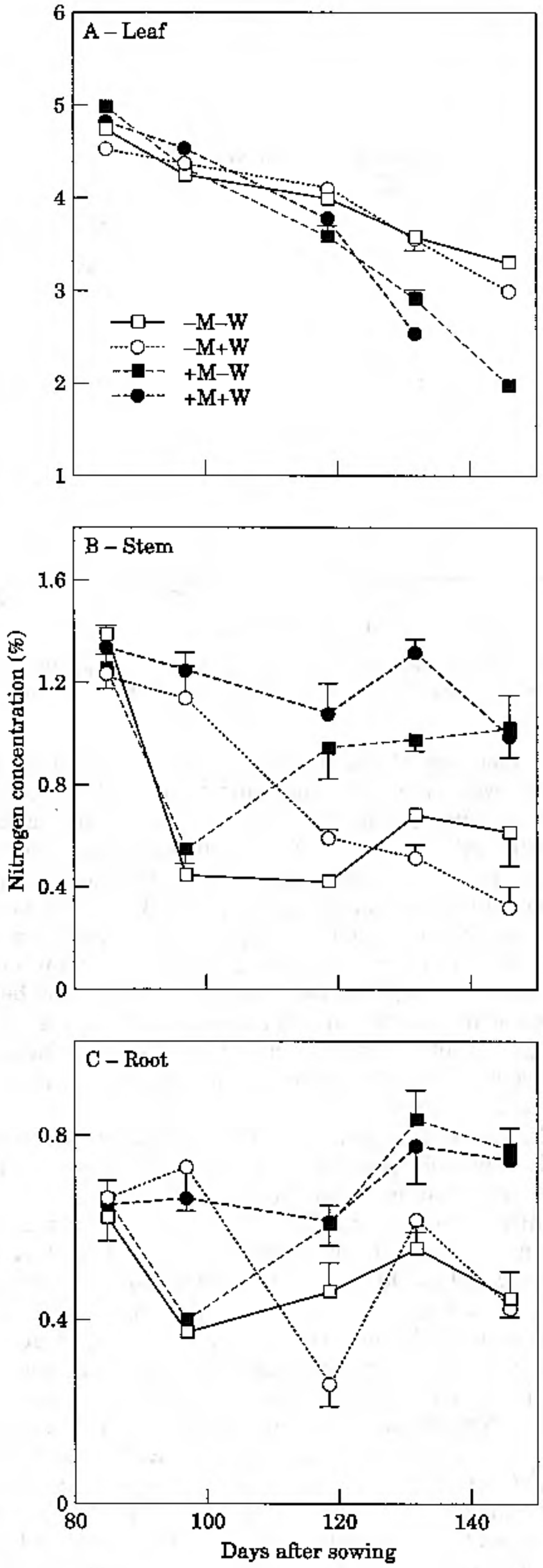


FIG. 10. Dynamics of nitrogen concentration in vegetative organs of cotton plants as affected by mite infestation and water deficit. Error bars are one s.e.m. and were not plotted when smaller than symbols.

leaves from well-watered plants (Table 1) reinforces the hypothesis that chemical and/or physical changes in cotton leaves due to water-stress made them less suitable for mites. Water-stressed leaves had greater penetration resistance than leaves from well-watered plants (Fig. 4), a factor that probably contributed to the greater damage on (Figs 2B, C and 3) and preference of mites for leaves from well-watered plants (Table 1). Jiang and Ridsdill-Smith (1996) also found a negative association between redlegged earth mite (*Halotydeus destructor* Tucker) feeding damage and penetration resistance of subterranean clover (*Trifolium subterraneum* L.) cotyledons. Causes of increased leaf penetration resistance in water-stressed plants and its consequences on herbivory are discussed further in the next section. Other changes induced by water deficit that may have reduced leaf suitability for mites include: (*a*) more, and qualitatively different, epicuticular waxes (Bondada *et al.*, 1996) that are known to influence herbivory (Eigenbrode and Espelie, 1995); and (*b*) changes in concentration of nutrients and of secondary metabolites in plant tissues, often invoked to explain differences in herbivore responses to host plant water status (Jones and Coleman, 1991).

Effects of mites and water deficit on cotton

Well-watered, uninfested crops maintained canopy temperature within the optimal 'window' of 23 to 32 °C (Fig. 4) (see Introduction). Transpirational cooling was restricted by water deficit and, as mite colonies grew, by mite infestation. As the intensity of both stresses increased through the season, interactions were increasingly significant. Likewise, leaf water potential was sequentially affected by water stress, mite infestation and by the interaction of both stresses (Table 2). For uninfested crops, or for infested crops with less than about 20 adult female mites per leaf, there was (*a*) a negative association between canopy temperature and leaf water potential (Table 2), similar to that found by Reddy, Hodges and McKinion (1997) and (*b*) a positive association between leaf water potential and leaf water content (Table 2) comparable to those reported previously (Jordan and Ritchie, 1971; Ackerson *et al.*, 1977). Mites decoupled these variables (Table 2) when their density was over 20 adult females per leaf, a threshold that coincides with that for RUE responses to mites in well-watered cotton (Sadras and Wilson, 1997*a*). Histological studies and details of leaf water relations are needed to elucidate the mechanisms of mite injury in water-stressed cotton, including physical damage, stomatal conductance as affected by both hydraulic and chemical root signals, and changes in leaf osmotic potential and turgor. Irrespective of the mechanisms, it is worth emphasizing that crops with both stresses were cooler and their leaf water potential was higher than expected from the additive effects of mites and water deficit.

Specific leaf weight usually increases with water stress (Wright *et al.*, 1996) in part because leaf expansion is more sensitive than photosynthesis to water deficit (Sadras and Milroy, 1996). Greater specific leaf weight is related, in some cases, to differences in the amount of cell wall material (Dijkstra, 1989). In our study, leaves from water stressed relocated from senescing leaves accounted for the increase in nitrogen concentration of stems, roots and reproductive organs of mite-infested plants (Figs 10 and 11) (Sadras and Wilson, 1997*c*). Despite changes in trajectory, final concentration of nitrogen in stems and roots was unaffected by water stress or the interaction between water and mite treatments. In contrast, significant effects of both water deficit and water × mite interaction were still evident 146 DAS for capsule walls (Fig. 11). The accelerated loss of leaf nitrogen and the nitrogen 'enrichment' in stems, roots and reproductive structures of mite-infested cotton can further affect mites and other herbivores (Sadras and Wilson, 1997*c*).

Mites can reduce cotton oil yield by reducing both seed mass and seed oil concentration (Sadras and Wilson, 1996). Reduction in seed oil concentration due to mite feeding was more severe in well-watered crops than in water-stressed ones (Fig. 11B) indicating again that mite damage was greater in well-watered plants.

CONCLUSIONS

th *Tetranychus urticae* infestation and water deficit had detrimental effects on several aspects of the water, carbon and nitrogen economies of cotton plants and crops. Under our experimental conditions, mites caused more damage to well-watered plants than to their water-stressed counterparts, i.e. mite-infested, well-watered plants had more extended and more intense symptoms of leaf injury, lower reproductive partitioning and lower lint yield than their water-stressed counterparts. The magnitude and consistency of the interaction between both stresses indicates that mechanisms of adjustment to water deficit may have enhanced cotton resistance to mites.

ACKNOWLEDGEMENTS

We thank J. Ridsdill-Smith and G. Constable for comments on the manuscript, M. Laird, D. O'Connor, D. Johnson and M. Mennell for their technical assistance, I. Rose for advice with oil measurements, D. Magann and his staff for crop husbandry and the Cotton Research and Development Corporation for financial support (grants CSP46C, P68C).

LITERATURE CITED

Ackerson RC, Krieg DR, Miller TD, Zartman RE. 1977. Water relations of field grown cotton and sorghum: temporal diurnal changes in leaf water, osmotic and turgor potentials. *Crop Science* **17**: 76–84.

Bondada BR, Oosterhuis DM, Murphy JB, Kim KS. 1996. Effect of water stress on the epicuticular wax composition and ultrastructure of cotton (*Gossypium hirsutum* L.) leaf, bract, and boll. *Environmental and Experimental Botany* **36**: 61–69.

Bondada BR, Oosterhuis DM, Tugwell NP, Kim KS. 1995. Physiological and cytological studies of two spotted spider mites, *Tetranychus urticae* K., injury in cotton. *Southwestern Entomologist* **20**: 171–180.

Burke JJ, Mahan JR, Hatfield JL. 1988. Crop specific thermal kinetic windows in relation to wheat and cotton biomass production. *Agronomy Journal* **80**: 553–556.

Chapin FS, Bloom AJ, Field CB, Waring RH. 1987. Plant responses to multiple environmental factors. *BioScience* **37**: 49–57.

Charles-Edwards DA, Lawn RJ. 1984. Light interception by grain legume row crops. *Plant, Cell and Environment* **7**: 247–251.

Coleman JS, McConnaughay KDM, Ackerly DD. 1994. Interpreting phenotypic variation in plants. *Trends in Ecology and Evolution* **9**: 187–191.

De Barro PJ. 1991. A cheap lightweight efficient vacuum sampler. *Journal of the Australian Entomological Society* **30**: 207–208.

Dijkstra P. 1989. Cause and effect of differences in specific leaf area. In: Lambers H, Cambridge ML, Konings H, Pons LT, eds. *Causes and consequences of variation in growth rate and productivity of higher plants*. The Hague: SPB Academic, 125–140.

Doss BD, Scarsbrook CE. 1969. Effect of irrigation on recovery of applied nitrogen by cotton. *Agronomy Journal* **61**: 37–40.

Eigenbrode SD, Espelie EK. 1995. Effect of plant epicuticular lipids on insect herbivores. *Annual Review of Entomology* **40**: 171–194.

English-Loeb GM. 1989. Nonlinear responses of spider mites to drought-stressed host plants. *Ecological Entomology* **14**: 45–55.

English-Loeb GM. 1990. Plant drought stress and outbreaks of spider mites: a field test. *Ecology* **71**: 1401–1411.

Flint HM, Wilson FD, Hendrix D, Leggett J, Naranjo S, Henneberry TJ, Radin JW. 1994. The effect of plant water stress on beneficial and pest insects including the pink bollworm and the sweetpotato whitefly in two short-season cultivars of cotton. *Southwestern Entomologist* **19**: 11–21.

Giyasov TD, Kluyuikova AI, Yakubova MM, Alekhina ND. 1992. Functioning of nitrate reductase in germinating cotton seedlings: effect of light and substrate availability. *Soviet Plant Physiology* **39**: 532–536.

Grace J. 1995. On the measurement of plant competition intensity. *Ecology* **76**: 305–308.

Hare JD, Pehrson JE, Clemens T, Youngman RR. 1989. Combined effects of differential irrigation and feeding injury by the citrus red mite (Acari: Tetranychidae) on gas exchange of orange leaves. *Journal of Economic Entomology* **82**: 204–208.

Hatfield JL, Burke JJ, Mahan JR, Wanjura DF. 1987. Foliage temperature measurements: a link between the biological and physical environment. *International Conference on Measurement of Soil and Plant Water Status. Centennial of Utah State University, July 6–10, 1987*. **2**: 99–102.

Hearn AB, Constable GA. 1984. Irrigation of crops in a sub-humid environment. VII. Evaluation of irrigation strategies for cotton. *Irrigation Science* **5**: 75–94.

Herron GA, Edge V, Wilson LJ, Rophail J. 1997. Organophosphate resistance in spider mites (Tetranychidae) from cotton in Australia. *Experimental and Applied Acarology* (in press).

Hochuli DF. 1996. The ecology of plant/insect interactions: implications of digestive strategy for feeding by phytophagous insects. *Oikos* **75**: 133–141.

Hsiao TC. 1990. Measurements of plant water status. In: Stewart BA, Nielsen DR, eds. *Irrigation of agricultural crops*. Madison: ASA, CSSA, SSSA, 244–279.

Idso SB, Reginato RJ, Farah SM. 1982. Soil- and atmopshere-induced plant water stress in cotton as inferred from foliage temperatures. *Water Resources Research* **18**: 1143–1148.

Jiang Y, Ridsdill-Smith TJ. 1996. Examination of the involvement of mechanical strength in antixenotic resistance of subterranean clover cotyledons to the redlegged earth mite (*Halotydeus destructor*) (Acarina: Penthaleidae). *Bulletin of Entomological Research* **86**: 263–270.

Jones CG, Coleman JS. 1991. Plant stress and insect herbivory: Toward an integrated perspective. In: Mooney HA, Winner WE, Pell EJ, eds. *Response of plants to multiple stresses*. New York: Academic Press, 249–280.

Jordan WR, Ritchie JT. 1971. Influence of soil water stress on evaporation, root absorption, and internal water status of cotton. *Plant Physiology* **48**: 783–788.

Kittock DL, Henneberry TJ, Bariola LA, Taylor BB, Hoffman WC. 1983. Cotton boll period response to water stress and pink bollworm. *Agronomy Journal* **75**: 17–20.

Kytö M, Nimelä P, Larsson S. 1996. Insects on trees: population and individual response to fertilisation. *Oikos* **75**: 148–159.

Recovery of Cotton Crops after Early Season Damage by Thrips (Thysanoptera)

Víctor O. Sadras* and Lewis J. Wilson

ABSTRACT

The objective of this study was to assess the ability of cotton (*Gossypium hirsutum* L.) crops to recover after early-season damage by thrips (Thysanoptera). Such information may help clarify the actual need to control thrips. Ten experiments, resulting from the combination of two to four sites per season and three seasons, were carried out in commercial crops in the irrigation area of northwest New South Wales, Australia. Two treatments were compared: unprotected crops and crops protected with aldicarb{2-methyl-2-(methylthio)propanal *O*-[(methylamino)carbonyl]oxime} at sowing. Early season thrips communities were dominated by *Thrips tabaci* Lindeman, which accounted for 52 to 100% of the total phytophagous thrips present in the crops. Insecticide treatment consistently reduced the number of larval thrips compared with the unprotected crops. Number of larval thrips per plant ranged from 0 to 24. Thrips reduced crop leaf area in six experiments, dry matter production in four experiments, and yield in two experiments. Maximum differences in leaf area and dry weight between treatments were found about 40 d after sowing. In all cases, crops damaged by thrips recovered well and reached leaf areas and dry weights similar to protected crops after about 60 to 80 d after sowing. On average, protected crops reached maturity 3 d earlier than crops damaged by thrips, but differences were not statistically significant. Despite large reductions in early growth, yield reductions due to thrips were found in only two experiments. The magnitude of the reduction in yield in those experiments (11%) contrasts with the magnitude of the reduction in growth (about 40%) and highlights the ability of the cotton crop to recover after early season damage by thrips.

Young cotton crops host a range of insect pests, including thrips (Thysanoptera) (Hearn and Fitt, 1992). Common species of phytophagous thrips in high-input cotton cropping systems include *Thrips tabaci* and *Frankliniella* spp. (USA: Quisenberry and Rummel, 1979; Australia: Wilson and Bauer, 1993; Israel: Atakan et al., 1996).

Leaf distortion, reduced leaf area and plant height, and growth delay are often observed in thrips-damaged cotton and, in cases of severe infestation, loss of vegetative buds and branching after release of apical dominance have been reported (e.g., Watts, 1937; Quisenberry and Rummel, 1979; Attique and Ahmad, 1990). Because of these effects, thrips have the potential to reduce yield and delay the maturity of cotton crops (e.g., Watts, 1937; Attique and Ahmad, 1990). However, growth reduction and tissue destruction are "rarely, if ever, translated monotonically into a proportional reduction of final yield" (McNaughton, 1983). This is due to tolerance (sensu Belsky et al., 1993) mechanisms that allow plants to recover after damage has occurred. The mechanisms of plant tolerance to herbivory have recently been reviewed by Belsky et al. (1993), Trumble et al. (1993), and Rosenthal and Kotanen (1994).

Thrips control can be achieved either by using insecticide-treated seed, in-furrow treatment with systemic insecticides, or by foliar applications of broad spectrum systemic insecticides (Wilson and Bauer, 1993). However, many thrips species are opportunistic predators of mite (Acari: Tetranychidae) eggs (Wilson et al., 1996). Furthermore, experiments in the field showed that suppression of *T. tabaci* and *F. schultzei* with broad spectrum insecticides contributed to mite outbreaks in cotton (Wilson et al., 1996). Wilson et al. (1996) concluded that "preservation of thrips for the management of spider mites may be beneficial, yet they may also sometimes warrant control in their own right, which poses a pest management dilemma".

To assist in solving this pest management problem, we assessed to what extent early reduction in growth due to thrips translates into yield reduction and/or delay in maturity. Emphasis has been placed on analyzing the effects of thrips on plant growth and the subsequent recovery of plants after damage.

MATERIALS AND METHODS

Crops and Treatments

Ten experiments were carried out on commercial farms in northwest New South Wales, Australia (Table 1). Crops were fully irrigated and fertilized with nitrogen (100–150 kg N ha^{-1}) according to current practices in the area. Sowing dates were close to the recommended date (mid October) and plant densities ranged from 7 to 14 plants m^{-2}. Cultivar 'Siokra S324' was used in 1993-1994, and 'Siokra V-15' in 1994-1995 and 1995-1996.

Two treatments were compared: unprotected crops and crops protected with aldicarb applied in the soil at sowing (0.45 kg ha^{-1}). Each experiment used a randomized block design with three or four replicates; each plot was between 0.5 and 0.8 ha. No synthetic insecticides were used before 60 d after sowing (DAS). During this period *Heliothis* spp. were controlled, when necessary, with formulations of *Bacillus thuringiensis* var. *kurstaki* which are not toxic to non-lepidoptera. Thereafter, both treatments were managed identically for pest control by accepted commercial thresholds (Shaw, 1995).

Thrips: Species Composition and Abundance

We monitored thrips populations during the period of thrips occurrence as pests, viz., from seedling emergence to about 60 DAS (Wilson and Bauer, 1993). At weekly intervals, cotton shoots ($n \geq 5$) were collected from each plot and taken to the laboratory where insects were removed using a plant washing machine (Leigh et al., 1984). Numbers of adult and larval thrips, and all other insects present in the samples, were recorded. Estimates of the species composition of thrips were obtained by identifying subsamples of adults from each sample

---

V.O. Sadras, Universidad Nacional de Mar del Plata, Facultad de Ciencias Agrarias, CC 276, Balcarce (7620), Argentina; L.J. Wilson, CSIRO Plant Industry, Locked Bag 59, Narrabri 2390, NSW, Australia. Received 25 Feb. 1997. *Corresponding author.

Published in Crop Sci. 38:399–409 (1998).

Abbreviations: DAS, days after sowing, LA:LDWT, slope of the regression between log$_e$ leaf area and log$_e$ leaf dry weight; LDWT:SDWT, slope of the regression between log$_e$ leaf dry weight and log$_e$ shoot dry weight; ULR, unit leaf rate.

Table 1. Season, site, and sowing date of field experiments. Time of maturity of protected and unprotected crops is also shown.

Season	Site†	Sowing date	Maturity (days after sowing)‡	
			Protected	Unprotected
1993–1994	Abbey Green (3)§	11 Oct	153	162
	Norwood (4)	02 Oct	162	168
	Oakville (4)	13 Oct	156	160
	Redmill (4)	08 Oct	151	151
1994–1995	Abbey Green (3)	11 Oct	–¶	–
	Norwood (4)	17 Oct	–	–
	Oakville (4)	10 Oct	–	–
	Redmill (4)	06 Oct	166	168
1995–1996	Kooiyong (4)	24 Oct	179	181
	Merrigal (4)	16 Oct	188	189

† Commercial farms in the Lower Namoi Valley (Abbey Green, Oakville), Upper Namoi Valley (Kooiyong, Merrigal), and in the Gwydir Valley (Norwood, Redmill) of New South Wales, Australia.

‡ 60% of open bolls. Differences between treatments were not significant ($P > 0.05$) in all experiments.

§ Number of replicates.

¶ Not measured.

date for each site. Wilson and Bauer (1993) found that for the main phytophagous species, the species composition of larval thrips closely followed that of adults. Adult thrips were slide mounted and identified by the keys of Mound (1967, 1972), Mound and Waker (1982, 1986), Mound et al. (1976), Pitkin (1973), Mound and Houston (1987), and Palmer et al. (1989).

Cotton Growth and Yield

Separate samples were collected for plant growth analysis. In 1993-1994, shoots were cut at ground level while plants were pulled and shoots and attached tap roots were collected in 1994-1995 and 1995-1996. Samples were taken at weekly intervals (sample size = 0.5 m^2 per replicate). Plant components were separated and oven-dried to constant weight. Green leaf area of at least two whole plants was measured with a leaf area meter (LI-3100, LI-COR, Inc., Lincoln, NE) to estimate specific leaf area, and this variable used to estimate plant leaf area from leaf dry matter values. Sequential hand harvests were done to determine time of maturity (i.e., 60% of open bolls, Snipes and Baskin, 1994) for all sites in 1993-1994, for Redmill only in 1994-1995 and for both sites in 1995-1996 (sample size = 2 m^2 per replicate). Cotton seed was machine harvested from a two or four row section through the complete length of each plot, and yield (seed + lint) determined with calibrated load cell scales.

Data Analyses

Response variables analyzed include (i) number of adult thrips, (ii) number of larval thrips, (iii) plant leaf area, (iv) shoot dry matter, (v) tap root dry matter, (vi) time of maturity, and (vii) yield. Effects of treatments were tested with analysis of variance (ANOVA) for each sampling date (variables i–v) and each experiment (all variables). Thrips numbers were $\log_e$ transformed before analyses.

Shoot relative growth rate and unit leaf rate (or "net assimilation rate") were calculated as in Evans (1972). Two allometric coefficients were calculated to explore relevant changes in partitioning due to thrips (i) LA:LDWT, the slope of the regression between $\log_e$ leaf area and $\log_e$ leaf dry weight, and (ii) LDWT:SDWT, the slope of the regression between $\log_e$ leaf dry weight and $\log_e$ shoot dry weight. Details and justification of this approach to analyze partitioning have been summarized by Coleman et al. (1994).

Table 2. Species composition of thrips on cotton crops.

Season	Site	n†	% Species			
			Thrips tabaci	*Frankliniella schultzei*	*Thrips imaginis*	Other‡
1993–1994	Abbey Green	107	82.2	3.7	0	14.1
	Norwood	88	85.2	10.2	1.1	3.5
	Oakville	57	63.1	36.8	0	0
	Redmill	66	51.5	28.8	0	19.7
1994–1995	Abbey Green	25	68.0	12.0	0	20.0
	Norwood	4	75.0	25.0	0	0
	Oakville	26	84.6	15.4	0	0
	Redmill	8	100.0	0	0	0
1995–1996	Kooiyong	24	95.8	4.2	0	0
	Merrigal	19	94.7	0	0	5.3

† Variation in number of adult thrips identified reflects, in part, their actual abundance; in 1994–1995 some samples were lost after thrips counting and before species identification.

‡ Non-phytophagous thrips.

RESULTS

Thrips Species

Consistent with previous studies (Wilson and Bauer, 1993), we found early-season thrips communities to be dominated by *T. tabaci* (Table 2). Averaged over all the sites and seasons, *T. tabaci* accounted for 80% of the total thrips species and for 89% of the phytophagous species. Thus, no attempt was made to separate thrips species in the following analyses where we use the term "thrips" to refer to communities dominated by *T. tabaci.*

1993-1994 Experiments

Intensity and timing of thrips infestation varied among sites (Fig. 1). The insecticide treatment consistently reduced the number of larval thrips at all sites but was less effective at reducing numbers of adult thrips. In unprotected controls, the maximum number of larvae per plant varied between 2 (Oakville) and 24 (Norwood). The time of peak larval numbers ranged from 24 DAS (Redmill) to 44 DAS (Norwood).

Insecticide treatments affected crop leaf area and dry matter accumulation (Fig. 2). Effects on leaf area normally preceded effects on dry matter. Early in the season, unprotected crops usually had less leaf area and dry weight than protected crops, with significant reductions often observed in the period from 20 to 60 DAS. After about 50 to 60 DAS, leaf area and dry matter of unprotected crops usually recovered to the levels of protected crops.

Yield of protected crops ranged from 2 to 5 Mg ha^{-1}. Treatment effects on yield were only significant at one of the four sites, where the unprotected crop yielded 11% less than the protected one (Table 3). Unprotected crops normally reached maturity later than protected controls but differences were not significant (Table 1).

1994-1995 Experiments

As in the 1993-1994 season, the intensity and timing of thrips infestation varied among sites. Insecticide treatment consistently reduced the number of larvae at all sites and had a marginal effect on adult thrips (Fig. 3). Number of larvae were negligible at Norwood, great-

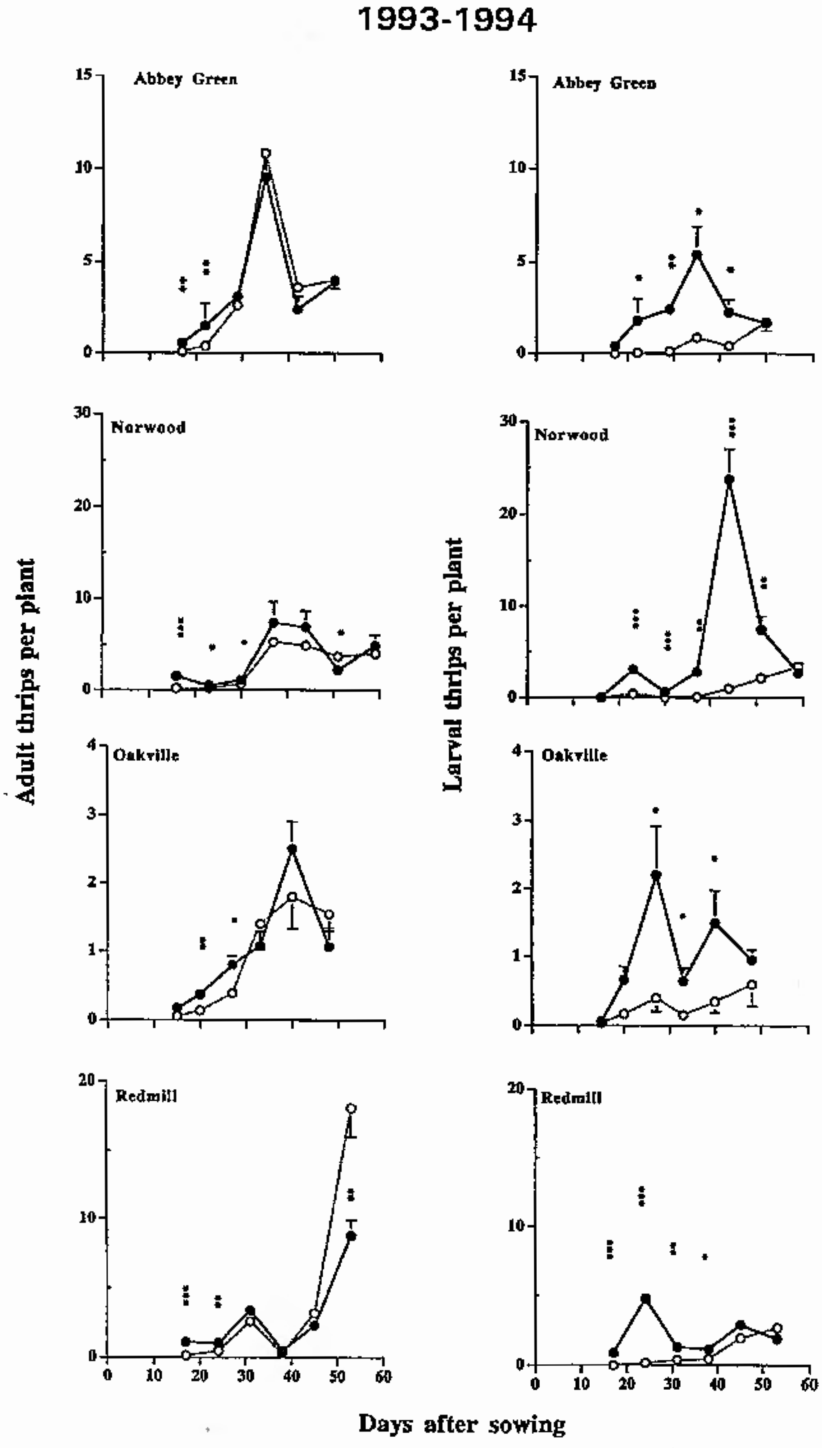


Fig. 1. Dynamics of thrips populations in four cotton crops during the 1993-1994 season. Closed symbols = unprotected crops, open symbols = protected crops. Levels of significance, from ANOVAs of $\log_e$-transformed variables, are: $P < 0.0001$ (***), $P < 0.01$ (**), $P < 0.05$ (*). Bars are one standard error of the mean and are not shown when smaller than symbols.

est at Abbey Green and Redmill and intermediate at Oakville (Fig. 3). Redmill was the only site where a significant number of thrips developed early in the season.

Insecticide treatment did not affect crop growth at Oakville, Abbey Green, or Norwood (not shown). Comparison between unprotected and protected crops at Redmill (Fig. 4) showed early season reductions in: leaf

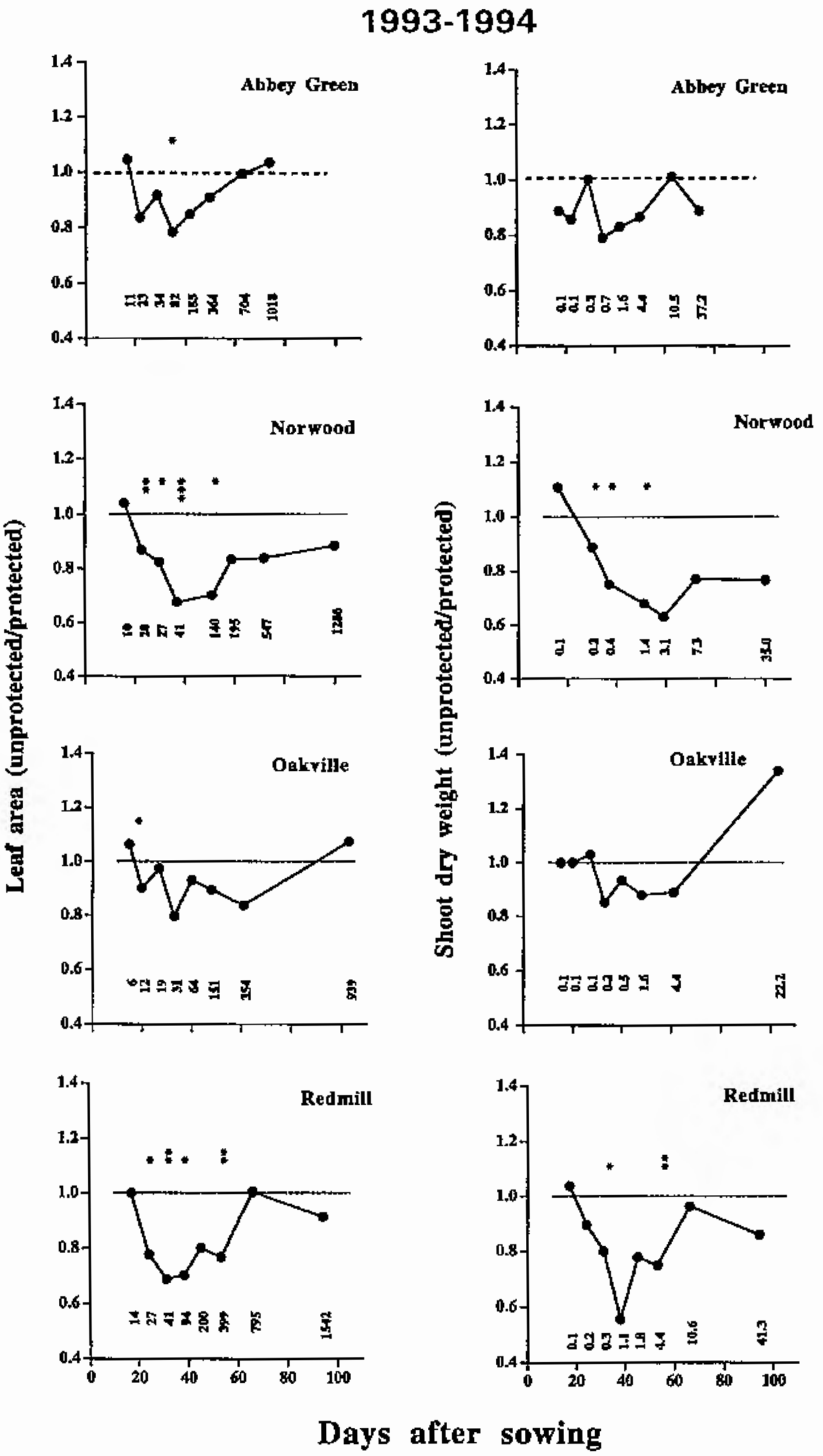


Fig. 2. Effect of insecticide treatment on leaf area and shoot growth of cotton at four sites in 1993-1994. The magnitude of treatment effect can be visualized as the divergence between the solid line and the $y = 1$ (dashed) line. Levels of significance, from ANOVAs comparing protected and unprotected treatments, are $P < 0.0001$ (***), $P < 0.01$ (**), $P < 0.05$ (*). Numbers below the plot are absolute values of protected crops in square centimeters per plant (leaf area) and grams per plant (shoot dry weight).

Table 3. Yield of cotton crops as affected by early-season thrips damage.

Experiment		Seed cotton (Mg ha^{-1})		P values from ANOVA
Season	Site	Protected	Unprotected	
1993–1994	Abbey Green	2.23	2.20	0.71
	Norwood	2.51	2.56	0.62
	Oakville	3.36	3.17	0.27
	Redmill	4.94	4.41	0.02
1994–1995	Abbey Green	5.15	4.95	0.30
	Norwood	6.25	6.22	0.82
	Oakville	4.89	4.57	0.21
	Redmill	5.46	4.88	0.05
1995–1996	Kooiyong	4.02	3.94	0.73
	Merrigal	3.87	3.89	0.90

area (up to 48% at 39 DAS), shoot dry weight (up to 43% at 48 DAS), and tap root dry weight (up to 59% at 53 DAS). At about 70 DAS, differences between protected and unprotected crops were no longer evident.

Yield of protected crops ranged from 5 to 6 Mg ha^{-1}. At Redmill, the unprotected crop yielded 11% less than the protected one; no effect of insecticide was found at any other site (Table 3). At Redmill, maturity was unaffected ($P > 0.6$) by insecticide treatment (Table 1).

1995-1996 Experiments

Again, insecticide treatment affected number of larvae markedly and number of adult thrips marginally. These effects were mostly evident at Merrigal, where thrips abundance was greater than at Kooiyong (Fig. 5). Insecticide treatments affected crop growth in Merrigal (Fig. 6) but not in Kooiyong (not shown). As in the previous seasons, treatments affected leaf area first, and then dry weight (Fig. 6). Despite severe growth reductions early in the season, unprotected crops recovered to the level of protected controls by about 80 DAS. Treatments did not affect maturity (Table 1, $P > 0.2$) nor yield (Table 3).

General Yield and Growth Responses to Insecticide Treatments

Fig. 7 shows the relationship between growth and yield, both expressed as the ratio between unprotected and protected treatments, for the 10 experiments in this study. No yield reductions were observed when shoot growth reductions early in the season were less than about 40%.

DISCUSSION

Effects of Insecticide Treatments on Thrips and Other Arthropods

Because of the high mobility of thrips, adults were found in both protected and unprotected crops in similar numbers (Fig. 1, 3, and 5). This probably reflects continuous influxes of adult thrips into the cotton crops as nearby spring hosts of thrips senesced (Wilson and Bauer, 1993). However, protected crops had consistently less larvae than unprotected crops (Fig. 1, 3, and 5), indicating that the insecticide treatment effectively reduced the colonization of crops by thrips. Despite the presence of adults in the protected treatment, there were no signs of damage to plants, indicating that the thrips probably died before causing visible injury to the crop.

Regular insect and mite counts in our study showed that aldicarb did not affect the abundance of beneficial arthropods or arthropod pests other than thrips (Wilson and Sadras, 1996, unpublished). Scott et al. (1985) in cotton cropping systems in the USA and Soares et al. (1996) in Brazil also found no effects of aldicarb on populations of beneficial arthropods.

Effects of Aldicarb on Crop Growth

Responses of crop growth (Fig. 2, 4, and 6), time of maturity (Table 1) and yield (Table 2) to insecticide treatment could be related to (i) effects of insecticide on arthropods other than thrips (see previous section), (ii) direct effects of insecticide on plant growth, and/or (iii) effects of insecticide on thrips.

In the absence of insects, mites and nematodes, aldicarb can increase, reduce or have no effect on plant growth (Womack and Schuster, 1986; Barker and Powell, 1988; Barker et al., 1988). In reviewing the effects of aldicarb on cotton growth, Terry (1992) highlighted the inconsistency of the responses; genotype, soil type, fertility, and soil moisture are among the factors that can influence plant responses to aldicarb (Barker and Powell, 1988; Barker et al., 1988). The inconsistent responses of plant growth to aldicarb are in sharp contrast to the consistent pattern of plant growth of unprotected and aldicarb-protected plants found in our study despite the environmental variation derived from a combination of locations and seasons (Fig. 2, 4, and 6). It is worth emphasizing the contrast between the cooler environment of the Upper Namoi Valley (Kooiyiong, Merrigal) where protected crops reached maturity at 179 to 188 DAS in comparison with the warmer Lower Namoi and Gwydir Valleys where crops reached maturity at 151 to 162 DAS (Table 1).

Thus, even though direct effects of aldicarb cannot be discarded, it is very unlikely that the pattern of plant growth in the present experiments could be due to direct effects of aldicarb. It is reasonable to assume, therefore, that the differences in growth and yield between protected and unprotected crops were mostly mediated by the effects of aldicarb on thrips. This premise is further supported by (i) the correspondence between thrips dynamics (Fig. 1, 3, and 5) and plant growth dynamics (Fig. 2, 4, and 6), and (ii) the known effects of thrips in reducing leaf area (see Introduction) and the sequence of responses whereby unprotected crops usually had reductions in leaf area preceding significant growth reductions (Fig. 2, 4, and 6).

Effects of Thrips on Crop Growth, Maturity and Yield

In six out of 10 experiments, thrips significantly affected cotton leaf area (Fig. 2, 4, and 6). Reductions in leaf area translated into growth reductions in four of

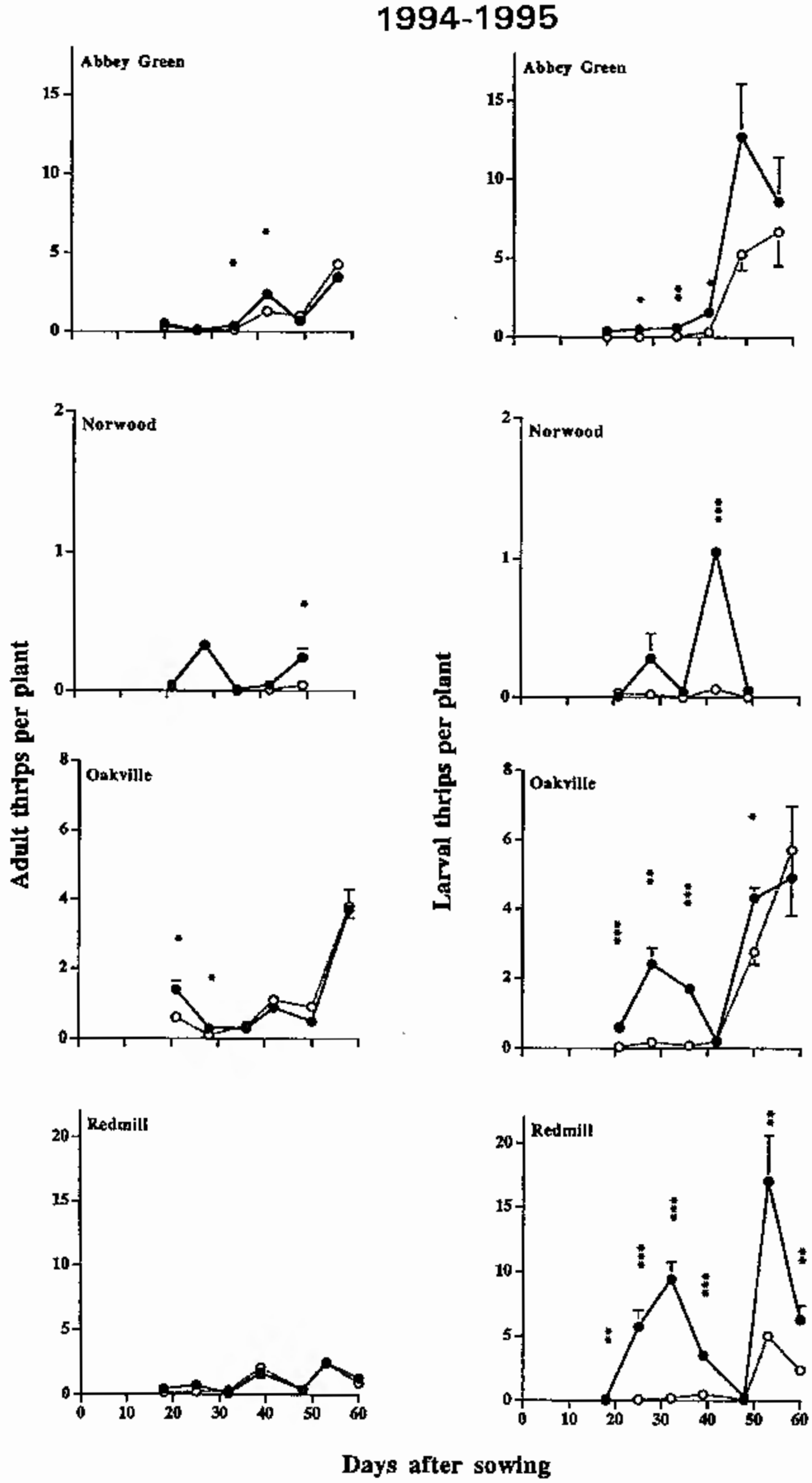


Fig. 3. Dynamics of thrips populations in four cotton crops during the 1994-1995 season. Closed symbols = unprotected crops, open symbols = protected crops. Levels of significance, from ANOVAs of $\log_e$-transformed variables, are $P < 0.0001$ (***), $P < 0.01$ (**), $P < 0.05$ (*). Bars are one standard error of the mean and are not shown when smaller than symbols.

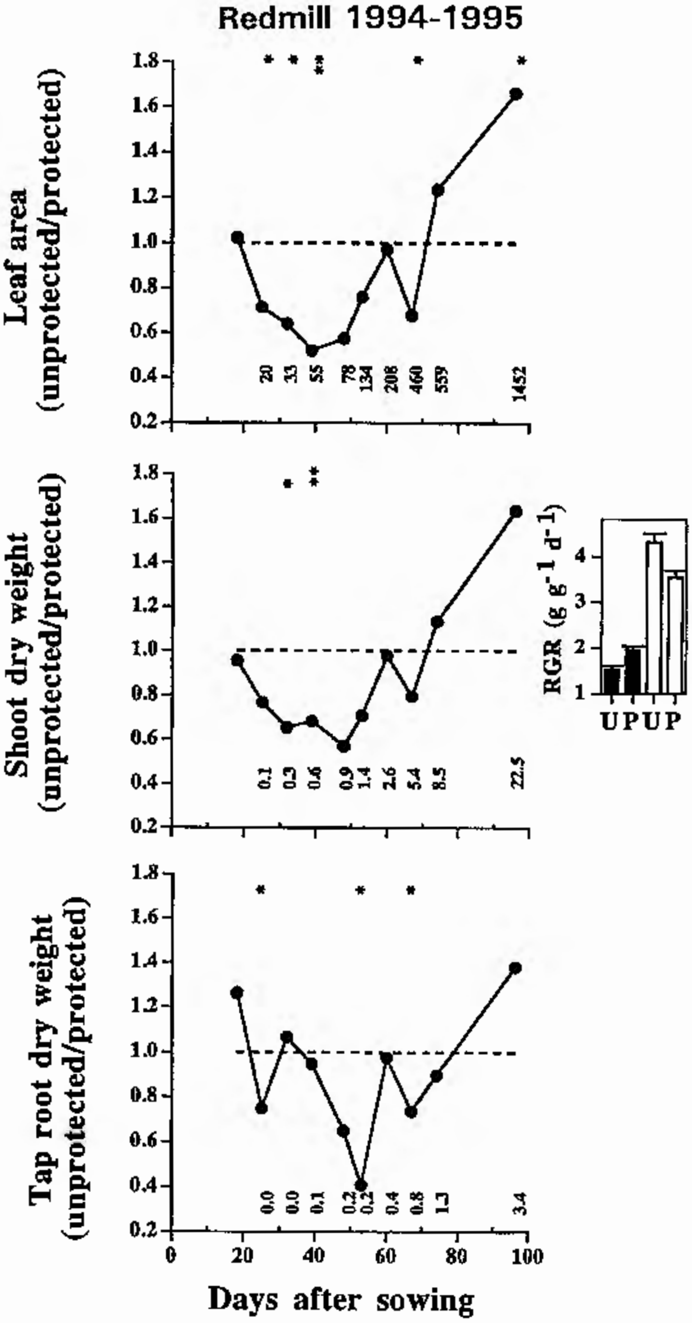


Fig. 4. Effects of insecticide treatment on leaf area, shoot and tap root growth of cotton at Redmill in 1993-1994. The magnitude of treatment effect can be visualized as the divergence between the solid line and the $y = 1$ (dashed) line. Levels of significance, from ANOVAs comparing protected and unprotected treatments, are $P < 0.01$ (**), $P < 0.05$ (*). Numbers below the plot are absolute values of protected crops in square centimeters per plant (leaf area) and grams per plant (shoot and root dry weight). Inset shows relative growth rates of unprotected (U) and protected (P) shoots during the period 18 to 48 DAS (closed bars) and 48 to 96 DAS (open bars). Bars are one standard error of the mean.

the 10 experiments (Fig. 2, Norwood and Redmill, Fig. 4 and 6). Reductions in growth translated into reductions in yield in only two cases (Fig. 7, Table 3). Thus, the general statement by McNaughton (1983), that tissue destruction is rarely translated into a proportional yield reduction, seems to be valid for the cotton-thrips system under study.

The dynamics of leaf area, expressed as the ratio between unprotected and protected treatments, showed a biphasic pattern (Fig. 2, 4, and 6). In the first phase, protected crops grew faster than unprotected crops, and the ratio declined consistently. A minimum value of the ratio, ranging from 0.8 to 0.5, was usually reached by 40 DAS. In the second phase, leaf area in crops damaged by thrips increased faster than in protected crops, and significant differences between treatments were not evi-

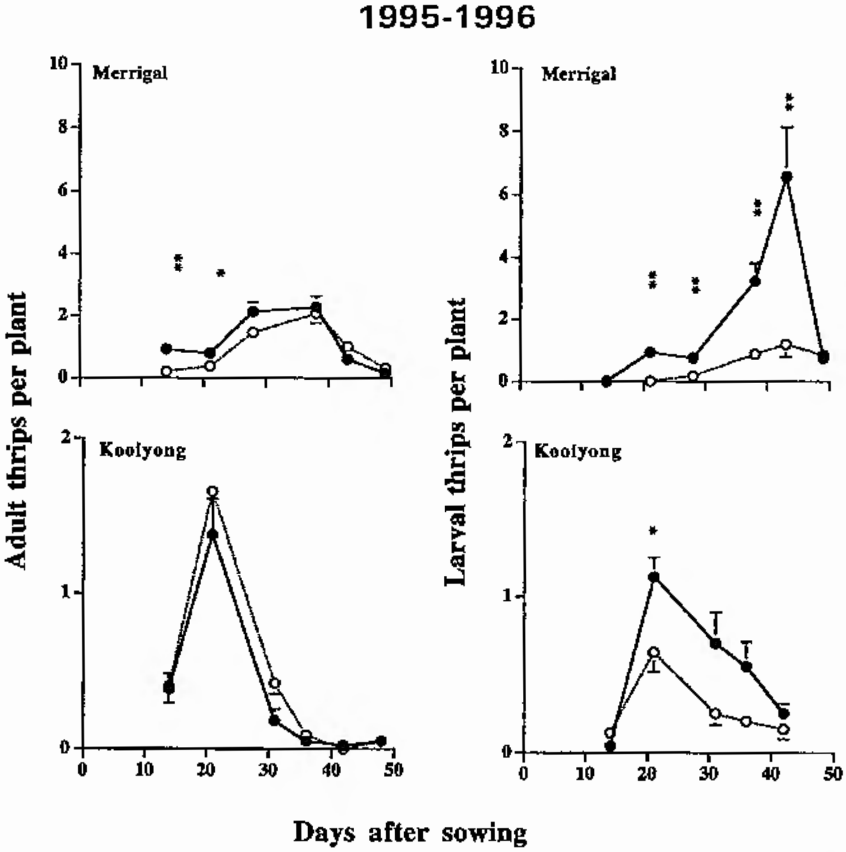


Fig. 5. Dynamics of thrips populations in two cotton crops during the 1995-1996 season. Closed symbols = unprotected crops, open symbols = protected crops. Levels of significance, from ANOVAs of log$_e$-transformed variables, are $P < 0.01$ (**), $P < 0.05$ (*). Bars are one standard error of the mean and are not shown when smaller than symbols.

dent after about 60 to 80 DAS. A similar biphasic pattern, that was displaced in time by about 5 to 10 d, was observed for shoot and tap-root growth. This pattern is further illustrated by the insets of Fig. 4 and 6: a first phase, in which protected crops had higher relative growth rates than their unprotected counterparts was followed by a phase in which the opposite was true. The capacity of cotton plants to recover after substantial reductions in leaf area caused by thrips, found in this study (Fig. 2, 4, and 6), is consistent with other studies involving leaf area loss in this species (e.g., Lane, 1959; Gutierrez et al., 1975).

Four main mechanisms could be involved in plant recovery after reduction in leaf area. First, changes in partitioning, viz., increase in leaf area : leaf weight ratio and/or increase in leaf weight : shoot weight ratio could increase the relative growth rate of damaged plants. Second, new leaf addition can partially compensate for leaf loss due to insects (Lane, 1959; Bishop et al., 1978). Third, if leaves are involved in apical dominance (Töpperwein, 1993), then enhanced branching following leaf damage may also be a factor in the recovery of damaged crops. Fourth, there may be an increase in the photosynthetic rate of undamaged leaves in a damaged plant and/or in undamaged areas of damaged leaves, i.e., compensatory photosynthesis (Trumble et al., 1993). Our data allowed investigation of the first and, to some extent, the fourth mechanism.

Allometric analysis was used to explore relevant changes in partitioning during the first (i.e., growth reduction) and second (i.e., recovery) phases of cotton responses to thrips defined before. The consistent and substantial reduction in LA:LDWT caused by thrips in the first phase (Table 4) indicates that leaf expansion was more severely reduced than leaf dry matter accumulation. Reduction in export of carbohydrates from leaves damaged by thrips might also have contributed to reductions in LA:LDWT. Effects of thrips on LDWT:SDWT in this phase were small and inconsistent (Table 4). In the recovery phase, both LA:LDWT and LDWT:SDWT were consistently higher in crops damaged by thrips than in their protected counterparts (Table 4). Although differences between treatments were small (≤8%), small changes in dry matter partitioning may have a large impact on subsequent plant growth (Körner, 1991). Thus, an increased partitioning to photosynthetic tissue may have contributed to the recovery of damaged crops.

Unit leaf rate was reduced by thrips in the first phase (Table 4). Hence, thrips may have reduced dry matter accumulation of young cotton crops by reducing not only leaf area but also photosynthetic rate. Unit leaf

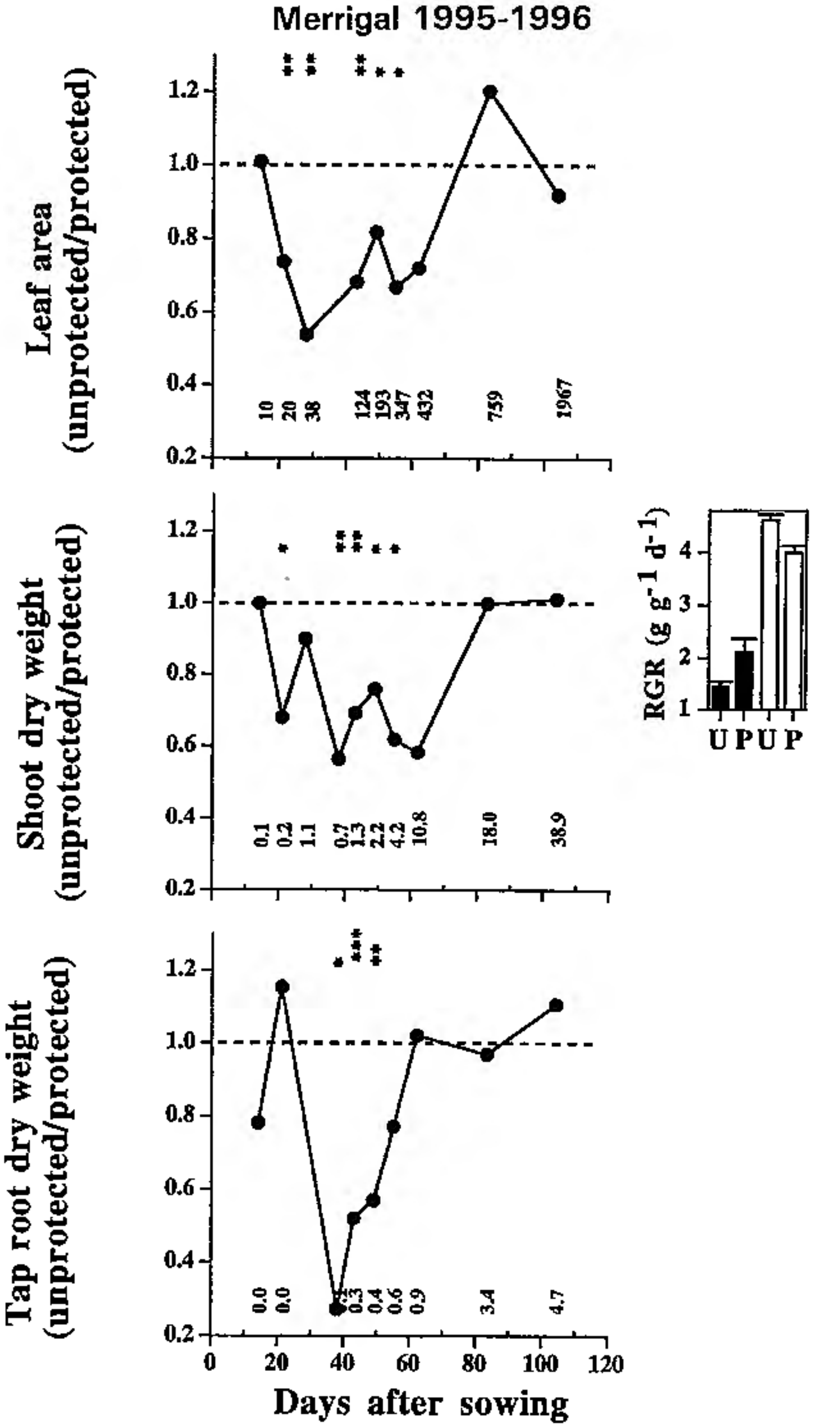


Fig. 6. Effects of insecticide treatment on leaf area, shoot and tap root growth of cotton at Merrigal in 1993-1994. The magnitude of treatment effect can be visualized as the divergence between the solid line and the $y = 1$ (dashed) line. Levels of significance, from ANOVAs comparing protected and unprotected treatments, are: $P < 0.0001$ (***), $P < 0.01$ (**), $P < 0.05$ (*). Numbers below the plot are absolute values of protected crops in square centimeters per plant (leaf area) and grams per plant (shoot and root dry weight). *Inset* shows relative growth rates of unprotected (U) and protected (P) shoots during the period 14 to 38 DAS (closed bars) and 38 to 104 DAS (open bars). Bars are one standard error of the mean.

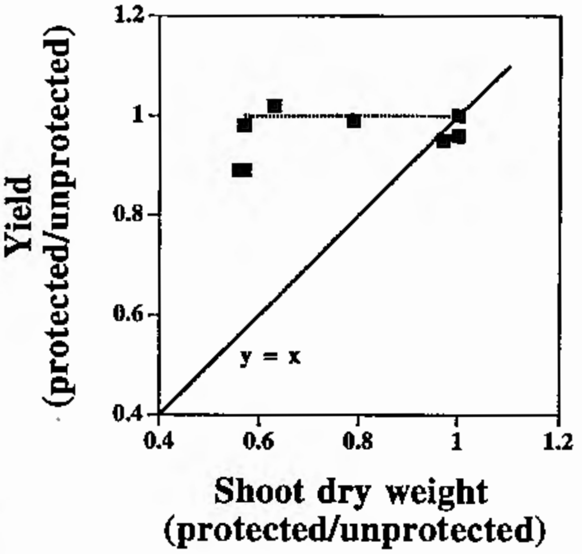


Fig. 7. Comparison of yield and shoot growth responses to thrips in 10 field experiments. Both variables are expressed as ratios between protected and unprotected crops. For shoot dry weight, the lowest ratio found in each experiment was used. The horizontal line joins data points from experiments where insecticide treatment did not affect yield (Table 3).

rate of crops damaged by thrips increased with respect to protected controls during the recovery phase in three out of four experiments (Table 4). Compensatory photosynthesis could therefore be a factor in the recovery of these crops. However, owing to limitations associated with the calculation of unit leaf rate (Evans, 1972; Monteith, 1994) our conclusions about putative effects of thrips on cotton photosynthesis should be considered with care. Direct measurements of leaf and/or crop photosynthesis are required to further assess these effects.

Implications for Pest Management

Key pests are those that are persistent, occur perennially, and usually reach economically damaging levels (Hearn and Fitt, 1992). For cotton in Australia, thrips clearly meet the first two criteria as they are often found in significant numbers in young crops (Fig. 1,3, 5; Wilson et al., 1994). Similarly, early-season thrips infestations are common in cotton crops in the USA (e.g., Quisenberry and Rummel, 1979). The economic impact of thrips is less clear, however. We found yield reductions attributable to thrips in two out of 10 field experiments. Similarly, we found significant yield reductions in one out of seven experiments carried out in commercial farms in 1991-1992 and 1992-1993 (Wilson et al., 1994). The same picture arises for the peanut-thrips system in southeastern USA: *Frankliniella fusca* (Hinds) cause early-season foliar injury which often leads to stunting of peanut plants, but the economic justification for thrips suppression remains controversial and, in general, controlling thrips is not recommended (Brecke et al., 1996).

Although thrips had only minor effects on yield and maturity in the present study (Tables 1 and 2) and in previous experiments (Wilson et al., 1994), they reduced seedling growth dramatically (Fig. 2, 4, and 6). Given the contrasting visual aspect of healthy protected crops and typically stunted crops damaged by thrips, the perception of growers that thrips need to be controlled is understandable. The use of insecticides for "cosmetic" reasons has a number of side effects, however. First, it may reduce the number of beneficial arthropods early in the season, interfering with the implementation of integrated pest management programs. Second, it eliminates "phytophagous" thrips of cotton crops that are, in fact, facultative predators of twospotted spider mites (Wilson et al., 1996). Spider mites are an important secondary pest of cotton crops and have the potential to reduce severely lint yield, oil yield, and fiber quality (Wilson, 1993; Sadras and Wilson, 1996, 1997).

The quantification of thrips/yield relationships and development of thresholds for thrips management require experiments that cover a wider range of thrips densities. Our study has shown, however, the significant ability of cotton to recover after severe growth reduction caused by thrips. This observation, together with recognition of the negative side effects of using insecticides for thrips control, could assist in the rational assessment of the actual need to use insecticides for their control.

ACKNOWLEDGMENTS

We thank each of the co-operators, Steve, Andrew, and Elliot Benham, Jeremy Killen, Mike Logan, Steve Brown, John Mohr-Bell, Peter Glennie, Kylie May, Jeff Carolan, Phil Warmoll, and their staff for their interest in this research and

Table 4. ULR, LA:LDWT, and LDWT:SDWT in experiments where thrips reduced crop growth. ULR, unit leaf rate, was calculated using eq. 16.9.2 of Evans (1972), LA:LDWT is the slope of the regression between $\log_e$ leaf area and $\log_e$ leaf dry weight, and LDWT:SDWT is the slope of the regression between $\log_e$ leaf dry weight and $\log_e$ shoot dry weight.

		ULR ($g\ m^{-2}\ d^{-1}$)				LA:LDWT ($cm^2\ g^{-1}$)				LDWT:SDWT ($g\ g^{-1}$)			
Experiment	**Treat.†**	**Phase 1‡**	**Δ%¶**	**Phase 2**	**Δ%**	**Phase 1**	**Δ%**	**Phase 2**	**Δ%**	**Phase 1**	**Δ%**	**Phase 2**	**Δ%**
Redmill 1993–1994	P	9.2 ± 2.16§		10.5 ± 0.99		0.83 ± 0.030		0.92 ± 0.014		0.99 ± 0.013		0.79 ± 0.019	
	U	7.0 ± 0.90	−24	11.2 ± 1.16	+7	0.64 ± 0.054	−23	0.93 ± 0.035	+1	1.01 ± 0.022	+2	0.82 ± 0.017	+4
Norwood 1993–1994	P	8.5 ± 0.48		9.9 ± 1.07		0.79 ± 0.030		0.93 ± 0.014		0.89 ± 0.009		0.82 ± 0.017	
	U	8.1 ± 0.69	−5	9.1 ± 0.42	−8	0.45 ± 0.021	−43	1.00 ± 0.019	+8	0.89 ± 0.008	0	0.85 ± 0.014	+4
Redmill 1994–1995	P	6.1 ± 1.24		7.6 ± 1.52		1.00 ± 0.070		1.02 ± 0.022		0.98 ± 0.050		0.87 ± 0.013	
	U	5.5 ± 1.55	−10	10.3 ± 1.54	+35	0.75 ± 0.093	−25	1.06 ± 0.022	+4	0.94 ± 0.050	−4	0.89 ± 0.014	+2
Merrigal 1995–1996	P	5.7 ± 1.23		5.9 ± 0.33		0.43 ± 0.080		0.89 ± 0.020		1.01 ± 0.060		0.82 ± 0.018	
	U	3.1 ± 0.51	−46	6.8 ± 0.73	+15	0.23 ± 0.060	−47	0.93 ± 0.026	+4	0.94 ± 0.030	−7	0.83 ± 0.015	+1

† Treatments are protected with insecticide (P) and unprotected (U).

‡ Two phases were distinguished in the responses of cotton to thrips: Phase 1, growth reduction, and Phase 2, recovery. See text for details.

§ SE.

¶ $\Delta\% = 100(U - P)/P$.

their willingness to provide experimental sites and to assist with crop management. We also thank P. Walker and R. Mensah for comments on the manuscript; D. Lally, S. Warden, G. Nehrkon, M. Hickman, L. Bauer, T. Staines, M. Laird, and L. Gett for technical assistance; D. Lally for thrips identification; and the Cotton Research and Development Corporation for financial support (grants CSP46C, CSP39C, CSP68C).

REFERENCES

Atakan, E., M. Coll, and D. Rosen. 1996. Within-plant distribution of thrips and their predators: effects of cotton variety and developmental stage. Bull. Entomol. Res. 86:641–646.

Attique, M.R., and Z. Ahmad. 1990. Investigation of *Trips tabaci* Lind. as a cotton pest and the development of strategies for its control in Punjab. Crop Protection 9:469–473.

Barker, K.R., and N.T. Powell. 1988. Influence of aldicarb on the growth and yield of tobacco. J. Nematol. 20:432–438.

Barker, K.R., S.R. Koenning, A.L. Bostian, and A.R. Ayers. 1988. Growth and yield responses of soybean to aldicarb. J. Nematol. 20:432–438.

Belsky, A.J., W.P. Carson, C.L. Jensen, and G.A. Fox. 1993. Overcompensation by plants: Herbivore optimization or red herring? Evol. Ecol. 7:109–121.

Bishop, A.L., P.R.B. Blood, R.E. Day, and J.P. Evenson. 1978. The distribution of cotton looper (*Anomis flava* Fabr.) larvae and larval damage on cotton and its relationship to the photosynthetic potential of cotton leaves at the attack sites. Aust. J. Agric. Res. 29: 319–325.

Brecke, B.J., J.E. Funderbuk, I.D. Teare, and D.W. Gobert. 1996. Interaction of early-season herbicide injury, tobacco thrips injury, and cultivar on peanut. Agron. J. 88:14–18.

Coleman, J.S., K.D.M. McConnaughay, and D.D. Ackerly. 1994. Interpreting phenotypic variation in plants. Trends Ecol. Evol. 9:187–191.

Evans, G.C. 1972. The quantitative analysis of plant growth, vol. 1. Blackwell Scientific Publications, Oxford.

Gutierrez, A.P., L.A. Falcon, W. Loew, P.A. Leipzig, and R. van der Bosch. 1975. An analysis of cotton production in California: A model for Acala cotton and the effects of defoliators on yield. Environ. Entomol. 4:125–136.

Hearn, A.B., and G.P. Fitt. 1992. Cotton Cropping Systems. p. 85–142. *In* C.J. Pearson (ed.) Field crop ecosystems. Elsevier, Amsterdam.

Körner, C. 1991. Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. Funct. Ecol. 5: 162–173.

Lane, H.C. 1959. Simulated hail damage experiments in cotton. Texas Agricultural Expt. Station Bulletin 934.

Leigh, T.F., V.L. Maggi, and L.T. Wilson. 1984. Development and use of a machine for the recovery of arthropods from plant leaves. J. Econ. Entomol. 77:271–276.

McNaughton, S.J. 1983. Compensatory plant growth as a response to herbivory. Oikos. 40: 329–336.

Monteith, J.L. 1994. Principles of resource capture by crop stands. p. 1–15. *In* J. L. Monteith et al. (ed.) Resource capture by crops. Proc 52nd Easter School, Univ of Nottingham, School of Agriculture. Nottingham Univ. Press, Nottingham, UK.

Mound, L.A. 1967. A taxonomic revision of the Australian Aeolothripidae (Thysanoptera). Bull. Brit. Mus. (Nat. Hist.) (Entomol.). 20:41–74.

Mound, L.A. 1972. Further studies on Australian Aeolothripidae (Thysanoptera). J. Aust. Entomol. Soc. 11:37–54.

Mound, L.A., and K.J. Houston. 1987. An annotated check-list of Thysanoptera from Australia. Occas. Pap. Systematic Entomol. 4:1–28.

Mound, L.A., and A.K. Walker. 1982. Terebrantia (Insecta: Thysanoptera). Fauna NZ 1:1–113.

Mound, L.A., and A.K. Walker. 1986. Tubulifera (Insecta: Thysanoptera). Fauna NZ 10:1–140.

Mound, L.A., G.D. Morison, B.R. Pitkin, and J.M. Palmer. 1976. Thysanoptera. p. 1–79. *In* A. Watson (ed.) Handbooks for the identification of British insects. Royal Entomological Society of London, London.

Palmer, J.M., L.A. Mound, and G.J. Du Heaume. 1989. Thysanoptera. p. 1–77. *In* C. R. Bretts (ed.) CIE guides to insects of importance to man, vol. 2. CAB International, Wallingford, UK.

Pitkin, B.R. 1973. A revision of the Australian Haplothripini, with descriptions of three new species (Thysanoptera: Phlaeothripidae). J. Aust. Entomol. Soc. 12:315–339.

Quisenberry, J.E., and D.R. Rummel. 1979. Natural resistance to thrips injury in cotton as measured by differential leaf area reduction. Crop Sci. 19:879–881.

Rosenthal, J.P., and P.M. Kotanen. 1994. Terrestrial plant tolerance to herbivory. Trends Ecol. Evol. 9:145–148.

Sadras, V.O., and L.J. Wilson. 1997. Growth analysis of cotton crops infested with spider mites. II. Partitioning of dry matter. Crop Sci. 492–497.

Sadras, V.O., and L.J. Wilson. 1996. Effect of timing and intensity of spider mite infestation on the oil yield of cotton crops. Aust. J. Exp. Agric. 36:577–580.

Scott, W.P., J.W. Smith, and G.L. Snodgrass. 1985. Response of cotton arthropod populations in cotton to various dosages of aldicarb applied in the furrow at planting. J. Econ. Entomol. 78:249–257.

Shaw, A.J. 1995. Cotton pesticides guide 1995-96. NSW Agriculture Agdex 151/680.

Snipes, C.E., and C.C. Baskin. 1994. Influence of defoliation on cotton yield, seed quality, and fiber properties. Field Crops Res. 37: 137–143.

Soares, J.J., A.C. Busoli, and F.T. Tanagaw. 1996. Efeito de aldicarb em populacoes de pulgao em artropodes beneficos e na fisiologia do algodoneiro. Pesquisa Agropecuaria Brasileira 31:549–554.

Terry, L.I. 1992. Effect of early season insecticide use and square removal on fruiting patterns and fiber quality of cotton. J. Econ. Entomol. 85:1402–1414.

Töpperwein, H. 1993. Relationships in the apical region of angiosperms. Angew. Bot. 67:22–30.

Trumble, J.T., D.M. Kolodny-Hirsh, and I.P. Ting. 1993. Plant compensation for arthropod herbivory. Annu. Rev. Entomol. 38: 93–119.

Watts, J.G. 1937. Reduction of cotton yield by thrips. J. Econ. Entomol. 30:860–863.

Wilson, L.J. 1993. Spider mites (Acari:Tetranychidae) affect yield and fiber quality of cotton. J. Econ. Entomol. 86:566–585.

Wilson, L.J., and L.R. Bauer. 1993. Species composition and seasonal abundance of thrips (Thysanoptera) on cotton in the Namoi Valley. J. Aust. Entomol. Soc. 32:187–192.

Wilson, L.J., V.O. Sadras, and L. Bauer. 1994. Effects of thrips on growth, maturity and yield of cotton—Preliminary results. p. 113–120. Proc. 7th Australian Cotton Conference, Broadbeach, Australia. 10–12 Aug. 1994. Australian Cotton Growers Research Association, Wee Waa, N.S.W. Australia.

Wilson, L.J., L.R. Bauer, and G.H. Walter. 1996. "Phytophagous" thrips are facultative predators of two spotted spider mites (Acari: Tetranychidae) on cotton in Australia. Bull. Entomol. Res. 86: 297–305.

Womack, C.L., and M.F. Schuster. 1986. Testing the reported positive growth response for cotton, *Gossypium hirsutum*, treated with aldicarb. J. Econ. Entomol. 79: 1118–1120.

ELSEVIER

Field Crops Research 56 (1998) 287–299

Field Crops Research

Herbivory tolerance of cotton expressing insecticidal proteins from *Bacillus thuringiensis*: responses to damage caused by *Helicoverpa* spp. and to manual bud removal

V.O. Sadras *

CSIRO Plant Industry, Locked Bag 59, Narrabri, NSW 2390, Australia

Received 26 June 1997; revised 19 August 1997; accepted 29 August 1997

Abstract

Transgenic cotton varieties expressing Cry IA(c) insecticidal proteins from *Bacillus thuringiensis* ('Bt cotton') remain vulnerable to non-lepidopteran insects. In addition, they are susceptible to lepidopteran pests when the efficacy of Bt toxins fails because of ontogenetic and/or environmental factors. Hence the importance of knowing to what extent Bt cotton is able to tolerate damage. The degree of tolerance of Bt cotton to actual and simulated insect damage was assessed in three field experiments. Exp. 1 compared the effects of *Helicoverpa* spp. (Lepidoptera: Noctuidae) on the growth, development and yield of Bt cotton with those of its near isogenic non-Bt counterpart in two genetic backgrounds (Siokra V15, Sicala V2) under two regimes of chemical control of insects (S1: nine insecticide applications during the growing cycle, S2: six insecticide applications). Exp. 2 compared insecticide-protected Bt crops with crops manually damaged to simulate (a) early-season loss of vegetative buds, (b) loss of flowerbuds, and (c) loss of both vegetative and reproductive buds. Also using manual damage, Exp. 3 evaluated the effect of timing of flowerbud loss on the yield and maturity time of insecticide-protected Bt crops. In Exp. 1, well-protected Bt crops (S1) yielded 24% more than their less-protected counterparts (S2). The less protected crops had, however, substantially more immature fruit at the end of the season highlighting a considerable potential for recovery. Poor soil conditions, interacting with season length accounted for the difference between potential and actual compensation in crops that were exposed to almost continuous damage by *Helicoverpa* spp. Under more favourable growing conditions, maturity was delayed but yield of damaged Bt crops was unaffected by discrete episodes of simulated herbivory (Exps. 2 and 3). The introduction of *B. thuringiensis* genes into cotton does not seem to have reduced the considerable capacity of the crop to tolerate insect damage, and this attribute should be considered in the development of pest management strategies for Bt crops. © 1998 Elsevier Science B.V.

Keywords: Herbivory; Compensation; Lepidoptera; *Gossypium hirsutum*; *Bacillus thuringiensis*; *Helicoverpa* spp.

---

1. Introduction

Helicoverpa armigera (Hübner) and *H. punctigera* (Wallengren) (Lepidoptera: Noctuidae) are the major pests of cotton in Australia (Fitt, 1994). Lepidopteran pests are also important in other cotton cropping systems including those of North America and Africa (Hearn and Fitt, 1992). The chemical control of these insects is costly and environmentally disruptive (Fitt, 1994). Moreover, in some cropping systems the chemical control of Lepidoptera is often

---

* Corresponding author. Tel.: +61-67-991539; fax: +61-67-931186; e-mail: victors@mv.pi.csiro.au.

PII S0378-4290(97)00096-8

ineffective owing to their increasing resistance to commonly used insecticides such as endosulfan and pyrethroids (Forrester et al., 1993).

Cotton varieties carrying *Bacillus thuringiensis* subsp. kurstaki genes encoding insecticidal proteins (hereafter 'Bt cotton') provide a platform for cropping systems that are less dependent on chemical control of lepidopteran pests. The overall performance of Bt cotton has been evaluated in a series of field trials (Benedict et al., 1996; Fitt et al., 1994; Wilson et al., 1992, 1994) and commercial Bt varieties have already been released in the U.S.A. and in Australia. The capacity of Bt crops to tolerate (sensu Belsky et al., 1993) insect damage has not been, however, explicitly examined.

Herbivory tolerance or 'compensation' of Bt cotton is important for two reasons. First, and most obviously, Bt crops are vulnerable to non-lepidopteran pests. Second, the efficacy of Bt toxins in plants declines during the period of fruit maturation (Fitt et al., 1994) and crops can be damaged by lepidopteran pests during this phase. Furthermore, under some environmental conditions, the efficacy of Bt toxins can be low even in young crops, and commercial Bt crops have been found that have shed flowerbuds ('squares') and young fruits ('bolls') as the result of damage caused by lepidopteran larvae (Forrester and Pyke, 1997; Moss, 1996).

This study assessed the tolerance of Bt cotton crops to damage caused by (a) naturally occurring populations of *Helicoverpa* spp., and (b) simulated insect damage including early season loss of vegetative buds, as caused by Lepidoptera larvae, sucking mirid bugs (Hemiptera: Miridae) and heavy thrips (Thysanoptera) infestation, and/or fruit loss, as caused by Lepidoptera larvae and mirids.

2. Materials and methods

2.1. General

Three experiments were carried out at Narrabri (30°S, 150°E) in the 1996/97 season. Two experiments were designed to characterise the dynamics of growth and development, and the yield responses of Bt cotton crops subjected to actual (Exp. 1) or simulated (Exp. 2) insect damage. Damage treatments in Exp. 2 included early-season loss of vegetative buds and/or loss of flowerbuds. Experiment 3, also using manual damage, evaluated the effect of the timing of flowerbud loss on crop yield and maturity.

Crops were grown on grey clay soils (Ug5.25) characterised by Northcote (1979). Nehl et al. (1996) further described the variability of physical and biological properties of these soils; according to their classification, the soil in Exp. 1 belongs to Type A-B, i.e., more sodic and of lighter texture, hence more prone to waterlogging, and less favourable for mycorrhizal colonisation than the soil Type C of Exps. 2 and 3.

Experiment 1 was sown on October 10 and Exps 2 and 3 on October 14. Plant density was 9.2 plants m^{-2} in Exp. 1 and 12.5 plants m^{-2} in Exps 2 and 3; inter row space was 1 m in all three experiments. Crops were fertilised with 150 kg N ha^{-1}, treated with aldicarb (450 g ha^{-1}) to control thrips, and irrigated as required throughout the season. Cultivar Sicala V2i expressing the CryIA(c) insecticidal protein from *B. thuringiensis* subsp. kurstaki was used in Exps 2 and 3; cultivars used in Exp. 1 are described below. Table 1 summarises meteorological conditions during the trials.

Time available for recovery is a key determinant of compensation in damaged crops (Sadras, 1995) thus the importance of defining time of harvest. Methods used in commercial crops were applied to decide time of harvest in each experiment. All crops in each experiment were treated with chemical defoliant when the most advanced treatment (treatment

Table 1
Photosynthetically active radiation (PAR), maximum (T_{max}) and minimum (T_{min}) temperature during field experiments at Narrabri in 1996/97. Values are monthly averages ± s.e.

Month	T_{max} (°C)	T_{min} (°C)	PAR ($MJ\,m^{-2}\,d^{-1}$)
October	26.1 ± 0.6	11.8 ± 0.6	10.7 ± 0.6
November	30.0 ± 1.1	13.3 ± 0.8	12.5 ± 0.5
December	30.7 ± 0.6	17.8 ± 0.5	12.6 ± 0.7
January	29.8 ± 0.5	18.0 ± 0.5	12.6 ± 0.7
February	31.5 ± 0.5	20.2 ± 0.5	11.2 ± 0.6
March	30.1 ± 0.4	15.0 ± 0.6	10.8 ± 0.2
April	27.7 ± 0 3	9.7 ± 0.5	9.0 ± 0.2

+BtS1 in Exp. 1, undamaged controls in Exps 2 and 3, see below for definitions) reached the stage of 60% mature fruits ('open bolls') (Snipes and Baskin, 1994). Crop yield was thus measured at 204 in Exp. 1, and at 189 days after sowing, DAS in Exps. 2 and 3.

2.2. Experiment 1

Eight treatments resulted from the factorial combination of (1) two varieties (Sicala V2, a normal leaf variety, and Siokra V15, an okra leaf variety) (2) with (+Bt) or without (−Bt) CryIA(c) insecticidal protein genes, and (3) two regimes of insecticide application (S1 vs. S2, see below). A split-plot design with three replicates was used; insecticide regime was applied to main plots and cultivar × Bt combinations to subplots. Each subplot included 6 rows 630 m long. The whole experimental area was 82 ha and buffers between S1 and S2 blocks were 3.1 ha (50 rows). Although the possibility of insecticide drift between S1 and S2 plots cannot be discounted, detailed monitoring of insects allowed for the growth and yield of cotton in each individual plot to be related to the actual density of insects measured in the same plot.

Key arthropod pests, as summarised by Fitt (1994), were monitored weekly; these included thrips, mirids, spider mites (Acari: Tetranychidae), *H. armigera* and *H. punctigera*. Special attention was paid to populations of *Helicoverpa* spp., the main pest in our cropping system and the main target of Bt cotton. Data were recorded for each of six life stages of *Helicoverpa* spp: white (newly laid) eggs, brown (developing) eggs, very small larvae (< 3 mm), small (3–7 mm), medium (8–20 mm) and large (> 20 mm) larvae; further details of sampling procedures can be found in Dillon and Fitt (1995).

Current recommendations for pest management in Australian cotton farms are based on twice-weekly insect counts. Thus, in addition to the weekly assessment of arthropod pests described before, independent scouting of *Helicoverpa* spp. was done twice weekly; these data and recommended thresholds were used to define two regimes of insecticide application (S1, S2). Thresholds for the S1 regime were as recommended for non-Bt crops and thresholds for the S2 regime were as recommended for Bt crops; for details see Shaw (1996). Using these thresholds and actual insect counts, S1 plots were treated with insecticides nine times and S2 plots six times during the season (Fig. 1a).

Shoots were sampled 13 times between 36 and 166 DAS (sample size = 0.5 m^2). Plant components were separated and dried to constant weight. Green leaf area of whole plants ($n \geq 2$) was measured with a leaf area meter (LI-3100, LICOR, Lincoln, NE, USA) to estimate specific leaf area, and this variable used to estimate leaf area index (LAI) of the crop from green laminae biomass values. Reproductive organs (flowerbuds, immature and mature fruit) were counted in these samples and, in addition, mature fruits were counted weekly between 144 and 204 DAS in 2 m^{-2} samples.

At approximately weekly intervals, the fraction of photosynthetically active radiation (PAR, 0.4–0.7 μm) intercepted by the canopy at noon (Qn) was calculated from measurements with a ceptometer (AccuPAR, Decagon Devices, Pullman, WA, USA)

2.3. Experiment 2

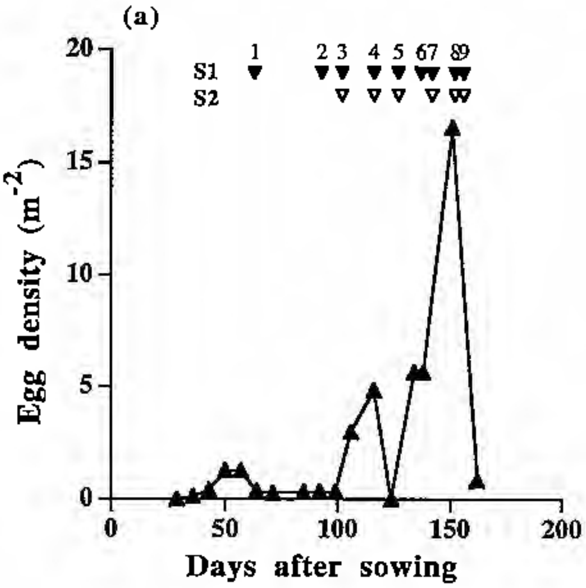
Five treatments were compared, C: undamaged control, V: early vegetative damage, involving the manual removal of the mainstem apex at 36 DAS, R1: reproductive damage involving the removal of all the flowerbuds longer than 1 cm at 64 DAS (total removed: 25 flowerbuds m^{-2}), R2: removal of randomly chosen 25 flowerbuds m^{-2} at 71 DAS, and the combination of V + R2. The rationale of these treatments is as follows. Treatment V simulates early-season vegetative damage as can be caused by mirids, thrips or Lepidoptera while treatment R1 simulates a single episode of severe flowerbud shedding as normally induced by mirids or Lepidoptera. In some cases, crops are exposed to both vegetative and reproductive damage. Due to the delay in squaring associated with vegetative damage (Sadras, 1996c), a second treatment of reproductive damage was included one week later (R2) that simulated the shedding of the same number of flowerbuds removed in R1. Treatment R2 and V were combined to evaluate the responses of crops exposed to both vegetative and reproductive damage.

Treatments were arranged in a randomised block design with four replicates. Each block comprised 20 rows 30 m long, and the trial was in the centre of a 6.7 ha cotton field. Insects were monitored twice a week and controlled with insecticides when required according to thresholds for non-Bt crops (Shaw, 1996); insecticides were applied at 56, 73, 81, 95, 113, 116, 134 and 144 DAS.

Crop growth and development was assessed in a similar way to that described for Exp. 1. In addition, phenological development of crops was assessed by twice-weekly observation of ten plants per plot and calculation of the proportion of plants with flowerbuds, immature and mature fruit.

2.4. *Experiment 3*

Gibb (1995) showed that 50-60% fruit retention in the first fruit position maximises yield of non-Bt cotton crops in our region. The proportional retention of fruit necessary to maximise yield, however, may change during the growing season and the relationship between retention and yield for Bt cottons may differ from that of non-Bt crops. The responses of Bt cotton to timing of flowerbud shedding was assessed in an experiment in which 50% of randomly chosen flowerbuds were removed at five stages between early and peak squaring (Table 2). Treatments were laid out in a randomised block design with four replicates in the same field as Exp. 2. Each plot was 3 rows 2 m long. Mature fruits were counted and seed cotton harvested at weekly intervals between 140 and 189 DAS to evaluate the effects of treatments on time of maturity and yield.



Insecticides applied and rates (g a.i./ha)
1: endosulfan (735),
2: beta-cyfluthrin (20)
3: dimethoate (200) + fenvalerate (140)
4: bifenthrin (80)
5: profenofos (1000) + beta-cyfluthrin (20)
6: amitraz (400) + beta-cyfluthrin (20)
7: beta-cyfluthrin (20) + PBO (350)
8: beta-cyfluthrin (20) + parathion (900)
9: beta-cyfluthrin (20) + propargite (1500)

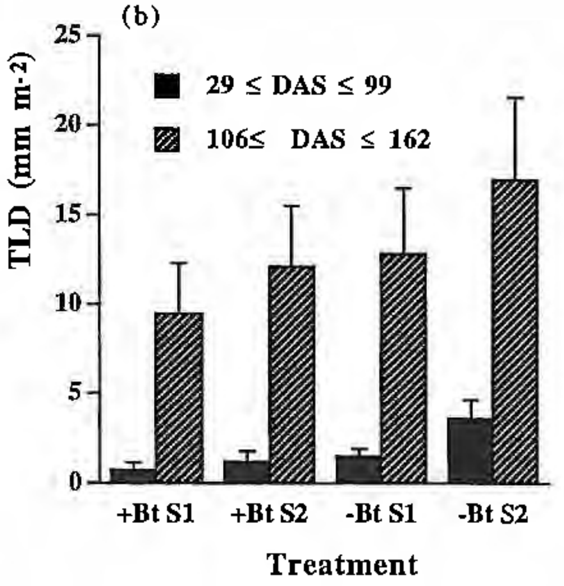


Fig. 1. (a) Changes with time in the density of *Helicoverpa* spp. eggs and (b) average TLD before fruit set (29–99 DAS) and during active fruit growth (106–162 DAS). In (a) data were pooled across cultivar, Bt and insecticide treatments after ANOVA of square root transformed data showed these factors and interactions between them did not affect egg density ($P > 0.05$); back transformed data are presented for easier interpretation. Arrows indicate the timing of insecticide application in the S1 and S2 treatments. In (b) data are also averages across varieties. Error bars are one s.e.m. and are not shown when smaller than symbols. Data from Exp. 1.

Table 2
Treatments in Experiment 3

Treatment code	Time of flowerbud removal (DAS)	No. flowerbuds removed ± s.e. (m^{-2})
W1	58	4±0.5
W2	64	15±3
W3	73	25±1
W4	80	50±7
W5	85	46±7
Control (C)	–	0

2.5. *Data analysis*

In Exp. 1, insect numbers were square root transformed before statistical analyses. For each sampling date, an index of total larval density (TLD, mm m^{-2}) was calculated weighting the density of each larval class (defined in Section 2.2) by the middle size of each class, i.e.,

$$\text{TLD} = \sum_{i=1}^{i=4} \text{larval density}_i \times \text{size}_i. \qquad (1)$$

In Exps. 1 and 2, the daily fraction of PAR intercepted by the crop (Q) was calculated according to Charles-Edwards and Lawn (1984): $Q = 2Qn/(1 + Qn)$. Previous tests with cotton showed that this equation yields estimates of daily light interception that are statistically indistinguishable from estimates based on continuous measurements of light interception obtained with tube solarimeters (Sadras, 1994, unpublished). The amount of PAR intercepted by the canopy (IPAR) was estimated using daily values of solar radiation, measured in a meteorological station 0.5 km from the experimental site, and Q. Quadratic polynomials were used to describe the progression of Q with time (Sadler and Karlen, 1994; Trápani et al., 1992). Least squares linear regression between dry matter and cumulative IPAR was used to estimate RUE in the period from 71 to 161 DAS (Exp. 1) and between 49 and 155 DAS (Exp. 2). Intra-seasonal changes in RUE were explored by assessing the significance of quadratic terms in the regressions (Sadras and Wilson, 1997; Steer et al., 1993). Statistical comparison of fitted curves was done with the F-test described by Potvin et al. (1990).

3. Results and discussion

3.1. *Experiment 1*

The density of *Helicoverpa* spp. eggs was unaffected by treatments ($P > 0.05$). Across treatments, it averaged 1 ± 0.2 m^{-2} before fruit set (< 100 DAS) and 5.3 ± 1.4 m^{-2} afterwards (Fig. 1a). Seasonal analysis of TLD indicated that survival of larvae was significantly lower in +Bt than in −Bt crops ($P < 0.02$) and it was also lower in crops more frequently treated with insecticide (S1 vs. S2, $P < 0.05$). Before 100 DAS, average TLD decreased with increasing protection from 3.6 mm m^{-2} in −BtS2 crops to 0.72 mm m^{-2} in +BtS1 crops (Fig. 1b), with a significant effect of Bt ($P < 0.02$) and a marginal effect of insecticide ($P = 0.06$); effects of Bt and insecticide treatments were additive (interaction: $P > 0.20$). After 100 DAS, the ranking of TLD for the four treatments remained the same as before 100 DAS, but differences among treatments were not significant (Fig. 1b).

The effects of cultivar and interactions between cultivar and other experimental sources of variation were normally non-significant for all the crop variables measured in this experiment. Thus, results are

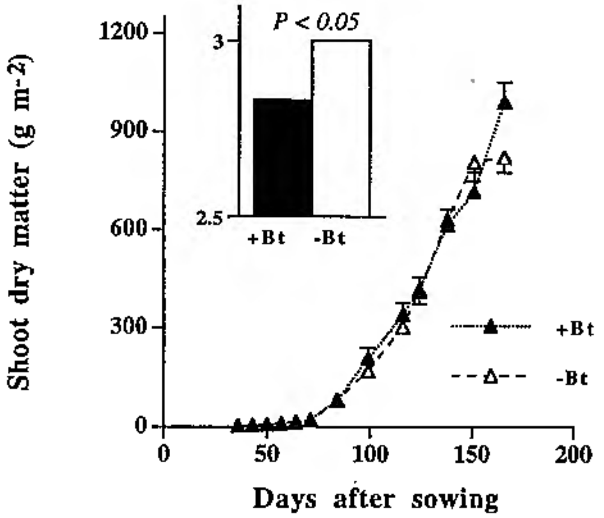


Fig. 2. Dynamics of shoot dry matter in +Bt and −Bt cotton crops. Inset shows shoot dry matter at the first sampling date (36 DAS). Error bars are one s.e.m. and are not shown when smaller than symbols. Data from Exp. 1.

presented as averages across cultivars. None of the treatments affected LAI, which reached a maximum of 2.1 ± 0.11 at 138 DAS, or fractional PAR interception, which reached a maximum of 0.92 ± 0.01 at 154 DAS.

Shoot growth was unaffected by insecticide treatment ($P > 0.05$). Shortly after emergence (36 DAS) +Bt crops were lighter than their −Bt counterparts, differences between +Bt and −Bt were not significant between 43 and 151 DAS, and +Bt crops were heavier than −Bt crops on the last sampling date, 166 DAS (Fig. 2). Recovery of Bt crops after initially slow growth was in part due to a greater specific leaf area; at 50 DAS it was 87 ± 1.8 cm^2 g^{-1} in +Bt crops compared with 80 ± 2 cm^2 g^{-1} in −Bt crops ($P < 0.05$).

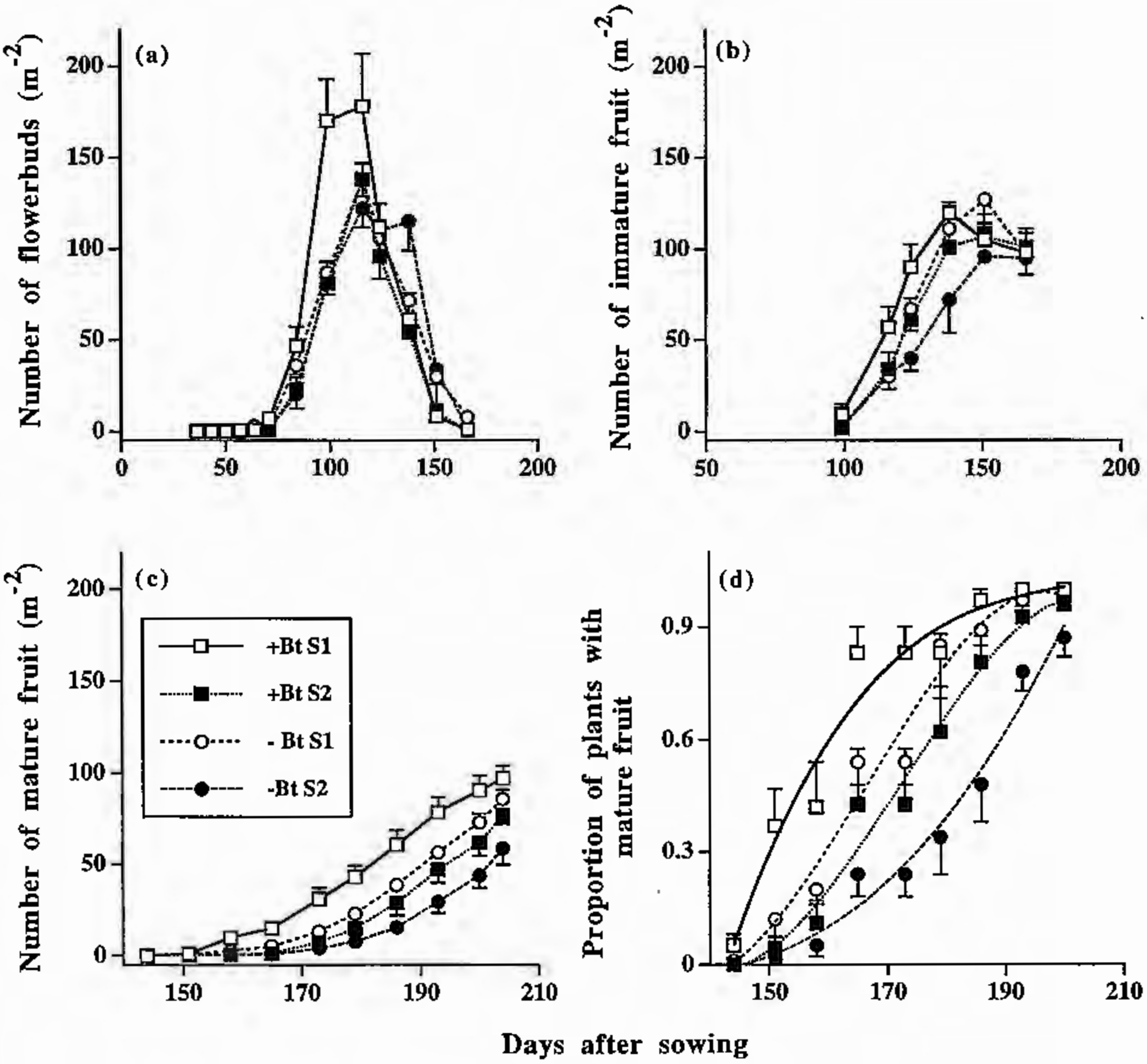


Fig. 3. Fruiting dynamics of cotton crops as affected by Bt and insecticide treatments. Production of (a) flowerbuds, (b) immature fruit, and (c) mature fruit, and (d) proportion of plants in the crop with mature fruit. Values are averages across two cultivars that had similar fruiting dynamics and responded similarly to Bt and insecticide treatments. Error bars are one s.e.m. and are not shown when smaller than symbols. In (d) fitted curves are 3rd degree polynomials ($r^2 > 0.97$, $P < 0.0002$) that were significantly different according to the F-test described in Potvin et al. (1990) ($F_{16,15} = 8.09$, $P < 0.005$). Data from Exp. 1.

Table 3
Seed cotton per fruit in three experiments at Narrabri. Values are averages across treatments ± s.e.

Experiment	Seed cotton per fruit (g)		Effect of treatment
	Maximum	Minimum	
1	8.5 ± 0.5 (158)[a]	3.7 ± 0.1 (204)	not significant
2	7.6 ± 0.2 (154)	3.1 ± 0.2 (189)	crops with reproductive damage had 14% more seed per fruit than controls at 154 DAS ($P < 0.05$)
3	8.1 ± 0.3 (154)	3.3 ± 0.1 (189)	not significant

[a] Time when maximum or minimum was attained (DAS).

and the importance of time available for recovery as a key determinant of actual compensation (Sadras, 1995; Sadras, 1996a,b,c).These issues are discussed further in Section 4.

3.2. *Experiment 2*

Damage treatments did not affect LAI ($P > 0.13$; maximum: 2.0 ± 0.08 at 127 DAS) or shoot dry matter ($P > 0.07$; maximum: 892 ± 40 g m^{-2} at 155 DAS). The intensity of reproductive damage was not enough to increase vegetative growth (Sadras, 1995) except for a significant ($P < 0.05$) but transient 20% increase in stem biomass of R1 crops with respect to controls at 78 DAS. In the period from 52 to 66 DAS, V crops tended to intercept less light than undamaged controls. Differences in fractional PAR interception were significant at 58 DAS (control: 0.19 ± 0.006, V: 0.14 ± 0.018; $P < 0.05$) and marginal at 52 and 66 DAS (both $P = 0.06$). Similar reductions in PAR interception associated with the loss of vegetative buds have been found before, and were related to changes in canopy structure rather to changes in LAI (Sadras, 1996c). Fractional PAR interception was unaffected by treatments after 66 DAS; its maximum was 0.91 ± 0.01 at 132 DAS. Treatments did not affect RUE which averaged 0.98 ± 0.03 g MJ^{-1}.

Damage treatments had marked effects on reproductive development (Fig. 5). Loss of vegetative buds delayed the production of flowerbuds, as found previously (Sadras, 1996c); the stage at which 50% of plants had flowerbuds was delayed from 57 DAS in controls to 63 DAS in V crops (Fig. 5a). At 65 DAS, crops with early reproductive damage (R1) had 60% less flowerbuds than controls and crops with vegetative damage (V and V + R2) had 78% less flowerbuds than controls ($P < 0.001$, Fig. 5b). Compensatory responses were observed at 100 and 114 DAS when damaged crops had significantly more flowerbuds than controls ($P < 0.05$, Fig. 5b); this is a common response of cotton to reproductive damage (e.g., Dale, 1962). The treatment that combined vegetative and reproductive damage (V + R2) reached the stage at which 50% of plants had immature fruit at 95 DAS, 10 days later than control crops; delays caused by R1, R2 and V treatments were 4, 5, and 7 days, respectively (Fig. 5c). Despite delays in reproduction caused by damage treatments (Fig. 5a–e), all crops had the same final number of mature fruit ($P > 0.30$, Fig. 5f). This attenuation of differences in development through the crop cycle resembles the phenomenon of phenological convergence described for wheat (Hay and Kirby, 1991).

Owing to the delay in reproductive development, accumulation of dry matter in reproductive organs was initially slower in damaged crops than in controls (Fig. 6a). Differences in reproductive dry matter were significant at 65 DAS ($P < 0.01$), reached a maximum at 100 DAS($P < 0.0001$) and disappeared at 155 DAS ($P > 0.98$). Yield was unaffected by damage treatments (Fig. 6b) but time of maturity was significantly delayed (Fig. 6c). Seed cotton per fruit ranged from 3.1 to 7.6 g, and it was greater in crops that had reproductive damage than in controls at 154 DAS (Table 3).

Analysis of fruiting dynamics and yield components highlight two of the compensatory mechanisms described by Brook et al. (1992b): (a) removal of fruit simulating insect-induced shedding substituted for fruit that would have been shed physiologically, as indicated by the large difference between peak fruit number and peak flowerbud number in undamaged crops (Fig. 5d vs. b), and to a lesser extent (b) increased fruit mass (Table 3).

3.3. *Experiment 3*

Removing 50% of the flowerbuds present in the crop had dramatic but transient effects on cotton development (Fig. 7). At 140 DAS, the proportion of

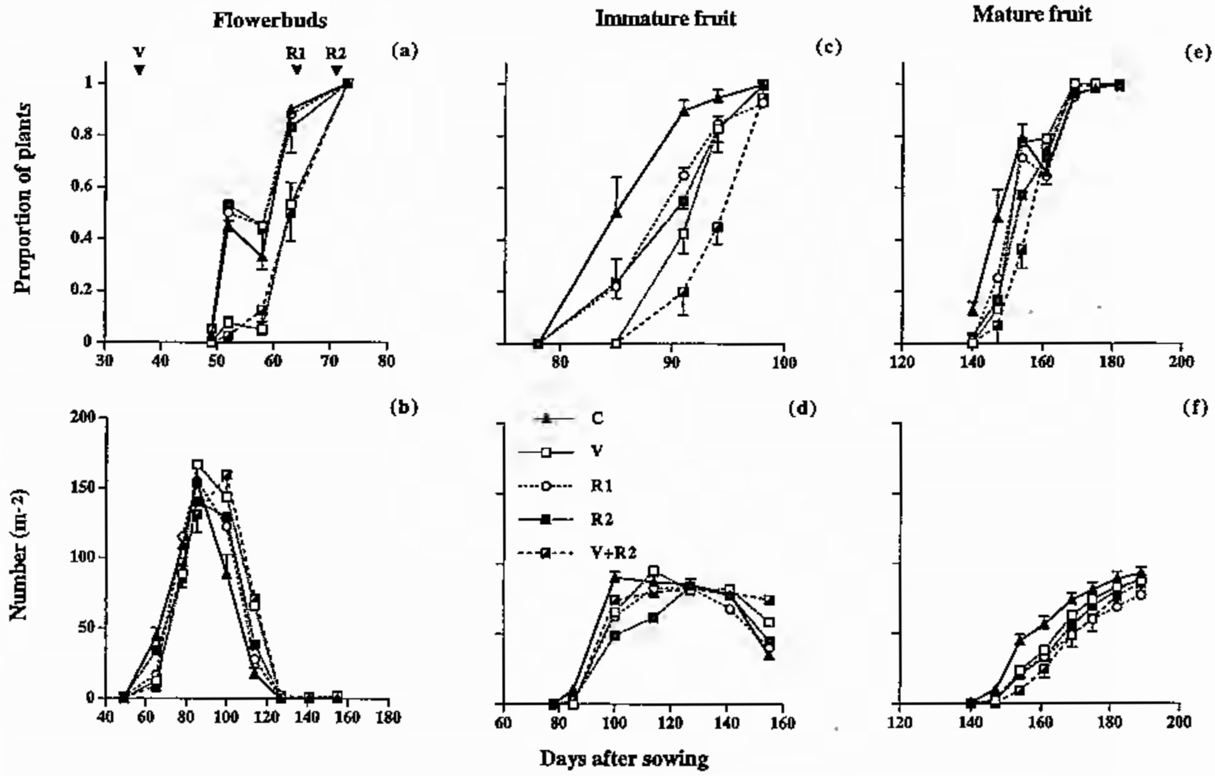


Fig. 5. Effects of simulated vegetative and/or reproductive damage on the proportion of plants in the crops with (a) flowerbuds, (c) immature and (e) mature fruit, and on the number of (b) flowerbuds, (d) immature and (f) mature fruit. Arrows in (a) show the timing of treatments. Error bars are one s.e.m. and are not shown when smaller than symbols. Data from Exp. 2.

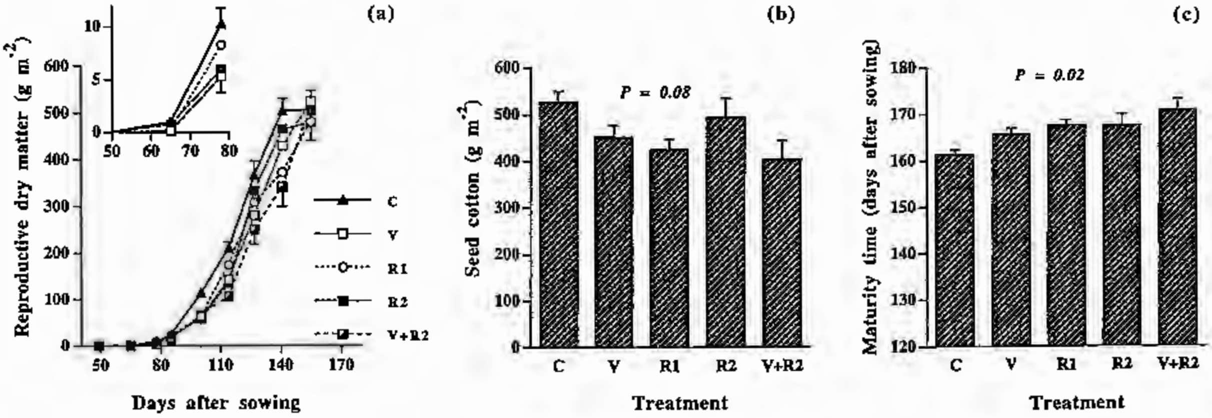


Fig. 6. Effects of simulated vegetative and/or reproductive damage on (a) dynamics of reproductive dry matter accumulation, (b) yield and (c) time of maturity. P values indicate effect of treatments according to ANOVA. Data from Exp. 2.

plants with mature fruit in W1-W3 treatments was only 0.02 to 0.06 in comparison with the controls were this proportion was 0.2 (Fig. 7a). Crops that were damaged earlier recovered faster, e.g., mature fruit number in the W1 treatment recovered to the level of control crops at 161 DAS while W5 crops reached the level of controls at 189 DAS (Fig. 7b). The mass of seed cotton per fruit was unaffected by treatments ($P > 0.10$, Table 3). At the end of the growing cycle, all treatments had similar yield (Fig. 7c), and negligible (2 m^{-2}) and similar ($P > 0.25$) number of immature fruit. Damaged crops tended to reach maturity later than the undamaged control but differences were not significant (Fig. 7d).

4. General discussion: implications for pest management

Bt cotton provides a basis to reduce the use of insecticides aimed at lepidopteran pests. Previous

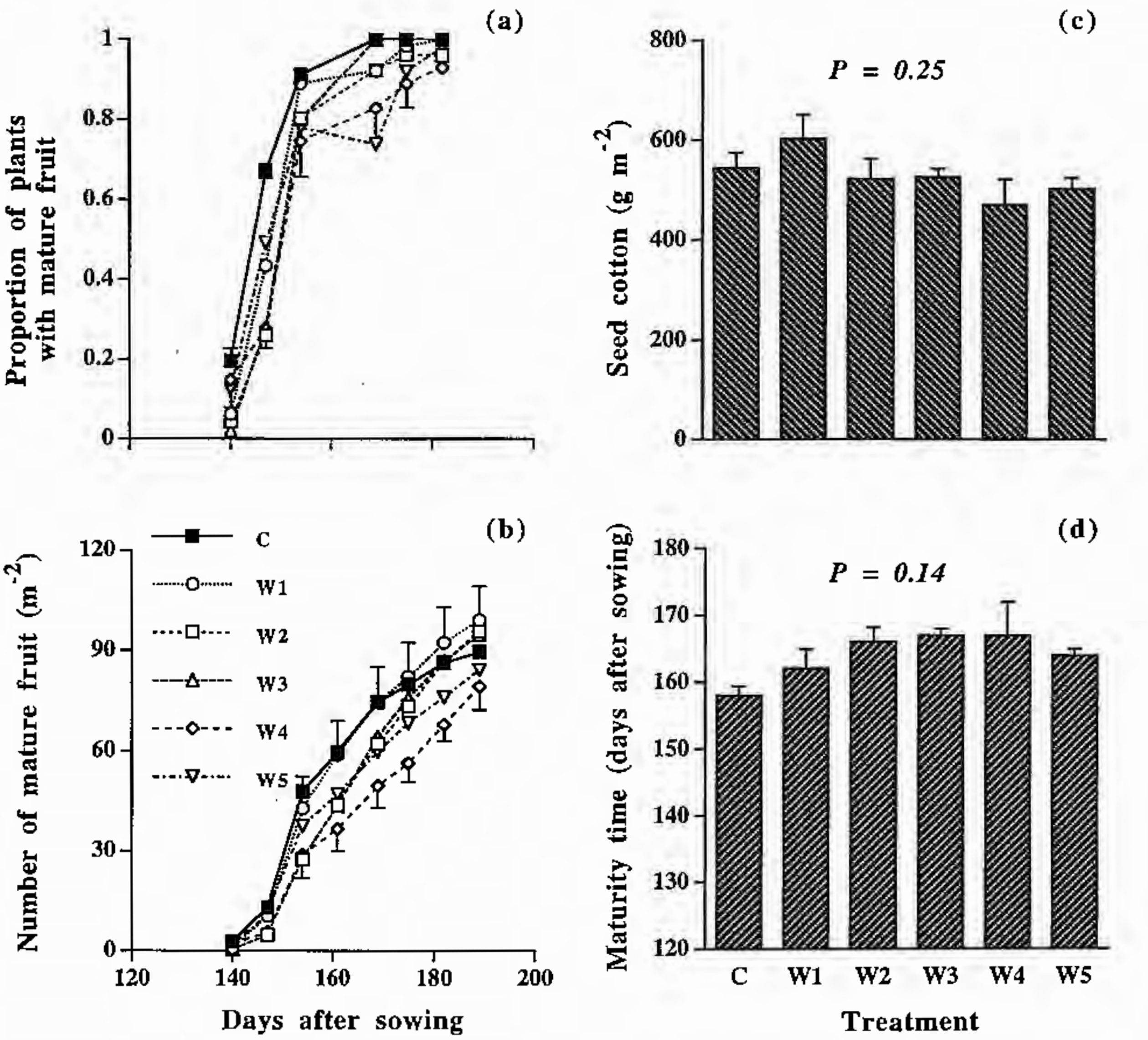


Fig. 7. Effect of timing of flowerbud removal on (a) the proportion of plants with mature fruit, (b) number of mature fruit, (c) yield, and (d) time of maturity. Error bars are one s.e.m. P values in (c) and (d) indicate the effect of treatments (ANOVA). Data from Exp. 3; see Table 2 for treatment details.

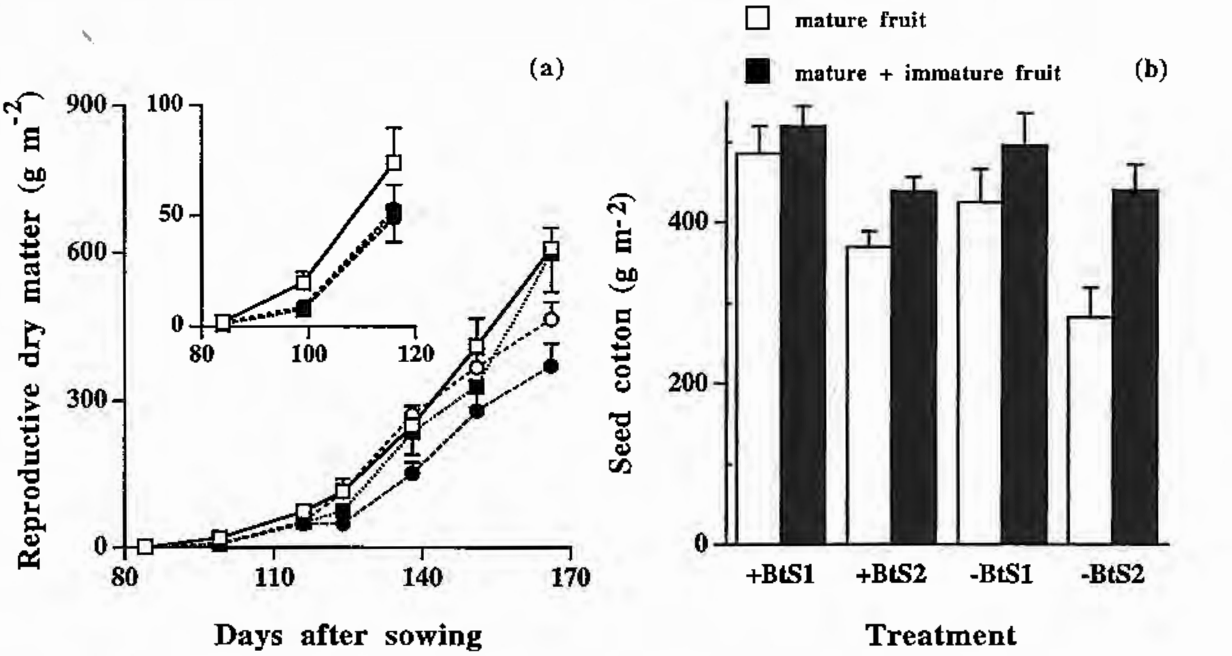


Fig. 4. Effects of Bt and insecticide treatments on (a) the accumulation of dry matter in reproductive organs (symbols as in Fig. 3), and (b) seed cotton yield; seed cotton in mature fruit is the actual (harvestable) yield whereas seed cotton in mature and immature (not harvestable) fruit is taken as a measure of yield 'potential'. Error bars are one s.e.m. and are not shown when smaller than symbols. Data from Exp. 1.

Radiation-use efficiency was unaffected by insecticide treatment; average RUE in the period from 71 to 161 DAS was 1.32 ± 0.02 g MJ^{-1} for +Bt crops and 1.21 ± 0.04 g MJ^{-1} for −Bt, values that are comparable to those previously reported for reproductive cotton (Rosenthal and Gerik, 1991; Sadras, 1996b). A conservative conclusion from this comparison is that Bt genes did not reduce cotton RUE, hence standard RUE values can be applied in modelling the growth of Bt cotton.

Reproductive growth was substantially affected by both Bt and insecticide treatments (Figs. 3 and 4). Between 56 and 99 DAS, +BtS1 crops had a net rate of flowerbud production of 3.96 ± 0.49 flowerbuds per day, about twice the rate measured in the other treatments (Fig. 3a). The rate of fruit set was greatest in the more protected crops (+BtS1), lowest in the least protected (−BtS2) and intermediate in the +BtS2 and −BtS1 treatments (Fig. 3b). Fruit maturity was increasingly delayed with decreasing protection (Fig. 3c,d). For instance, the stage at which 50% of plants had mature fruit was attained at 156 DAS in +BtS1 and at 185 DAS in −BtS2 (Fig. 3d). Accumulation of dry matter in reproductive organs (Fig. 4a) paralleled the differences in fruiting dynamics depicted in Fig. 3b. Seed cotton per fruit was unaffected by treatments (Table 3).

Yield of +Bt crops was 17% greater than that of −Bt crops ($P < 0.05$), and it was 28% greater in S1 than in S2 crops ($P < 0.001$); the effects of Bt and insecticide treatment were additive (interaction: $P > 0.70$) (Fig. 4b). The ranking of treatments based on yield measured in 2 m^{-2} samples (Fig. 4b) agreed with the ranking based on lint yield measured in 0.11 ha samples (S. Deutscher, unpublished data). The number of immature fruit per m^2 remaining in the crops at the end of the growing season (204 DAS) was: 7 ± 2 in +BtS1, 15 ± 2 in +BtS2, 15 ± 3 in −BtS1, and 24 ± 8 in −BtS2; effects of Bt and insecticide treatments were significant (both $P < 0.05$) and additive (interaction: $P > 0.78$). Taking seed cotton of mature and immature fruit together as a measure of yield potential, no differences were found between +Bt and −Bt treatments ($P > 0.72$) and the effect of insecticide treatment was less (13% difference between S1 and S2) but still significant ($P < 0.05$; Fig. 4b). This highlights the potential ability of cotton crops to compensate for damage, studies showed a consistent decline of Bt efficacy during the last part of the growing season, and some cases of reduced efficacy early in the season have also been observed in commercial Bt crops (Introduction). This, together with the obvious need to protect the crops against non-lepidopteran pests, means that information on crop tolerance to damage is important to devise effective pest management strategies for Bt crops.

Studies of tolerance to damage in non-Bt cotton demonstrated (see references in Table 4): (a) that crop yield is unlikely to be reduced by losses of vegetative buds similar in timing and intensity to those investigated in Exp. 2, (b) a substantial capacity of the crop to recover after reproductive damage similar to that in Exps. 1–3, and (c) important influences of growing conditions on the actual degree of compensation. Morphological and physiological mechanisms underlying these responses have been discussed in detail by Brook et al. (1992b) and Sadras (1995). Experiments 2 and 3 indicate that the degree of tolerance to early-season loss of vegetative buds and to the loss of reproductive buds in Bt crops is comparable to that usually observed in non-Bt crops (Table 4).

Table 4

Comparative tolerance to vegetative and reproductive damage of Bt (+) and non-Bt (−) cotton. The ratio between the yield of manually damaged crops and that of undisturbed controls is taken as an approximate measure of tolerance

Bt	Damage[a]	Yield ratio	Source
+	V	0.86	Exp. 2
−	V	0.72 to 1.06	Bishop et al. (1977)
−	V	1.0 to 1.10	Brook et al. (1992b)
−	V	0.96 to 0.98	Evenson (1969)
−	V	0.92 to 1.29	Sadras (1996c)
+	R	0.81 to 0.94	Exp. 2
+	R	0.86 to 1.11	Exp. 3
−	R	0.59 to 1.12	Brook et al. (1992b)
−	R	0.80 to 1.03	Evenson (1969)
−	R	0.20 to 1.24	Kennedy et al. (1986)
−	R	0.64 to 1.12	Kincade et al. (1970)
−	R	0.99 to 1.27	Kletter and Wallach (1982)
−	R	0.97 to 1.03	Pettigrew et al. (1992)
−	R	0.81 to 0.92	Sadras (1996a)
−	R	0.56 to 1.13	Ungar et al. (1987)
−	R	0.82 to 1.21	Wilson and Bishop (1982)
+	V and R	0.76	Exp. 2
−	V and R	0.97 to 1.05	Brook et al. (1992b)

[a] V: removal of vegetative buds, R: removal of reproductive buds and/or fruit.

The recovery of damaged crops in Exps. 2 and 3 seem to contrast with the results of Exp. 1, in which Bt crops with 6 insecticide applications yielded 24% less than their counterparts with 9 insecticides. There are three possible reasons for these contrasting results. First, crops in Exp. 1 were damaged by *Helicoverpa* spp. larvae while crops in the other experiments were manually damaged. Although differences in plant responses to insect and simulated damage cannot be disregarded, the key cotton responses to *Helicoverpa* spp. can be reproduced realistically with the methods used in this study, as demonstrated by Brook and colleagues in comparative studies of cotton responses to insect and manual damage (Brook et al., 1992a,b). The validity of using manual bud removal to simulate insect damage is further supported by the similar patterns of fruiting dynamics and accumulation of reproductive dry matter of crops damaged manually (Figs. 5, 6a, 7) and those damaged by *Helicoverpa* spp. (Figs. 3 and 4a). Second, crops in Exp. 1 grew in poorer soil than crops in Exps. 2 and 3, i.e., soil in Exp. 1 was more sodic and of lighter texture, hence more prone to waterlogging, and less favourable for mycorrhizal colonisation (see Section 2.1). Although the yield of the best protected crops was similar in all experiments (Figs. 4, 6 and 7) crops in Exp. 1 took two weeks longer than crops in the other experiments to achieve this yield, an indication of poorer growing conditions. Third, less protected treatments in Exp. 1 were exposed to continuous insect damage during most of the growing season (Fig. 1) in contrast to Exps. 2 and 3 in which damage treatments were well defined and restricted in time. The second and third propositions are the most relevant from the viewpoint of the physiology of the crop and its implications for pest management.

Growing conditions are known to affect the capacity of plants and crops to recover after episodes of herbivory. Depending on the kind of factor/s that restrict growth, cotton compensates better under ‘poor’ (Brook et al., 1992a) or ‘favourable’ (Sadras, 1996a) growing conditions (see interpretation of conflicting results in Sadras, 1995). Under the poorer growing conditions of Exp. 1, damaged crops had a substantial mass of immature fruit at the end of the growing cycle. The magnitude of unrealised yield, i.e., the difference between harvestable and potential yield (Fig. 4b) highlights the importance of the interaction between growing conditions and time available for recovery in the outcome of compensatory responses in cotton (Sadras, 1995, 1996a). Pest management decisions could thus be improved if practical means are developed to account for the influence of growing conditions and season length on cotton compensation.

The contrasting responses between experiments could also be due to the continuous insect pressure to which crops were exposed in Exp. 1 compared to the discrete damage episodes of Exps. 2 and 3. If so, single cohorts of insects that escape the effects of Bt toxins and cause up to 50% flowerbud shedding should not be of great concern unless this situation persists through the growing season and/or other non-lepidopteran pests, such as mirids, also damage the crop.

This is the first study of tolerance to damage in Bt cotton and certainly the responses of the crop to damage could be expected to be influenced by factors such as nitrogen supply, water availability, temperature and radiation. Studies specifically designed to investigate the interactions between these factors, the crop and its pests are required. In principle, this study indicates that the introduction of *B. thuringiensis* genes into cotton did not reduce the considerable capacity of the crop to tolerate insect damage.

Acknowledgements

I thank Mike Mennell for technical assistance, Sandra Deutscher for crop and pest management in Experiment 1, Lewis Wilson, Steve Milroy, and Gary Fitt for comments on the manuscript, and the Cotton Research and Development Corporation of Australia for financial support (grant CSP68C).

References

Belsky, A.J., Carson, W.P., Jensen, C.L., Fox, G.A., 1993. Overcompensation by plants: herbivore optimization or red herring?. Evol. Ecol. 7, 109–121.

Benedict, J.H., Sachs, E.S., Altman, D.W., Deaton, W.R., Kohel, R.J., Ring, D.R., Berberich, S.A., 1996. Field performance of cotton expressing transgenic CryIA insecticidal proteins for resistance to *Heliathis virescens* and *Helicoverpa zea* (Lepidoptera: Noctuidae). J. Econ. Entomol. 89, 230–238.

Bishop, A.L., Day, R.E., Blood, P.R.B., Evenson, J.P., 1977. Effect of damaging main stem terminals at various stages of flowering, on yield of cotton in south-east Queensland. Aust. J. Exp. Agric. Anim. Husb. 17, 1032–1035.

Brook, K.D., Hearn, A.B., Kelly, C.F., 1992a. Responses of cotton, *Gossypium hirsutum* L., to damage by insect pests in Australia: Compensation for early season fruit damage. J. Econ. Entomol. 85, 1378–1386.

Brook, K.D., Hearn, A.B., Kelly, C.F., 1992b. Responses of cotton, *Gossypium hirsutum* L., to damage by insect pests in Australia: Manual simulation of damage. J. Econ. Entomol. 85, 1368–1377.

Charles-Edwards, D.A., Lawn, R.J., 1984. Light interception by grain legume row crops. Plant Cell Environ. 7, 247–251.

Dale, J.E., 1962. Fruit shedding in cotton. Cotton Grow. Rev. 39, 170–176.

Dillon, G.E., Fitt, G.P., 1995. Reassessment of sampling relationships for *Helicoverpa* spp. (Lepidoptera: Noctuidae) in Australian cotton. Bull. Ent. Res. 85, 321–329.

Evenson, J., 1969. Effects of floral and terminal bud removal on the yield and structure of the cotton plant in the Ord Valley North Western Australia. Cotton Grow. Rev. 46, 37–44.

Fitt, G.P., 1994. Cotton pest management: 3. An Australian perspective. Annu. Rev. Entomol. 39, 543–562.

Fitt, G.P., Mares, C.L., Llewellyn, D.J., 1994. Field evaluation and potential ecological impact of transgenic cottons (*Gossypium hirsutum*) in Australia. Biocontrol Sci. Technol. 4, 535–548.

Forrester, N.W., Cahill, M., Bird, L.J., Layland, J.K., 1993. Management of pyrethroid and endosulfan resistance in *Helicoverpa armigera* (Lepidoptera: Noctuidae) in Australia. Bull. Entomol. Res. Supplement 1, 132.

Forrester, N.W., Pyke, B., 1997. The Bt Report. Aust. Cottongrower 17, 23.

Gibb, D., *Heliothis* thresholds—pre flowering. Research Review —Cooperative Res. Centre for Sustainable Cotton Production Newsletter, 2 (1995) pp. 1–4.

Hay, R.K.M., Kirby, E.J.M., 1991. Convergence and synchrony—a review of the coordination of development in wheat. Aust. J. Agric. Res. 42, 661–700.

Hearn, A.B., Fitt, G.P., Cotton cropping systems. In: Pearson, C.J. (Ed.), Ecosystems of the world. Field crop ecosystems. Elsevier, Amsterdam, 1992, pp. 85–142.

Kennedy, C.W., Smith, W.C., Jones, J.E., 1986. Effect of early season square removal on three leaf types of cotton. Crop Sci. 26, 139–145.

Kincade, R.T., Laster, M.L., Brazzel, J.R., 1970. Effect on cotton yield of various levels of simulated *Heliothis* damage to squares and bolls. J. Econ. Entomol. 63, 613–615.

Kletter, E., Wallach, D., 1982. Effects of fruiting form removal on cotton reproductive development. Field Crops Res. 5, 69–84.

Moss, I., 1996. Bollgard: deep in the heart of Texas. Aust. Cottongrower 17, 18–20.

Nehl, D.B., Allen, S.J., Brown, J.F., 1996. Mycorrhyzal colonisation, root browning and soil properties associated with a growth disorder of cotton in Australia. Plant Soil 179, 171–182.

Northcote, K.H., A factual key for the recognition of Australian soils, Rellim, Glenside, 1979.

Pettigrew, W.T., Heitholt, J.J., Meredith, W.R.J., 1992. Early season floral bud removal and cotton growth, yield, and fiber quality. Agron. J. 84, 209–214.

Potvin, C., Lechowicz, M.J., Tardif, S., 1990. The statistical analysis of ecological response curves obtained from experiments involving repeated measures. Ecology 71, 1389–1400.

Rosenthal, W.D., Gerik, T.J., 1991. Radiation use efficiency among cotton cultivars. Agron. J. 83, 655–658.

Sadler, E.J., Karlen, D.L., 1994. Higher-order analysis of nutrient accumulation data. Agron. J. 86, 26–31.

Sadras, V.O., 1995. Compensatory growth in cotton after loss of reproductive organs. A review. Field Crops Res. 40, 1–18.

Sadras, V.O., 1996a. Cotton compensatory growth after loss of reproductive organs as affected by availability of resources and duration of recovery period. Oecologia 106, 432–439.

Sadras, V.O., 1996b. 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.

Sadras, V.O., 1996c. Population-level compensation after loss of vegetative buds: Interactions among damaged and undamaged cotton neighbours. Oecologia 106, 432–439.

Sadras, V.O., Wilson, L.J., 1997. Growth analysis of cotton crops infested with spider-mites. I. Light interception and light-use efficiency. Crop Sci. 37, 481–491.

Shaw, A.J., 1996. Cotton pesticides guide 1996–97. NSW Agriculture Agdex 151/680.

Snipes, C.E., Baskin, C.C., 1994. Influence of defoliation on cotton yield, seed quality, and fiber properties. Field Crops Res. 37, 137–143.

Steer, B.T., Milroy, S.P., Karmona, R.M., 1993. A model to simulate the development, growth and yield of irrigated sunflower. Field Crops Res. 32, 83–99.

Trápani, N., Hall, A.J., Sadras, V.O., Vilella, F., 1992. Ontogenic changes in radiation-use efficiency of sunflower (*Helianthus annuus* L.) crops. Field Crops Res. 29, 303–316.

Ungar, E.D., Wallach, D., Kletter, E., 1987. Cotton response to bud and boll removal. Agron. J. 79, 491–497.

Wilson, L.T., Bishop, A.L., 1982. Responses of Deltapine 16 cotton *Gossypium hirsutum* L. to simulated attacks by known populations of *Heliothis* larvae (Lepidoptera: Noctuidae) in a field experiment in Queensland, Australia . Prot. Ecol. 4, 371–380.

Wilson, F.D., Flint, H.M., Deaton, W.R., Fischhoff, D.A., Perlak, F.J., Armstrong, T.A., Fuchs, R.L., Berberich, S.A., Parks, N.J., Stapp, B.R., 1992. Resistance of cotton lines containing a *Bacillus thuringiensis* toxin to pink bollworm (Lepidopetra: Gelechiidae) and other insects. J. Econ. Entomol. 85, 1516–1521.

Wilson, F.D., Flint, H.M., Deaton, W.R., Buehler, R.E., 1994. Yield, yield components, and fiber properties of insect-resistant cotton lines containing a *Bacillus thuringiensis* toxin gene. Crop Sci. 34, 38–41.

Compensation in cotton following pest damage: potential and limitations

Tom Lei

CSIRO Cotton Research Unit and Australian Cotton Cooperative Research Centre, PO Box 59, Narrabri NSW 2390

Key words: compensation, yield, cultivar, pest damage, *Helicoverpa*, fruiting dynamics, tip damage, canopy development

Abstract

Damage caused by chewing and sucking pests does not necessarily lead to a yield loss in cotton. There is ample evidence indicating that cotton can fully recover from levels of vegetative and fruit damage above the current industry threshold. The ability to compensate for tissue loss in cotton is attributed to an improved canopy development stimulated by pre-squaring tip damage, and to fruit substitution for damage and increased fruit production during the reproductive stage. However, cotton's ability to compensate for fruit loss declines dramatically as boll development accelerates (3-4 weeks after first square), therefore, a more cautious pest management is necessary for about 2 months (until cut-out) to avoid yield loss. A look-up table of the estimated fruit damage caused by *Helicoverpa* larvae at different fruiting stages is provided to allow assessment of a crop's ability to tolerate fruit loss. To ensure full compensation, it is important to maintain a healthy crop canopy (i.e., keeping mite damage under control) but not one with excessive leaf area (which leads to yield loss), particularly during the boll forming stage. Excessive growth response to pest damage may be minimised by selecting okra leaf cultivars and by managing nitrogen and irrigation properly. A well managed crop may even respond to damage such as early season tipping out with yield gain over an undamaged crop. Clearly, the potential for reduced pesticide use in early and mid-season clearly exists and so do the attendant benefits of that. Harnessing the compensatory capacity of cotton is a key component of Integrated Pest Management and sustainable cotton cropping. This research continues the effort to ascertain ways of fully utilising the compensation potential of cotton for future incorporation into decision support systems for pest management.

Why is compensation important?

"It will become increasingly rare for farmers to use pesticides when the damage is not of economic importance" Wilson (1986). This observation has taken on a greater imperative in the current cotton cropping system in Australia. Knowing the full capacity of a cotton crop to recover from pest damage means we can raise the threshold for *Helicoverpa* and other pests without suffering economic penalty. Moreover, there are important benefits to reducing pesticide use:

- reduced cost
- less impact on the environmental
- slow the development of insect resistance
- encourage beneficial arthropods
- minimise flaring of secondary pests
- possible yield gain

While the introduction of transgenic cotton represents a significant advance in cotton pest management, compensation remains important. The current Bt cottons do not protect the crop throughout the season and even with the forthcoming 2-gene lines, non-lepidopteran pests remain a threat. Given that different cultivars have different sensitivities and recovery patterns to pest damage, the key question is at what level would pest damage become "economically important"? Of equal importance is the question of how compensation varies under different agronomic conditions and in different cropping regions. Information from this study can help us to develop guidelines for pest management which take full advantage of the compensation capacity of cotton.

How tolerant is cotton to damage?

As early as the 1930s, cotton researchers had begun to assess the tolerance of cotton plants to pest damage (e.g., Eaton, 1931). Since then, a substantial number of studies have found full or over- compensation of yield in crops even after fairly heavy damage to leaves, terminals and fruit. Sadras (1995) presented a review of the evidence supporting the case that damage episodes at levels above the current threshold do not necessarily reduce yield. In our own field trials in the last two years, we simulated more realistic damage by imposing multiple damage events including both pre-squaring tip damage and fruit removal. We also used several levels of artificial pest damage ranging from no additional damage to 8 larvae per metre (Fig. 1). The results of the two-year trial demonstrate two key points. Firstly, cotton can compensate from repeated damage at levels as high as 8 *Helicoverpa* larvae per metre without significant yield loss (note that histograms in Fig. 1 have a break which accentuates the differences among treatments). Secondly, even though the yield potential may have differed considerably (Yr 2 was twice that of Yr 1), the ability to compensate was not strongly affected.

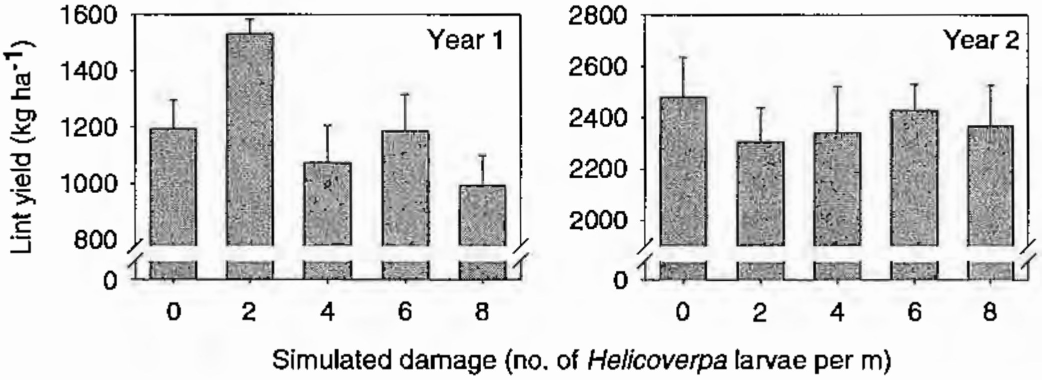


Figure 1. A two-year field trial conducted at Narrabri examining the ability of cotton to compensate from repeated damage simulating 0-8 *Helicoverpa* larvae per metre. The damage imposed consisted of two tip damage events before first square (80% of plants tipped out) and 2 fruit removal events (last event was about 130 DAS). Sicala V2 (Yr 1) and Sicala V2i (Yr 2) were grown using standard N and irrigation management and plant stand at 10 plants per metre. The number of fruit removed for each simulated larval level was calculated using actual fruit count and the *Helicoverpa* Feeding model (see Table 1), fruit were removed in a random fashion by hand.

How does cotton recover from damage?

Cotton plants respond to different types of pest damage in different ways. Early season tip damage induces a strong response for lateral branch growth. We will look at this more closely later. When leaf area is reduced either by defoliation or through mite infestation, the plant experiences reduced vegetative growth and fruit development. Moderate levels of leaf loss may not have an economic effect on yield (see below). Loss of fruit can lead to an increase in vegetative or reproductive growth depending on the number of fruit remaining on the plant. If there is a sufficient number of fruit remaining, then substitution of lost fruit can maintain the carbon demand by fruit without resuming vegetative growth. If few fruit remain, then the surplus carbon will be used for a spurt of vegetative growth until fruit numbers build up again. In the later case, because fruit development is temporarily interrupted, there may be a delay in boll maturation.

Structural changes resulting from tip damage or reduced leaf area

When early season pests damage the terminal of a young cotton plant, the plant is stimulated to produce lateral branches from main stem leaf nodes below the terminal. The number and position of lateral branches produced differs between cultivars and may be related to their degree of apical dominance (Sadras and Fitt, 1997). Figure 2 shows a significant increase in the number of branches produced from manual tip damage prior to squaring. With the development of lateral branches, the cotton canopy usually becomes more efficient in intercepting light and therefore could accumulate more carbon. More branches also means more potential fruiting sites and a larger square production. Since plants with more fruit can tolerate more damage (through substitution of lost fruit), we believe tip damage could also help cotton to resist fruit damage later in the season.

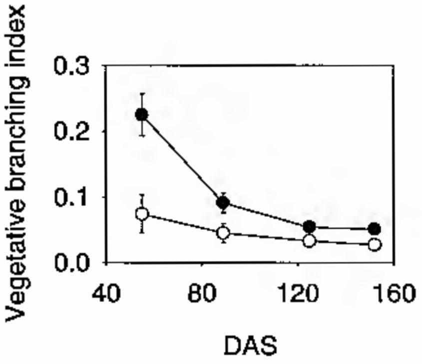


Figure 2. This graph shows the increase in the number of vegetative branches resulting from manually imposed tip and fruit damage across the 1998-99 season. The vegetative branching index represents the number of branches per 0.5 m row of cotton standardised to plant height. The variety planted in this trial was Sicala V2i with 60 kg N / ha applied and at 10 plants per metre.

Relative to tip damage, early season defoliation appears to have a greater impact on the subsequent growth of the cotton plant. In a series of field trials conducted by CRC Industry Development Officers in 1999, tip damage showed little influence on (or even a slight boost to) yield while 100% defoliation of true leaves had a larger negative effect (Fig. 3). These results highlight the difference between depriving a plant of its current growing tip and of its carbon source. The former involves little tissue mass and can be readily replaced by dormant buds while the latter requires major re-establishment of canopy by a carbon-impoverished plant. Such drastic loss of leaves is clearly undesirable but rare (such as a result of hail). Other studies found no yield effect with as much as 80% of leaf area removed (Wilson and Sadras 1998). This shows that when plants are young, they have sufficient time to recover fully from only a small amount of leaf area left. Another issue Fig. 3 raises is the effect of climate on compensation. Because of a lower mean temperature and a shorter season, cotton grown in cooler regions have a reduced ability to compensate and a greater risk of delays in maturity from both tip and leaf damage. Therefore, a full account of the safety margin for full recovery for various cropping regions is essential and is key part of the continuing compensation research.

Cotton response to fruit removal

Damage to cotton fruit is a great concern to growers since it is generally perceived as having a direct impact on final yield. This perception, however, is not always true. In the extreme case, cotton can lose all its fruit without yield loss if the loss occurred early (Sadras, 1996b). In a realistic situation, pests cause damage to a portion of the fruit on the plant and if there is sufficient fruit remaining to replace the lost fruit, there may

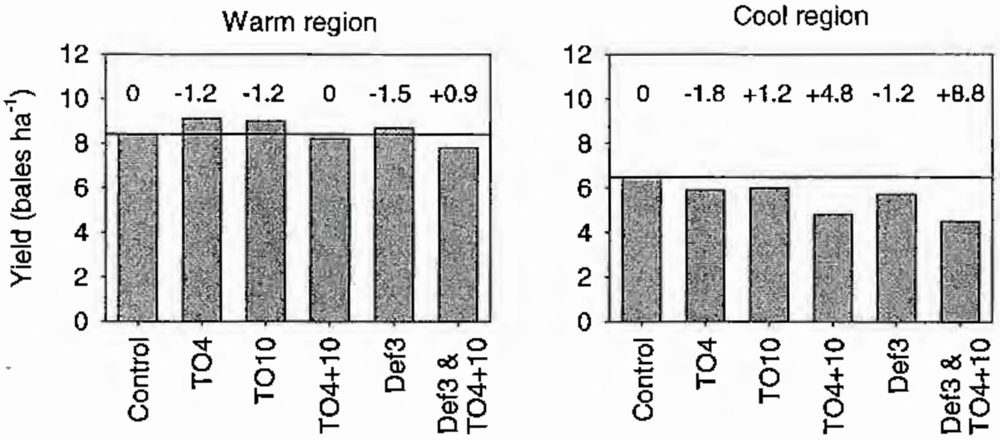


Figure 3. Yield and maturity (numbers above bars) of various tip damage and defoliation treatments conducted in warm (central Queensland) and cool (upper Namoi) cotton cropping regions by CRC Industry Development Officers. Early or delay (in days) in maturity to the control was indicated by – and + numbers respectively. Treatment codes: Control – (no damage), TO4, TO10 and TO4+10 – tipped out at main stem node 4, 10 and both, respectively, Def3 – 100% defoliation (excpet for cotyledons) at node 3.

not be a yield consequence. Taking an average crop as an example, within a metre row, 300 squares may be initiated. However, the crop will lose 2/3 of them through physiological shedding, and will mature typically 120 bolls/m at the end of the season. Physiological shedding occurs because cotton produces more squares than its carbon supply can support. But if a portion of squares was shed through pest damage, then a similar number of remaining squares will be retained to maintain a balance in carbon supply to fruit. Therefore, so long as there are sufficient fruit left on the plant to substitute for that lost to pests and to maintain a fruit load at the plant's carrying capacity (e.g., 120 fruit per metre), then no significant yield loss should occur. How many damaged fruit can cotton substitute? Table 1 gives some idea of the number. This table is derived from the larval feeding model developed by Wilson and Gutierrez (1980) and tested in Australia by Wilson and Waite (1982). Given the developmental stage of the crop (i.e., early squaring with only squares and flowers), we can estimate the number of fruit taken by a cohort of *Helicoverpa* larvae over a 2-week period (from first instar to pupation). Clearly, a healthy crop has enough fruit to substitute for losses caused by 6 or 8 larvae per meter more than once. However, as boll development progresses, there will be fewer squares and more feeding on bolls (lower part of Table 1). Replacing damaged bolls is more energetically demanding than replacing squares. Because there is less time for recovery as the season progresses, boll damage could result in no loss of yield but a significant delay in maturity, or in a yield loss if the damage occurred very late in the season. The limit to compensation late in the season means it is prudent to protect the boll load against damage starting about peak flowering until cut out. Thereafter, without small squares and young terminals on the plants after cut out, first instar *Helicoverpa* larvae will not survive to the next stage. In addition, the combined effect of less attractive maturing bolls (Table 1 – compare LB with other fruit classes when all fruit classes are present) and feeding on young but economically inconsequential bolls means control will not be necessary, particularly after about 15% of bolls have opened (Gibb 1999).

Associated with compensation, first position boll retention is an issue of concern for growers. Currently, a first position fruit retention rate of 50-60% is considered ideal while excessively high rates (above 80%) could incur a yield penalty (ENTOpak, Cotton CRC). With fruit damage, our concern is whether a lower level of retention relates directly to a decrease in yield? This appears not to be the case in the example given in Figure 4. This graph shows no direct relationship between first position boll retention and yield for both transgenic and conventional cotton trialed in the Upper Namoi in 1999. Another key point in this graph is that the two low yielding trials (open circles) were unsprayed but they have retention rates similar to the sprayed trials suggesting that more sprays do not necessarily increase fruit retention. While retention of fruit is important to good yield in general, this can be achieved through larger and more second position bolls. This is one form of compensation where yield is maintained through the substitution of higher position fruit. In cropping areas such as Kununurra WA where the season warms up as fruiting progressed, late forming bolls make up a large portion of the yield (Kay 1998, S. Yeates personal communication). In this situation, the loss of first position bolls lower in the stem will have even less effect on yield.

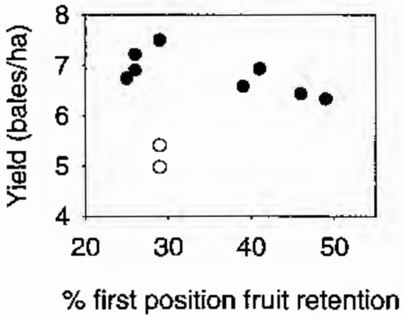


Figure 4. Relationship between fruit retention and yield taken from field trial results conducted by Industry Development Officers in the upper Namoi Valley in 1999. These trials included conventional and INGARD cotton managed under various pest control regimes.

How to harness the compensation potential of cotton?

To be successful in achieving compensation, it is critical to maintain a safety margin between potential pest damage and the crop's ability to tolerate and recover at any given time during the season. Because agronomic and environmental factors vary with time of the season and location, spray decisions should not always be based on static pest thresholds but on the risk of yield loss given the status of the crop and likely weather ahead. The concept of a sliding scale of pest threshold depending on canopy development and fruiting dynamics has been proposed by Hearn and Room (1979) and Wilson (1986). Because we are not yet able to forecast the yield impact at different pest levels and crop conditions, a truly dynamic threshold for pest management has not been widely implemented. Achieving good compensation involves a multitude of interacting factors, the following are a few key points warrant consideration.

Any factor involved in regulating cotton growth may influence how cotton recovers from pest damage. Conditions favourable for rank growth (e.g., irrigated cotton under high soil N) may exacerbate the response to pest damage such as excessive leaf production following tip damage. To reduce the risk of under compensation due to excessive growth, appropriately managing N and irrigation and choosing the right cultivar will help. Okra leaf cultivars with their higher light penetration and better resistance to mites and *Helicoverpa*, may both incur less damage and suffer less impact from responses to pest damage resulting in excessive leaf production.

Good accounting of the time required to recover lost fruit is essential. If fruit damage exceeds the level where substitution can occur (cf. Table 1), then the plant will initiate more fruit development. This could lead initially to a resumption of vegetative growth which may improve the radiation use efficiency (Sadras, 1996a) and a faster recovery of the crop but it could also delay fruit development resulting in a late crop. Therefore it is important to monitor damage during the early fruiting stage to ensure it does not exceed the level of sufficient substitution. For *Helicoverpa*, one way to do this is by comparing the potential fruit damage of larval number per meter (using Table 1) with actual fruit count. The current fruit retention guidelines given in ENTOpak and the Australian Cotton Industry Best Management Practices Manual

(Integrated Pest Management section) should also be consulted. In the future, we will make available a decision support system for the assessment of compensation potential (see Future work below).

There is strong evidence suggesting that most cotton crops can tolerate or even benefit from some tip damage as this can lead to an improvement in canopy structure and resource utilisation. However, there is a risk that high input crops may respond to tip damage by excessive leaf growth. This could increase self-shading and respiratory cost, reduce carbon gain, spray penetration and boll number through boll rot. Therefore, maximising compensation must include measures (e.g., cultivar selection, planting density or growth regulator application) to minimise excessive growth.

Encourage the establishment of beneficial insects to reduce secondary pests such as mites and aphids. Crops with fewer sprays or sprayed with softer chemicals could maintain healthier predator populations and inherit fewer problems with secondary pests later in the season. Other options to increase beneficial insects such as adding refuge crops and food supplements such as Envirofeast should also be considered (e.g., Mensah, 1997).

The use transgenic cultivars will significantly alter future pest management strategies. The current one-gene cultivars offer an enhanced early season protection against lepidopteran pests but the efficacy declines with the start of fruiting. Notwithstanding the potential increase in non-Lepidopteran pests (e.g., mirids), the early season *Helicoverpa* protection alone should be used to its full advantage through the promotion of predator / parasitoid populations. Mid- to late season fruit protection of current INGARD cultivars should follow that proposed for conventional cotton.

Future work

The implementation of compensation potential in decision making on pest control is the next major step in our research. To do so, we must make good predictions on the safety margin between crop tolerance and potential pest damage at any stage of the crop development. This involves a large number of variables (e.g., weather, cultivar, fruiting dynamic, damage history) which can only be processed with a computer simulation model. Based on a substantial amount of existing information, we have begun to describe the processes involved in compensation in a cotton growth model (OZCOT, Hearn, 1994). We are currently incorporating into this model response parameters of cotton to vegetative and fruit damage by *Helicoverpa*, mites and other major pests. The value of such a model lies not only in making spray decisions based on its projected yield for a given pest damage event through simulation, but also in finding the best agronomic options such as cultivar, N application, and planting density prior to planting to maximise compensation.

References cited

Eaton, F. M. (1931). Early defloration as a method of increasing cotton yields, and the relation of fruitfulness to fiber and boll characters. Journal of Agricultural Research 42, 447-462.

ENTOpak. (1999) A compendium of information on insects in cotton. CRC for Sustainable Cotton Production. Cotton Technology Resource Centre, ACRI, Narrabri NSW.

Hearn, A. B. (1994). OZCOT: A simulation model for cotton crop management. Agricultural Systems 44, 257-299.

Hearn A.B., and Room, P.M. (1979). Analysis of crop development for cotton pest management. Protection Ecology 1: 265-277.

Gibb, D. (1999). Late season *Heliothis* management. CCA Cotton Production Seminar. 1999.

Kay, A. (1998). Ord Cotton Update. The Australian Cotton Grower. Cotton Yearbook 1998: 42-22.

Mensah, R.K. (1997). Local density responses of predatory insects of *Helicoverpa* spp. to a newly developed food supplement 'Envirofeast' in commercial cotton in Australia. International Journal of Pest Management 43, 221-225.

Sadras, V. O. (1995). Compensatory growth in cotton after loss of reproductive organs. Field Crops Research 40, 1-18.

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

Sadras, V.O. (1996b). Cotton compensatory growth after loss of reproductive organs as affected by availability of resources and duration of recovery period. Oecologia 106, 432-439.

Sadras, V. O., and Fitt, G. P. (1997). Apical dominance - variability among cotton genotypes and its association with resistance to insect herbivory. Environmental and Experimental Botany 38, 145-153.

UC (1996). IPM for Cotton in the Western Region of the United States, 2nd Ed. UC DANR Publication 3305.

Wilson, L.J. and Sadras, V.O. (1998) How important is early season damage? The Ninth Australian Cotton Conference Proceedings. Aug. 13-14, 1998, Gold Coast, Queensland.

Wilson, L.T. (1986). The compensatory response of cotton to leaf and fruit damage. Beltwide Cotton Production Research Conference 1986, 149-153.

Wilson, L. T., and Gutierrez, A. P. (1980). Fruit predation submodel: *Heliothis* larvae feeding upon cotton fruiting structures. Hilgardia 48, 24-35.

Wilson, L. T., and Waite, G. K. (1982). Feeding pattern of Australian Heliothis on cotton. Environmental Entomology 11, 297-300.

Table 1. This is a look-up table of the number of fruit that will be damaged when fed upon by a given number of *Helicoverpa* larvae. The number of damaged fruit varies according to the developmental stage and the availability of fruit types on the plant. It can be used to assess the ability of a crop to replace lost fruit given the number of fruit currently on the plants. This table was generated using the *Heliothis* feeding model developed by Wilson and Gutierrez (1980) and Wilson and Waite (1982). Fruiting classes are: SS=small squares <0.5 cm, MS=medium squares 0.5 – 1 cm, LS=large squares >1 cm, FL=flowers, SB=small bolls <2.5 cm, MB= maturing bolls >2.5 cm but with soft boll wall, and LB=late bolls >2.5 cm with hard boll walls.

Fruit development	larvae per metre	SS	MS	LS	FL	SB	MB	LB	Total
Only small to large squares									
	0.5	0.1	1.0	2.5	0.0	0.0	0.0	0.0	3.7
	1	0.3	2.0	5.1	0.0	0.0	0.0	0.0	7.4
	2	0.5	4.1	10.1	0.0	0.0	0.0	0.0	14.8
	4	1.1	8.1	20.3	0.0	0.0	0.0	0.0	29.5
	6	1.6	12.2	30.4	0.0	0.0	0.0	0.0	44.3
	8	2.2	16.3	40.6	0.0	0.0	0.0	0.0	59.1
Squares and flowers									
	0.5	0.1	0.7	1.1	1.3	0.0	0.0	0.0	3.2
	1	0.3	1.4	2.1	2.6	0.0	0.0	0.0	6.4
	2	0.5	2.8	4.3	5.2	0.0	0.0	0.0	12.9
	4	1.1	5.7	8.6	10.4	0.0	0.0	0.0	25.7
	6	1.6	8.5	12.8	15.7	0.0	0.0	0.0	38.6
	8	2.1	11.4	17.1	20.9	0.0	0.0	0.0	51.5
Squares, flowers and small bolls									
	0.5	0.1	0.7	0.9	1.0	0.6	0.0	0.0	3.3
	1	0.3	1.4	1.8	2.0	1.2	0.0	0.0	6.6
	2	0.5	2.7	3.5	3.9	2.4	0.0	0.0	13.1
	4	1.0	5.4	7.0	7.9	4.9	0.0	0.0	26.2
	6	1.6	8.1	10.5	11.8	7.3	0.0	0.0	39.3
	8	2.1	10.8	14.0	15.7	9.7	0.0	0.0	52.4
All except hard bolls									
	0.5	0.1	0.7	0.7	0.7	0.4	0.2	0.0	2.9
	1	0.3	1.3	1.5	1.5	0.8	0.5	0.0	5.9
	2	0.5	2.6	2.9	2.9	1.7	1.0	0.0	11.7
	4	1.0	5.3	5.9	5.9	3.4	1.9	0.0	23.4
	6	1.6	7.9	8.8	8.8	5.1	2.9	0.0	35.1
	8	2.1	10.6	11.8	11.7	6.7	3.9	0.0	46.9
All fruit classes present									
	0.5	0.1	0.7	0.7	0.7	0.4	0.2	0.0	2.8
	1	0.3	1.3	1.4	1.4	0.8	0.4	0.1	5.6
	2	0.5	2.6	2.8	2.7	1.5	0.8	0.2	11.2
	4	1.0	5.3	5.6	5.4	3.0	1.7	0.4	22.4
	6	1.6	7.9	8.5	8.1	4.5	2.5	0.5	33.7
	8	2.1	10.6	11.3	10.8	6.0	3.4	0.7	44.9

Recovery of cotton in growth and yield after repeated damage

T.T. Lei
CSIRO Cotton Research Unit, Locked Bag 59, Narrabri NSW 2390 Australia

Introduction

The issue of compensatory growth in cotton is central to IPM. Cotton has been shown to produce more leaf area and more fruiting sites after early and mid-season pest damage (e.g., Sadras 1996). Therefore it is possible for cotton to recover from infestations by pests such as *Helicoverpa* without a loss of yield. The potential for full or over-compensation in growth and yield parameters exists for cotton and is well documented (e.g., Brook, Hearn and Kelly 1992a, b; 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. Brook et al. have also shown a high recovery potential under intermediate resource availability but the ability to fully recover declines at very high and very low resource levels. The mechanism for the observed patterns of recovery remains unclear. However, we suspect that adjustments in canopy structure and photosynthesis are important. To examine these possible mechanisms of compensation, we conducted field trials where plant responses were monitored after shoot terminals, squares and bolls were manually removed.

Methodology

A field trial was conducted at ACRI in 1998-99. We examined the responses in plant architecture and leaf level physiology following simulated *Helicoverpa* damage at 0 (Control) and 6 small larvae m^{-1} (Damage, Figure 1). Plants were given three levels of soil nitrogen: 0 (LN), 60 (MN) and 120 (HN) kg ha^{-1} to assess the pattern of recovery under different resource availability. Seed of Sicala V2i were sown in mid-October and thinned to 10 plants per meter. Standard irrigation and pest management were applied. We made five sequential harvests where the biomass of above- and below-ground tissue and the number of vegetative branches and reproductive structures were recorded for each treatment combination. There were four replicate plots per treatment combination.

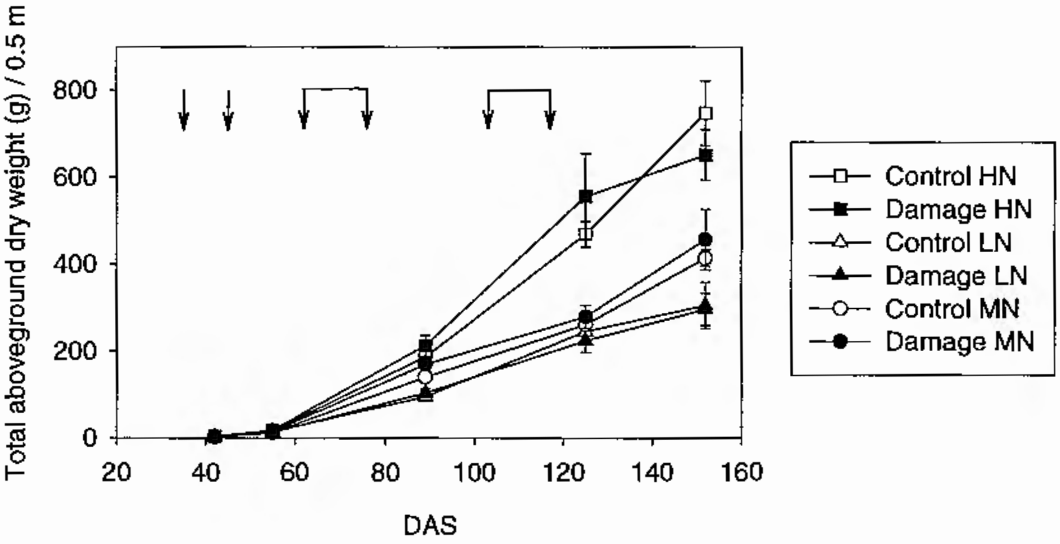


Figure 1. The increase in aboveground dry matter was clearly affected by soil N. The dates and duration of simulated damage during the growing season are indicated by the arrows.

To mimic realistic levels of *Helicoverpa* damage, we imposed repeated (4 times) damage to cotton plants during both the pre-squaring and the reproductive stages (Figure 1). For this experiment, we simulated the effect of 6 small larvae m^{-1}. The first damage event was at the pre-squaring stage where plants were tipped out. Pre-squaring tipping out has significant physiological consequences on the because it stimulates the production of lateral vegetative branches and so alters the crop's canopy structure. Subsequent damages involved the removal of reproductive structures simulating the realistic preferences and feeding rates of *Helicoverpa*. We used the actual number of fruiting structures of various sizes on the plant as the input for the Predation Model developed by LT Wilson (Table 1; Wilson and Gutierrez 1980). This model generates the number of squares, flowers and bolls to be removed over a 2-week period which simulates the developmental progression of a cohort of feeding larvae.

Table 1. Using the actual number of reproductive structures, we calculated how many of those structures 6 larvae will remove over a 2-week period. Note that the amount of damage to the large 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 from the fourth damage event (see Figure 1).

Nitrogen	S sq	M sq	L sq	flower	S bolls	L bolls
Actual number of fruiting structures per m						
HN	105.7	84.0	170.5	8.2	8.7	0.0
MN	58.3	58.7	125.3	4.7	6.7	0.0
LN	39.3	47.8	58.8	0.0	0.8	0.8
Fruiting structures removed per m						
HN	1.5	7.6	30.2	2.0	1.4	0.0
MN	1.2	7.5	31.0	1.6	1.5	0.0
LN	1.3	10.9	30.6	0.0	0.4	0.3

Abbreviations: S sq - small squares (<0.5 cm), M sq – medium squares (0.5-1.0 cm), L sq – large squares (>1.0 cm), S bolls – small bolls (<2.5 cm), and L bolls – large bolls (>2.5 cm, soft)

Findings of last year's experiment

Our results support the expected trend of yield recovery under different resource situations. Table 1 shows an overcompensation at moderate N, full compensation at low N and incomplete compensation at high N. There was a slight delay associated with damaged plots grown in moderate and low N, but a greater delay for those in high N. Clearly, even after repeated damages simulating 6 larvae per meter, cotton plants can recover fully under certain growth conditions.

Table 2. Lint yield and maturity date of Sicala V2*i* grown under 3 nitrogen regimes and 2 damage levels.

Nitrogen	Damage	lint (kg/ha)	60% boll open (DAS)	Delay (days)
HN	Control	2334	165±4	
HN	Damage	**1893**	**177±6**	12
MN	Control	1355	158±2	
MN	Damage	**1825**	**164±5**	6
LN	Control	1400	157±3	
LN	Damage	**1399**	**163±3**	6

The manner in which full compensation is achieved appears to be related to plant architecture. When the cotton plant loses its terminal, lateral branching is induced (Sadras and Fitt 1997). In our experiment, damaged plants of all three nitrogen treatments had significantly more lateral branches than their control counterpart (Figure 2, left panel). Not only did the lateral branch growth changed the canopy shape, it also maintained a number of fruiting sites above or equal to the control from early squaring onward (Figure 2, right panel).

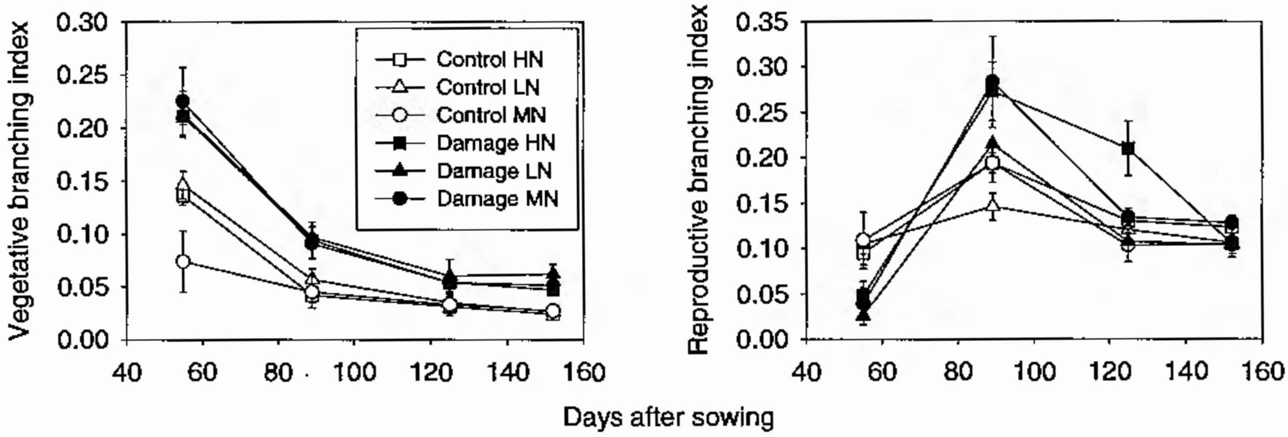


Figure 2. Two indices of how simulated damage changed the growth form of cotton during the growing season. The vegetative branching index represents the number of lateral branches per meter row of cotton corrected for the height of the plants. The reproductive branching index was similarly calculated using the number of fruiting branches.

The development of lateral branches following damage improved light interception in low and medium N treatments. Figure 3 shows the medium N results where the total amount of light intercepted at mid-canopy and at the ground level was greater for damaged plants, particularly later in the season. We helieve this allowed damaged plants to produce more carbon for the maturing bolls and led to a higher yield.

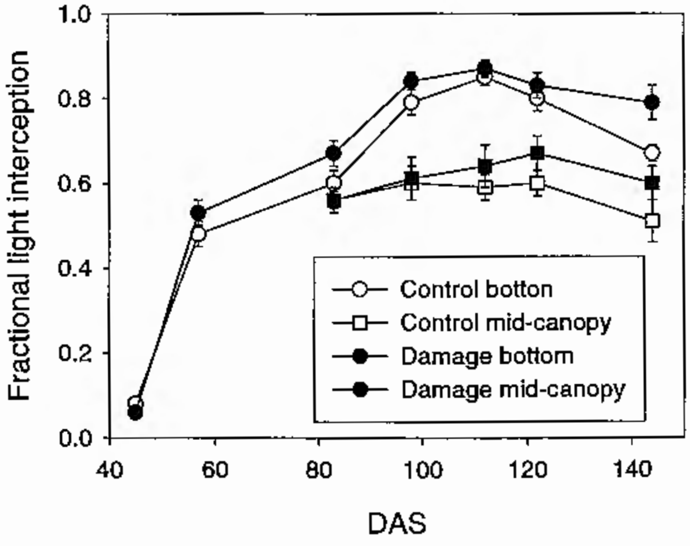


Figure 3. These are the patterns of light interception at mid-canopy and at the ground level across season for the moderate N treatment only.

Conclusions

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. In a sense, the stimulation of lateral branch growth increased the compensation capacity of cotton and makes them more tolerant of later season fruit damage.

But the recovery is resource-dependent: high in mid-resource situations and low at both the high and low resource extremes. The lack of full compensation in high resource-grown plants may be due to high self shading from their vigorous growth which nullifies the improvement in canopy structure of damaged plants. In low resource-grown plant an insufficient nutrient supply to maintain boll development is the likely cause of a lower compensation. We plan to carry out further experiments to confirm these inferences, and to explore differences in the compensation potential of a wider range of modern cotton varieties.

References

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

Brook KD, Hearn AB, Kelly CF. 1992b. Response of cotton to damage by insect pests in Australia: compensation for early season fruit damage. Journal of Economic Entomology 85: 1378-1386.

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.

Sadras VO. 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 Research 48: 199-208.

Wilson LT, Gutierrez AP. 1980. Fruit predation submodel: Heliothis larvae feeding upon cotton fruiting structures. Hilgardia 48: 24-36.