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ENHANCING CERCOT TO MEET INDUSTRY NEEDS
(CSP90C)

FINAL REPORT

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CSIRO
AUSTRALIA

CSIRO Cotton Research Unit
Narrabri

January, August & Final Reports

Part 1 - Summary Project Details

REPORTS

Please use your TAB key to complete parts1,2,4 & 5

CRDC Project Number:
CSP90C

January Report:	☐	Due 29-Jan-01
August Report:	☐	Due 03-Aug-01
Final Report:	☒	Due within 3 months of project completion
Project Title:	**Enhancing CERCOT to meet industry needs**	

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Part 3 – Final Report Format

1. Outline the background to the project.

Dynamic simulation models for cotton growth are powerful tools for the industry. Such models have a number of important features. (i) Models are essentials tools for investigating long term issues. This includes questions such as the long term impact of management decisions and the sustainability of cropping systems. (ii) When used as components of decision support systems they effectively extend the experience of managers, allowing the assessment of the impact of decisions in the context of the full climatic record. (iii) They allow integration of the influences of a range of factors acting on the crop simultaneously including pests, nutrition, moisture and weather and the interaction of these forces.

The work proposed in this project will:

(a) Use the capacity of the model to integrate responses of cotton to insect damage and to varying environmental conditions to yield improved tools for pest management that can account for compensation. This will also result in a capacity to assess the likely extent and value of compensation under different conditions.

(b) Make the model applicable to a wider section of the cotton industry by incorporating the capacity to deal with skip row cotton and with short and long season cotton cultivars. These are two key limitations noted by grower groups currently using the Ozcot model in decision support.

(c) Put the model into a simulation environment in which it can be readily applied to production decisions and which will enhance both model development and the ability of other researchers to work with the model; thus increasing its availability to industry.

The original intention was to develop these areas in the CERCOT model, which was under development. Intractable problems in calibrating CERCOT to properly simulate the fruiting dynamics of cotton occurred. In combination with the need to quickly meet the increasing demand for a model that could meet the needs of on farm simulation, this lead to the decision to concentrate on further development of the Ozcot model. It was considered that this change would consolidate the efforts of the modelling group and thus allow more rapid development of the model. It would also enhance our ability to respond to the increasing interest in the model.

Incorporating plant responses to insect damage. Previous research at ACRI by Ken Brook and colleagues showed that cotton plants could compensate for pest damage if yield potential was low but not when yield potential was high. This outcome was contrary to our understanding at the time and showed that our knowledge of the mechanisms of cotton responses to pests was limited. This was surprising in view of the economic and environmental importance of pest management in high-input cotton production systems.

To address this problem two projects were conducted by Dr Victor Sadras (CSIRO Cotton research Unit; CRDC projects CSP39C, CSP68C), with the specific aim of investigating the physiology of compensation in order to be able to predict it and use it in tactical pest management decisions. Using plant growth analysis, the responses of plant growth processes after insect damage have been quantified. Dr Sadras has compiled a comprehensive data base from his field experiments that will be used to test our model and to modify it in order to improve its ability to predict yield responses to pest damage.

Incorporating capacity to simulate skip row cotton and short and long season cultivars. Ozcot is currently being used by APSRU (QDPI/CSIRO Agricultural Production Systems Research Unit) as part of a decision support system in the Farmscape project. Ozcot is incorporated into a larger model known as ASPIM which provides linkages to simulation models for a range of crops. APSIM is being used with grower groups to answer questions regarding cropping options and management. From these grower groups, two key limitations to Ozcot have become apparent: the inability to allow for differences in development between individual cotton cultivars and the inability to reliably simulate water extraction and crop growth of cotton grown using skip row configuration. These are key features requested by growers and consultants.

Dryland cotton production, and with it skip row sowings, continues to increase in area. In the 1996 season approximately 50,000 ha of dryland cotton was sown, the majority being in skip row configurations. To be able to explore management options and strategic questions for this sector of the industry requires the model to be able to simulate the growth of cotton and its response to environment and management factors when grown under a range of planting configurations.

Dr P.J.Goyne of the Department of Primary Industries Queensland (DAQ77C), conducted a research project examining the crop-level processes involved in evaporative demand and soil water extraction of cotton crops of different row configuration. The results from these experiments will be used as a basis for developing the ability to simulate these processes.

Growers in situations were season length may be limiting, such as cooler areas or late plantings, often wish to consider management options specifically for short season cultivars. This requires the model to accurately reflect growth, maturity and yield of cultivars of different season length. Using a generic development pattern in a short season situation can falsely increase the risk of the results being effected by frost.

A series of experiments is being conducted on the development of short and long season cultivars as part of current projects (CSP57C and CSP67C). The timing of cut out in cotton is effected by the rate fruit are produced, the rate they develop and by the ability of the crop to support the fruit produced. Therefore data are being collected both on fruiting characteristics and dry matter production and partitioning. After analysis has been completed this data will provide the basis for parameter inputs to allow the model to reflect differences in the timing of crop maturity between cultivars.

These two modifications will allow the model to be used to the benefit of a larger section of the industry. While these limitations are of immediate significance for the

Farmscape project they are also important for the wider application of the model to both strategic and tactical decision making.

Including CERCOT into the APSIM shell. Incorporation of CERCOT into the APSIM model will have both direct and indirect benefits to the industry. The OZCOT model is already linked into the APSIM shell and is being used in this framework for decision support in the Farmscape project. Including CERCOT in place of OZCOT will bring the benefit of greater responsiveness to soil type and more realistic simulation of nitrogen processes to the benefit of decision support applications. In addition, using the crop template developed as part of the APSIM suite to re-code CERCOT will provide cleaner, more thoroughly documented code and access to the code maintenance protocols already established by APSRU. These benefits will result in more efficient program development, reduce time lost due to changes in personnel and make the code more accessible to other researchers who might work with it. APSIM will also be a valuable tool for strategic studies.

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

The aim of the project was to enhance the cotton simulation model to meet demands for applications to industry issues. There were four specific objectives, originally framed with reference to CERCOT but, as indicated in section 1, since August 1999 the objectives have been pursued in relation to Ozcot.

- *To incorporate into the model the capacity to simulate crop responses to insect damage, including compensation responses.*

  The capacity to respond to information on the timing and intensity of fruit loss due to insect damage has been re-introduced by modifying code from the Siratac system. Because the model has been extensively redeveloped since this code was previously used, further modification is necessary for the model to give accurate results in all scenarios. This work is continuing. A first version of code to allow mite levels to be input and their impact on cotton growth processes to be simulated has been developed. It will be necessary to test this against independent data sets collected by Sadras and Wilson.

- *To incorporate into the model the capacity to reliably simulate water extraction, growth and yield of skip row cotton.*

  The capacity to simulate skip row crops was incorporated into Ozcot by Brian Hearn as part of a consultancy funded from this project. Single skip is well simulated but with a higher variability than solid plant crops.

- *To develop parameters to reliably describe the fruiting dynamics of different cotton cultivars and modify the model to simulate the development of short and long season cultivars.*

  Parameters for a range of cultivars are now available in Ozcot, the contribution of these parameters in improving simulation results has not yet been quantified. Parameters relating to dry matter production and partitioning have been assessed experimentally. New temperature responses for a number of developmental processes have been derived.

- *To incorporate CERCOT into the APSIM crop simulation shell. This will allow linkages to other crop modules, provide access to an expanding library of meteorological and soils data and access to the state of the art management routines and model development tools*

  Methods to achieve the desired outcomes in this area are currently under review. Progress has been made toward incorporating Ozcot into the APSIM crop simulation template. Outside this project, a user friendly user interface has also been developed by CSIRO software developers in Narrabri and has been demonstrated to extension staff.

3. How has your research addressed the Corporations three outputs: Sustainability of natural resources, profitability and competitiveness, and/or people and communities?

Simulation models provide useful tools to explore the value of management options either in a strategic or tactical sense. Demand from researchers and producers for the model is significant and is increasing. Producer demand has included requests for assessing the potential for production in new areas, assessing alternative crop choices and cropping sequences and crop management questions. Research demands have included assessing the impact of management options in a strategic sense, water supply assessment, the impact of cropping potential on regional economics and the interaction of combinations of stresses, in particular the interaction of compensation capacity with other growth stressors.

4. Methodology, Results and Discussion.

The majority of the information approaching methodology, results and discussion are included in the attached papers. A brief discussion will be presented here with reference made to the appropriate articles as required.

Methods:

Incorporate capacity to simulate responses to insect damage. The explicit dry matter production and partitioning routines in CERCOT enable the incorporation of data from growth analysis studies such as those conducted as part of Dr Victor Sadras' projects CSP39C and CSP68C on plant responses to insect damage. This is important for pests which effect yield *via* processes involved in dry matter production and partitioning. In collaboration with Dr Sadras, we aimed to incorporate parameters/processes derived from his projects into CERCOT. The model was then to be tested against data collected as part of Dr Sadras' ongoing research.

Incorporation of capacity to simulate skip row cotton. Concurrent with this project Dr Phil Goyne (CRDC project DAQ77C) was conducting an investigation into water extraction under skip row cotton on a range of soil types. The findings from Dr Goyne's project could be incorporated into CERCOT by developing functions to describe the rate of water extraction from different soil layers as effected by planting configuration and soil type. A hedgerow evaporation model could also be used to account for the differences in evaporative demand of skip row and solid planted crops. In addition to the programming exercise, the skip row capability of the model was to be evaluated against independent data collected both by Dr Goyne and as part of the proposed project.

Incorporation of capacity to simulate early and late cultivars. As part of CSP28C and CSP57C a series of experiments have been conducted to derive stable parameters to characterise fruiting development in cotton cultivars and to allow development of the capacity to simulate short and long season cultivars. The experiments to develop these parameters are nearing completion. In the proposed project, the data collected in the two previous projects was analysed to derive stable parameters for general use. As part of the modelling exercise, the data was to be further explored to extract a minimum set of parameters necessary to reliably simulate the development of long and short season cultivars. Independent data sets were also collected so that the reliability of this capacity could be tested.

Include CERCOT in the APSIM shell. The Agricultural Production System Research Unit has developed a powerful modelling shell (APSIM) expressly for the analysis of cropping systems questions. OZCOT is currently linked into this shell. CERCOT was firstly to be linked into the shell as the most direct means of providing access to the new capabilities offer by CERCOT. Using the crop template developed as part of APSIM, the model was to be re-engineered to provide cleaner, more thoroughly documented code and access to the code maintenance protocols already established by APSRU.

Achievements:

Model code:

Code maintenance: The increasing use of the Ozcot model in on-farm application has increased the need to ensure that this model is both well maintained and modified in a timely manner to be able to approach new questions. For this reason, the last 12 months of this project have focussed on ensuring proper maintenance of this code. Tests have been conducted on various versions of the model to ensure that the response to yearly variation in weather and to time of sowing are both realistic and are similar to those of the original model developed and validated by Brian Hearn. Recent versions which account for the effect of weather on stand density at establishment and include the ability to simulate skip row crops were found to be less responsive to seasonal variation.

This was traced to the subroutine simulating leaf area development and a modified response of carrying capacity to moisture stress. In addition, improved quality of patched weather data (that is data where missing whether observations have been estimated) required a minor adjustment to the processing of the data files. Most of the subroutines in the model which contain alterations from the original 1995 version have been verified as not negatively effecting model performance. Tests on the remaining subroutines are continuing.

Capacity to simulate crop responses to insect damage. As a component of the research of Tom Lei (CSIRO) it is planned to use Ozcot to investigate the capacity of the cotton crop to compensate for insect damage under different combinations of weather and crop management. To do this, it is necessary to input into the model information on the timing and intensity of fruit loss. This capacity was re-introduced by modifying code from the Siratac system. Because the model has been extensively redeveloped since this code was previously used, further modification is necessary for the model to give accurate results in all scenarios. This work is continuing.

To be able to accurately predict compensation it may also be necessary to test the importance of modifications to canopy architecture, partitioning and the importance of tip damage. These effects were not accounted for in the early versions. Initially, the impact of changes in architecture will be explored by Tom Lei using simulation models for canopy light interception. The impact of partitioning and tip damage can be estimated through the validation of the current version of Ozcot against experimental data sets from artificial damage experiments. These have already been collected. If the initial investigations indicate a significant impact, the importance of these factors can be explored further.

The work of Lewis Wilson and Victor Sadras has quantified the impact of mite damage on leaf area development and radiation use efficiency. A first version of code to allow mite levels to be input and the impact on cotton growth processes has been developed. It will be necessary to test this against independent data sets collected by Sadras and Wilson. Testing is also required to explore the importance of modified nitrogen dynamics in the simulation of mite damage.

To incorporate CERCOT into the APSIM crop simulation shell. A first stage cotton model has been assembled based on the APSIM crop template. Development, dry matter accumulation and partitioning and responses to environmental stressors in the model are based on parameters from Ozcot. Currently the harvest index approach to yield development is used, in which the number and size of the fruit are not simulated but only the proportion of the total plant dry matter that is partitioned to the fruit. The data were derived from earlier work by Mike Bange, Victor Sadras and Steve Milroy. The model gave promising results in preliminary tests. The next step is to develop a routine to simulate the development of individual cohorts of fruit, as in Ozcot, to replace the harvest index component.

Experimental:

Nitrogen and RUE: Radiation use efficiency (RUE) is the amount of dry matter that can be produced per unit of photosynthetically active radiation intercepted by a crop. RUE is a widely used concept in simulation modelling. Currently Ozcot uses a simple photosynthesis calculation to estimate dry matter production. It is planned to convert to an RUE approach in the near future to allow the use of a wider range of available data in deriving model parameters and to allow a more comprehensive validation of this part of the simulation. The conversion also makes apparent more of the assumptions underlying the simulation of dry matter production.

RUE varies with nitrogen levels in the leaves. In cotton, it also appears to vary with development. RUE can be effected by the way nitrogen is distributed between leaves high in the canopy and low in the canopy. We conducted two experiments to explore whether the vertical distribution of nitrogen in a cotton canopy varied during the development of the crop. The gradients were found to vary during development, as too were the light interception characteristics of the canopy (Milroy, Bange and Sadras 1998; Milroy, Bange and Sadras, 2001). An initial analysis of the impact of this variation suggests that the magnitude of any effect is small (Bange and Milroy 1998a) due to the relatively small leaf area developed in many cotton crops compared to other crop species. However, this analysis was limited by the availability of data on the response of photosynthesis to leaf nitrogen content in cotton. The available response was developed in a controlled environment facility. Collection of appropriate data for field grown cotton began in the 1999-2000 season and will continue in the 2000-2001 season.

The information from these experiments is important for our understanding of the way nitrogen effects crop growth and also the interaction of development and nitrogen on RUE. Because the distribution of nitrogen can also effect the RUE for a given average canopy nitrogen concentration, gradients also need to be considered when simulating the effect of nitrogen supply on plant growth using an explicit plant nitrogen balance. This approach uses canopy nitrogen content and concentration as components of the plant nitrogen balance and to drive the canopy activity.

Establishment: Whilst developing routines for the impact of weather on stand density, Brian Hearn found that there were limited data available for Australian conditions. As a result all available data was used in the development of the code and no independent data were available for validation. Further, data that were available were primarily for obsolete cultivars and the question was raised as to whether there had been a change in the establishment percentage that could be expected under adverse conditions. A field experiment was therefore conducted to collect validation data using a current commercial variety. It comprised six times of sowing between September and November. A set number of seeds were sown in each eight metre plot and the number of plants that had emerged each day were counted in two rows. Daily minimum air temperature and soil surface temperature was recorded along with 9am soil temperatures at 5cm. Soil moisture content was recorded on a weekly basis. Time to emergence and final establishment was related to temperature parameters. The experiment is being repeated in the 2000-2001 season.

Cultivars of different maturity times: Because of the need to be able to simulate cultivars of different maturity class, we conducted a series of experiments to investigate the importance of growth and developmental parameters in governing the timing of cutout and crop maturity in different cotton cultivars. The aim was to derive stable parameters which could reliably describe the development of short and long season cultivars. Field experiments were conducted using S324 (short) and L22 (long) to investigate whether they differed significantly in their dry matter production and partitioning or fruiting dynamics. The results indicated that the cultivars differ little in dry matter production characteristics. Their light interception traits were similar and there was no difference in the efficiency with which they converted intercepted light to dry matter. However, S324 partitioned a significantly higher proportion of its dry matter to bolls during early fruiting than did L22. The methods and results are presented in more detail in the attached articles (Bange and Milroy, 1998b; Bange and Milroy, 2000).

Analysis of the fruiting dynamics showed that the S324 had a significantly higher rate of site production than L22. An analysis of the interaction of fruiting dynamics and dry matter dynamics suggest that the difference in partitioning is probably due to the higher demand by the fruit in S324 due to the higher squaring rate. There was no evidence that the cultivars differed in the way their fruiting pattern responded to the plants' dry matter status (Milroy and Bange 2001).

In deriving developmental parameters for the different cultivars, it became apparent that the temperature responses being used did not robustly describe the impact on development over the range of temperatures being used. Therefore, experiments have been conducted in the CSIRO Plant Industry phytotron in Canberra to explore the response to temperature of the rate of developmental processes over a wide range of temperatures. Excellent results have been obtained for the rate of development toward first square. When compared to field data from a number of experiments, the response function derived appears to represent a maximum rate which may or may not be obtained in the field depending on other factors such as tip damage, drought or cold shock which would delay the appearance of first square. The results for the rate of site production were unexpected. They suggest a constant rate at moderate temperatures followed by an increasing rate at high temperatures. The results are presented in more detail in the conference paper attached (Bange and Milroy 2001). No link could be found in the variation in site production with the rate of early shedding or with the node at which the first fruiting branch was developed. Further data are being collected to attempt to verify the response. Preliminary results were presented to industry at the ACGRA cotton conference (Milroy and Bange 1998) and the CRC Research Review (Milroy and Bange 1999).

The results to date confirm that the key variables to differ between cultivars of different maturity class relate to fruiting development rather than carbon supply. Another series of experiments has been started to test the application of these principles to a wider group of genotypes. Six cultivars were sown in the field at the ACRI at two times. The experiment is being repeated in the 2000-2001 season. Data collection is also starting this season on four important commercial cultivars for direct use in the model.

The results of these experiments are important for a number of reasons. Firstly they are necessary to develop methods of reliably quantifying and predicting the development of a cultivar. The parameters are also important for allowing cotton simulation models to account for the differences in yield development between cultivars. This is needed particularly when considering scenarios with reduced season length. It may also prove important when considering compensation responses by different cultivars. A capacity to reliably describe crop development is also necessary for monitoring crop development and may improve the use of decision support tools or management procedures which incorporate crop development. In addition to these direct practical applications, the research also adds to our understanding of crop development and the interaction of fruiting dynamics and plant carbon status.

5. **Provide an assessment of the likely impact of the results and conclusions of the research project for the cotton industry. Where possible include a**

statement of the costs and potential benefits to the Australian cotton industry and future research needs.

Ozcot can provide producers with an obective assessment of the likely outcomes of changes to management practices under their own particular conditions. By using the full historic weather record for their particular location it can provide a probabilistic comparison of two or more options. The options that can be manipulated include: sowing date, nitrogen, irrigation, planting density and row configuration. Some capacity to deal with cultivar differences is also available.

The demand for this technology is high and it is envisaged that it will continue to increase as more producers are exposed to the value of using simulation models in discussion group situations.

6. **Describe the project technology (eg. commercially significant developments, patents applied for or granted licenses etc).**

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7. **Provide a technical summary of any other information developed as part of the research project. Include discoveries in methodology, equipment design, etc.**

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8. **State the recommendations on the activities or other steps that may be taken to further develop, disseminate, or to exploit the project technology.**

The increasing demand for this technology is stretching the resources of the CSIRO team to support it. IDOs are therefore being offered training in using the model. This is an important initiative which needs to be ongoing and needs to be encouraged.

Model development needs to continue to ensure the model provides satisfactory output under the increasing range of conditions in which it is being used. This will require continued commitment to both scientific and computing personnel. The lack of computing support within TA for model development means that researchers time is being used less effectively than it could be.

9. **List the publications arising from the research project.**

Refereed Journal Papers

Milroy,S.P. and Bange,M.P. (2001) Profiles of leaf nitrogen and light in reproductive canopies of cotton. *Annals of Botany,* 87: 325-333.

Bange,M.P. and Milroy,S.P. (2000) Timing of crop maturity in cotton: dry matter production and partitioning of an early and late season cultivar. *Field Crops Research* 68: 143-155.

Scientific Conference Papers

Bange,M.P. and Milroy,S.P. (2001) Effect of temperature on the rate of early fruiting developmental processes of cotton. *Proceedings of the 10th Australian Agronomy Conference, Hobart, Jan 2001* (CD).

Milroy,S.P. and Bange,M.P. (2001) Fruit production rates in cotton cultivars of different maturity times. *Proceedings of the 10th Australian Agronomy Conference, Hobart, Jan 2001* (CD).

Bange,M.P. and Milroy,S.P. (1998a) Assessing effects of canopy nitrogen and light distribution on radiation use efficiency of cotton. *Proceedings of the Second World Cotton Research Conference, Athens, Greece, 1998,* pp. 498-501.

Bange,M.P. and Milroy,S.P. (1998b) Growth analysis of short and long season cotton cultivars. *Proceedings of the 9th Australian Agronomy Conference, Wagga Wagga, 1998,* pp. 415-416.

Milroy,S.P., Bange,M.P. and Sadras,V.O. (1998) Leaf nitrogen gradients in cotton canopies vary with ontogeny and nitrogen supply. *Proceedings of the 9th Australian Agronomy Conference, Wagga Wagga, 1998,* pp. 417-418.

Industry Papers

Milroy,S.P., Bange,M.P. and Richards,D.Q. (2000) Cool starts: what is normal. *The Australian Cottongrower* 21 (2): 70-73.

Milroy,S.P. and Bange,M.P. (1999) Agronomic research to support the development of crop simulation models. *Proceedings of the Cotton CRC Research Conference, Narrabri, NSW, 21-22 July 1999.* pp. 309-313.

Milroy,S.P. and Bange, M.P. (1998) Do degree days accurately describe the rates of cotton development? *Proceedings of the 1998 Australian Cotton Conference, Broadbeach, Qld.* pp. 209-214.

Part 4 – Final Report Plain English Summary

The aim of the project was to enhance the CERCOT cotton model to meet demands for applications to industry issues. Due to the demand for improvements in the Ozcot model which was already in use by researchers and on-farm, the focus was shifted to that model.

(a) A key concem noted by researchers and grower groups currently using the Ozcot model in decision support is the limited capacity to simulate cultivars of differing maturity type. A series of field experiments was conducted over three years to investigate the differences between a long and a short season cultivar in terms of fruiting dynamics and in dry matter production and partitioning. The results indicated little difference in dry matter production but a difference in partitioning. It is suggested that the difference in partitioning is a result of the observed differences in fruiting rate.

(c) Whilst investigating the fruiting dynamics of the cultivars it became apparent that problems were arising with the standard degree-day function used to account for the influence of temperature. A study including both field and glasshouse experiments has yielded a more robust description of the effect of temperature.

(d) No research had been conducted into the vertical distribution of nitrogen within the cotton canopy. In other species the distribution has been shown to influence the efficiency with which the crop can use light. Therefore it was important to check the magnitude of the gradients and there impact on light use efficiency to assess its significance in simulating the response of cotton to nitrogen. In two field experiments the observed gradients were found to changed during the development of the crop, but the impact on the efficiency of light use was small.

(e) Subroutines have been reinstated to allow the cotton model to accept inputs of observed fruit numbers. Because the model has changed in many ways since this code was last used, testing is continuing to ensure that including this code has not interfered with the reliability of simulation output. The capacity to input fruit numbers will be used in research to improve tools for pest management that can account for compensation and a capacity to assess the likely extent and value of compensation under different conditions.

(c) A first stage cotton model has been assembled based on the APSIM crop template. Development, dry matter accumulation and partitioning and responses to environmental stressors in the model are based on parameters from Ozcot. The model gave promising results in preliminary tests. This is an important development which could greatly streamline ongoing development of cotton simulation models. It will also enhance d the ability of other researchers and extension officers to work with the model; thus increasing its usefulness to the industry.

Profiles of Leaf Nitrogen and Light in Reproductive Canopies of Cotton (*Gossypium hirsutum*)

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During vegetative growth, the vertical profile of leaf nitrogen (N) often parallels the profile of light distribution within the canopy. This gives an advantage in canopy photosynthesis over a uniform distribution of leaf N. We investigated the influence of both reproductive growth and N supply on the profiles of N and light in canopies of irrigated cotton crops (*Gossypium hirsutum* L.). Regular samplings were made from soon after the onset of reproductive growth up to crop maturity. Each two weeks a 1 m^2 sample of the canopy was cut in four successive vertical layers of equal thickness. The leaf area and N concentration (%) in each layer was measured. The vertical N gradient became more marked with ongoing reproductive development. It is hypothesised that because of the high rate of growth after the onset of reproductive development and the long duration of this phase compared to other species, the whole canopy photosynthetic benefit that would accrue from maintaining the N gradient is likely to be accentuated. The rate of decline in leaf N concentration in a layer was not related to either the initial concentration in the leaves nor the boll load within the layer.

Key words: *Gossypium hirsutum*, leaf nitrogen, light profile, nitrogen, nitrogen distribution, remobilization, reproductive growth

INTRODUCTION

In vegetative canopies, the profile of nitrogen (N) concentration in leaves has been shown to be positively correlated to the light environment experienced by the leaves (Werger and Hirose, 1991). That is, the N concentration in a leaf layer can be related to the proportion of the incoming light that reaches that layer. While N concentration also declines with leaf age, most of the difference in the concentration of nitrogen per unit leaf area (N_A, $gm^{-2}{}_{leaf}$) among leaves at different heights in canopies of lucerne (*Medicago sativa* L.) was associated with light intensity

(Lemaire *et al.*, 1991). Hikosaka, Terashima and Katoh (1994) elegantly separated light and leaf age as sources of variation, and demonstrated the role of light in modulating leaf N distribution by training *Ipomoea tricolor* Cav. to grow horizontally and varying the light intensity of leaves of different ages.

For a given total N content per unit ground area (N_C, gm^{-2}_{ground}) in the canopy, preferential distribution of N to upper leaves gives higher canopy photosynthesis rates compared to a uniform distribution (Field, 1983; Hirose and Werger, 1987; Werger and Hirose, 1991; Sinclair and Shiraiwa, 1993; Wright and Hammer, 1994; Leuning *et al.*, 1995; Connor, Sadras and Hall, 1995). This is because the strong correlation between leaf N and photosynthetic enzymes means that the photosynthetic apparatus are placed where they are best utilised (Charles-Edwards *et al.*, 1987; Evans, 1989).

However, Sadras, Hall and Connor (1993) found that in sunflower (*Helianthus annuus* L.), while the association between N_A and light receipt held in vegetative canopies, it did not hold during the period of active reproductive growth. It was postulated that this deviation was due to translocation of nitrogen from leaves to the developing seed, since the seed accrues a high concentration of protein. It was also found that N was removed faster from the leaves near the top of the plant than from the lower leaves. Whether this was being governed primarily by the proximity of these leaves to the capitulum or the greater proportion of labile N in leaves of high N concentration could not be ascertained.

Like sunflower, the seed of cotton (*Gossypium hirsutum* L.) is high in protein and comprises a significant nitrogen sink in the plant (Leffler, Elmore and Hesketh, 1977; Hearn, 1981). Unlike sunflower, which is determinate, cotton's indeterminate growth habit means (i) that fruit production is widely spread in time and space within the canopy, and (ii) there is a substantial overlap between vegetative and reproductive growth. In addition, a significant proportion of the leaf area of cotton is produced on lateral branches exserted from the mainstem nodes (Wullschleger and Oosterhuis 1992). Therefore, leaves of different ages are present in the same canopy layer and are thus exposed to similar light regimes. For these reasons, cotton provides a useful model for studying the mechanism underlying changes in leaf nitrogen distribution in reproductive canopies. We thus investigated the influence of both reproductive growth and nitrogen supply on the profiles of nitrogen and light in canopies of irrigated cotton crops.

The aims of this research were: firstly to determine whether a clear N gradient existed in cotton canopies and whether any gradient could be related to light distribution; secondly to record whether the gradient was maintained with the increasing dominance of reproductive growth over time; and thirdly to see whether any changes in the N concentration in a layer could be explained in terms of proximity to the reproductive N sink or the initial leaf N concentration.

This information can be used in simple frameworks to scale from leaf to canopy photosynthesis to explore the impact of N gradients on crop photosynthetic rates (Kull and Jarvis, 1995; Leuning *et al.*, 1995). This may assist in capturing the impact of ontogeny and N supply on radiation use by the crop (Wright and Hammer, 1994; Bange, Hammer and Rickert, 1997; Bange and Milroy, In Press).

MATERIALS AND METHODS

Cultural techniques

Two field experiments were conducted on a uniform grey cracking clay (Vertosol) at the Australian Cotton Research Institute, Narrabri (30° S, 150° E); a semi-arid environment of north-west New South Wales, Australia. The crops were sown with a commercial row crop planter with a 1 m row spacing and were established and grown with full irrigation and using high input management and insect control as described in Hearn and Fitt (1992).

In the first experiment (Exp. 1), an okra leaf cotton cultivar, Siokra L22, was sown on 11 October 1995 and a population of eight plants per m^{-2} was established. Nitrogen was applied as anhydrous ammonia 62 days before sowing at a rate of 15 g m^{-2}. This is the optimal rate for pre-plant N application in this farming system (Constable and Rochester, 1988; Rochester, Constable and Saffigna, 1997). Each plot was 175 m long and 4 rows wide and there were three replicates. In the second experiment (Exp. 2), Sicala V-2*i*, a normal leaf cultivar, was sown on 14 October 1996 with a plant population of 13 plants per m^{-2} being established. Treatments received either nil or 15 g m^{-2} of N as anhydrous ammonia applied 47 d before sowing. A randomised complete block design and four replicates were used. Plots were 75m long by 4 rows wide.

Measurements

Beginning around the time of first flower, when reproductive growth was negligible, destructive samplings were made at approximately 14 d intervals. In each plot a 1 m^2 area of the crop canopy was cut in four successive layers of equal vertical thickness (layer 1 being the top, layer 4 the bottom). The leaf area (and hence leaf area index, LAI) in each layer was then measured with a calibrated planimeter (Licor 3100, Nebraska, USA). The leaf samples were dried in a forced draught oven at 70°C and weighed. The material was then ground and analysed for N concentration on a mass basis (N_M, g N g^{-1} dry weight) using a near infrared refractometer (Perten Inframatic 8100, Germany) calibrated against the Kjeldahl method or, if the sample was too small, using complete combustion and thermal conductivity analysis (LECO FP-228, St Joseph MI, USA) also calibrated against the Kjeldahl method. Stratified samplings continued until the period of maximum fruit (boll) growth was over and the crop was approaching maturity. A total of seven stratified harvests were made in Exp. 1 and six in Exp. 2.

In Exp. 1, reproductive dry matter (including flower buds (squares), green bolls and open bolls) was measured on the weeks alternate to the stratified samplings. In Exp. 2 this was measured using the stratified sample. In both cases, reproductive structures were separated from the rest of the plant, dried, ground and analysed for N using the methods described above.

Measurements of photosynthetically active radiation (PAR, 0.4-0.7 μm) were taken in each plot above (PAR_O) and below of the canopy (PAR_T) at approximately weekly intervals. At each date, three measurements were made on each plot using a ceptometer (Decagon, Delta-T Devices Ltd., Cambridge, UK). Measurements were taken between 1100 and 1300 hours (Eastern Standard Time).

Light distribution coefficient

For each plot, the proportion of radiation intercepted by the crop (Q_I) was calculated as:

$$Q_I = (PAR_O - PAR_T)/PAR_O \qquad (1)$$

This was then regressed on days after sowing (DAS) to allow interpolation between measurement dates. An exponential function was fitted to the data collected from each plot:

$$Q_I = a[1 - \exp(-b.DAS)] + c \qquad (2)$$

where *a*, *b*, and *c* are fitted coefficients.

Using values of Q_I for the day of the stratified biomass samplings as derived from eqn (2), a canopy light extinction coefficient (k_L) was calculated for each plot from a non-linear regression between Q_I and leaf area index (LAI):

$$Q_I = d[1 - \exp(-k_L.LAI)] + f \qquad (3)$$

where d and f are fitted coefficients.

For subsequent analysis, light intensity at the midpoint of each layer was calculated using the k_L derived for the particular treatment and sampling date and the cumulative LAI from the top of the canopy to the midpoint of the layer of interest. This assumes that k_L varied little with vertical position in the canopy. Light intensity measured at six levels within a crop of V-2*i* grown in 1999 in the same location as our experiments indicated no variation in k_L with depth in the canopy (data not presented). The data fitted Beer's law closely ($R^2 = 0.94$; $n = 10$).

Nitrogen distribution coefficient

The nitrogen distribution coefficient (k_N) as defined by Hirose and Werger (1987) quantifies the distribution of N between leaves at different levels in the canopy. For each plot k_N was derived using linear regression and the function:

$$N_A / N_{A,top} = \exp(-k_N(LAI_{cum} / LAI_{tot})) \qquad (4)$$

where N_A is the leaf N per unit leaf area in the layer (g N m^{-2}_{leaf}), $N_{A,top}$ is the N_A in the top layer, LAI_{cum} is the cumulative LAI from the top of the canopy to the midpoint of the layer, LAI_{tot} is the total LAI of the canopy. The coefficient (k_N) is usually greater than zero, and increases when leaves in the upper canopy have higher N concentrations relative to the canopy below. When k_N equals zero the canopy has a uniform N distribution. This relationship has been successfully used for both wild and cultivated species (Hirose and Werger, 1987; Hirose *et al.*, 1988; Lemaire *et al.*, 1991). An average k_N was calculated for each crop; pooling data from all times of sampling and all replicates. Stepwise regression analysis was then used to assess whether k_N varied between sampling dates.

Relationship between profiles of nitrogen and light

The putative association between the pattern of foliar N and the distribution of light in the canopy was explored with two complementary approaches. First, we explored the relationship between relative N_A and relative irradiance (RI) using regression analysis. Relative N_A for the ith-layer was calculated as the ratio $N_{A,i}/N_{A,top}$. Likewise, we calculated RI as the ratio of the light intensity at the midpoint of each layer to that above the canopy. The power function derived by Hirose *et al.* (1988) was then fitted to the data:

$$Relative\ N_A = m.RI^n \tag{5}$$

where m and n are fitted parameters. Our second approach was to explore the variation in k_N and k_L with development.

RESULTS

Whole canopy growth and nitrogen dynamics

The dynamics of leaf area and total biomass accumulation were generally similar for the two fertilized crops (Fig. 1a to d). In the unfertilized crop, LAI began to plateau when reproductive growth started and then remained relatively constant. The pattern and timing of total biomass and boll biomass was similar between the high and nil N treatments in Exp 2 (Fig. 1d and f), but the rates of accumulation were slower in the nil treatment.

In Exp. 1, leaf N concentration, on both a leaf area (N_A) and leaf mass basis (N_M), declined with crop age; at maturity, it was about half the value measured 60 DAS (Fig. 2a and c). In Exp. 2, both N_A and N_M showed a biphasic pattern with an initial declining phase followed by an increase (Fig. 2b and d). These two phases were more marked in the unfertilized than in the fertilized crop; the end of the declining phase occurred earlier and the increase was sharper in unfertilized crop. The biphasic pattern was not seen in Exp 1. In both experiments, leaf area per unit mass (LAM, $gm^{-2}{}_{leaf}$) increased early in the season and then declined from 90 DAS to maturity in Exp. 1 and from 70 DAS to maturity in Exp. 2 (Fig. 2e and f). The fertilized treatment tended to have greater LAM than the unfertilized (Fig. 2f).

Nitrogen and LAI dynamics within layers

In each experiment N_A gradients were consistently found over the duration of measurements (Fig. 3). N_A was always lower in the lower layers of the canopies (Fig. 4a to c). In Exp. 1, the N_A of the top layer was relatively stable over time apart from a high value at 130 DAS. On the other hand, the lowest layer declined steadily from approximately 1.8 g m^{-2} at 82 DAS to 0.8 g m^{-2} at 166 DAS. In Exp. 2, the trend was for each layer to show an initial declining period followed by an increase reflecting the pattern of total canopy N_A (Fig. 2b). The duration of the declining phase was least in the top layer and the rate of increase was greater in the higher layers. As a consequence, in each of the three crops an increasing differential in N_A developed between the layers over time. This was most accentuated in the unfertilized crop of Exp. 2 and least in Exp. 1.

In both fertilized crops, LAI in the top layer generally declined over the period of measurement whilst each of the other layers showed an increase followed by a gradual loss of leaf area (Fig. 4d to f). In the unfertilized crop, there was limited variation in the LAI of the individual layers, reflecting the relatively constant total LAI over this period (cf Fig. 4f *vs*. Fig. 1b).

The amount of leaf N per unit ground area (N_C, Fig. 4g to i) can be analysed as the product of leaf area (Fig. 4 d to f) and N_A (Fig. 4a to c) in each layer of the canopy. In the fertilized treatment of Exp. 2, the large variation in LAI strongly influenced the dynamics of N_C per layer: the top layer generally declined over the period of measurement whilst each of the other layers showed an increase followed by a loss of N. In contrast, owing to the limited variation in LAI, the pattern of N_C in the unfertilized crop was more clearly related to the dynamics of N_A. Of interest is that the amount of foliar N did not decline in any layer in the canopy of unfertilized crop. In Exp. 1, both LAI and N_A appeared to contribute similarly to the pattern of N_C.

In Exp. 2, the rate of change of N_C of a given layer was unrelated to the rate of accumulation of N in the reproductive organs of that layer or the rate of accumulation of N in the reproductive organs summed over the whole crop (data not presented). N content of reproductive organs was not available for Exp 1.

Relationships between profiles of nitrogen and light

In both experiments, relative N_A decreased with distance below the canopy surface and hence with decreasing RI (Fig. 5a to c). The power function (eqn 5) gave a significant ($P < 0.0001$) fit to N_A *versus* RI for each crop when the data was pooled across sampling dates. In the unfertilized crop of Exp. 2, the power term increased significantly with time ($P < 0.02$) (Fig. 6b). For the high N crop, while stepwise regression showed a significant difference in the relationship for the different sampling dates ($P < 0.001$), there was no obvious trend with time (Fig. 6b). In the first experiment, while the relationship was not tight for the combined data ($R^2 = 0.70$), there was no significant difference between the sampling dates (Fig. 6a).

When considered across all harvests relative N_A was only loosely related to LAI_{cum} (eqn 4). Given the variation in the N_A *versus* RI relationship with sampling date, we fitted eqn (4) and calculated N extinction coefficients (k_N) for each sampling date. In both experiments, but more markedly in Exp. 2, k_N increased significantly ($P < 0.05$) with crop age (Fig. 6c and d). The light extinction coefficient, k_L, also changed with crop age; it remained stable around 0.6 until about 120 DAS, and then increased (Fig. 6e and f), possibly in association with the increased fruit component (Fig 1e and f). Neither k_N nor k_L differed significantly between the high and nil N treatments at any sampling in Exp 2.

DISCUSSION

The purpose of this study was to determine whether clear N gradients could be found in cotton and how reproductive growth effected any gradients found.

Profiles of foliar N

Despite the coexistence of leaves of varying ages in the same canopy layer, a clear N gradient was apparent at each time of sampling (Fig. 3). Relative irradiance (RI) or LAI_{cum} accounted for much of the variation in leaf N per unit leaf area (N_A) provided the ontogenetic influence was considered (Figs. 5 and 6). It could be alternatively hypothesised that the gradient was due to different average leaf age in the different layers. While N_M in individual cotton leaves declines with age (Thompson *et al.*, 1976) and there are more older leaves lower in the canopy (Constable and Oosterhuis, In Press), the pattern of change in the concentrations of different layers showed that the gradients were not simply reflecting leaf age. This is indicated by the fact that, although the lower layers decreased in concentration, the upper layers actually increased in concentration even after new leaf initiation had ceased. If the concentration in each layer was merely reflecting leaf age, the concentration in the upper layers might be expected to follow the same pattern as the lower layers; with concentration declining and approaching the same minimum. These results are consistent with findings in other species which indicate that the effect of leaf age on N_M can be overridden by light intensity, although it does not explain all the variation in N distribution (Hirose *et al.*, 1988; Lemaire *et al.*, 1991; Evans, 1993).

The relationship between relative N_A and RI remained relatively stable over development in the fertilized crops but was accentuated as reproductive growth increased in the nil N crop. The magnitude of the N gradient against LAI (reflected in k_N), however, was found to increase throughout reproductive development in all three crops (Fig. 6). This resulted from N_A increasing in the upper, and decreasing in the bottom layers of the canopy (Fig. 4a to c).

The contrasting decline in the leaf N gradient during grain filling in sunflower (Sadras, Hall and Connor, 1993) was associated with a) a close association between N efflux from leaves and N influx to the seed, and b) faster decline in N concentration in leaves at the top of the canopy. We postulated that cotton could provide a useful model to separate the two influences because the distribution of fruit in the plant would mean the initial leaf N concentration should not be correlated with proximity to the sink. In fact, neither of the proposed mechanisms appeared to operate in cotton.

The influence of sink proximity on the rate of efflux from cotton leaves was assessed by comparing the rate of N efflux from the leaves to the rate of influx to the fruit but no association was found. Close nutritional relations have been found between leaves associated with a sympodium and the fruit on that sympodium. That is, a large proportion of the N and carbohydrate exported by the leaves on a sympodium and the subtending mainstem leaf moves to the bolls on that sympodium (Brown, 1973; Constable, 1982; Oosterhuis, Zhu and Wullschleger, 1989). Further, Zhu and Oosterhuis (1992) found that the increase in boll N on a given sympodium coincided with the decline in leaf N for that branch. However, it should be noted that the amount of N accumulated in the bolls on the sympodium was six times the loss of N from the sympodial leaves and the associated mainstem leaf combined (Zhu and Oosterhuis, 1992). Thus, the rest of the N (85%) must either have been translocated from other parts of the plant or have been supplied by concurrent uptake from the soil. Presumably, this level of movement overrode any association caused by the movement of N from the leaves to the bolls of each sympodium. Moreover, in both our experiments while N_C (Fig 2g and h) and N_A (Fig 4a to c) of the lower layers declined in time, we found an increase in the upper portions of the canopy during the period of rapid development of the reproductive sink (Fig. 1).

There was also no correlation between initial N concentration of leaves in a layer and the rate of depletion of N in that layer. In fact, N_A decreased most rapidly in the lower layers with the lowest initial N_A. The leaves in the upper layers with the highest initial N_A tended to either remain stable or increased in N_A. This was most noticeable in the nil N treatment of Exp 2.

Implication for cotton growth

The increase in k_N after the onset of reproductive growth indicates more marked gradients of N distribution in the canopy (Fig. 6) although this was only related to a change in the N_A *versus* RI relationship in the nil N crop of Exp. 2. Working with *Solidago altissima*, Werger and Hirose

(1991) concluded that optimizing the distribution of N in the reproductive phase was less critical than in the vegetative phase, and that the advantage in terms of canopy photosynthesis was less, in part because of declining LAI in the reproductive phase. This was based on the fact that it has been shown on theoretical grounds that the photosynthetic advantage accruing from optimizing N distribution is less with smaller LAI (Hirose and Werger, 1987). In cotton, the production of fruit is morphologically related to the production of leaves. Therefore, while in some species there is a decline in LAI during reproductive growth, cotton differs in that LAI is increasing for approximately the first half of this period (Fig. 1), thus increasing the likely advantage to accrue from optimizing N distribution.

Furthermore, maintenance of photosynthesis after the onset of the reproductive phase is important in cotton to sustain the high rates of dry matter accumulation typical of this stage, and because of the extended duration of crop growth after the onset of reproductive development (Fig. 1). Thus, in contrast to the conclusion of Werger and Hirose (1991), both the importance of maintaining optimal N distribution during reproductive growth, and the likely benefit to accrue in terms of canopy photosynthesis, are high.

The contrast between the changing *n* parameter of the power function for the relationship between relative N_A and RI (eqn 5) in the nil N treatment of Exp. 2 and its stability in the high N treatment may relate to the difference in the N_C of the two canopies. While the analysis of Hirose and Werger (1987) indicates that there is likely to be a greater photosynthetic benefit from optimizing N distribution in canopies with a greater N_C, that of Leuning *et al.* (1995) suggested the benefit was greater in a canopy with low N_A or N_C. During boll filling, the high N treatment had two to three times the N_C of the nil N treatment and higher N_M and N_A(Fig. 2).

CONCLUSIONS

A clear vertical N gradient was established in canopies of irrigated cotton crops. N_A of a layer could be related to the light intensity at the mid point of that layer. The gradient of N_A against LAI_{cum} became stronger during the period of increasing reproductive growth. Neither the proximity of leaves to N sinks nor the initial N_A of leaves in a given layer appeared to govern the rate of N decline in the leaves. Furthermore, the steeper gradient which developed during reproductive growth involved depletion of N in the lower layers but either maintenance or accumulation of N in leaves in the upper layers of the canopy. The persistence of vertical N gradients in cotton may relate to the need to maintain high growth rates over a prolonged period.

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LITERATURE CITED

Bange MP, Hammer GL, Rickert KG. 1997. Effect of specific leaf nitrogen on radiation use efficiency and growth of sunflower. *Crop Science* **37**: 1208-1214.

Bange MP, Milroy SP. Effects of specific leaf nitrogen on the radiation use efficiency of cotton. In: *Proceedings of the Second World Cotton Conference*. Athens, Greece. 6-12 Sep 1998. Athens, Greece: (In Press).

Brown KJ. 1973. Factors affecting translocation of carbohydrates to fruiting bodies of cotton. *Cotton Growing Review* **50**: 32-42.

Charles-Edwards DA, Stutzel H, Ferraris R, Beech DF. 1987. An analysis of spatial variation in the nitrogen content of leaves from different horizons within a canopy. *Annals of Botany* **60**: 421-426.

Connor DJ, Sadras VO, Hall AJ. 1995. Canopy nitrogen distribution and the photosynthetic performance of sunflower crops during grain filling - a quantitative analysis. *Oecologia* **101**: 274-281.

Constable GA. 1982. *Carbon fixation and distribution in cotton: implications of single leaf measurements to plant performance.* Ph.D. Thesis, Australian National University.

Constable GA, Oosterhuis DM. Temporal dynamics of cotton leaves and canopies. In: Stewart JM, Oosterhuis DM, eds. *Cotton Physiology*. 2nd Edition. The Cotton Foundation, Memphis Tenessee, USA (In Press).

Constable GA, Rochester IJ. 1988. Nitrogen application to cotton on clay soil: Timing and soil testing. *Agronomy Journal* **80**: 498-502.

Evans JR. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* **78**: 9-19.

Evans JR. 1993. Photosynthetic acclimation and nitrogen partitioning within a lucerne canopy. II Stability through time and comparison with a theoretical optimum. *Australian Journal of Plant Physiology* **20**: 69-82.

Field C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: Leaf age as a control on the allocation program. *Oecologia* **56**: 341-347.

Hearn AB. 1981. Cotton nutrition. *Field Crops Abstracts* **34**: 11-34.

Hearn AB, Fitt GP. 1992. Cotton cropping systems. In: Pearson CJ, ed. *Field Crop Ecosystems.* Amsterdam: Elsevier, 85-142.

Hikosaka K, Terashima I, Katoh S. 1994. Effects of leaf age, nitrogen nutrition and photon flux density on the distribution of nitrogen among leaves of a vine (*Ipomoea tricolor* Cav.) grown horizontally to avoid mutual shading of leaves. *Oecologia* **97**: 451-457.

Hirose T, Werger MJA. 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* **72**: 520-526.

Hirose T, Werger MJA, Pons TL, van Rheenen JWA. 1988. Canopy structure and leaf nitrogen distribution in a stand of *Lysimachia vulgaris* L. as influenced by stand density. *Oecologia* **77**: 145-150.

Kull O, Jarvis PG. 1995. The role of nitrogen in a simple scheme to scale up photosynthesis from leaf to canopy. *Plant, Cell and Environment* **18**: 1174-1182.

Leffler HR, Elmore CD, Hesketh JD. 1977. Seasonal and fertility related changes in cottonseed protein quantity and quality. *Crop Science* **17**: 953-956.

Lemaire G, Onillon B, Gosse G, Chartier M, Allirand JM. 1991. Nitrogen distribution within a lucerne canopy during regrowth: relation with light distribution. *Annals of Botany* **68**: 483-488.

Leuning R, Kelliher FM, de Pury DGG, Schulze E-D. 1995. Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies. *Plant, Cell and Environment* **18**: 1183-1200.

Oosterhuis DM, Zhu B, Wullschleger SD. 1989. The uptake of foliar-applied nitrogen in cotton. In: Oosterhuis DM, ed. *Proceedings of the Cotton Research Meeting. Monticello, Arkansas. 14 Feb 1989.* Fayetteville, Arkansas: Arkansas Agricultural Experiment Station, 23-26.

Rochester IJ, Constable GA, Saffigna PG. 1997. Retention of cotton stubble enhances N fertilizer and lint yield of irrigated cotton. *Soil and Tillage Research* **41**: 75-86.

Sadras VO, Hall AJ, Connor DJ. 1993. Light-associated nitrogen distribution profile in flowering canopies of sunflower (*Helianthus annuus* L.) altered during grain growth. *Oecologia* **95**: 488-494.

Sinclair TR, Shiraiwa T. 1993. Soybean radiation-use efficiency as influenced by nonuniform specific leaf nitrogen distribution and diffuse radiation. *Crop Science* **33**: 808-812.

Thompson AC, Lane HC, Jones JW, Hesketh JD. 1976. Nitrogen concentrations of cotton leaves, buds, and bolls in relation to age and nitrogen fertilization. *Agronomy Journal* **68**: 617-621.

Werger MJA, Hirose T. 1991. Leaf nitrogen distribution and whole canopy photosynthetic carbon gain in herbaceous stands. *Vegetatio* **97**: 11-20.

Wright GC, Hammer GL. 1994. Distribution of nitrogen and radiation use efficiency in peanut canopies. *Australian Journal of Agricultural Research* **45**: 565-574.

Wullschleger SD, Oosterhuis DM. 1992. Canopy leaf area development and age-class dynamics in cotton. *Crop Science* **32**: 451-456.

Zhu B, Oosterhuis DM. 1992. Nitrogen distribution within a sympodial branch of cotton. *Journal of Plant Nutrition* **15**: 1-14.

Caption for figures:

Fig. 1: Whole canopy dynamics of (a,b) leaf area index, (c,d) shoot biomass and (e,f) reproductive biomass in experiments 1 and 2. In experiment 2 closed symbols are for fertilized crops; open symbols are unfertilized crops. Error bars are twice the standard error of the mean.

Fig. 2: Whole canopy dynamics of (a,b) leaf nitrogen per unit leaf area, N_A; (c,d) leaf nitrogen per unit leaf mass, N_M; (e,f) leaf area per unit mass, LAM; and (g,h) leaf N content per unit ground area, N_C; in experiments 1 and 2. In experiment 2 closed symbols are for fertilized crops; open symbols are unfertilized crops. Error bars are twice the standard error of the mean.

Fig. 3: Leaf nitrogen per unit leaf area, N_A, in the four canopy layers at the first sampling, during reproductive growth, and at the last sampling in (a) experiment 1 and for the (b) high N treatment and (c) nil N treatment in experiment 2 (layer 1 being the top, layer 4 the bottom). Error bars are twice the standard error of the mean.

Fig. 4: Dynamics of (a,b,c) leaf N per unit leaf area, N_A; (d,e,f) leaf area index, LAI; and (g,h,i) leaf N per unit ground area, N_C; for the four canopy layers in experiments 1 and 2 (layer 1 being the top, layer 4 the bottom). Error bars are twice the standard error of the mean.

Fig. 5: Relationship between relative leaf N per unit leaf area (N_A) in each layer and relative irradiance (RI) at the mid-point of the layer in (a) experiment 1 and for the (b) high N treatment and (c) nil N treatment in experiment 2 using data from all sampling dates.

Fig. 6: Ontogenetic changes in (a,b) the power term n (eqn 5), (c,d) the nitrogen distribution coefficient k_N, and (e,f) in the light extinction coefficient k_L. All coefficients are dimensionless; see eqns (3) and (4) for definitions. In experiment 2 closed symbols are for the fertilized crops; open symbols are unfertilized crops. Error bars are twice the standard error of the mean. In (c) and (d) the standard error was calculated from the final model in the stepwise regression analysis.

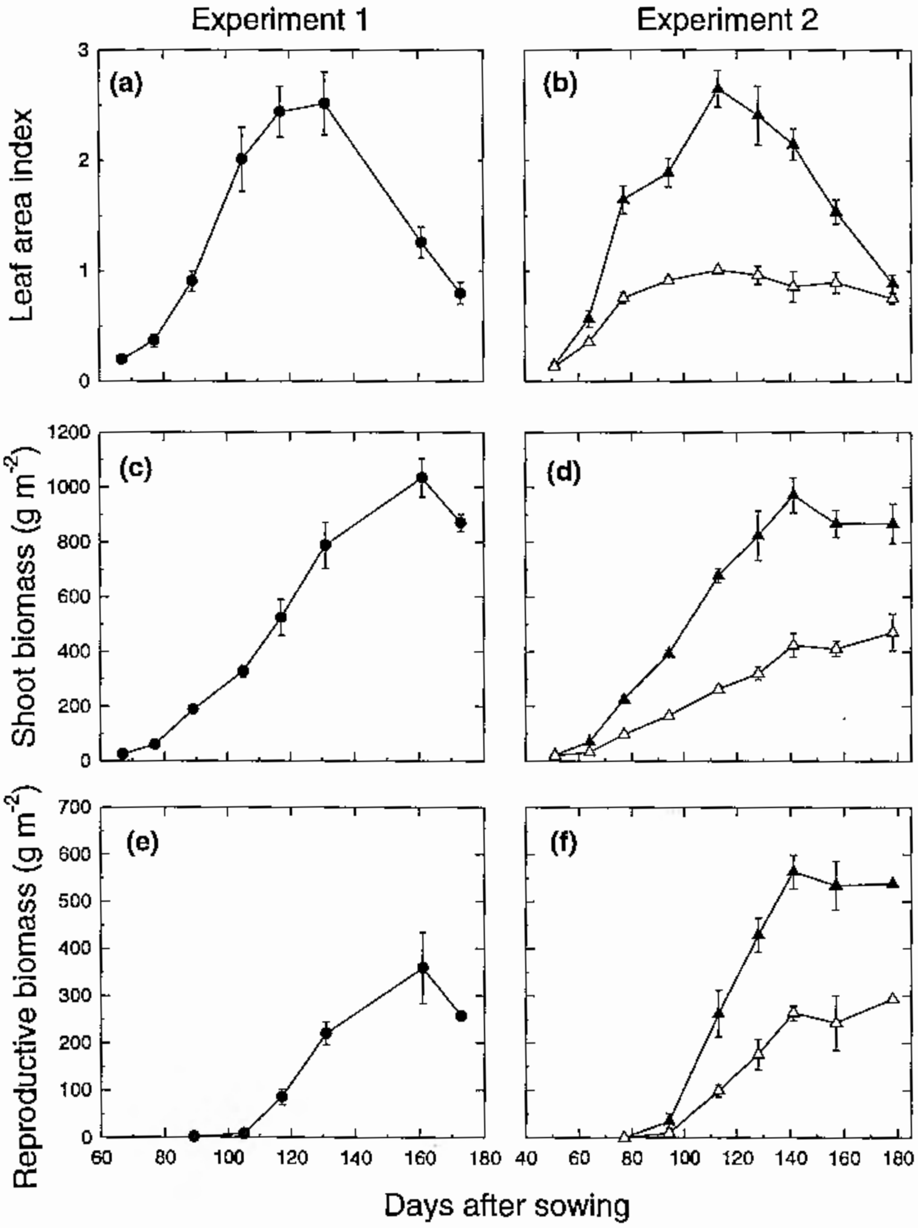
Experiment 1
Experiment 2
(a)
(b)
(c)
(d)
(e)
(f)
Leaf area index
Shoot biomass (g m-2)
Reproductive biomass (g m-2)
Days after sowing
0
1
2
3
0
200
400
600
800
1000
1200
0
100
200
300
400
500
600
700
60
80
100
120
140
160
180
40
60
80
100
120
140
160
180

Figure 1

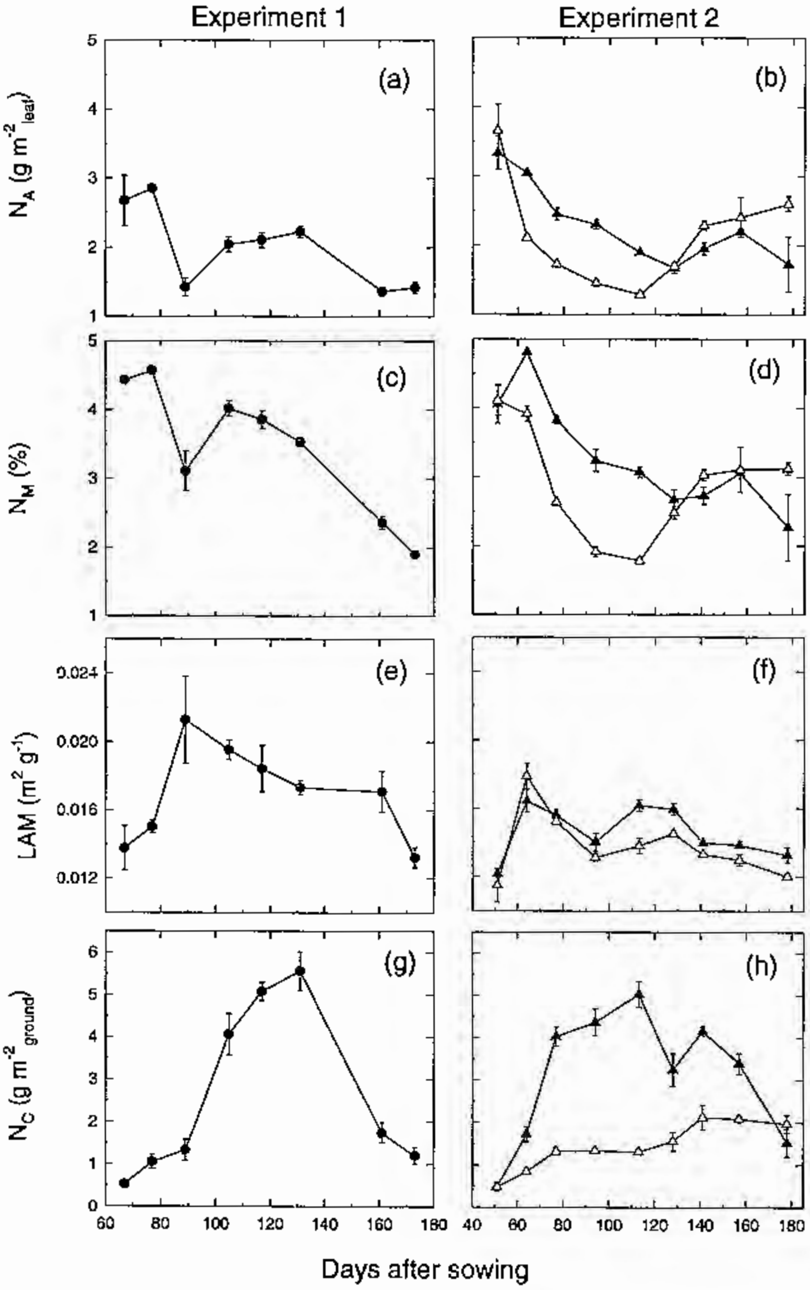

Experiment 1
Experiment 2
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
N_A (g m^{-2}$_{leaf}$)
N_M (%)
LAM (m^2 g^{-1})
N_C (g m^{-2}$_{ground}$)
1
2
3
4
5
0.012
0.016
0.020
0.024
0
6
60
80
100
120
140
160
180
40
Days after sowing

Figure 2

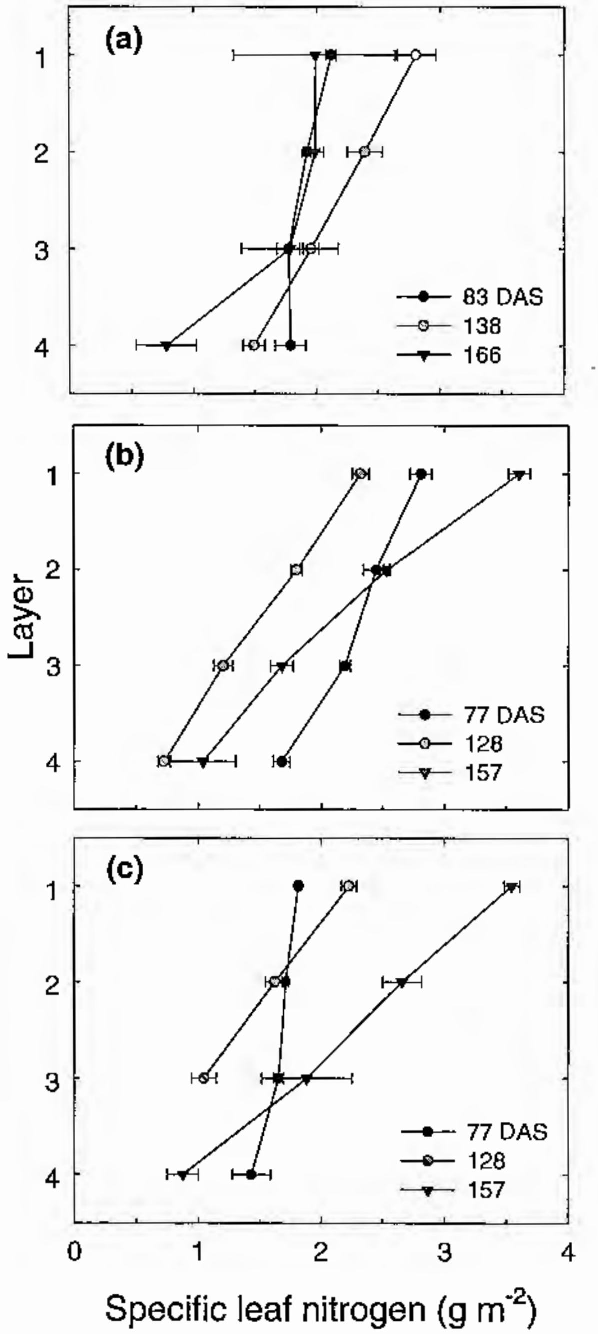

(a)
1
2
3
4
83 DAS
138
166
(b)
Layer
77 DAS
128
157
(c)
77 DAS
128
157
0
1
2
3
4
Specific leaf nitrogen (g m-2)

Figure 3

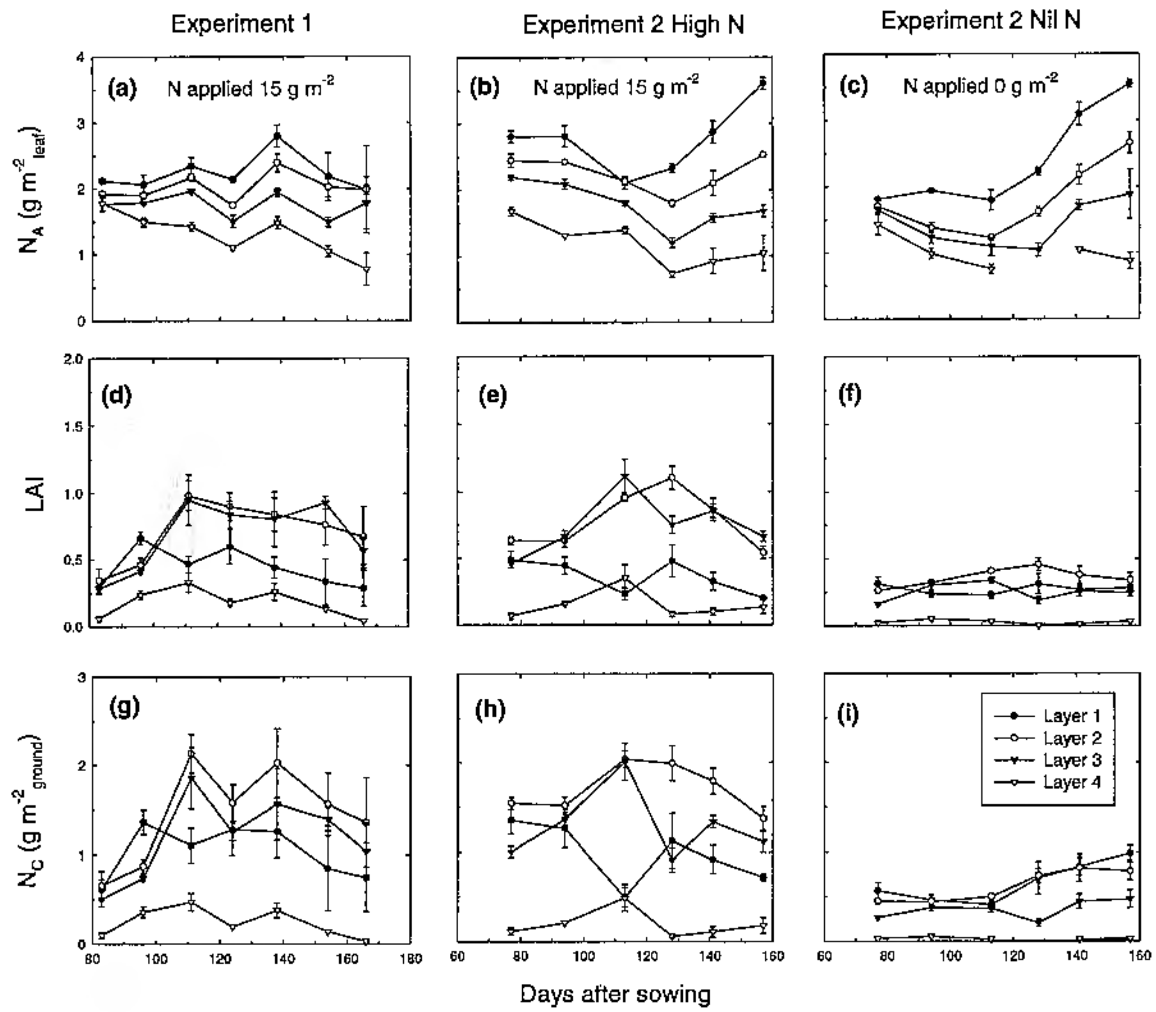
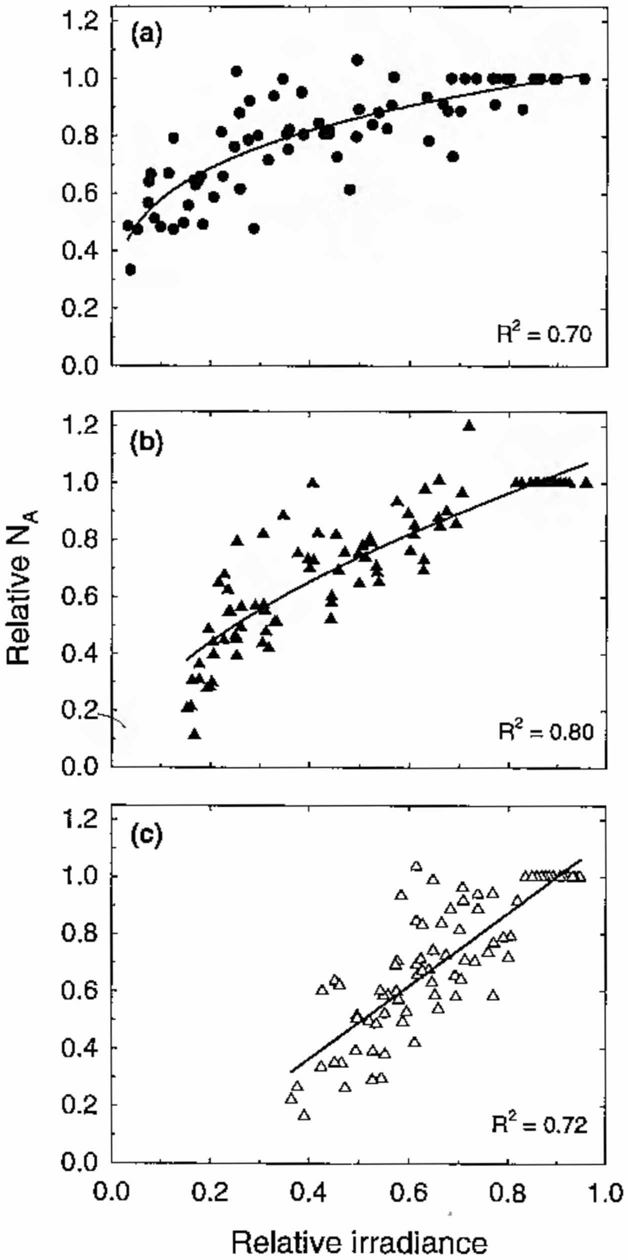

Experiment 1
Experiment 2 High N
Experiment 2 Nil N
(a)
N applied 15 g m^{-2}
(b)
N applied 15 g m^{-2}
(c)
N applied 0 g m^{-2}
N_A (g m^{-2}$_{leaf}$)
0
1
2
3
4
(d)
(e)
(f)
LAI
0.0
0.5
1.0
1.5
2.0
(g)
(h)
(i)
N_C (g m^{-2}$_{ground}$)
0
1
2
3
Layer 1
Layer 2
Layer 3
Layer 4
80
100
120
140
160
180
60
80
100
120
140
160
60
80
100
120
140
160
Days after sowing

Figure 4



(a)
R² = 0.70
(b)
R² = 0.80
(c)
R² = 0.72
Relative N_A
Relative irradiance
0.0
0.2
0.4
0.6
0.8
1.0
1.2

Figure 5

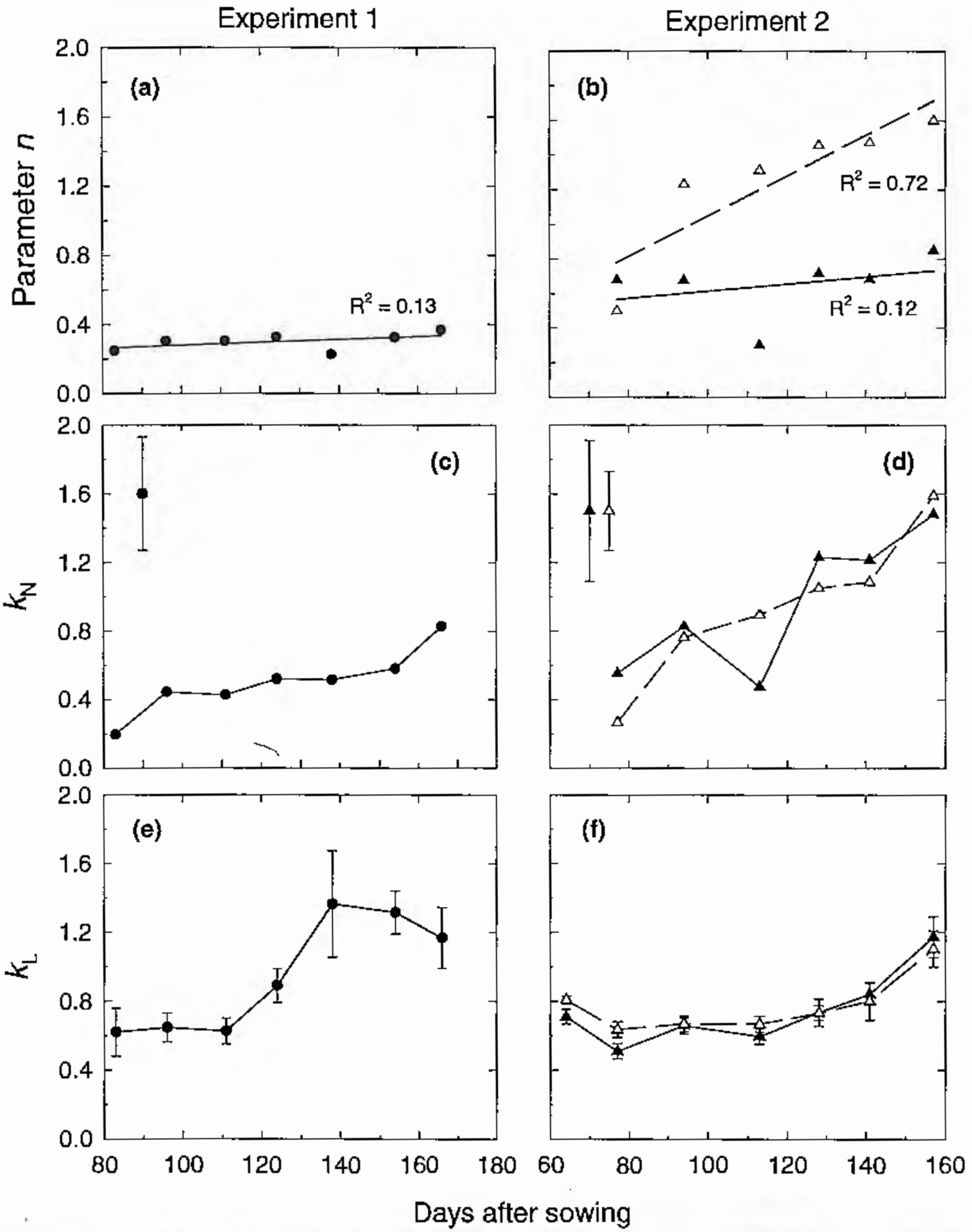

Experiment 1
Experiment 2
Parameter n
(a)
R² = 0.13
(b)
R² = 0.72
R² = 0.12
kN
(c)
(d)
kL
(e)
(f)
2.0
1.6
1.2
0.8
0.4
0.0
80
100
120
140
160
180
60
Days after sowing

Figure 6

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Timing of crop maturity in cotton
Impact of dry matter production and partitioning

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Abstract

Cotton is an indeterminate species; the timing of crop maturity is determined by the capacity of the plant to continue the production of new fruiting sites. According to the nutritional hypothesis, the cessation of fruit production ('cutout') occurs when the demand on the resource supply by growing fruit leaves none for the initiation of new fruiting sites. The aim of this work was to determine whether differences between cultivars in dry matter production or partitioning contributed to the timing of crop maturity. Growth analysis was conducted on a short- and a long-season cultivar grown in four fully irrigated field experiments. The production of dry matter, as a function of radiation-use efficiency (RUE) and light interception, and its partitioning to various plant parts were calculated as indirect measures of resource supply.

The cultivars rarely differed in total dry matter production. When differences were measured, the earlier cultivar produced more dry matter due to greater RUE and light interception. Its light interception was greater due to an earlier production of a larger canopy and not differences in light extinction coefficient. Early in reproductive growth, the shorter-season cultivar consistently partitioned a greater proportion of dry matter into reproductive structures than the long-season cultivar in a pattern consistent with its higher growth rate at that time. There was therefore no indication that fruiting in the long-season cultivar was maintained due to greater dry matter production. While differences in partitioning were found, it is not clear whether this contributed to differences in timing of maturity or was a consequence of an earlier development of fruit demand in the early cultivar due to its higher rate of square production. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: *Gossypium hirsutum*; Development; Radiation-use efficiency (RUE); Light interception; Canopy extinction coefficient

1. Introduction

Differences in the timing of crop maturity or 'earliness' of cotton (*Gossypium hirsutum* L.) cultivars in different environments is an important consideration in crop management. Late maturing cultivars are suited to regions with long growing seasons, while early maturing cultivars are used in short season areas for late sowing times, or to avoid late season pest infestations.

Cotton is an indeterminate species. Fruiting forms develop on lateral branches which are exserted at the main stem nodes. As the boll load on the crop develops, the rate of node production (and hence site production) declines below the potential and the rate of shedding increases until the net change in fruit numbers becomes zero (Ehlig and LeMert, 1973; Patterson et al., 1978; Jackson and Gerik, 1990). The crop is said to have 'cutout' (Hearn, 1981).

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The crop finishes maturing the bolls on the plant before fruit production is resumed.

Following the nutritional hypothesis of Mason (1922) and based on crop level measurements, Hearn (1969, 1972, 1994) proposed that both the declining rate of fruit production and the decreasing rate of retention of the fruit are related to the ratio between boll growth rate and crop growth rate. The results of Guinn and co-workers (Mauney et al., 1978; Guinn, 1974, 1985), who manipulated photosynthesis and respiration rates, suggest that the imbalance between photosynthate supply and demand is a major cause of this process; although the involvement of plant hormones cannot be excluded (Guinn and Brummett, 1989). Consistent with this, investigations into nitrogen nutrition and water stress indicate that these stresses effect fruiting dynamics predominantly through their impact on assimilate supply (Turner et al., 1986; Jackson and Gerik, 1990; Gerik et al., 1994).

The timing of crop maturity is thus determined by the balance between the rate at which the boll demand develops and the capacity of the plant to meet this demand. The accumulation of boll demand is in turn effected by the time at which the first square is produced, the rate of site production and the rate of fruit shedding. Conceptually, the demand by each individual fruit is the product of the period it takes for the boll to mature (boll period) and the final potential size of the boll. The timing of first square, the potential rate of site production, boll period and potential boll size are known to be genetic characteristics of a cultivar (Moraghan et al., 1968; Yfoulis and Fasoulas, 1973; Hesketh et al., 1975; Young et al., 1980). The rate of shedding, the actual rate of site production and the final boll size realised are mediated through resource supply.

Thus the capacity of the crop to supply resources to the fruit modulates the rate of site production and the rate of shedding, which together determine the timing of cutout and thence crop maturity. As indicated above, this is in the context of fruiting parameters which are under more direct genetic control. In the work presented in this paper, we aimed to determine whether differences in dry matter production or partitioning between a short- and long-season cultivar contributed to the timing of crop maturity. Dry matter production was decomposed into light interception and radiation-use efficiency. In turn, light interception was characterised by differences in leaf area dynamics and light extinction within the canopy.

The dynamics of dry matter production and reproductive demand may also have significant impact on yield of various cultivars (Wells and Meredith, 1984) and there is some evidence to suggest that there is a trade-off between early maturation and yield potential in cotton (Quisenberry and Roark, 1976). This paper does not approach the question of yield potential but focuses only on the relationship between dry matter production, reproductive partitioning, and the timing of crop maturity.

2. Materials and methods

2.1. Cultural details

Three field experiments were conducted at the Australian Cotton Research Institute (ACRI) and one (experiment 3) on a neighbouring farm at Narrabri (30°S 150°E), in a semi-arid environment of north-west New South Wales, Australia. The experiments included a range of sowing times so as to generate variation in temperature and radiation regimes which in turn would influence dry matter production and fruiting patterns. Two okra leaf cultivars, Siokra S324 and Siokra L22 (hereafter S324 and L22), were used in all experiments. S324 represents the earliest cultivars currently in commercial use in Australia. These cultivars are used for late times of sowing or in short season areas. L22 is later maturing and represents those cultivars suitable for areas with longer, hotter growing seasons. These cultivars represent the range of maturity types used in Australia, although earlier maturing types than S324 are available in other countries.

The first experiment (experiment 1) consisted of three sowing times and two cultivars arranged factorially. Plots (4 m × 75 m), containing four rows spaced at 1 m, were sown on 10 October (S1), 20 November (S2) and 5 December 1995 (S3). A completely randomised design was used with four replications. All experiments were sown with a commercial row crop planter.

The second experiment (experiment 2) consisted of two sowing times with two cultivars arranged factorially. Plots (8 m × 20 m), containing eight rows spaced at 1 m, were sown on 11 October (S1) and

13 November (S2) 1996. For this experiment, a randomised complete block design was used with four replications.

The third field experiment (experiment 3), sown in the same season as the second experiment but on a neighbouring farm, had a single sowing time using the two cultivars. Plots (4 m × 150 m), containing four rows spaced at 1 m, were sown on 14 October and arranged in a randomised complete block design with three replications.

The fourth field experiment (experiment 4) also had two sowing times with two cultivars arranged factorially. Plots (8 m × 15 m), containing eight rows spaced at 1 m, were sown on 16 October (S1) and 5 November 1997 (S2). A completely randomised design was used with four replications.

All experiments were established and grown with full irrigation on a grey-clay soil utilising high-input management and insect control as described in Hearn and Fitt (1992). Nitrogen was applied as anhydrous ammonia at a rate of 150 kg ha^{-1} 62 days before the first sowing in experiment 1, 113 kg ha^{-1} 44 days before the first sowing in experiment 2, 142 kg ha^{-1} 61 days before sowing in experiment 3, and 200 kg ha^{-1} 35 days after the first sowing in experiment 4. Meteorological data for the experimental period was measured 2 km from the sites at a fully serviced weather station.

2.2. Measurements

Plant samples were taken approximately every 2 weeks in experiments 1–3, and approximately every three weeks in experiment 4. Sampling started just prior to the appearance of the first square in each sowing and involved taking all plants from within 1 m of row, selected randomly from the inner two or four (from eight row plots) rows of each plot. Total fresh biomass was measured and a sub-sample of four plants was taken. Sub-samples were partitioned into green leaf (laminae), stem (including petioles), squares, green bolls and open bolls. The number and type of fruits were recorded. A square was defined as being present when the leaf that subtended the square had unfolded. Fruits were defined as green bolls from the day of anthesis and as open bolls once two sutures had split. Leaf area was measured in each sub-sample using a planimeter (Licor 3100, Nebraska, USA).

All samples were dried in a forced draught oven at 70°C for at least 48 h, weighed and measurements were then converted back to m^{-2} basis using a drying ratio. Masses are presented on an oven-dry basis. Measurements of photosynthetically active radiation (PAR, 0.4–0.7 μm) were taken in each plot above (PAR_O) and below the canopy (PAR_T) at approximately weekly intervals. Three measurements were made on each plot using a ceptometer (Decagon, Delta-T Devices, Cambridge, UK) between 1100 and 1300 h (Australian Eastern Standard Time). Timing of crop maturity (60% bolls open) was estimated by taking repeated weekly counts of the number of open bolls on 1 m^2 in each plot.

2.3. Data analysis

LAI was calculated using the product of specific leaf area of the sub-sample and the total mass of leaf material (m^{-2} of ground area), both measured at each biomass sampling.

To account for the high synthesis cost of cotton fruit relative to vegetative tissue, biomass of all components was converted to glucose equivalents using production values (gram glucose per gram dry matter) from Wall et al. (1994) for cotton leaves, stems, squares and fruits. A glucose-adjusted total shoot dry matter (TDM_g) and total fruit dry matter (squares, green bolls and open bolls; FDM_g) were then derived.

The proportion of radiation intercepted by the crop (Q_I) was calculated as

$$Q_I = \frac{PAR_O - PAR_T}{PAR_O}. \tag{1}$$

This was then regressed on days after sowing (DAS) to allow interpolation between measurement dates. An exponential function was fitted to the data collected from each plot:

$$Q_I = a[1 - \exp(-b\,\mathrm{DAS})] + c \tag{2}$$

where a, b, and c are fitted coefficients.

Using values of Q_I for the day of the biomass samplings as derived from Eq. (2), a canopy light extinction coefficient (k) was calculated for each plot from a non-linear regression between Q_I and leaf area index (LAI):

$$Q_I = d[1 - \exp(-k\,\mathrm{LAI})] + f \tag{3}$$

where d and f are fitted coefficients. Treatment effects on k were tested using forward stepwise regression analysis.

Charles-Edwards and Lawn (1984) reported that the proportion of intercepted PAR for a day is underestimated if instantaneous measurements are used instead of integrating them over the day. Therefore, before deriving radiation-use efficiency (RUE, g MJ^{-1}), Q_I was adjusted using their relationship

$$Q_\mathrm{D} = \frac{2Q_\mathrm{I}}{1 + Q_\mathrm{I}} \qquad (4)$$

where Q_D is an estimate of the proportion of PAR intercepted over the day. Again, because light interception measurements were not always taken on the same day as the biomass samplings, Q_D was regressed on DAS to allow interpolation between measurements using a function of the same form as Eq. (2). The period of measurement always covered the period of maximum growth and light interception; however, measurements were not always terminated at the same developmental stage for the different sowing dates. While comparison of cumulative light interception between cultivars is still valid, this renders comparison between sowing dates and years invalid.

Average RUE for the season was derived from the linear regression of $\mathrm{TDM_g}$ against cumulative intercepted radiation ($\mathrm{RUE_g}$). In each sowing, the period over which this could be determined was dictated by the availability of light interception and dry matter data. In experiment 1 measurements used were from 67 to 131 DAS in S1, 41 to 111 DAS in S2, and from 48 to 90 DAS in S3; in experiment 2 from 54 to 137 DAS in S1, 34 to 119 DAS in S2; in experiment 3 from 59 to 162 DAS and in experiment 4 from 38 to 147 DAS in S1 and 35 to 127 DAS in S2. Forward stepwise regression analyses were used to test for differences between cultivars and among times of sowing.

To test whether there was a significant trend for one cultivar to partition more dry matter to fruit over time, a distribution ratio (DR) for the partition of dry matter to fruit was calculated for the interval between each sampling. This was derived as the ratio of the increment in $\mathrm{FDM_g}$ to the increment in $\mathrm{TDM_g}$. The DR for L22 was then plotted against DR for S324 using data from all experiments and up to the time of peak green boll number. Since simple ratios can be biased descriptors of partitioning if development or dry matter production differ markedly (Coleman et al., 1994), reproductive partitioning was also examined allometrically by plotting ln $\mathrm{FDM_g}$ against ln $\mathrm{TDM_g}$ for the two cultivars. The slope of such a plot is equivalent to the ratio between the relative growth rate of the two plant components. Significant differences are expressed at the 95% ($P < 0.05$) confidence level unless otherwise stated.

3. Results

3.1. Fruit production

Cultivar S324 developed a significantly higher peak number of squares than L22 in five of the eight sowings (Figs. 1–3); in the rest the cultivars were not significantly different. In all cases except experiment 4, the rate of increase in square numbers was greater in S324 than L22. Across all experiments, the average rate of square production was 7.08 (±0.52) squares per day for S324 and 5.13 (±0.53) for L22. It should be noted that this rate was affected both by the rate of square production and the degree of early shedding.

The higher peak square number of S324 was translated into a higher peak number of green bolls (Figs. 1–3). The exceptions were S1 in experiment 2, in which the two cultivars showed very similar patterns of green boll numbers over time and experiment 4, sowing 1 in which peak green boll numbers were similar for the two cultivars but with S324 peaking markedly earlier. In the very late sowing (S3) of experiment 1, development of the crop was severely truncated so that the comparison was not possible. Reflecting the rate of increase in square numbers in S324, this cultivar set more green bolls sooner than L22. Interpolating between sampling dates indicates that S324 set 100 green bolls m^{-2} at least 10 days earlier than L22 in six out of seven cases. In S1 of experiment 2, it was only 3 days earlier.

S324 produced more open bolls in each of the normal sowing times (Figs. 1–3): experiment 3 and S1 in experiments 1, 2 and 4. For the November times of sowing in experiments 1 and 2 the cultivars produced similar numbers of open bolls at similar rates. It was not possible to assess the timing of crop maturity

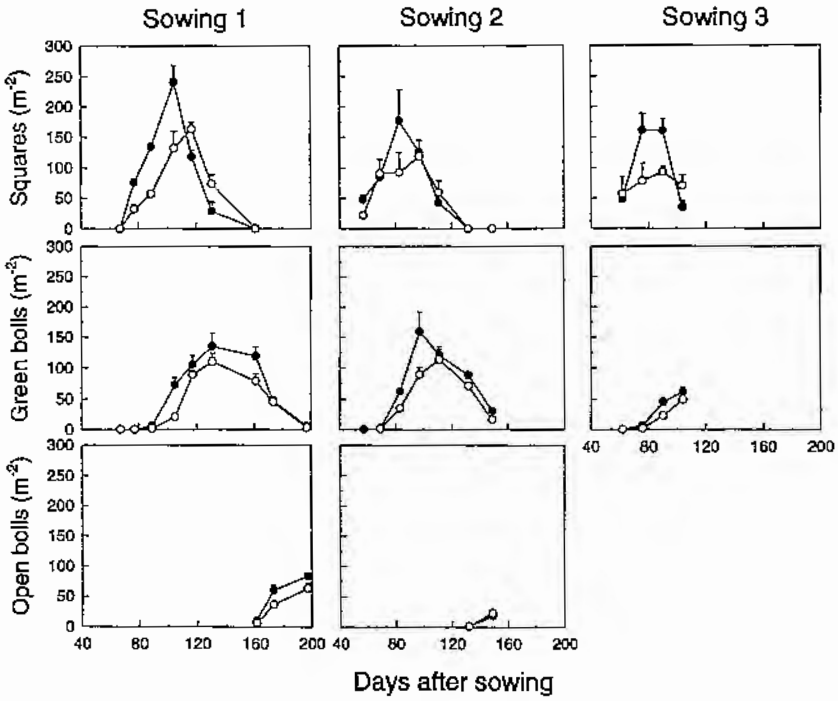

Fig. 1. Fruit numbers versus DAS for cultivars (●) S324 and (○) L22 across three sowings of experiment 1 1995/1996 season (sowing 1, 10 October; sowing 2, 20 November; sowing 3, 5 December). Error bars are one standard error of the mean.

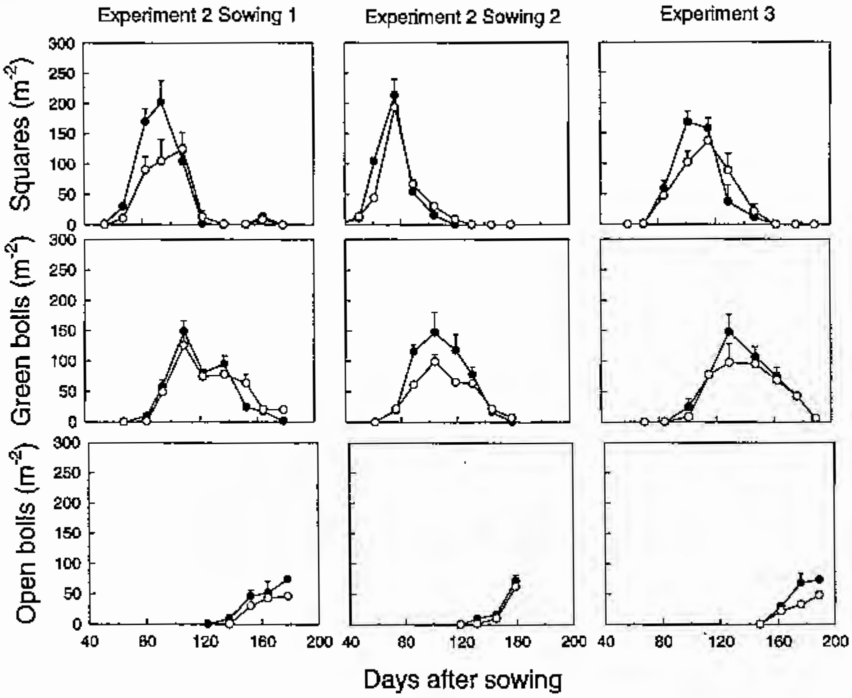

Fig. 2. Fruit numbers versus DAS for cultivars (●) S324 and (○) L22 across two sowings of experiment 2 1996/1997 season (sowing 1, 11 October; sowing 2, 13 November) and the single sowing of experiment 3 1995/1996 (sown 14 October). Error bars are one standard error of the mean.

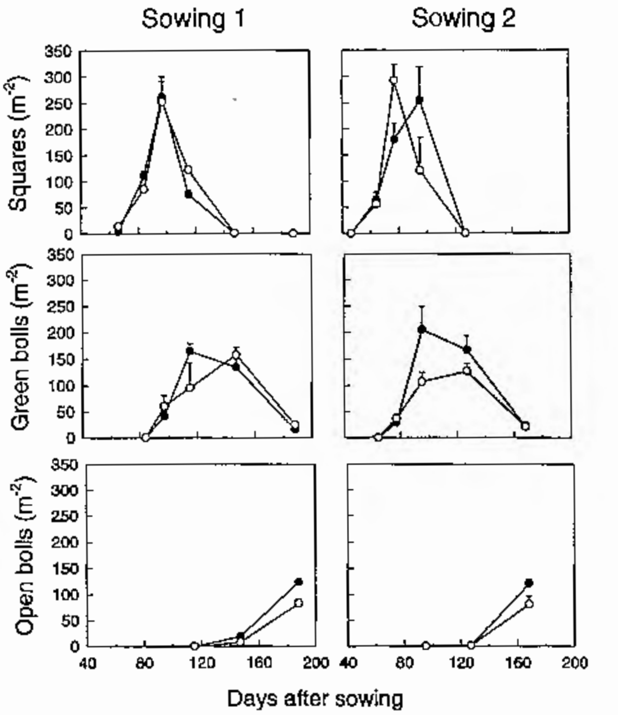

Fig. 3. Fruit numbers versus DAS for cultivars (●) S324 and (○) L22 across two sowings of experiment 4 1998/1999 season (sowing 1, 16 October; sowing 2, 5 November). Error bars are one standard error of the mean.

for the two truncated crops from the 1995 sowing. Of the remaining six crops, S324 reached 60% bolls open significantly earlier in five cases (Table 1).

Fruit numbers varied between times of sowing. Excluding S3 in experiment 1, the peak number of squares varied between 160 and 235 m^{-2} for S324, and 120 and 190 m^{-2} for L22. Peak green boll numbers also varied but to a lesser extent: S324 ranged between 130 and 160 m^{-2} and L22 between 100 and 120 m^{-2}. In S3 of experiment 1 the peak square number was 155 m^{-2} for S324 and 90 m^{-2} for L22, these numbers were translated into only 65 and 50 green bolls, respectively.

3.2. *Dry matter production*

The two cultivars were similar in the overall pattern of accumulation of total shoot dry matter (TDM$_g$; Fig. 4). In experiment 1 S1 and S2, S324 produced a slightly higher peak TDM$_g$ than L22 and a slightly earlier increase with significantly greater TDM$_g$ during the early part of the rapid growth phase. In experiment 2 S2, S324 accumulated dry matter rapidly around 100 DAS resulting in maximum dry matter earlier than L22. On the occasions where TDM$_g$ differed significantly, this was generally reflected in differences in both LAI and RUE. These differences will be discussed below.

Total fruit dry matter (FDM$_g$) increased earlier in S324 than L22 with the earlier cultivar having significantly higher FDM$_g$ during most of the boll-filling period in four of the eight times of sowing (Fig. 4). In experiment 3 and S2 of experiment 4, S324 had significantly higher FDM$_g$ at only one sampling. In a number of cases the two cultivars tended to converge again toward the end of boll growth after S324 had gained maximum FDM$_g$.

3.3. *Radiation interception and leaf area index*

Eq. (2) was fitted to radiation interception data collected from each plot to allow interpolation of

Table 1
Maturity (60% bolls open) in DAS for cultivars S324 and L22 for each sowing and experiment (numbers in parentheses are standard error of the mean)

Experiment	Sowing	Sowing date	Maturity (DAS)	
			S324	L22
1	S1	10 October 1995	172.9 (2.5)	176.2 (1.7)[a]
2	S1	11 October 1996	157.0 (0.9)	166.0 (1.4)[*]
	S2	13 November 1996	148.8 (1.0)	155.8 (1.4)[*]
3	–	14 November 1996	178.0 (0.8)	180.0 (0.0)[*]
4	S1	16 October 1998	173.0 (0.6)	181.0 (2.0)[*]
	S2	5 November 1998	160.0 (1.2)	164.0 (0.6)[*]

[a] Non-significant.

[*] Significant at $P < 0.05$.

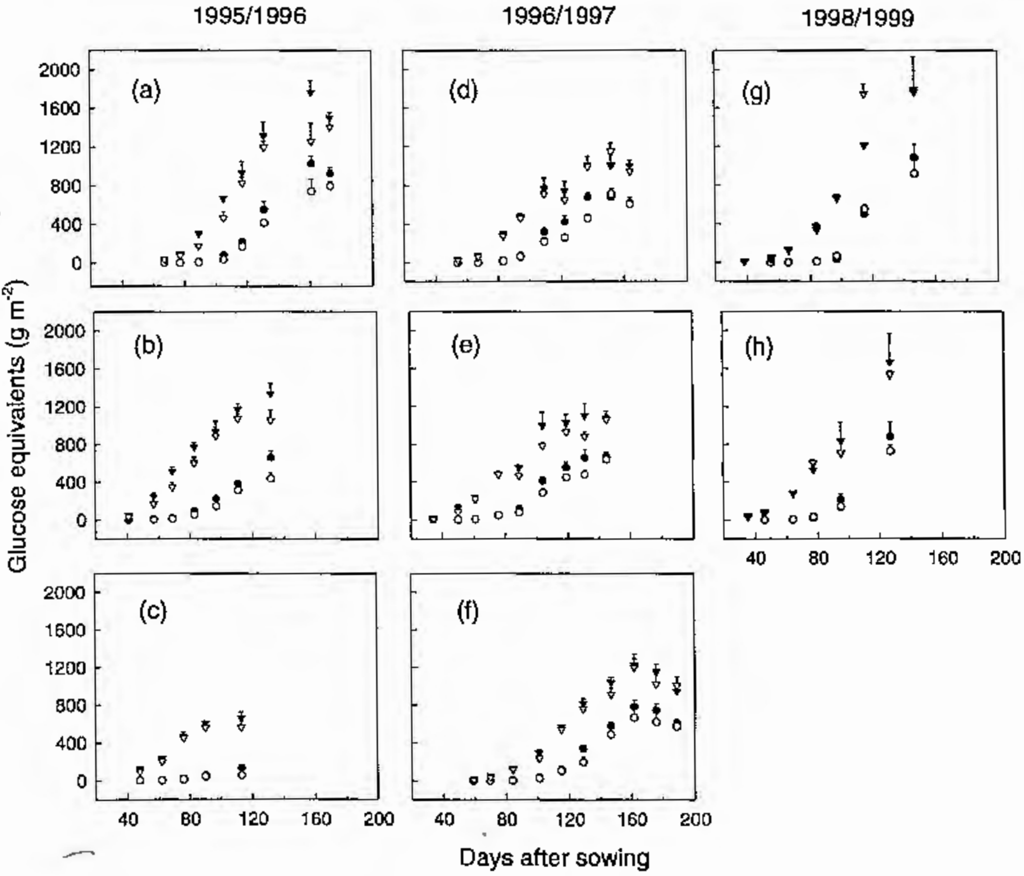

Fig. 4. Total dry matter (triangles) and fruit dry matter (circles) production adjusted for glucose equivalents for cultivars S324 (closed symbols) and L22 (open symbols) for experiment 1 (sowing 1 (a); sowing 2 (b); sowing 3 (c)), experiment 2 (sowing 1 (d) and sowing 2 (e)), experiment 3 (f), and experiment 4 (sowing 1 (g) and sowing 2 (h)). Error bars are one standard error of the mean.

Q_D between measurements. For each plot the responses were used in conjunction with measured daily PAR to derive accumulated intercepted PAR (Accum. PAR$_i$) for the period of measurement. In experiment 1 S1 and S2 and experiment 4 S2, cultivar S324 intercepted significantly more radiation than L22 during these periods (Table 2). There were no significant differences between cultivars in experiment 2 or 3. As mentioned in Section 2, measurements were not always terminated at the same developmental stage, so comparison between sowing dates and years are invalid.

In each sowing of experiment 1, regression analysis indicated that S324 intercepted a higher proportion of light sooner than L22, but by the end of the season L22 had attained the same level of light interception as S324 (Fig. 5). There was little apparent difference between cultivars during growth of the crop in experiments 2 and 4 but in experiment 3 L22 intercepted a higher proportion in the last weeks of measurement.

LAI differed significantly between cultivars in experiment 1 (Fig. 6). In each sowing S324 developed its canopy sooner than L22. There were no consistent differences between the LAI of the cultivars in experiment 2, 3 or 4. Both cultivars produced higher peak LAI in S1 of experiments 1 and 4 than for later sowing dates. Like the proportion of light intercepted, LAI increased later in S1 than in later times of sowing.

Using data from all replicates, Eq. (3) was used to fit a regression of Q_I against LAI to estimate canopy light extinction coefficient (k). Forward stepwise regression analyses were used to test for differences between cultivars and among times of sowing for each experiment. No significant differences between cultivars

Table 2
Radiation-use efficiency (RUE$_g$, g MJ^{-1}) adjusted for glucose equivalents and accumulated intercepted photosynthetically active radiation (PAR$_i$, MJ^{1}) for cultivars S324 and L22 for each time of sowing and experiment. The duration of the period over which intercepted PAR was accumulated (from sowing to the specified DAS) is indicated for each experiment and time of sowing.[a]

Experiment	Sowing	RUE$_g$		Accum. PAR$_i$		
		S324	L22	Duration	S324	L22
1 (1995)	S1	1.62 (0.06)	1.31 (0.08)*	161	1024 (11)	975 (13)*
	S2	1.41 (0.09)	1.30 (0.09)^{b}	111	754 (6)	724 (9)*
	S3	1.21 (0.19)	1.16 (0.19)^{b}	90	395 (18)	386 (17)^{b}
2 (1996)	S1	1.59 (0.09)	1.56 (0.10)^{b}	137	626 (18)	599 (22)^{b}
	S2	1.70 (0.07)	1.47 (0.05)*	119	602 (13)	611 (24)^{b}
3 (1996)	–	1.67 (0.09)	1.54 (0.09)^{b}	162	780 (10)	776 (21)^{b}
4 (1998)	S1	1.01 (0.08)	1.16 (0.08)^{b}	115	1236 (36)	1151 (21)*
	S2	0.96 (0.09)	0.95 (0.10)^{b}	127	1639 (17)	1442 (195)^{b}

[a] Numbers in parentheses are standard error of the mean.
[b] Non-significant.
* Significant at $P < 0.05$.

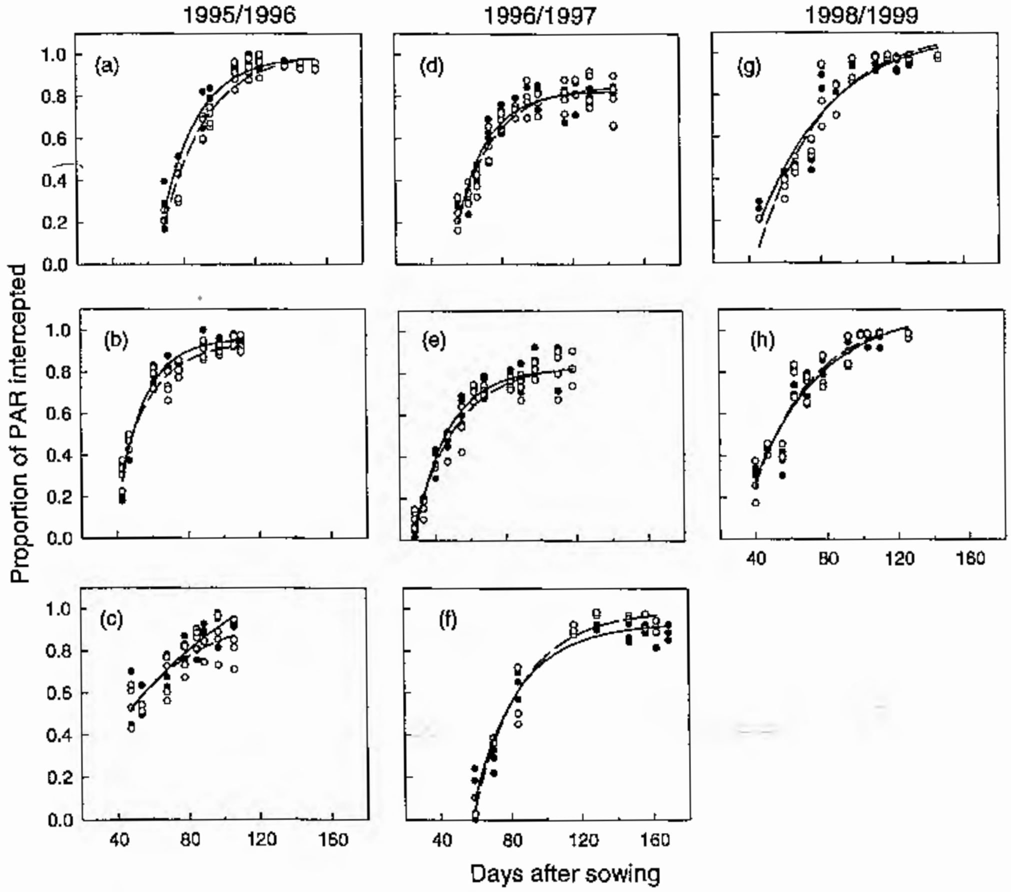

Fig. 5. Proportion of photosynthetically active radiation (PAR; MJ) intercepted versus DAS for cultivars (●) S324 (solid line) and (○) L22 (broken line) for experiment 1 (sowing 1 (a); sowing 2 (b); sowing 3 (c)), experiment 2 (sowing 1 (d) and sowing 2 (e)), experiment 3 (f), and experiment 4 (sowing 1 (g) and sowing 2 (h)).

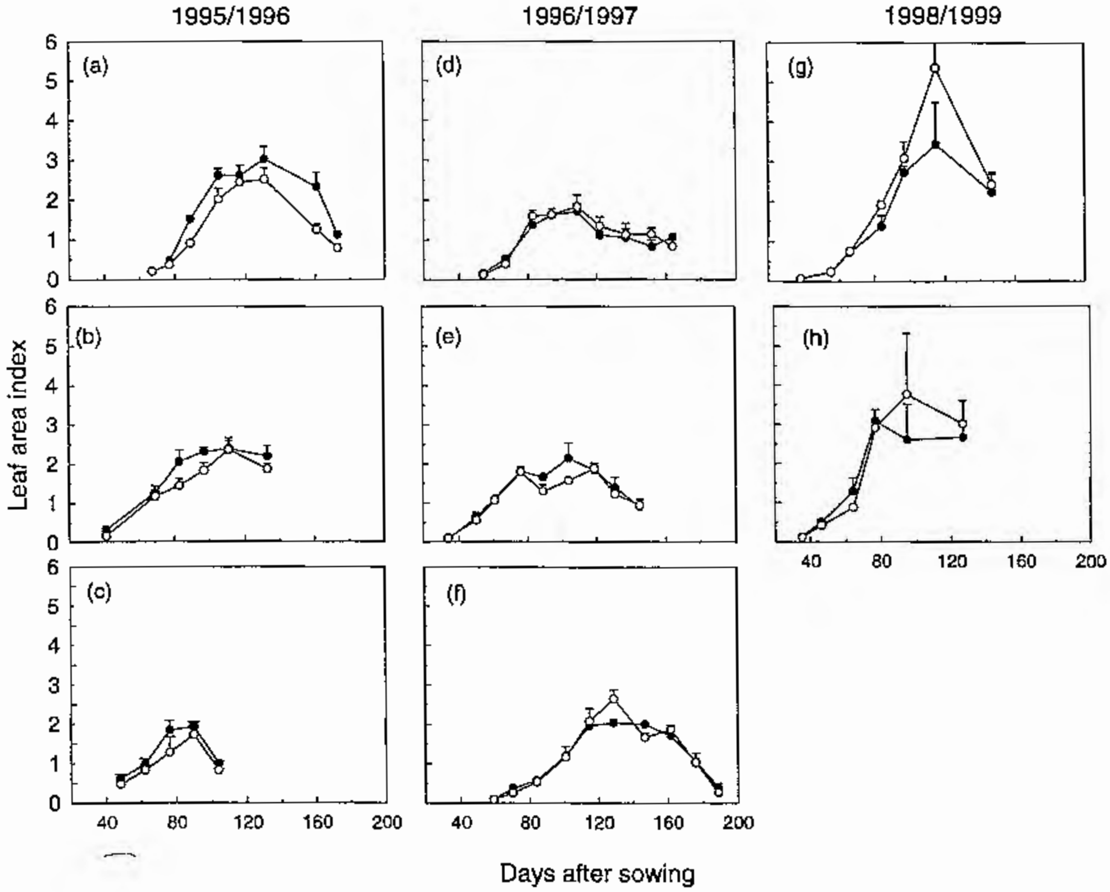

Fig. 6. Leaf area index dynamics for cultivars (●) S324 and (○) L22 versus DAS for experiment 1 (sowing 1 (a); sowing 2 (b); sowing 3 (c)), experiment 2 (sowing 1 (d) and sowing 2 (e)), experiment 3 (f), and experiment 4 (sowing 1 (g) and sowing 2 (h)). Error bars are one standard error of the mean.

were found in any experiment. Pooled across times of sowing and cultivars, k was 0.75 (±0.13, $P < 0.05$) in experiment 1, 0.74 (±0.14, $P < 0.01$) in experiment 3 and 0.65 (±0.04, $P < 0.01$) in experiment 4. In experiment 2 differences were identified between times of sowing. The k value for S2 (0.58 ± 0.04, $P < 0.01$) was significantly less ($P < 0.05$) than for S1 (0.68 ± 0.03, $P < 0.01$).

3.4. Radiation-use efficiency

There was no consistent difference in RUE_g between the two cultivars but on the occasions when they did differ S324 had the greater value (Table 2). In experiment 1, significant differences were found between cultivars; S324 being greater than L22 when pooled across times of sowing. In experiment 2 the cultivars had similar RUE_g in S1, but in S2 S324 had a significantly greater RUE_g than L22. There were no significant differences between cultivars in RUE_g in experiments 3 and 4. No significant differences between times of sowing were found in experiment 1 or 2.

3.5. Dry matter partitioning

While S324 had higher FDM_g during most of the boll filling period, it also tended to have a greater TDM_g. Comparing the distribution ratios (DRs) for the two cultivars indicated that S324 partitioned significantly more of the current increment of dry matter to fruit during the initial period of boll growth than did L22. When DR for L22 was plotted against DR for S324, using data up to the time of peak green boll

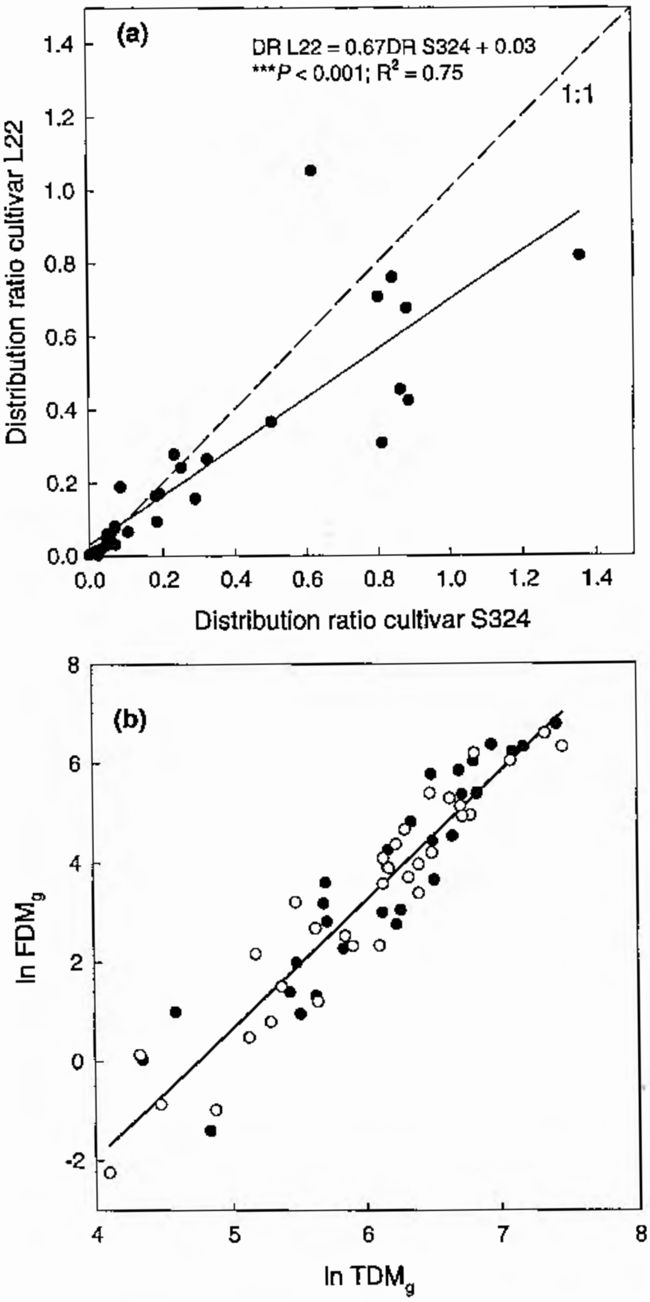

Fig. 7. Reproductive partitioning in the two cultivars up to peak green bolls. (a) Comparison of distribution ratios between cultivars S324 and L22 across all experiments and times of sowing. Distribution ratio (DR) was calculated as the ratio of the change between samplings in fruit dry matter (glucose adjusted) relative to the change in total dry matter (glucose adjusted). (b) Allometric partitioning between fruit dry matter (glucose adjusted) and total dry matter (glucose adjusted) for cultivars (●) S324 and (○) L22.

number from all experiments (Fig. 7a), the regression line had a slope of 0.67, which was significantly different from unity ($P < 0.001$). Stepwise regression showed no significant difference between years or times of sowing. When the cultivars were examined using an allometric approach, the relative growth rate of total plant dry matter and total fruit dry matter showed a constant relationship up to the time of peak green boll number. This is demonstrated by the linear relationship between $\ln \mathrm{FDM_g}$ and $\ln \mathrm{TDM_g}$

($P < 0.001$). Furthermore, this relativity was identical for the two cultivars (Fig. 7b).

4. Discussion

The aim of this work was to determine whether differences between cultivars in dry matter production or partitioning contributed to the timing of crop maturity. As expected, cultivar S324 generally matured before L22. This was associated with a more rapid accumulation of squares and hence green bolls and open bolls.

According to the nutritional hypothesis (Hearn, 1981), cutout occurs when fruits that are already on the plant monopolise the resource supply, thus precluding the production of any new fruiting sites. Total dry matter production (TDM_g) was never greater in the late maturing cultivar: either the two cultivars had the same TDM_g or S324 had an earlier accumulation of dry matter. The later maturity of L22 was therefore not due to a greater total dry matter production allowing it to sustain squaring for longer.

When the two cultivars were compared on a common time basis, S324 showed a markedly greater distribution of dry matter to the fruit during the period up to peak green boll number. However, the two cultivars were identical when the relative growth rate for total plant dry matter and for fruit dry matter were compared. That is, S324 partitioned more dry matter to the fruit early in the fruiting cycle in a manner that was commensurate with its higher growth rate at that time. Therefore, the ability of L22 to meet the fruit demand for carbon was not greater due to partitioning either. Pace et al. (1999) found that when ^{14}C was applied to the uppermost mainstem leaf during early vegetative growth, an early cultivar partitioned a greater proportion of labelled C into reproductive organs than did a late-maturing cultivar. This is consistent with our results measured at the crop level.

There are two possible explanations for the earlier reproductive partitioning in S324. Firstly the earlier dry matter production may reflect a greater assimilate supply to the fruit. Since the allometric pattern of partitioning was the same, at any time a greater proportion of the greater total DM supply in S324 was going to the fruit. According to the nutritional hypothesis, this could be expected to have allowed a higher rate of fruit retention, resulting in the higher fruit numbers observed. Alternatively, the greater rate of growth and partitioning may have been driven by the more rapid fruit development which in turn increased the sink for assimilates. There is some evidence to support the idea that early assimilate accumulation in cotton may be limited by sink capacity: associations between fruit load and leaf level photosynthetic rates (Perry et al., 1983; Rasulov, 1987) are mirrored in changes in RUE throughout ontogeny (Sadras, 1996). The higher rate of fruit production in S324 resulted in an earlier development of both reproductive and vegetative sinks since the production of fruiting sites and leaves are morphologically linked. Removing the constraint on the sinks would have lead to an increase in the growth of both components as was observed. Whether the difference in partitioning is a cause or effect of earliness is yet to be determined.

In the instances when differences did occur between TDM_g of S324 and L22, they were associated with differences in RUE_g and/or accumulated light interception. The earlier maturing cultivar S324 was found to intercept more PAR over the period of measurement. This was not due to a difference in the light interception characteristics of the canopy but rather canopy size. S324 developed its canopy sooner. This may have resulted from differences in fruiting site production between the two cultivars due to the morphological association of leaves and fruiting sites which leads to the correlation between leaf area and site production (Jackson et al., 1990). However, there was not a clear association between the cases in which S324 had a more rapid increase in canopy size than L22 and the cases where it had higher rates of squaring. Variation in the size of individual leaves between the cultivars, differences in the proportion of squares shed or differences in the number of vegetative branches produced could each modify the association between leaf area and site production. The leaf area produced per site could not be derived from our data. The similarity of the light extinction coefficients (k) between cultivars is consistent with the results of Heitholt et al. (1992) and Sadras (1996); although they did not specifically compare early and late cultivars. While they found variation in k with growing conditions, in each case the cultivars involved had similar extinction coefficients.

Rosenthal and Gerik (1991) found differences in the full season RUE of three American cultivars based on dry matter production. However, they attributed this to the different amounts of fruit carried by the cultivars and the higher energy requirement for the production of fruit relative to vegetative tissues. To circumvent this difficulty, they considered the RUE for the period prior to fruit production and found similar RUEs for the different cultivars. In our work the greater energy requirement of the fruit was incorporated by converting dry matter to glucose equivalents. This approach showed that, consistent with the results of Rosenthal and Gerik, the RUE of the two cultivars was similar in the majority of cases. In the two cases where there was a significant difference, it was the shorter-season cultivar which had the greater RUE. The RUE for both cultivars in our experiments lie within the range of Sadras (1996), who reported glucose adjusted RUE ranging from 1.18 to 1.71 g MJ^{-1}.

In summary, no evidence was found for the differences in crop maturity between S324 and L22, being caused by differences in total dry matter supply to reproductive development. However, the earlier maturity of S324 may have resulted from differences in the priority to partition dry matter to reproductive organs. Whether the observed difference in partitioning was a cause or an effect needs to be clarified. This paper has focussed on dry matter production and partitioning to the fruit. Within the nutritional framework being considered, earliness may also have resulted from differences in the resource demand due to the differences in fruiting dynamics. The development of reproductive demand as a result of the rate of increase in fruit numbers and the rate of boll growth is currently being investigated. Linking these two aspects is the question of whether the regulation of the rate of fruiting processes, as a function of internal carbon balance, differs between genotypes.

Acknowledgements

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References

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

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

Ehlig, C.F., LeMert, R.D., 1973. Effects of fruit load, temperature, and relative humidity on boll retention of cotton. Crop Sci. 13, 168–171.

Gerik, T.J., Jackson, B.S., Stockle, C.O., Rosenthal, W.D., 1994. Plant nitrogen status and boll load of cotton. Agron. J. 86, 514–518.

Guinn, G., 1974. Abscission of cotton floral buds and bolls as influenced by factors affecting photosynthesis and respiration. Crop Sci. 14, 291–293.

Guinn, G., 1985. Fruiting of cotton. III. Nutritional stress and cutout. Crop Sci. 25, 981–985.

Guinn, G., Brummett, D.L., 1989. Fruiting of cotton. IV. Nitrogen, abscisic acid, indole-3-acetic acid, and cutout. Field Crops Res. 22, 257–266.

Hearn, A.B., 1969. The growth and performance of cotton in a desert environment. II. Dry matter production. J. Agric. Sci. Cambridge 73, 75–86.

Hearn, A.B., 1972. The growth and performance of rain-grown cotton in a tropical upland environment. II. The relationship between yield and growth. J. Agric. Sci. Cambridge 79, 137–145.

Hearn, A.B., 1981. Cotton nutrition. Field Crop Abst. 34, 11–34.

Hearn, A.B., 1994. OZCOT: a simulation model for cotton crop management. Agric. Syst. 44, 257–299.

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

Heitholt, J.J., Pettigrew, W.T., Meredith, W.R., 1992. Light interception and lint yield of narrow row-cotton. Crop Sci. 32, 728–733.

Hesketh, J.D., Lane, H.C., Alberte, R.S., Fox, S., 1975. Earliness factors in cotton: new comparisons among genotypes. Cotton Growing Review 52, 126–135.

Jackson, B.S., Gerik, T.J., 1990. Boll shedding and boll load in nitrogen stressed cotton. Agron. J. 82, 483–488.

Jackson, B.S., Arkin, G.F., Hearn, A.B., 1990. COTTAM: a cotton plant simulation model for an IBM PC microcomputer. The Texas A&M University, College Station, TX.

Mason, T.G., 1922. Growth and abscission in sea island cotton. Ann. Bot. 36, 457–484.

Mauney, J.R., Fry, K.E., Guinn, G., 1978. Relationship of photosynthetic rate to growth and fruiting of cotton, soybean, sorghum and sunflower. Crop Sci. 18, 259–263.

Moraghan, B.J., Hesketh, J., Low, A., 1968. Effects of temperature and photoperiod on floral initiation among strains of cotton. Cotton Growing Review 52, 126–135.

Pace, P.F., Cralle, H.T., Cothren, J.T., Senseman, S.A., 1999. Photosynthate and dry matter partitioning in short- and long-season cotton cultivars. Crop Sci. 39, 1065–1069.

Patterson, L.L., Buxton, D.R., Briggs, R.E., 1978. Fruiting of cotton as affected by cotton boll set. Agron. J. 70, 118–122.

Perry, S.W., Krieg, D.R., Hutmacher, R.B., 1983. Photosynthetic rate control in cotton: photorespiration. Plant Physiol. 73, 662–665.

Quisenberry, J.E., Roark, B., 1976. Influence of indeterminate growth habit on yield and irrigation water-use efficiency in upland cotton. Crop Sci. 16, 762–765.

Rasulov, B.K., 1987. Photosynthetic parameters of cotton leaves under conditions of different source–sink relations in the whole plant. Sov. J. Plant Physiol. 33, 707–713.

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

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

Turner, N.C., Hearn, A.B., Begg, J.E., Constable, G.A., 1986. Cotton (*Gossypium hirsutum* L.): physiological and morphological responses to water deficits and their relationship to yield. Field Crops Res. 14, 153–170.

Wall, G.W., Amthor, J.S., Kimball, B.A., 1994. COTCO2: a cotton growth simulation model for global change. Agric. For. Meteorol. 70, 289–342.

Wells, R., Meredith, W.R., 1984. Comparative growth of obsolete and modern cotton cultivars. III. Relationship of yield to observed growth characteristics. Crop Sci. 24, 868–872.

Yfoulis, A., Fasoulas, A., 1973. Interactions of genotype and temperature on cotton boll period and their implications for breeding. Exp. Agric. 9, 193–201.

Young Jr., E.F., Taylor, R.M., Petersen, H.D., 1980. Day-degree units and time in relation to vegetative development and fruiting for three cultivars of cotton. Crop Sci. 20, 370–374.

Effect of temperature on the rate of early fruiting developmental processes of cotton.

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ABSTRACT

Degree days are commonly used within the Australian cotton industry to estimate expected crop development during early season growth. This assumes that cotton's early potential development is largely a function of temperature. Information collected on crop development over a range of field and controlled environment studies shows that the function currently used to calculate degree days does not fully reflect the effect of very high or low temperatures on development. More complex functions are available which can better represent the effect of temperature on cotton development as seen in the experimental data. Refining this function will enable better predictions of cotton development in a greater range of environments and seasons; which is important for the geographically expanding cotton industry.

KEY WORDS: base temperature; degree days; development; cotton; *Gossypium hirsutum*; squaring

INTRODUCTION

Within the cotton industry, the rate of cotton development is widely described as a function of degree days. The degree day approach is based on the near linearity of the response of a rate to temperature over the range most likely to be encountered by a given species in the field. The function used for cotton in Australia, degree days with base 12^{o}C, was developed by Constable and Shaw (4) based on experiments conducted by Constable (2). The function is used in protocols for nutrient monitoring and simulation modelling for on-farm decision support.

Constable's experiments concentrated mainly on the rate of early development at Narrabri, NSW, and therefore on the effect of low temperatures on development. However, Constable indicated that a plateau in the rate of development may have occurred at around 25^{o}C. More recently, Reddy *et al.* (8) working in a controlled environment reported a decline in development rate at temperatures above approximately 25^{o}C. Consistent with these findings, inflated thermal durations for the time to the appearance of the first square (flower bud) have been found for cotton sown under high temperatures in the field in Kununurra, WA (S. Yeates, CSIRO, unpublished data) and Narrabri, NSW (A.T. Wells, CSIRO, unpublished data).

An alternative approach to degree days is to describe the rate of a process, or the rate of progress toward a developmental stage, directly as a function of temperature (5). This allows non-linear functions to be used to more accurately reflect the variation in rate over a wider range of temperatures. With the continued expansion of the cotton industry into more extreme environments, there is a need to modify the current temperature response to account for the non-linearity of the response at both high and low temperatures.

In the research presented here, our aim was to explore temperature response functions to describe (i) the duration of the period between sowing and the appearance of the first square and (ii) the initial rate of production of fruiting sites. Fruiting sites are the nodes on the branches at which a square is produced although the fruiting form may or may not have been shed at the time of counting. Two approaches were used. Firstly, data were collated from four field experiments conducted under a range of temperature environments. Secondly, to extend the range of temperatures available and to avoid possible extraneous effects on development, a controlled environment study was conducted.

MATERIALS AND METHODS

Controlled environment study

A series of experiments was conducted in a temperature controlled glasshouse under natural light conditions. In the first experiment (sown October 7 1996) day/night temperatures varied sinusoidally between maxima and minima of: 12/20, 18/26, 21/29, 23/31 and 28/32^{o}C. In the second experiment (sown October 23 1998), the temperature regimes were 15/23, 20/28, 24/32^{o}C and in the third experiment (sown October 11 1999) 15/23, 20/28, 24/32, 26/34°C. Nine plants of cultivar Siokra L22 were grown singularly in 9L pots spaced at nine plants m^{-2}. This density was similar to that used in commercial practice, although in the field cotton is grown on a 1m row spacing. Pots received a basal N-P-K slow release fertiliser and Hoagland's solution was applied twice weekly. Pots were trickle irrigated daily. Pest control requirements were small, however two to three insecticidal sprays were required to control spider mites and aphids, and predatory mites were also released.

Observations were made on an individual plant basis. Plants were inspected three times per week. It was possible to estimate accurately the date of events occurring on intermediate days. The date of appearance of the first square was recorded together with the node number at which it occurred. The appearance of a square was defined as the date when the subtending leaf unfolded (3). The rate of development between sowing and the appearance of the first square was calculated as the inverse of the duration of the period between the two events. From first square until one week after the opening of the first flower, the date of appearance of each fruiting site was recorded for all positions on all sympodia.

Determining the rate of fruiting in cotton is complicated by two factors. Firstly, as the plant develops, the number of fruiting branches (exserted at each mainstem node) increases and thus the number of terminals producing fruiting sites is increased. This leads to a quadratic pattern of fruit production over time during early reproductive development (6). The rate was therefore determined from the slope of the regression of the square root of the cumulative number of fruiting sites against time in days. Secondly, the rate of fruiting declines in response to an increasing fruit load (6,7). To avoid this feedback, the rate was assessed only up to the time of the first open flower

Collated field data

In the field trials, the date of sowing and of first square production were obtained along with daily maximum and minimum temperatures for the location. From these data the duration of the period between the two events was calculated and the rate of development derived as the inverse of that duration. The experiments used are listed in Table 1. Squaring rate was calculated from experiments in which the production of fruiting sites on individual plants was monitored prior to the first flower opening.

Table 1: Field experiments used in collating data from a range of temperature regimes for estimating the rate of development to the appearance of the first square and the initial rate of site production.

Location	Date of Experiment	Source	Time of first square	Rate of site production
Narrabri	1972-74	Constable (2)	*	
Narrabri	1994-98	Bange and Milroy (1)	*	
Narrabri	1990-92	Wells (previously unpublished)		*
Kununurra	1995-97	Yeates (previously unpublished)	*	

RESULTS

The data from the field experiments indicate that the duration of the period from sowing to first square decreased with increasing temperature and thus the rate of development increased (Fig. 1). The linear regression through the data was significant ($P<0.001$, $R^2=0.62$, $n=91$) and a quadratic or exponential regression did not improve the fit significantly. In spite of this, the data from the experiments grown in Kununurra indicate little response of development rate to temperatures above approximately 25°C and the data of Constable (2) showed a relatively high response at lower temperatures. This suggests curvature in the overall response although no statistical improvement was found. The slope of the overall linear regression was less than that through the data of Constable (.0016 cf .0021) and the base temperature was lower (9.1°C cf 11.0°C). Because of the long extrapolation required to the x axis, small variations in the data cause large shifts in the estimated base temperature.

In the controlled environment experiment, the rate of development to first square increased with temperature (Fig. 1), but in contrast to the field data, the response showed a significant curvature. The data was well described by an exponential rise to a maximum function:

$$\text{Rate} = -0.9134+0.9474(1-\exp(-0.2135*\text{Temp}) \qquad (R^2=0.90;\ P<0.001).$$

At high temperatures, a maximum rate of 0.034 was approached and the rate fell to zero at an average temperature of around 15^{O}C. The curve fitted to the controlled environment data lay at the upper edge of the field data.

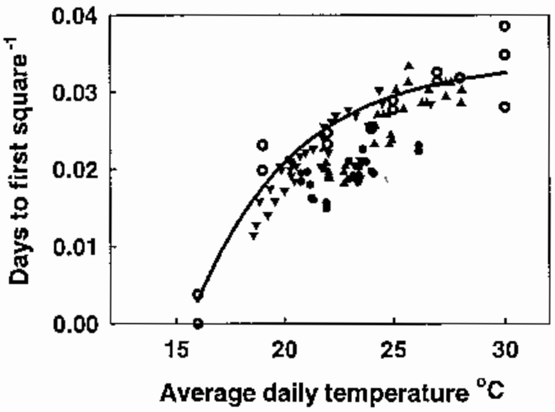

Fig. 1: Rate of development toward the production of first square in field trials (solid points) and controlled environment (open points), as a function of average temperature. Bange and Milroy (1), ●; Constable (2), ▼; Yeates, ▲. The curve represents the regression through the controlled environment data ○.

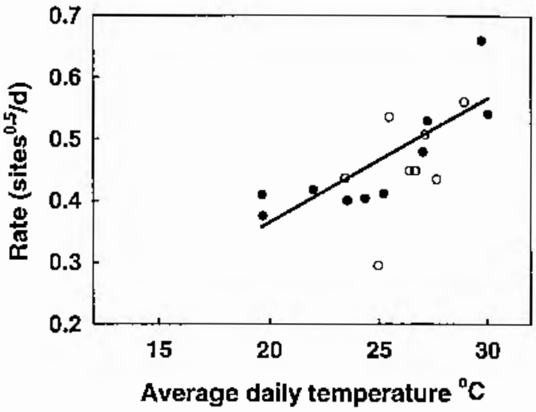

Fig. 2: Rate of production of squares in field trials of Wells (open symbols) and controlled environment (closed symbols) as a function of average temperature. The line is the linear regression through the controlled environment data.

In the controlled environment experiment, the shape of the response of fruiting rate to average temperature was unexpected (Fig. 2). The rate remained approximately constant at approximately 0.4 over the range of 19 to 26^{O}C and above this temperature the rate was found to increase. There was no clear indication of the response to temperature flattening at high temperatures. A linear regression through the data indicated an increasing rate with temperature and a base temperature around 2^{O}C. The field data was variable but lay reasonably well around the controlled environment data.

DISCUSSION

The data confirms the limitations of the degree day approach when used to describe early cotton development under a wide range of temperatures and also indicates that the responses are not necessarily transferable between processes.

The controlled environment data indicate that the rate of development to first square does not respond linearly to temperatures over the range used. This range of temperatures reflects the range of environments within which cotton is now grown in Australia. The results are consistent with those of Constable (2) who suggested a plateau in the response at about 25^{O}C. This shape of response explains the higher estimates of the thermal duration to first square found for cotton sown in high temperatures (A.T. Wells unpublished data and S. Yeates unpublished data). At higher temperatures the rate of development does not actually proceed faster but the estimated degree day accumulation each day is inflated by the linear extrapolation of the function.

Although the field data are highly variable, there is an indication of the same curvature as seen in the phytotron. The use of more refined analyses to account for the daily temperature conditions rather than using the average temperatures between two events might remove some of this noise. Other factors will also contribute to this variation, however. Cold shock early in crop growth or insect damage to the apical meristem can delay the appearance of the first square (4) and thus reduce the apparent rate of development. The fact that the curve fitted to the controlled environment data lies at the upper edge of the scatter of field data suggests that it represents a maximal rate of development with other factors reducing the estimated rate for individual field observations.

Similarly, drought stress and insect damage can alter the rate of fruit production (7,9). These effects would have increased the variability seen in the field data and rendered it more difficult to detect any curvature in the response to temperature. The shape of the phytotron response is unexpected and suggests the possibility of some sort of homeostasis in the fruiting rate over a range of temperatures. Additional data are currently being collected in a further phytotron experiment to confirm this response. Particular emphasis is being given to temperatures below 19°C.

The responses derived from this research will be important for monitoring crop development in the field against expected progress and for application in simulation models. Research is continuing to examine other developmental processes and also to assess differences between cultivars.

CONCLUSIONS

For controlled environment data, the response of the rate of development to first square in cotton was well described by an exponential rise to a maximum function. This appears to represent a potential rate which was approached by the field grown crops. The temperature response functions for development to first square and the initial rate of site production differed.

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REFERENCES

1. Bange and Milroy, S.P. 2000. *Field Crops Res.*, **68**, 143-155.
2. Constable, G.A. 1976. *Aust. J. Exp. Agric. Anim. Husb.*, **16**, 905-910.
3. Constable, G.A. 1991. *Agron. J.*, **83**, 374-378.
4. Constable, G.A. and Shaw, A.J. 1988. Agfact P5.3.5., New South Wales Agriculture and Fisheries.
5. Hammer, G.L., Goyne, P.J. and Woodruff, D.R. 1982. *Aust. J. Agric. Res.*, **33**, 263-274.
6. Hearn, A.B. and da Roza, G.D. 1985. *Field Crops Res.*, **12**, 49-69.
7. Patterson, L.L., Buxton, D.R. and Briggs, R.E. 1978. *Agron. J.*, **70**, 118-122.
8. Reddy, K.R., Hodges, H.F. and McKinion, J.M. 1997. *Adv. Agron.*, **59**, 225-290.
9. Sadras, V.O. 1996. *Oecologia.*, **106**, 432-439.

Fruit production rates in cotton cultivars of different maturity times.

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ABSTRACT

In cotton, the rate of production of new fruit decreases as the fruit (boll) load on the plant increases, eventually ceasing when the growth rate of the bolls is approximately equivalent to the growth rate of the whole plant. It is thought that the growing fruit monopolise resources within the plant and limit production of new fruit. We planted a short and a long season cultivar in the field on a number of dates and monitored their fruiting dynamics and growth rate to see whether there was any difference in the way fruiting responded to the carbon status of the plant. Initially, when there was no boll load to inhibit fruit production, the early maturing cultivar had a higher rate of fruit production than the late maturing cultivar. As the boll load developed and the amount of dry matter available for continued fruiting was limited, the impact on fruit production appeared to be similar for the two cultivars.

KEYWORDS: cotton; dry matter partitioning; fruit production; *Gossypium hirsutum*,

INTRODUCTION

To be able to simulate the growth and development of cotton cultivars of differing maturity length, we need to identify parameters which differ between cultivars of contrasting maturity. Cotton is an indeterminate species. The timing of crop maturity is not governed solely by temperature and photoperiod. Rather, according to the nutritional hypothesis, the timing of crop maturity is determined by when the fruit that are already growing monopolise resources and prevent the crop from producing new fruiting sites (3). Usually, the crop then finishes maturing the fruit that are already set. Crop maturity can therefore be affected by variation in either the supply of resources to the fruit or by the demand the fruit are generating by their number or growth rate.

Recent work (1) has shown that a short and a long season cultivar did not differ in total dry matter production but early in reproductive growth, the shorter season cultivar produced fruit more rapidly and partitioned a higher proportion of dry matter to fruit. It was not possible however, to identify whether the higher reproductive partitioning was caused of the more rapid fruiting or a result of it.

In this paper we aim to determine (i) whether the cultivars differ in their potential rate of fruit production and (ii) whether they differ in there ability to support a given rate of fruit production for a given level of carbon supply. To examine the rate of potential fruit production we compared fruiting site production before the onset of negative feedback by reproductive development. We then examined whether the cultivars differed in their rate of site production for a given amount of dry matter to support fruit production.

Both cultivars were sown on a number of occasions, to generate different growth rates and fruiting patterns, and grown in the field under full irrigation with excellent nutrition and pest control.

MATERIALS AND METHODS

Cultural details

Two field experiments were conducted at the Australian Cotton Research Institute (ACRI) Narrabri, New South Wales. The experiments included a range of sowing times so as to span a range of temperature and radiation regimes which in turn would influence dry matter production and fruiting patterns. Two okra leaf cultivars, Siokra S324 and Siokra L22 (hereafter S324 and L22), were used (S324 represents the earliest maturing cultivars currently in commercial use in Australia and it is used for late times of sowing or in shorter season areas). L22 is later maturing and is suitable for longer, hotter growing areas. These cultivars represent the range of maturity types used in Australia, although earlier maturing types than S324 are available in other countries.

The first experiment (Exp. 1) consisted of three sowing times and two genotypes arranged factorially. Plots (4 m by 75 m), containing four rows spaced at 1 m, were sown on 10 October (S1), 20 November (S2) and 5 December 1995 (S3). A completely randomised design was used with four replications. The second experiment (Exp. 2) consisted of two sowing times with two genotypes arranged factorially. Plots (8 m by 20 m), containing eight rows spaced at 1 m, were sown on 11 October (S1) and 13 November (S2) 1996. For this experiment a randomised complete block design was used with four replications.

Measurements

Starting just before first square (flower bud) plant samples (1 m^2) were taken approximately every two weeks and partitioned into leaf, stem, and fruit to determine their mass in dry matter. To account for the high cost of synthesis of cotton fruit relative to vegetative tissue, biomass of all components was converted to glucose equivalents using production values (g glucose per g dry matter) from Wall et al. (7) for cotton leaves, stems, squares and bolls. Vegetative dry matter (VDM_g) was calculated from the difference between glucose adjusted total shoot dry matter and total fruit dry matter.

To measure the rate of production of fruiting sites (hereafter sites), three plants in each plot were monitored three times a week. It was possible to estimate accurately the date of events occurring on intermediate days. The appearance of a square (which determines a new site) was defined as the date when the subtending leaf unfolded (2). Site production was measured from the appearance of first square till harvest maturity. In Exp.1 site production was only measured after the appearance of first flower.

The number of sites produced over time shows a quadratic increase during early reproductive development (4). The site production rate before the onset of flowering was therefore determined from the slope of the regression of the square root of the cumulative number of sites against time in days.

The production of new sites in cotton is dependent on vegetative growth; indeed it is morphologically linked to the production of new nodes and leaves (5). As the growing bolls consume more of the available resources, the amount available for vegetative growth, and hence new site production, declines. It is possible that the cultivars differed in their decline in site production with the decline in the amount of dry matter available for vegetative growth. We therefore plotted the rate of sites per day between consecutive harvests against the rate of increase in VDM_g over the same interval.

RESULTS

Initial rates of site production

In Exp. 2 the rate of site production ($sites^{0.5}\ d^{-1}$) before the onset of flowering between cultivars S324 and L22 was compared using linear stepwise regression analysis. When the two sowings of Exp. 2 were analysed individually, the inclusion of the cultivar as a factor in the regression of the rate of site production versus days after first square was significant ($P < 0.001$). In both sowings L22 had a lower rate of site production (Fig. 1). The slope of the regressions were 0.128 (±0.005) for S324, 0.086 (±0.004) for L22 in S1, and 0.120 (±0.003) for S324, 0.102 (±0.003) for L22 in S2. Thus on average S324 had a 32% higher rate of site production.

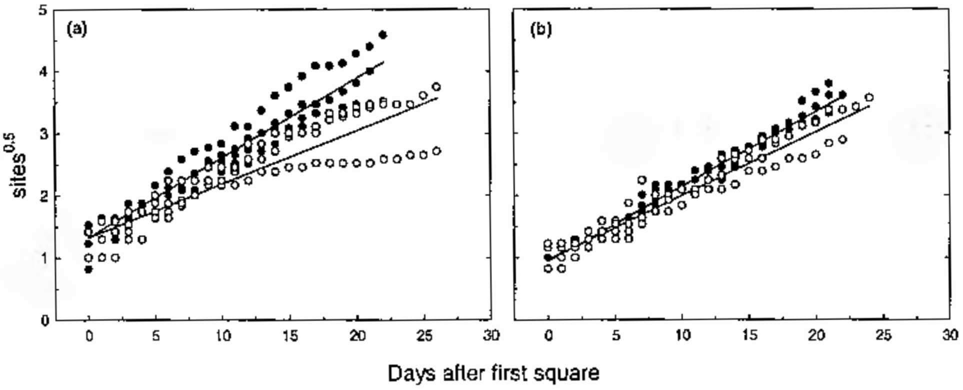

Fig. 1. Fruiting site production versus days after first square until the onset of flowering in Experiment 2 (a) sowing 1 and (b) sowing 2 for cultivars S324 (closed symbols) and L22 (open symbols). The slopes of the regressions represent the rate of early site production.

Carbon status and site production

Figure 2 presents examples of fitted curves of the general responses of site production rate and the rate of change of VDM_g for the first sowing of Experiment 2. Site production rate increased rapidly in both cultivars reaching a peak at approximately 70 days after sowing then declined rapidly. Cultivar S324 had a far higher rate of site production (Fig. 2a). Similarly the rate of change in VDM_g increased during early growth and reached a peak approximately 90 days after sowing then also declined rapidly. The rate of decline was far greater in cultivar S324 than for L22 (Fig.2b).

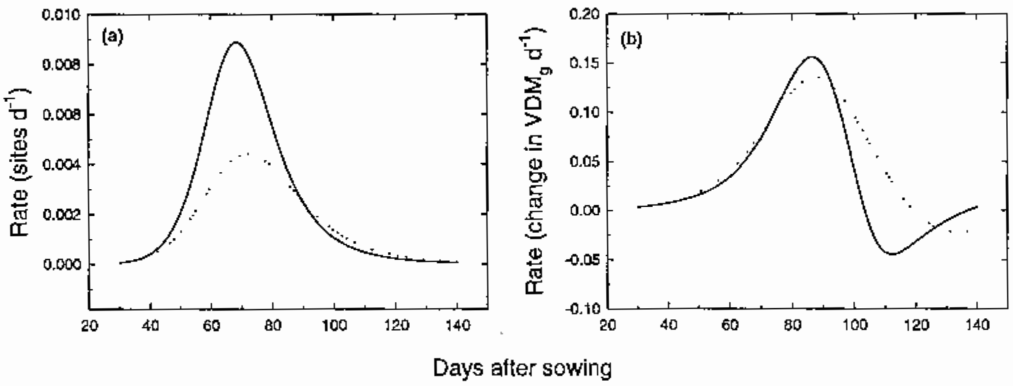

Fig. 2. Dynamics of site production rate and rate of change in vegetative dry matter production for sowing 1 of experiment 2. Solid line is cultivar S324 and dotted line is cultivar L22.

Carbon status and site production

To compare the relationship between internal carbon status and site production, the raw data for site production rate following flowering was plotted against the rate of change in vegetative dry matter (VDMg). Increases in the rate of vegetative growth rate during reproductive development mean that there is more capacity for sites being produced. This relationship is expected for cotton because the production of sites is morphologically linked to vegetative growth (5); new vegetative growth produces sites.

When the rate of site production was plotted against the rate of increase in VDM_g no single relationship was apparent (Fig. 3). Rather, the data are scattered below an apparent envelope curve showing a decline in site production with declining VDM_g. There was no difference between the cultivars either when each sowing or experiment was examined individually (data not shown) or with all the data combined (Fig. 3).

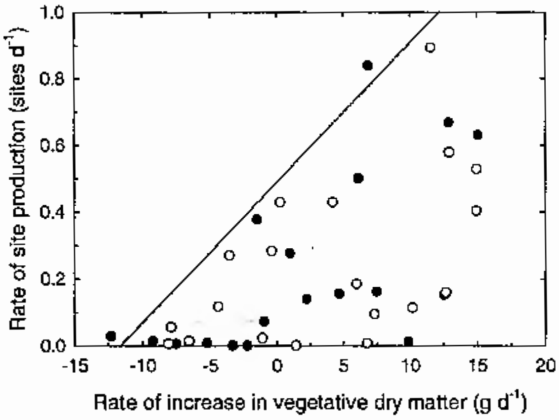

Fig. 3. Rate of fruiting site production versus rate of vegetative dry matter production (VDM_g) during reproductive development. Cultivars S324 (closed symbols) and L22 (open symbols).

DISCUSSION

We previously showed that the cultivar S324 accumulated squares more quickly than L22. This was translated into an earlier development of green and finally open bolls (1). However, the pattern of increase in the number of squares could have been influenced by either the rate of site production or the rate of early shedding. Fig. 1 shows that the cultivars differed in their initial rate of site production. Prior to the setting of any fruit load, the earlier cultivar S324 produced sites quicker than the later maturing L22.

Our earlier analysis also showed that the two cultivars did not differ significantly in their ability to intercept light or translate this into total dry matter but S324 did show a markedly greater distribution of dry matter to the fruit during the period up to peak green boll number (1). Consistent with this, Pace et al. (6) found that when ^{14}C was applied to the uppermost mainstem leaf during early growth, an early cultivar partitioned a greater proportion of labelled C into reproductive structures than did a later maturing cultivar. It was not possible to conclude whether the earlier fruit production was driving the greater proportion of DM going to the fruit or whether the greater distribution to the fruit was allowing a higher site production rate. However, Fig. 3 shows that as the supply of carbon in excess of the demand by the developing fruit became limiting, there was no difference between the cultivars in terms of their ability to continue to produce new sites. That is there was no apparent difference in the cultivars ability to utilise available dry matter during reproductive development for site production. The scatter of points below the apparent envelope curve may be due to a number of reasons. Initially, at the onset of reproductive development, site production rates increased rapidly and vegetative dry matter production was low. This means the points lie close to the line. When the rate of site production began to decrease, vegetative growth rate was high and thus the points fell away from the line. In addition to this, the fact that the vegetative organs continue to grow after a site is produced means that the pattern of VDM_g production lagged behind the pattern of site production. In the example from Fig.1 there was a 20-day lag between peak site production and peak rate of change in VDM_g.

Therefore it would seem unlikely that the greater rate of fruit production for cultivar S324 is due to the fact that the development of a site required less dry matter, enabling more sites to be produced. Rather it is likely that the greater partitioning of dry matter to reproductive development in S324 is a consequence of higher rate of site production which was then translated into bolls. To test this hypothesis, studies are being conducted to assess the impact of manipulating carbon supply on the rate of site production. In addition we are continuing our analysis of assessing whether cultivars differ in their rate of shedding in response to carbon status.

CONCLUSION

Past research (1) showed that the short season cultivar (S324) and the long season cultivar (L22) had similar RUE but differed in dry matter partitioning to reproductive growth. In this paper we show that S324 had the higher initial site production rate. As there appeared to be no difference in the way site production responded to VDMg we conclude that the higher site production rate in S324, which resulted in the more rapid increase in boll load, would cause the earlier termination of site production. Manipulative experiments are being conducted to test this hypothesis.

ACKNOWLEDGEMENTS

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REFERENCES

1. Bange, M.P. and Milroy, S.P. 2000. *Field Crops Res.*, **68**, 143-155.
2. Constable, G.A. 1991. *Agron. J.*, **83**, 374-378.
3. Hearn, A.B. 1981. *Field Crop Abs.*, **34**, 11-34.
4. Hearn, A.B. and Da Roza, G.D. 1985. *Field Crops Res.*, **12**, 49-69.
5. Mauney, J.R. 1986. In: Cotton Physiology. (Eds. J.R. Mauney and J.M. Stewart) (The Cotton Foundation: Memphis). pp. 11-28.
6. Pace, P.F., Cralle, H.T. Cothren, J.T., and Senseman, S.A. 1999. *Crop Sci.*, **39**, 1065-1069.
7. Wall, G.W., Amthor, J.S., and Kimball, B.A. 1994. *Agric. For. Meterol.*, **70**, 289-342.

Assessing Effects of Canopy Nitrogen and Light Distribution on Radiation Use Efficiency of Cotton.

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Abstract

As a surrogate for photosynthesis, biomass accumulation at the crop level can be estimated from the product of the amount of radiation intercepted and the amount of dry matter produced per unit of radiation intercepted (radiation use efficiency, RUE). The cotton crop simulation model CERCOT uses this approach and modulates RUE in response to canopy nitrogen status. However, the response of RUE of cotton to its nitrogen status is uncertain. Using a previously reported approach to scale from leaf photosynthesis to canopy RUE, we explored the significance of developmental changes in the vertical distribution of canopy N and canopy light interception characteristics on the response of RUE to nitrogen status. Tested against a field experiment, the framework performed reasonably well for high observed RUEs but over-estimated low RUEs. A number of avenues are being explored to improve its performance. A sensitivity analysis with the framework suggested that RUE in cotton was not effected by developmental changes in the vertical distribution of canopy N or light interception characteristics, but this needs to be tested in cotton crops with larger canopies where these effects are likely to be more important.

Introduction

The cotton crop simulation model CERCOT has been developed for use in research and to assist in tactical and strategic decision making. In CERCOT, biomass accumulation by the crop is estimated from the product of the amount of radiation intercepted each day and radiation use efficiency (RUE, the amount of dry matter produced per unit of radiation intercepted). RUE for a given day is modulated according to the canopy nitrogen status. However, changes in either light interception properties or the vertical distribution of N within the canopy can effect RUE for a given canopy N status (Hirose and Werger, 1987; Pons *et al.*, 1989). Developmental changes in both these factors have been observed in cotton (Sadras, 1996; Milroy *et al.*, 1998) and could effect the relationship between the canopy nitrogen status and RUE over the development of the crop. This would have implications for models which use RUE to simulate biomass production.

To explore the importance of these developmental changes for RUE in cotton, we used a simple framework developed by Hammer and Wright (1994) that scales from leaf photosynthesis to RUE which accounts for, amongst other factors, both the vertical distribution of N and the light interception characteristics of the canopy. The framework estimates the photosynthesis of sunlit and shaded leaves at each of the specified layers in the canopy as a function of their light receipt and N status. The photosynthesis of leaves in all the layers are totaled and adjusted for respiration to calculate a whole canopy photosynthesis. In this paper we aim (1) to test the suitability of the framework of Hammer and Wright (1994) for estimating RUE of field grown cotton crops and (2) use it to explore the predicted effects on RUE of average canopy N, the vertical distribution of N and the canopy light interception characteristics.

Materials and Methods

A field experiment was conducted at the Australian Cotton Research Institute Narrabri (30°S 150°E), a semi-arid environment in north-western New South Wales, Australia. The soil was a grey-clay. Cultivar Sicala V-2*i* was sown on 14 October with two nitrogen treatments; nil and 150 kg ha^{-1} of N applied as anhydrous ammonia. The crop was grown using full irrigation and commercial insect control methods. A completely randomised design was used with four replicates. Plots were 75m by four rows spaced at 1m. Incident solar radiation was measured throughout the experimental period at a meteorological station 3 km from the site.

From about the time of first square, 1 m^2 destructive plant samples were taken each fortnight. On each occasion, the canopy was cut in four successive strata of equal vertical thickness. For each layer, the leaf area (hence LAI) was measured using a planimeter and the leaf material dried and weighed. The total dry matter (TDM) in the sample was also measured. Leaf N concentration (g N/g DM) was determined using a near infrared refractometer or a Leco high temperature combustion system, both calibrated against the Kjeldahl method. The stratified cuts continued until boll growth was completed and the crop was approaching maturity, giving five samplings. Two additional samples were taken, one before the first and one after the last stratified cut, for TDM and N only. The proportion of photosynthetically active radiation (PAR) intercepted by the crop was measured using a ceptometer at approximately weekly intervals. Readings were taken above and below the canopy in each plot at around noon under clear conditions.

Instantaneous canopy light extinction coefficients (k), vertical specific leaf nitrogen (SLN, g N/m^2 of leaf) gradients within the canopy (henceforth referred to as SLN gradient) and average canopy SLN were calculated for each harvest date. The coefficient k was based on total global radiation and calculated from the light intensity above (I_o) and below (I) the canopy and LAI using the equation: $k = ln(I/I_o)/\text{-LAI}$. The SLN gradients were calculated from the regression of SLN in a given layer against cumulative LAI (LAI_{cum}) from the top of the canopy to the mid-point of that layer.

RUE was calculated for each date when a stratified harvest was taken by using data from three consecutive sampling dates centred on the date of interest. For each date RUE was calculated from the linear regression of accumulated biomass on cumulative intercepted PAR over the three dates. The proportion of light intercepted by the crop canopy over the day (Q) was estimated from the proportion of interception measured around noon (Q_n) using the equation of Charles Edwards and Lawn (1984): $Q = 2.Q_n/(1+Q_n)$. In calculating biomass, the high synthesis cost of cotton fruit relative to vegetative growth was taken into account by adjusting the reproductive biomass by the ratio of the biosythethic production costs (g glucose per g dry matter) of reprodnctive and vegetative tissues using the conversion factors of Wall *et al.* (1994). That is, the RUE is equivalent to that for the production of vegetative tissue.

The performance of the framework was tested by comparing the derived RUE's to those measured for each sampling date. For this purpose, the LAI for each layer, actual incident radiation, average canopy SLN, canopy SLN gradients and k as measured at each sampling date were used as inpnts to the framework. A limitation was the lack of a field based response of leaf photosynthesis (Pn) to SLN. The response equation used was based on that of Hammer and Wright (1994) but with a maximum Pn of 1.5 mg CO_2 m^{-2} s^{-1} at high SLN based on Australian cultivars grown in the field at Narrabri (Warwick Stiller CSIRO, unpublished data).

Results and Discussion

In the field experiment, RUE varied between 0.6 and 2.1 g MJ^{-1}. These values compare well to published data for the production of vegetative tissue by cotton which range between 1.2 and 2.1 g MJ^{-1} (Rosenthal and Gerik, 1991; Sadras 1996). Significant relationships were found between SLN in a layer and cumulative LAI from the top of the canopy ($P<0.05$). The negative slope of the relationship (ie: the SLN gradient) varied between the sampling dates and between nitrogen regimes ($P<0.05$, Fig. 1). Average canopy SLN also varied between treatments and sampling dates ($P<0.05$, Table 1), but k only varied significantly between sampling dates ($P<0.05$, Table 1). The k values in Table 1 appear low relative to previously published values for cotton (eg. Constable, 1986; Sadras, 1996) because they are based on total global radiation not PAR. On a PAR basis, the observations ranged from 0.51 to 0.81

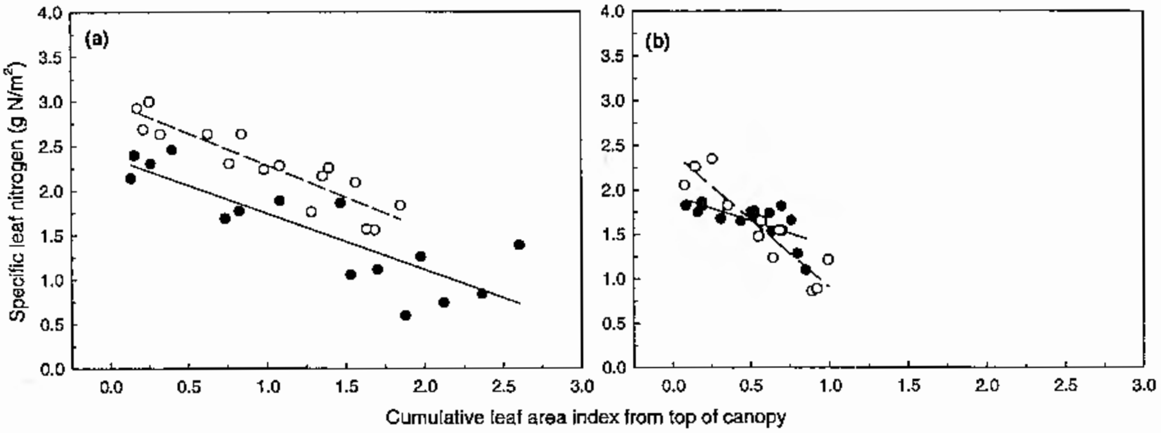

Fig. 1. Examples of the relationship between SLN and cumulative LAI for (a) the high N treatment and (b) the nil N treatment. Open symbols and broken lines are for 77 days after sowing (DAS), closed symbols and solid lines are 128 DAS.

Table 1. Observed values for the canopy light extinction coefficient, SLN gradient, total LAI and average canopy SLN for cotton crops grown under nil (LN) and high (HN) nitrogen for different sampling dates (DAS = days after sowing) and used as inputs to the framework.

DAS	Extinction Coefficient (k)		SLN Gradient		Total LAI		Average SLN (g N/m^2)	
	HN	LN	HN	LN	HN	LN	HN	LN
64	0.50	0.57	0.72	0.58	0.57	0.36	3.05	2.11
77	0.36	0.44	0.72	0.58	1.65	0.75	2.46	1.73
94	0.47	0.47	0.82	1.17	2.33	0.91	2.31	1.46
113	0.42	0.47	0.31	1.03	2.64	1.01	1.90	1.29
128	0.51	0.51	0.59	1.60	2.41	0.96	1.67	1.71

The RUEs calculated for the field experiment using the framework were plotted against the observed values (Fig 2a). The calculated RUEs were approximately correct for the higher observed values but were over estimated at moderate to low observed values, particularly for the nil N treatment. Part of the reason for the lack of response to low N supply is most likely due to the function used for the response of Pn to SLN. The function had been derived for peanut but was modified for cotton by changing the asymptotic maximum Pn rate. Although Reddy *et al.* (1979) have developed a relationship of this kind for cotton, it only used a limited range of SLN and was developed in a controlled environment. Significantly higher rates of Pn than the maxima reported by Reddy *et al.* (1979) or Constable and Rawson (1980) have been observed in the field (Warwick Stiller CSIRO, unpublished data). Leaf age may have also contributed to the over-estimation of RUE for the nil N treatment late in the season. The nil N treatment cut out earlier than the high N treatment and thus from this point onward the leaves at the top of the nil N canopy were older than those in the high N treatment. Thus, although they had only a slightly lower SLN (Fig. 1) they would have had significantly lower Pn rates (Constable and Rawson, 1980). Work is continuing to explore the response of Pn to SLN in the field and the interaction of leaf age and also light acclimation with this relationship. Non-linear canopy gradients (Hirose and Werger, 1987) may also have contributed to the scatter of the calculated RUEs. Research is continuing to quantify the importance of these aspects to the performance of the framework for cotton.

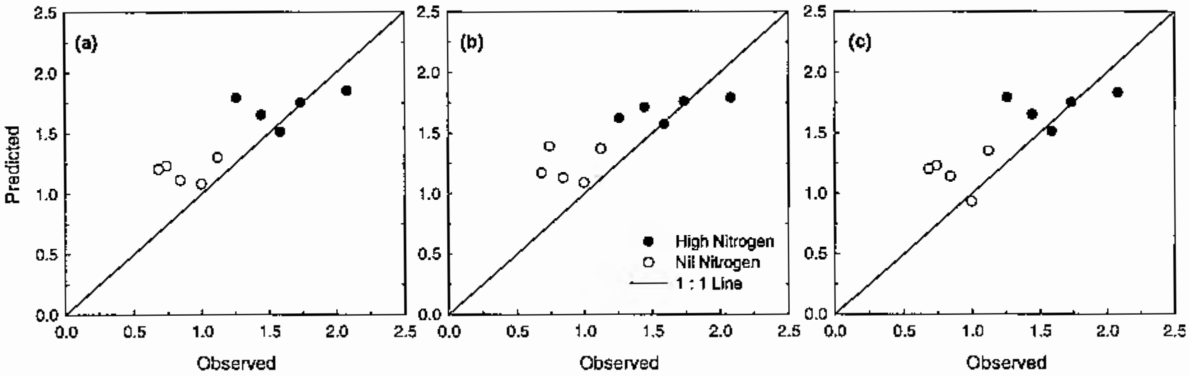

Figure 2: Derived versus observed RUE for the different dates in the field experiment using: (a) k and SLN gradient as measured for each date, (b) measured SLN and a common k calculated by pooling all the data and (c) measured k and a common SLN gradient.

To assess the significance of the observed developmental variation in k on the calculated RUE, we substituted a k derived across all dates and treatments in place of the actual k for each date. This had only a limited effect on the estimated RUE (Fig 2b). This was surprising given that a sensitivity analysis showed that the calculated RUE from the framework varied by 15% over the range of k values observed in the field trial (with SLN gradient = 0.61 and average SLN = 3.0). The small effect on the calculated RUEs for the field trial was presumably because, while there was statistical variation between the observed k values ($P<0.05$), most of the values lay near the overall value of 0.46. Thus only a few of the calculated RUE's where altered by using a common k.

When we tested the significance of the observed variation in SLN gradient by substituting an overall gradient in place of those specific for each date, it had even less effect than using a common k (Fig 2c). This was at least partially due to the low LAIs developed in the experimental crop. The analysis of Hirose and Werger (1987) indicated that canopy photosynthesis responded more strongly to SLN gradient at higher LAI; at an LAI of 2.12 the response was negligible. The highest LAI recorded in these crops was only 2.6 even though a yield of 2100kg ha^{-1} was obtained in the high N treatment.

The stability of the predicted RUE with changes in either k or canopy SLN gradient over the range observed in this study is promising for the development of a response of RUE to SLN which could apply through out the development of the crop. However, higher SLN gradients are likely with higher LAI (Sadras *et al.*, 1993) and also the consequences of variation in k or

SLN gradient are greater with higher LAI (Hirose and Werger, 1987). Therefore, it will be necessary to assess their importance in cotton crops which develop larger canopies than those in this study. This is the focus of ongoing experimentation.

Conclusions

The calculated RUE derived from the framework needs to be improved. This may be achieved through developing an appropriate field based response function for Pn versus SLN. Other aspects of the framework will also be examined to reduce the variability of the estimated RUE. The importance of developmental changes in SLN gradient and k for RUE in cotton needs to be quantified in crops with higher LAI than observed here.

Acknowledgments

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References

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

Constable, G.A. 1986. Growth and light receipt by mainstem cotton leaves in relation to plant density in the field. *Agric. Forest Meteorol.* **37**:279-292.

Constable, G.A. and Rawson, H.M. 1980. Effect of leaf position, expansion and age on photosynthesis, transpiration and water use efficiency of cotton. *Aust. J. Plant Physiol.* **7**:89-100.

Hammer, G.L., and Wright, G.C. 1994. A theoretical analysis of nitrogen and radiation effects on radiation use efficiency in peanut. *Aust. J. Agric. Res.* **45**:575-589.

Hirose, T. and Werger, M.J.A. 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* **27**:520-526.

Milroy, S.P., Bange, M.P. and Sadras, V.O. 1998. Leaf nitrogen gradients in cotton canopies vary with ontogeny and nitrogen supply. *Proceedings of the 9th Australian Agronomy Conference, Wagga Wagga, 1998.* pp. 417-418.

Pons, T.L., Schieving, F., Hirose,T., and Werger, M.J.A. 1989. Optimization of leaf nitrogen allocation for canopy photosynthesis in *Lysimachia vulgaris*. *In:* H. Lambers, M.L. Cambridge, H. Konings, T.L. Pons (eds) Causes and consequences of variation in growth rate and productivity of higher plants. Pp. 175-186, S.P.B Academic Pub., The Hague.

Reddy, K.R., Hodges, H.F. and McKinion, J.M. 1979. Crop modeling and applications: a cotton example. *Adv. Agron.* **59**:225-290.

Rosenthal, W.D. and Gerik, T. 1991. Radiation use efficiency among cotton cultivars. *Agron. J.* **83**:655-658.

Sadras, V.O., Hall, A.J. and Connor, D.J. 1993. Light-associated nitrogen distribution profile in flowering canopies of sunflower (*Helianthus annuus* L.) altered during grain growth. *Oecologia* **95**:488-494.

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

Wall, G.W., Amthor, J.S. and Kimball, B.A. 1994. COTCO2: a cotton growth simulation model for global change. *Agric. Forest Meteorol.* **70**:289-342.

Growth analysis of short and long season cotton cultivars

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Abstract

According to the nutritional hypothesis, the timing of crop maturity in cotton is affected by when the fruit that are already growing monopolise resources and prevent the crop from producing new fruiting sites. Maturity can therefore be influenced by either the supply of resources to the fruit or the level of demand generated by the fruit. Growth analysis was used to examine the supply of resources, in terms of the production and partitioning of dry matter, of an early and a late maturing cultivar grown in two fully irrigated field experiments. The two cultivars did not differ in peak leaf area index, above ground dry matter production or in allometric partitioning between the fruit and the rest of the shoot. Differences were however, found in light interception, canopy light extinction coefficient and radiation use efficiency in one experiment but not in a way that explain the differences in maturity.

Key words: extinction coefficient, *Gossypium hirsutum*, light interception, partitioning, RUE

Introduction

Cotton is an indeterminate species. The timing of crop maturity is not governed directly by temperature and photoperiod. Rather, according to the nutritional hypothesis, the timing of crop maturity is determined by when the fruit that are already growing monopolise resources and prevent the crop from producing new fruiting sites (1). Usually, the crop then finishes maturing the fruit that are already set. Crop maturity can therefore be affected by either the supply of resources to the fruit or the demand the fruit are generating in terms of their number or growth rate. In this paper we use growth analysis to examine the supply of resources in terms of the production and partitioning of dry matter, of an early and a late maturing cultivar.

Methods

An early maturing (Siokra S324) and late maturing (Siokra L22) cotton cultivar were studied in two field experiments grown on a uniform grey clay at Narrabri, NSW. The crops were sown on a 1 m row spacing with 10 plants/ m^2. Full irrigation and commercial insect control were used and N was applied as anhydrous ammonia six to eight weeks prior to sowing. Experiment 1 was sown on 10 Oct. 1995 and received 150 kg/ha of N. Plots were 175 m by 4 rows and a completely randomised design was used with three replicates. Experiment 2 was sown on 11 Oct. 1996 and received 113 kg/ha. A randomised complete block design and four replicates were used. Plots were 75 m by 4 rows. Starting just before first square, 1 m^2 samples were taken on a fortnightly basis and leaf area index (LAI) and dry weight of fruit, leaf and stem determined. The proportion of photosynthetically active radiation intercepted (PAR) by the canopies was measured weekly.

Results and discussion

The aim of this experiment was to determine whether differences in the dry matter production or partitioning could have contributed to the differences in crop maturity of a late and an early cotton cultivar. Differences were found between S324 and L22 in Experiment 1 in terms of accumulated light interception and radiation use efficiency (RUE) as measured over the whole period of measurement but not in a way that explained their maturity (Table 1). No differences were measured in Experiment 2. The difference in light intercepted between cultivars in Experiment 1 was due to a higher light extinction coefficient (k) and not greater canopy size (Table 1).

According to the nutritional hypothesis, a greater assimilate supply for the production of fruiting sites should result in prolonged fruit production and delayed maturity. The combination of the higher cumulative light interception and the higher RUE of S324 might suggest that S324, the early cultivar, would have the greater supply of photosynthate for the production of new fruiting sites. However, since the allometric partitionng (2) of the resources did not differ between the cultivars the greater supply of dry matter should lead merely to a larger plant in S324 (Fig. 1). In either case, the differences do not explain why it is the earlier cultivar. Further studies are considering within season variation of growth and partitioning, demand for resources by fruit, and are including a greater range of growth conditions.

Table 1: Comparison of peak LAI, cumulative PAR, k, total dry matter (TDM) and RUE for the two cultivars in the two field experiments. (n.s.d. - no significant difference).

Variable	Experiment	Cultivar S324	Cultivar L22	Pooled SE	Significance
LAI	1	3.02	2.52	0.30	n.s.d.
	2	1.70	1.82	0.27	n.s.d.
PAR (MJ/m^2)	1	1024	976	12	*($P < 0.05$)
	2	626	599	20	n.s.d.
k	1	0.64	0.77	0.03	* ($P < 0.05$)
	2	0.62	0.65	0.03	n.s.d.
TDM (g/m^2)	1	870	811	47	n.s.d.
	2	621	582	22	n.s.d.
RUE (g/MJ^1)	1	1.07	0.89	0.03	* ($P < 0.05$)
	2	1.03	1.00	0.03	n.s.d.

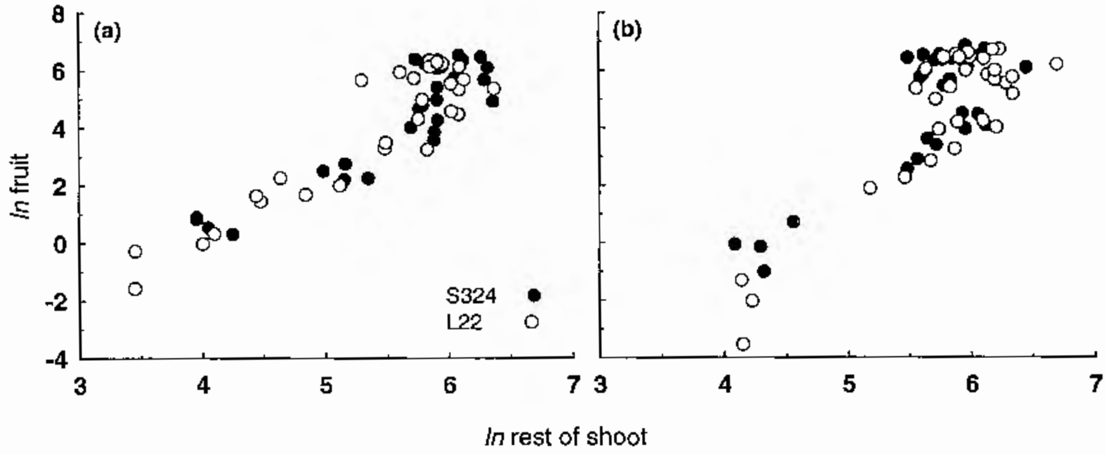

Figure 1: Comparison of the allometric partitioning of the two cultivars in the two field experiments.

Conclusions

The late and early cultivars did not differ in peak leaf area index, above ground dry matter production or in allometric partitioning between the fruit and the rest of the shoot. In one season differences were however, found in light interception and canopy light extinction coefficient. The short season cultivar also had a significantly higher radiation use efficiency, but this does not explain why it matures earlier.

Acknowledgments

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References

(1) Hearn, A.B. 1981. *Field Crop Abst.*, **34**, 11-34.
(2) Pearsall, W.H. 1927. *Ann. Bot.*, **41**, 549-556.

Leaf nitrogen gradients in cotton canopies vary with ontogeny and nitrogen supply

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Abstract

Leaf nitrogen (N) concentration usually declines with depth in plant canopies. For use in a framework to scale-up from leaf photosynthesis to canopy radiation use efficiency, we quantified the leaf N gradients in the canopies of three cotton crops. Stratified cuts were taken regularly, starting around the time of first square, and the leaf area index (LAI) and leaf N concentration in each layer determined. The slope of the regression of specific leaf nitrogen (SLN, g N /m^2 leaf) against cumulative LAI from the top of the canopy increased with ontogeny. It was also more marked under low N supply than high supply.

Key words: *Gossypium hirsutum*, leaf nitrogen, nitrogen distribution, ontogeny

Introduction

Radiation use efficiency (RUE) of cotton crops varies with ontogeny and leaf N accounts for part of this variation (6). Hammer and Wright (2) have developed a framework which can be used to scale-up from leaf photosynthesis to canopy RUE. The framework allows for the leaf N gradients within canopies and calculates photosynthesis by leaves at different levels in the canopy as a function of their N status and light receipt. This paper presents canopy gradients of SLN for use within this framework with the aim of exploring the mechanism by which ontogeny and leaf N affect RUE. The final purpose is to improve the response to nitrogen within the CERCOT cotton crop simulation.

Methods

Measurements were made on two field experiments grown on a uniform grey clay at Narrabri, NSW. The crops were sown on a 1 m row spacing with 10 plants/m^2. Full irrigation and commercial insect control were used. In Experiment 1, cotton (cultivar Siokra L22) was sown on 11 Oct. 1995. On 9 Aug., 150 kg/ha of N was applied as anhydrous ammonia. Each plot was 175 m × 4 rows and there were three replicates. In exp 2, two N treatments were established: nil and 150 kg/ha as anhydrous ammonia applied on 28 Aug. Cultivar Sicala V2i was sown on 14 Oct 1996. A completely randomised design and four replicates were used. Plots were 75 m × 4 rows. Each fortnight, beginning around the time of first square, 1 m^2 destructive samples were taken. The canopy was cut in four successive strata of equal vertical thickness. The leaf area (hence LAI) in each layer was measured and the leaves dried and weighed. N concentration (g N/g DM) was determined using a near infrared refractometer or a Leco machine, both calibrated against the Kjeldahl method. Sampling continued until the period of maximum boll growth was over and the crop was approaching maturity. Seven stratified harvests were made in Experiment 1 and six in Experiment 2.

Results and discussion

In Experiment 1, pooling data across all samplings, a strong linear relationship was found between *ln* SLN and cumulative LAI from the top of the canopy (Fig. 1). The production of branches by the cotton plant means that at any height in the canopy there are leaves of a variety of ages. Nevertheless, clear N gradients were still apparent. This is consistent with the hypothesis that leaf N concentration is influenced by light receipt as well as age (3, 5). In Experiment 2 the gradient varied with ontogeny and became steeper ($P < 0.01$) as the reproductive sink increased (Fig. 2). In contrast, N gradients in sunflower were more uniform in the reproductive than in the vegetative phase (7). This difference may be due to the indeterminate nature of cotton and/or the different distribution of reproductive sinks in the canopy. In Experiment 2, the gradient was greater for the low N treatment than for the high N treatment ($P < 0.001$) (Fig. 1). A non-uniform N distribution in plant canopies results in higher canopy photosynthesis than a uniform distribution by maximising N in leaves which receive the most light (4), although alternative reasons for the existence of gradients have been proposed (1). The greater N gradient in the low N treatment may reflect a mechanism that increases the efficiency with which limited N is used in photosynthesis. Investigations into the possible causes of ontogenetic changes in N gradients in cotton and their implications are continuing.

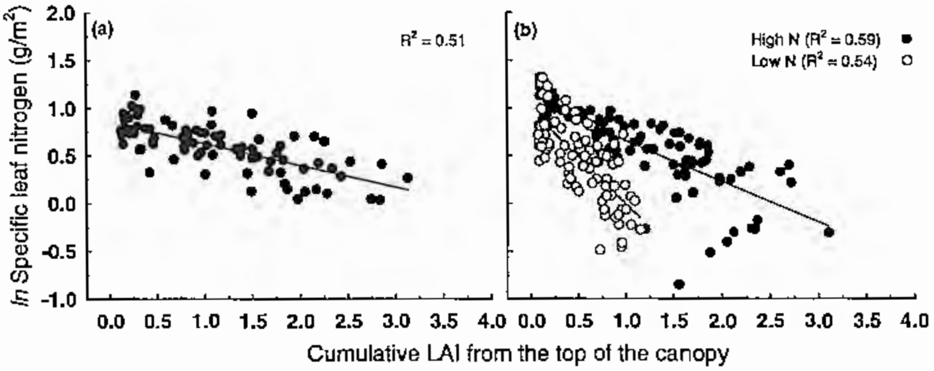

Figure 1: Relationship between *ln* SLN and cumulative LAI from the top of the canopy in (a) Experiment 1 and (b) 2, including data from all samplings.

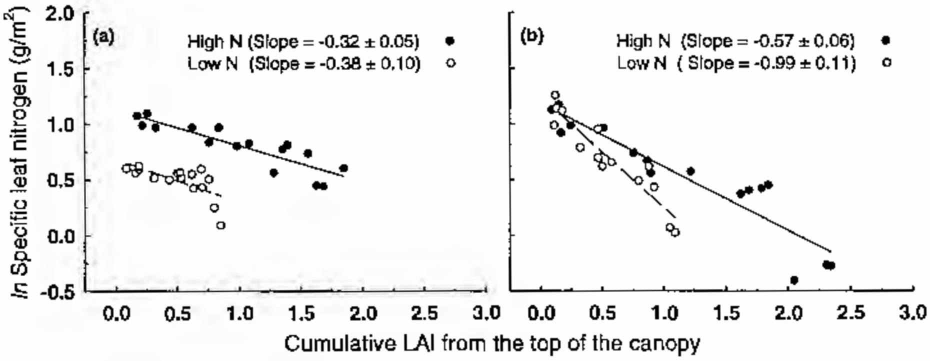

Figure 2: Relationship between *ln* SLN and cumulative LAI from the top of the canopy in Experiment 2 (a) near squaring (77 days after sowing) and (b) with a full boll load (141 days after sowing).

Conclusion

Leaf N gradients in cotton canopies were found to vary with N supply and ontogeny. In contrast to published data on other species they became steeper in the reproductive phase.

Acknowledgments

Thanks to the CRDC and the CRC for Sustainable Cotton Production for financial support of this work.

References

(1) Chen, J., Reynolds, J.F., Harley, P.C., Tenhunen, J.D. 1993. *Oecologia*, 93, 63-69.
(2) Hammer, G.L. and Wright, G.C. 1994. *Aust. J. Agric. Res.*, **45**, 575-589.
(3) Hikosaka, K., Terashima, I. and Katoh, S. 1994. *Oecologia*, **97**, 451-457.
(4) Hirose, T. and Werger, M.J.A. 1987. *Oecologia*, **72**, 520-526.
(5) Lemaire, G., Onillon, B., Gosse, G., Chartier, M. and Allirand, J.M. 1991. *Ann. Bot.*, **68**, 483-488.
(6) Sadras, V.O. 1996. *Field Crops Res.*, **48**, 199-208.
(7) Sadras, V.O., Hall, A.J. and Connor, D.J. 1993. *Oecologia*, **95**, 488-494.

Cool Starts: What is Normal?

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The cool starts to the last two seasons have again raised awareness of the problems of cold shock and slow crop development rates at low temperature. Low temperatures after sowing increase the time to emergence and reduce seedling vigour. These factors can lead to poor establishment, poor early growth and increased risk of seedling diseases. In addition they may increase susceptibility to herbicide damage and possibly reduce efficacy of Bt crops. Subsequently, the timing of crop maturity, yield and fibre quality may also be effected.

Staff at the Cotton CRC have received a number of inquiries about the weather we have had so far this season and how this compares to 'normal'. In this article we present the average day degrees, number of frosts, number of cold shocks, and occurrences of high temperatures for each week during the season from September through to May for locations in the major cotton growing areas. Together with the averages, the highest and lowest values in the climatic record are also presented to give an appreciation of the variation that exists for a particular region.

Day Degrees

In the cotton industry, day degrees are used for a variety of purposes, such as comparing the performance of crops within and across seasons, and for nitrogen fertiliser and pest management using CottonLOGIC.

In terms of development, the day degree calculation used by the industry can give an indication of the amount of development that can be expected on a given day. It is a useful tool for summarising the effect of variation in temperature on development using the daily maximum (Max) and minimum (Min) temperatures. If the daily minimum temperature is above 12 °C then day degrees are calculated as:

$$\text{Degree Days} = \left[(Max - 12) + (Min - 12)\right] / 2$$

If the daily minimum temperature is equal to or less than 12 °C then the day degrees are calculated as:

$$\text{Degree Days} = (Max - 12) / 2$$

A base temperature of 12 °C is used in this calculation and is the extrapolated temperature at which cotton crop development ceases. Note however, that this is not the temperature used to determine cold shocks which is 11 °C. Using day degrees assumes that cotton's potential development is largely a function of temperature. The actual rate of crop development at a given temperature in the field can differ depending on factors such as cultivar, soil condition, pest attack, disease, and herbicide damage.

Fig. 1 presents the average total day degrees for each week of the cotton season (September through to April). In addition to the averages, the highest and lowest accumulated values on record for a particular week are also shown. These analyses were conducted using weather data collected over a substantial number of years (Table 1). The analyses highlight the differences in climate between the regions and the degree of variation that can exist within each region and during the season. In southern areas, the day degrees per week increase more gradually in the early part of the season, giving the pattern over the growing season a skewed appearance. Prior to Christmas, the range of recorded values for any week is very large. For example in the first week of December at Goondiwindi the average value is 90 day degrees for one week but individual years range between 60 and 130 day degrees. In January, the hottest part of the season, the overall variability is at its maximum. Gunnedah is notable for its smaller variability for any week.

Fig.1: Historical cumulative day degrees for each week of the cotton season showing the average for each week as well as the maximum and minimum recorded for that week.

Frosts

Cotton requires warm soil conditions for emergence: three days with a minimum soil temperature above 14 °C are recommended before sowing. Because of this, frost is less commonly a problem than in some other crops which are planted earlier, but late frosts can occur and result in seedling death. At the other end of the season early frosts can terminate the crop prematurely reducing the crop's yield potential. Even before this occurs, most fibre properties are reduced when minimum air temperatures fall below 15 °C. Clearly the risk of frost will vary markedly with location and the severity of the frost (including the number of frosts that occur close together). In this analysis a frost was defined as a minimum air temperature of 2 °C recorded in a Stevenson screen which is approximately equivalent to a frost at ground level.

Fig. 2 presents the average number of frosts for each week of the cotton season (September through to April). In addition to the averages the highest and lowest recorded number of occurrences during a particular week are also shown. Table 1 presents the timing of the last frost (the start of the season) and the first frost (at the end of the season). In many cases the average dates of last and first frost fall outside the normal growing season. This shows up with the very low average frost occurrence in early September. However, as the analysis shows, in most regions there is a real chance that a frost can occur following planting or approaching crop maturity. Dalby stands out in this regard where the number of frosts per week in September and early October range from nil to six.

Fig. 2: Historical number of frosts for each week of the cotton season.

Cold Shocks

While the average number of frosts after sowing is very low, cotton growth can still be affected by chilling injury or cold shock. It has been identified that when daily minimum temperatures fall below 11 °C, growth and development the following day can be reduced regardless of the maximum temperature reached. Cold shocks particularly effect the rate of early development including the timing of emergence, squaring and flowering, but have no association with boll period. On average, the accumulated day degree requirement for flowering to occur is increased by 5.2 for each occurrence of a cold shock. In other crop species the physiological effects of cold shock have been shown to include effects on the function of the plants vascular system and photosynthetic apparatus. The physiological effects in cotton have not yet been fully established. Fig. 3 presents the average number of cold shocks recorded for each week of the cotton season (September through to April). It is notable that for most regions cold shocks can even occur in the middle of the growing season.

Fig 3. Historical number of cold shocks for each week of the cotton season. While the whole season is shown, cold shock is of most relevance during seedling development and approaching squaring.

Hot Temperatures

While variation in the rate of development can be caused by a number of environmental influences (such as waterlogging, pest attack, disease, cold shock), there is also evidence to suggest that some of this variation may be caused by excessively high daily temperatures.

Using day degrees to monitor crop development works well for early season growth. However, day degrees do not predict development as well when high temperatures occur, such as in the middle of the growing season. This is because the present day degree function assumes that the rate at which a process proceeds continues to increase as temperature increases although we know that at high temperatures many biological processes don’t respond as markedly to temperature as they do at moderate temperatures.

For example, recent examinations have shown that the present estimate of 505 day degree for the time from sowing to first square can actually vary from 510 to 695, especially in the hotter climates (eg. north-western Australia). Such variation devalues the usefulness of the present degree day function in predicting development when very hot conditions can be expected.

Fig. 4 shows the number of days during the week during the cotton season (September through to April) where the maximum temperature was recorded above 35 °C for a number of regions. This temperature was chosen arbitrarily as a high temperature likely to be approaching the limit beyond which the day degree calculation may no longer be robust. Continuing work is concentrating on refining the response of cotton development over a greater range of temperatures and for different developmental processes, as well as allowing for differences between cultivars. The new temperature functions are also being tested using field-grown crops.

Fig. 4: Historical high temperatures (greater than 35 °C) for each week of the cotton season.

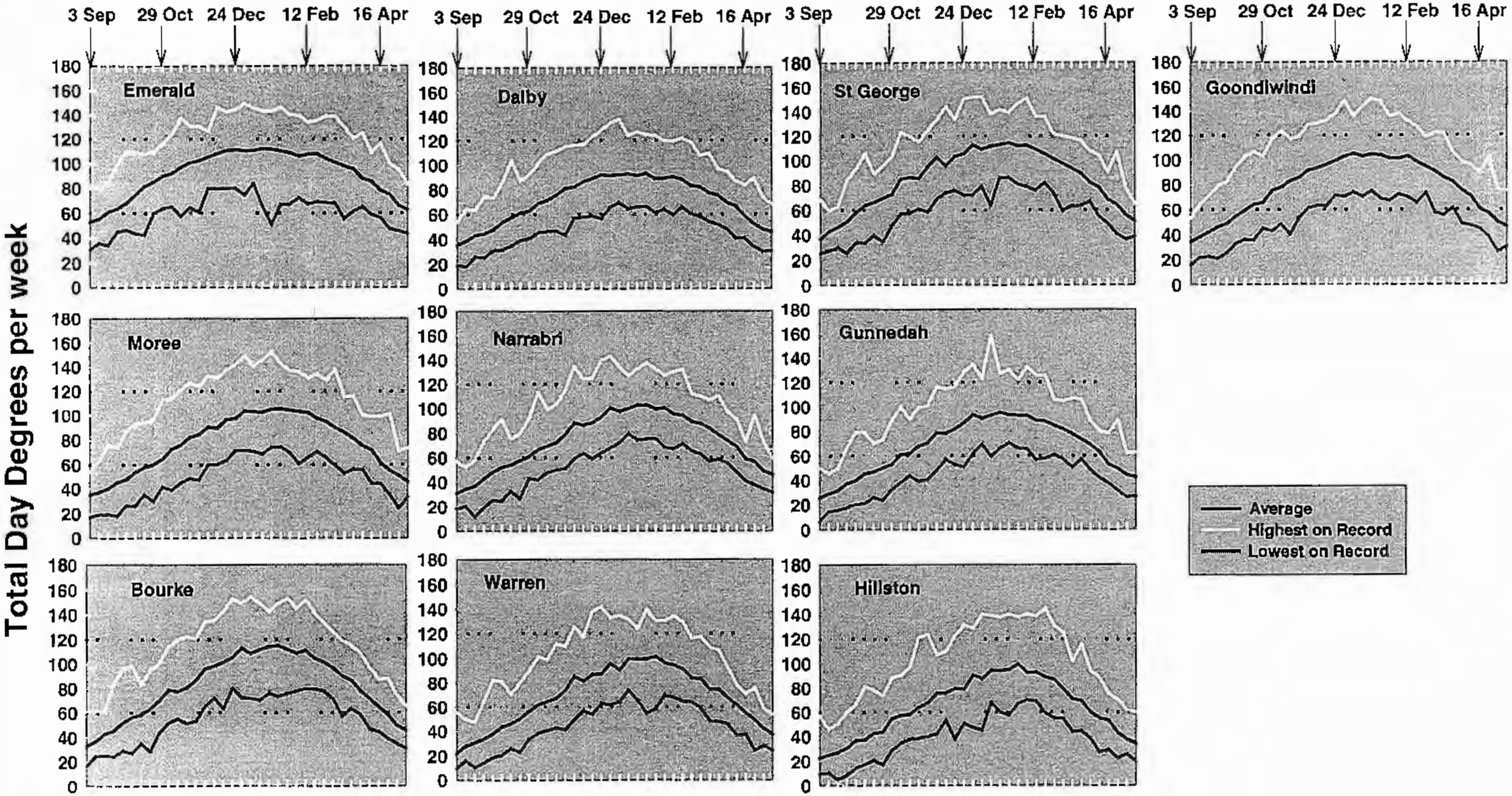
Accessing Weather Data and Day Degrees

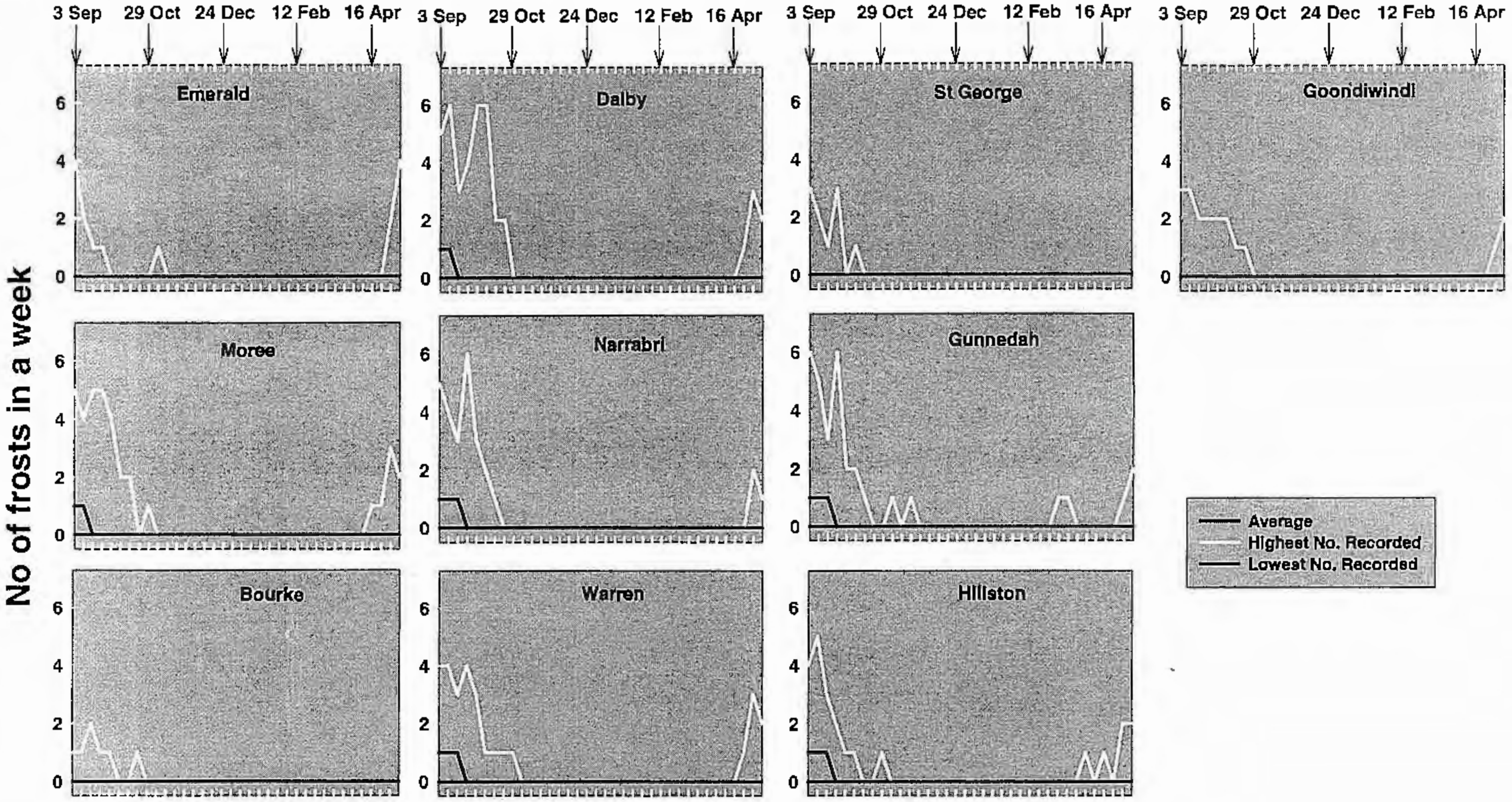
The data presented in this paper emphasises that for any of the climatic parameters which affect the growth of cotton a wide variation can occur from year to year and region to region. This provides a context against which to assess the current weather in your region. At the moment, there is no other convenient resource for accessing cold shock or day degree accumulation which will show the likely variation for your location. It should be born in mind that the degree of year to year variation that exists in one region will have a different impact on management or crop performance than in other regions.

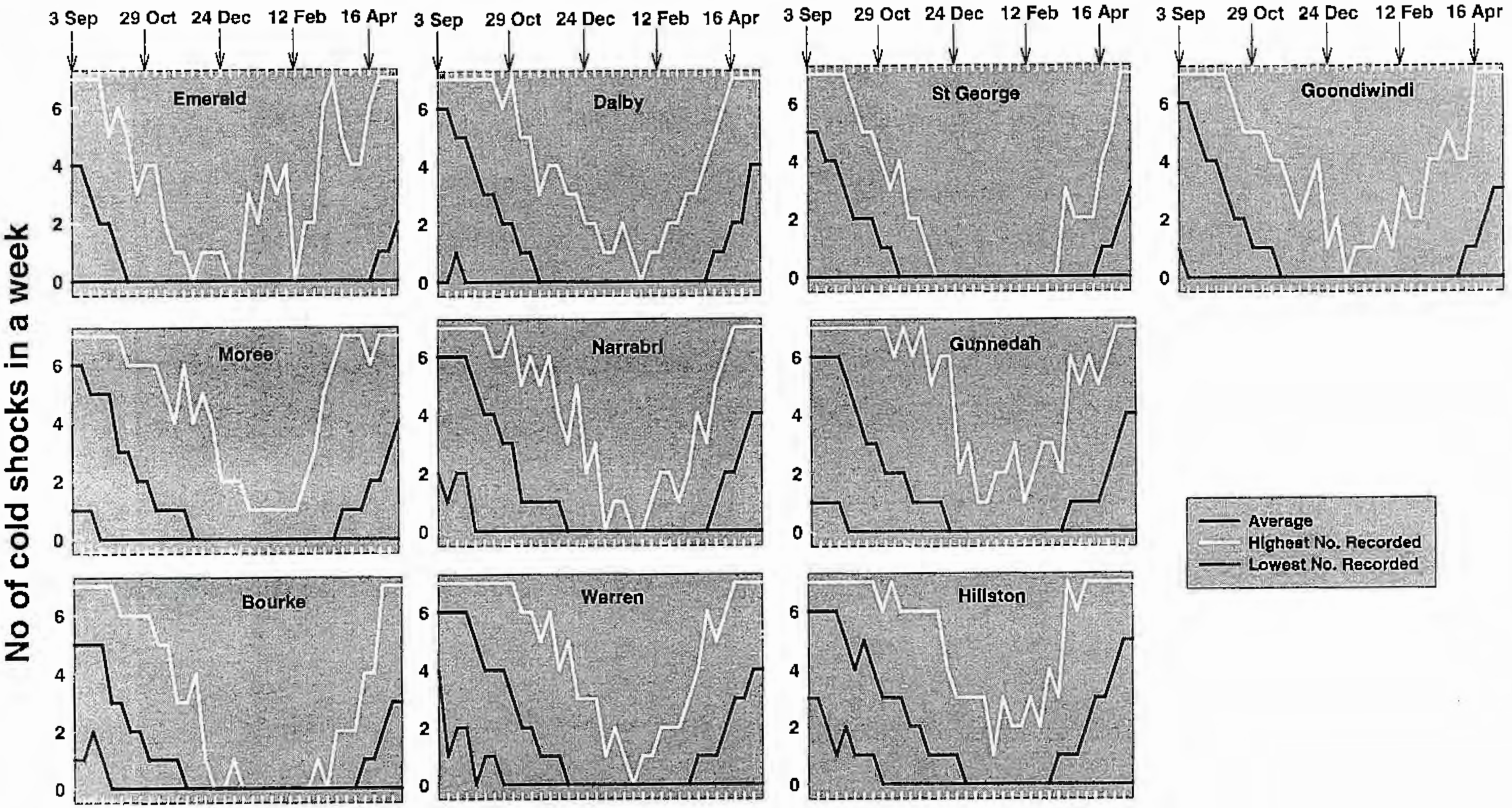
Although there isn't a tool for accessing the historic records of degree day accumulation or cold shock occurrences, the present season's day degrees and weather data can be accessed *via* the Australian Cotton CRC's web site www.cotton.pi.csiro.au. Through this site, information can be obtained from the cotton industry's weather stations or by using the new day degree calculator developed jointly by the Cotton CRC and the 'SILO' project funded by LWRDC. The degree day calculator uses a combination of the Bureau of Meteorology's data and interpolated data generated by the Queensland Department of Natural Resources. Present weather data is also available at SILO's web site www.bom.gov.au/silo .

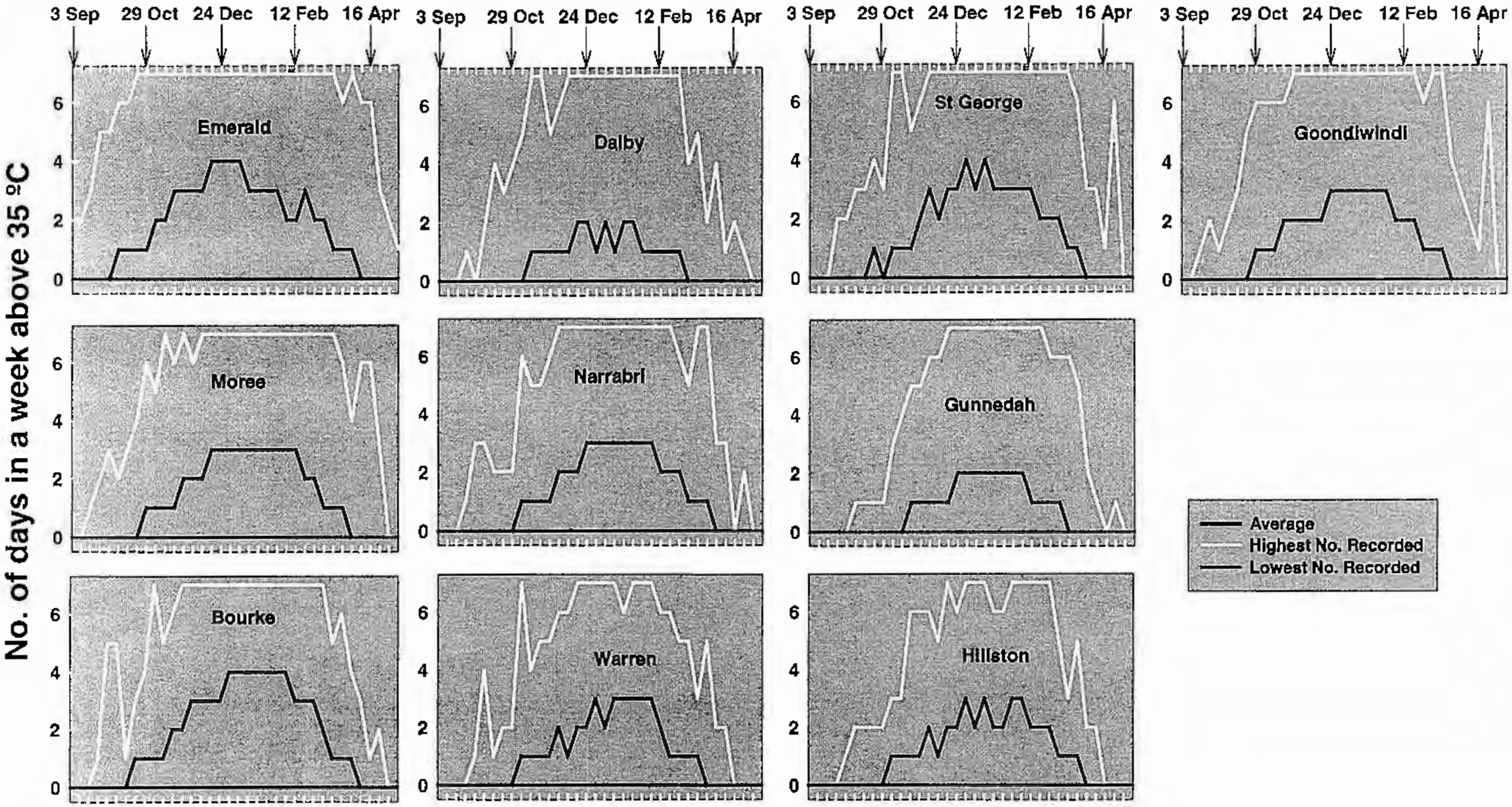
Table 1: Dates of first and last frost for cotton production.

Region	**Years of Climate Data**	**Average Date of Last Frost**	**Average Date of First Frost**	**Date of Latest Frost Recorded**	**Date of Earliest Frost Recorded**
Emerald	111	13 Aug	9 Jun	4 Nov	23 Apr
Dalby	111	8 Sep	26 May	18 Oct	17 Apr
St George	43	21 Aug	7 Jun	3 Oct	7 May
Goondiwindi	107	25 Aug	2 Jun	17 Oct	23 Apr
Moree	111	6 Sep	28 May	22 Oct	12 Apr
Narrabri	43	14 Sep	25 May	12 Oct	27 Apr
Gunnedah	62	14 Sep	22 May	18 Nov	11 Mar
Bourke	43	17 Aug	12 Jun	19 Oct	10 May
Warren	43	13 Sep	27 May	28 Oct	27 Apr
Hillston	43	14 Sep	17 May	28 Oct	1 Apr


Total Day Degrees per week
3 Sep
29 Oct
24 Dec
12 Feb
16 Apr
0
20
40
60
80
100
120
140
160
180
Emerald
Dalby
St George
Goondiwindi
Moree
Narrabri
Gunnedah
Bourke
Warren
Hillston
Average
Highest on Record
Lowest on Record


3 Sep
29 Oct
24 Dec
12 Feb
16 Apr
No of frosts in a week
0
2
4
6
Emerald
Dalby
St George
Goondiwindi
Moree
Narrabri
Gunnedah
Bourke
Warren
Hillston
Average
Highest No. Recorded
Lowest No. Recorded


No of cold shocks in a week
3 Sep
29 Oct
24 Dec
12 Feb
16 Apr
Emerald
Dalby
St George
Goondiwindi
Moree
Narrabri
Gunnedah
Bourke
Warren
Hillston
0
2
4
6
Average
Highest No. Recorded
Lowest No. Recorded


No. of days in a week above 35 ºC
3 Sep
29 Oct
24 Dec
12 Feb
16 Apr
Emerald
Dalby
St George
Goondiwindi
Moree
Narrabri
Gunnedah
Bourke
Warren
Hillston
0
2
4
6
Average
Highest No. Recorded
Lowest No. Recorded

AGRONOMIC RESEARCH TO SUPPORT THE DEVELOPMENT OF CROP SIMULATION MODELS

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BACKGROUND:

The work within the CRC relating to simulation model development encompasses links to a number of areas of agronomic and crop physiology research as well as important links to people involved in applying the model in various ways.

The involvement of research staff in the application of the model for on farm decision support provides a useful link back to those involved in model development. It allows rapid feedback on the robustness of the model under varying environmental and management conditions as well indicating priorities for developing new functionality required for decision support. In turn this helps indicate research priorities in terms of aspects of crop growth and response to environment where our understanding or the availability of quantitative results are limited.

Current research activities cover a number of areas of cotton agronomy and crop physiology. Some of these are outlined below.

WATER EXTRACTION BY SKIP ROW COTTON CROPS:

The increasing importance of dry land cotton production has resulted in a need to be able to reliably simulate cotton growth, development and yield when produced on different row configurations under limited water supply. To do this, one of the important processes which the model must simulate will be water extraction from different parts of the interrow space. Two successful projects have recently been completed by Dr Phil Goyne of DPIQ, Warwick, in which water extraction from five points within the planting row and the skip were monitored for solid planted cotton, single skip and double skip. The experiments encompassed a number of soil types and wide year to year variation in rainfall patterns. Some of his data is presented in his paper in these proceedings. This information will be used to improve the operation of the soil water balance in the simulation model for different row configurations.

DIFFERENCES BETWEEN COTTON CULTIVARS:

With the expansion of cotton production into many cooler areas, it is becoming increasingly important to be able to simulate cultivars of different season length. To this end, a series of experiments is being conducted to explore ways of deriving stable genotypic parameters to describe cultivars of varying crop maturity types. Because cotton is an indeterminate plant it is necessary to look at this in terms of the supply and demand of assimilate. Differences were found between Siokra S324 and Siokra L22 in Experiment 1 (1995-6) in traits that contributed toward carbon supply: accumulated light interception and radiation use efficiency (RUE) (Table 1). However, these did not explained their maturity types. No differences were detected in Experiment 2 (1996-97). The higher light interception by S324 in Experiment 1 was due to a higher efficiency of the canopy in intercepting light (canopy light extinction coefficient, k) and not greater canopy size. The greater light interception and greater efficiency with which this was converted into dry matter did not lead to a statistically significant difference between total dry matter (TDM) of the two cultivars.

Table 1: Comparison of peak LAI, cumulative PAR, canopy light extinction coefficient (k), total dry matter (TDM) and RUE for the two cultivars in the two field experiments. (nsd = no significant difference; * = cultivars different at $P<0.05$).

Variable	Experiment	Cultivar S324	Cultivar L22	
Peak LAI	1	3.02	2.52	nsd
	2	1.70	1.82	nsd
PAR (MJ/m^2)	1	1024	976	*
	2	626	599	n.s.d.
k	1	0.64	0.77	*
	2	0.62	0.65	nsd
TDM (g/m^2)	1	870	811	nsd
	2	621	582	nsd
RUE (g/MJ^1)	1	1.07	0.89	*
	2	1.03	1.00	nsd

Although no difference between the cultivars could be found in terms of TDM, there was a difference in the way the plants allocated dry matter between parts of the plant. At any point in time, S324 allocated a greater proportion of its new growth to fruit (Fig. 1). This is not necessarily the *cause* of S324's earliness. It may have been a *result* of its more rapid fruiting causing a higher demand by the fruit. Data on fruiting dynamics are still being processed but the data in Figure 2 show that, as expected, S324 had a higher peak square number than L22 at any sowing time. The research is widening to include a range of currently available cultivars.

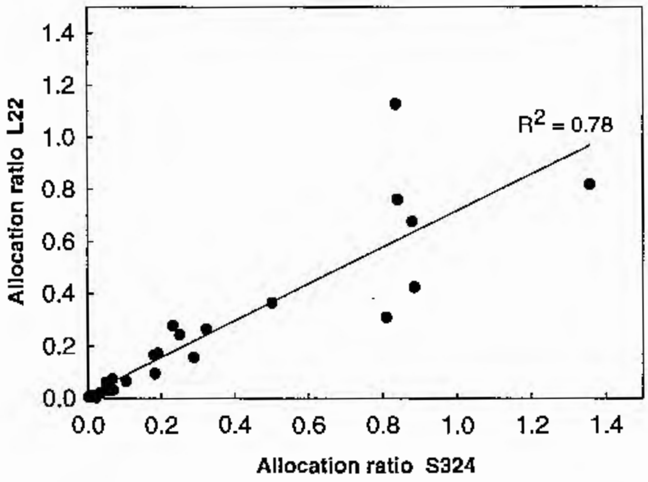

Figure 1: Comparison of the allocation ratio (proportion of new biomass going to fruit) of Siokra L22 compared to that of S324 in the first field experiment. S324 always partitioned proportional more biomass to the fruit.

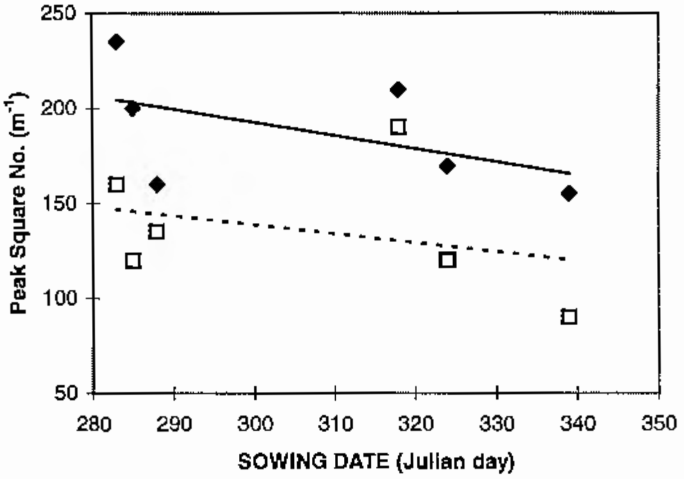

Figure 2: At all times of sowing Siokra S324 always had a higher peak square number than Siokra L22. Closed symbol and solid line = S324, open symbols and broken line = L22.

TEMPERATURE RESPONSES IN COTTON:

As part of developing parameters to describe the cultivar differences in growth and development, we have also conducted two control environment experiments into the response of fruiting processes to temperature. The processes being assessed include duration to first square, squaring rate, square period and boll period. The reason for doing these experiments is that a number of attempts to collect the cultivar specific development parameters have shown wider variation between years and times of sowing than between the cultivars. The controlled environment results show that the measures for development currently in use are not stable with temperature (Fig. 3). That means that the measurement made on a cultivar in the field will vary with environmental conditions. We are currently exploring a number of options for more stable descriptions of the processes using the controlled environment data. Any new relationships developed will then be tested against the field data collected on varieties of different maturity length. They will also then be used to analyse this data in terms of differences between cultivars.

WATERLOGGING OF COTTON:

A new project has recently commenced which has a twofold aim: to improve our understanding of the way waterlogging reduces cotton yield and to explore new possibilities for ameliorating its effects.

As described in his paper Marc Ellis (Australian Cotton CRC, CSIRO Plant Industry) has developed a number of transgenic lines which have been genetically modified to increase the activity of two key enzymes in the alcoholic fermentation pathway (*Pdc* and *Adh*). The aim is to allow metabolism to continue under low oxygen conditions. These lines are being tested in the field at Narrabri. To determine whether there is any benefit in the modifications, the growth and yield of the lines under waterlogged conditions is being compared to that under non-waterlogged conditions. Characters being assessed include leaf chlorophyll content, photosynthetic rate, fruit production and fruit retention.

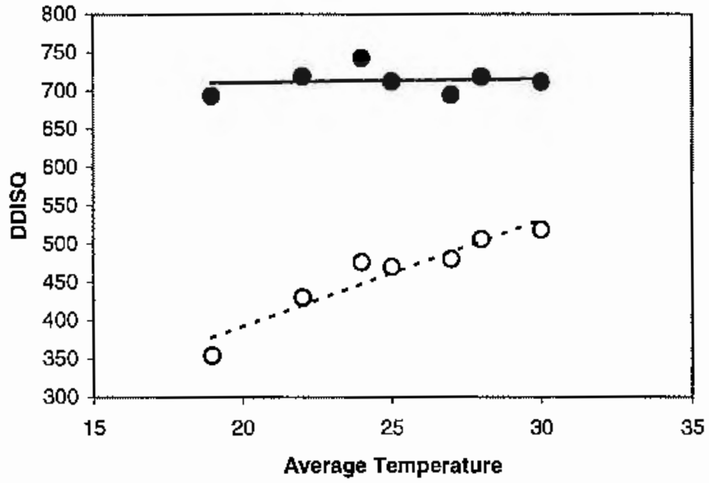

Figure 3: The thermal duration to first square (DDISQ) measured as degree days base 12 (open symbols) varied with temperature. Alternative functions (here a lower base temperature, closed symbols) gave more stable measnres.

The plant hormone AVG is also being trialed. This compound blocks the production of ethylene which is an important mediator in the senescence of organs, either naturally or in response to a stress such as waterlogging. However, this chemical may have negative impacts in terms of modifying rooting patterns and possibly delaying the maturation of the fruit. Its effects will need to be fully explored.

FUTURE DIRECTIONS:

Much of this work is still in progress. The first priority is the completion of the analysis for varieties of different maturity times and incorporating the results into the model. The work is being widened to include the collection of parameters for cultivars of different maturity lengths which cover a more diverse range of genetic backgrounds and to collect parameters for current cultivars.

The field research into waterlogging is just commencing. The new *Pdc* lines being generated by Marc Ellis and the new crosses of *Adh* and *Pdc* transformed lines will be included in the field program.

As well as increasing our understanding of how cotton responds to environmental factors and helping develop new ideas for cotton management, this research will be incorporated into the simulation model to enhance its ability to deal effectively with range of conditions. This will increase its usefulness and robustness in both research and decision support applications.

Do Degree Days accurately describe rates of cotton development?

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CRC for Sustainable Cotton Production

Summary

Degree days are commonly used by industry and researchers to estimate expected crop development. This assumes that cotton's potential development is largely a function of temperature. Controlled environment studies show that the function currently used to calculate Degree Days does not accurately reflect the effect of high temperatures on development. Preliminary analysis of the data shows that the inclusion of an optimum temperature in the degree day function in addition to the base temperature of 12°C can make more consistent predictions of cotton development. Improving this function will enable better predictions of cotton development in a greater range of environments and seasons.

Introduction

The rate of crop development is controlled by temperature and the relationship is often described using the convenient concept of degree days (DD). This is essentially the average temperature on a given day minus a base temperature of 12 °C; the temperature at which development ceases. The present function used in the Australian cotton industry to derive DD12 is:

$$\text{Degree Days } (°\text{C d}) = \frac{(\text{Tmax} - 12) + (\text{Tmin} - 12)}{2}$$

where Tmax and Tmin are daily maximum and minimum temperatures respectively. When Tmin is less than 12 °C, (Tmin - 12) is set to 0 (Constable and Shaw, 1988). Degree days can be accumulated over time to predict developmental phases or rates of cotton growth (eg. time to first square). In the cotton industry DD12 are used for a variety of purposes, such as comparing the performance of crops within and across seasons; nitrogen management (nutriLOGIC); pest management (entomoLOGIC); and the cotton crop simulations models OZCOT and CERCOT.

Since the DD12 function was derived from experiments which focused on the effects of early season development of cotton (Constable, 1976). The effects of low temperatures were the primary concern. Hence, this function describes the development of cotton ceasing when minimum air temperature drops below 12 °C. This minimum temperature for development is often referred to as the base temperature.

Recent studies into the effects of environment on crop development have highlighted some deficiencies in using this function to predict development. Constable and Shaw (1988) estimate that approximately 505 DD12 are required from sowing to first square. However, the measured DD12 for this period varied considerably (from 510 to 695 DD12) in a series of field experiments when calculated using the standard function (Table 1). Similarly, recent investigatious of dry season cotton production in the Ord (North West Australia) where high daily temperatures are experienced early in crop growth have shown that the time to first square varied between 440 and 600 DD12 (Yeates pers comm). Such variation devalues the usefulness of DD12 in predicting development. Especially when very hot conditions can be expected.

Table 1: Degree days (base 12) calculated for the time to first square for cultivars S324 and L22 (there was no significant difference between cultivars).

Season	Sowing date	Degree Days (°C d)
1995/1996	10 October 1995	696
	20 November 1995	608
	5 December 1995	644
1996/1997	11 October 1996	510
1997/1998	16 October 1997	622

While variation in development can be caused by a number of environmental influences (such as waterlogging, pest attack, disease, cold shock), there is evidence to suggest that some of this variation may be caused by high daily temperatures. The DD12 function assumes that the rate of a process continues to increase as temperatures increase. However, at high temperatures many biological processes don't respond as markedly to temperature as they do at moderate temperatures.

Studies conducted by Wells (1994) have shown a tendency for the rate of progress toward first square to increase only gradually when average daily air temperatures exceed the mid twenties (Figure 1). Constable (1976) in his studies in early cotton crop development also indicated that there appeared to be a plateau in the rate of crop development when temperatures exceeded 23° C.

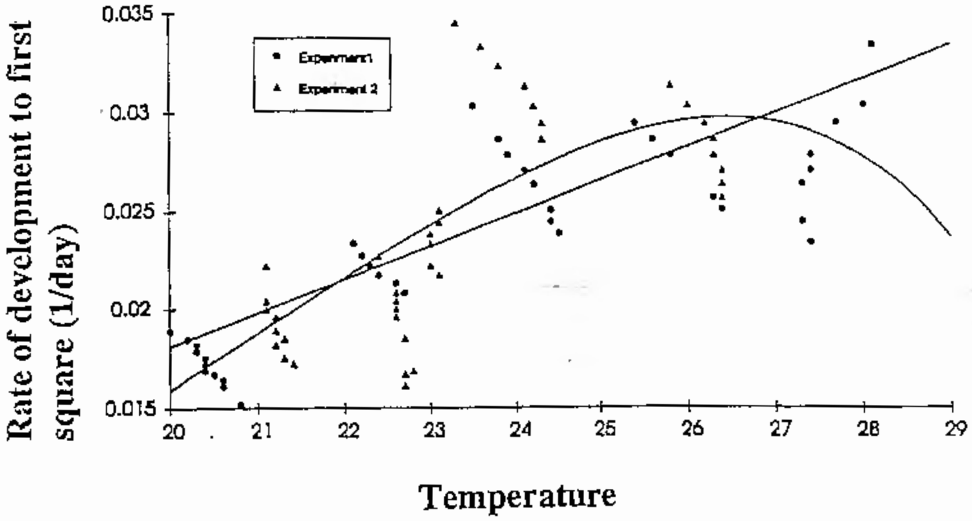

Figure 1. The rate of development to first square versus average daily air temperature (Wells, 1994).

Little work has been conducted to determine the effects of high temperature on the development of cotton. This paper outlines results from continuing studies to develop new functions that can be used to calculate DD that will account for both low and high temperature effects on cotton development.

Experimental Methods

To quantify the response of cotton development to temperature, specifically the time to first square and squaring rate, an experiment was conducted in a controlled temperature glasshouse under natural light. A short season (Siokra S324) and a long season (Siokra L22) cotton cultivar were sown on October 7 1996. Nine plants of each cultivar were grown under each of five maximum/minimum temperature regimes: 12/20, 18/26, 21/29, 23/31 28/32 °C (daily means of 16, 22, 25, 27 and 30 °C respectively).

Plants were observed three times per week and the date of appearance of the first square was recorded. The appearance of a square was defined as the date when the subtending leaf unfolded (Constable, 1991). From the appearance of the first square until one week after the opening of the first flower, the date of appearance of each square/site (sites analogous to new square production) was recorded for cultivar S324. This provides an estimate of the potential rate of squaring before the effects of increasing boll load could be expected to slow the rate of square production. Degree Days (DD12) were calculated using the function presented previously.

Results and Discussion

Rate of development calculated using the present cotton industry function (DD12) appeared to decrease as average daily temperature increased, in other words the apparent duration to first square in DD12 for both cultivars increased as average temperature increased (Figure 2). Degree Days to first square for cultivar S324 increased from 356 DD12 at 22 °C average daily temperature to 415 DD12 at 30 °C. This means that the DD12 calculation may not be adequately allowing for high temperatures. A better function would give similar estimates of developmental rate at all temperatures. A similar response was seen for cultivar L22, only the calculated DD12 were greater for each average temperature. No squares were produced in the 16 °C average daily temperature treatment in the experimental period.

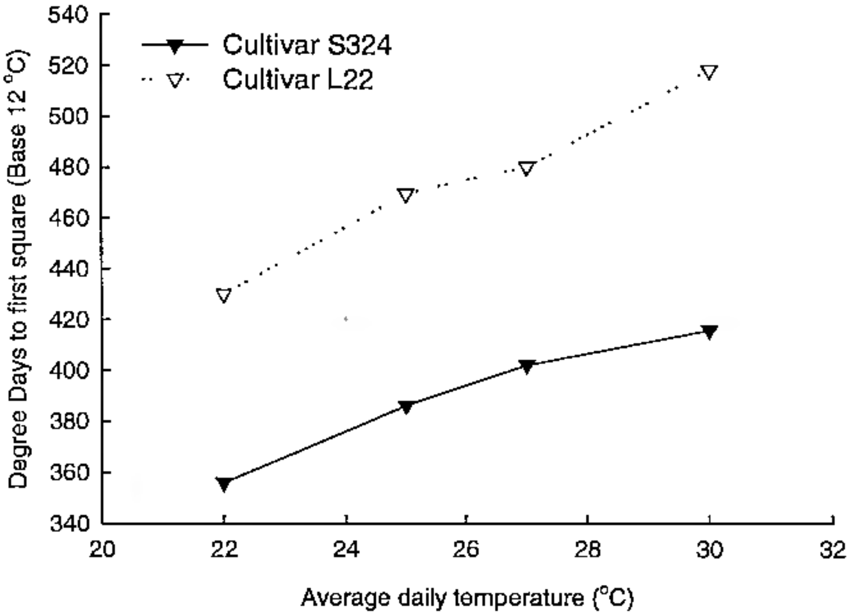

Figure 2. Degree Days (calculated using present industry function) to first square versus daily average temperature (°C) for cultivars S324 and L22.

After first square the rate of site production can be described by the squaring constant. The constant indicates the rate of square production as a function of temperature. It is a characteristic of the cultivar and should be constant across temperatures. Cultivars with a greater squaring constant have a higher rate of square production. The squaring constant for cultivar S324 calculated using the conventional DD12 function decreased as average temperatures increased (Figure 3). So again it would appear that the function did not adequately reflect the effects of high temperature.

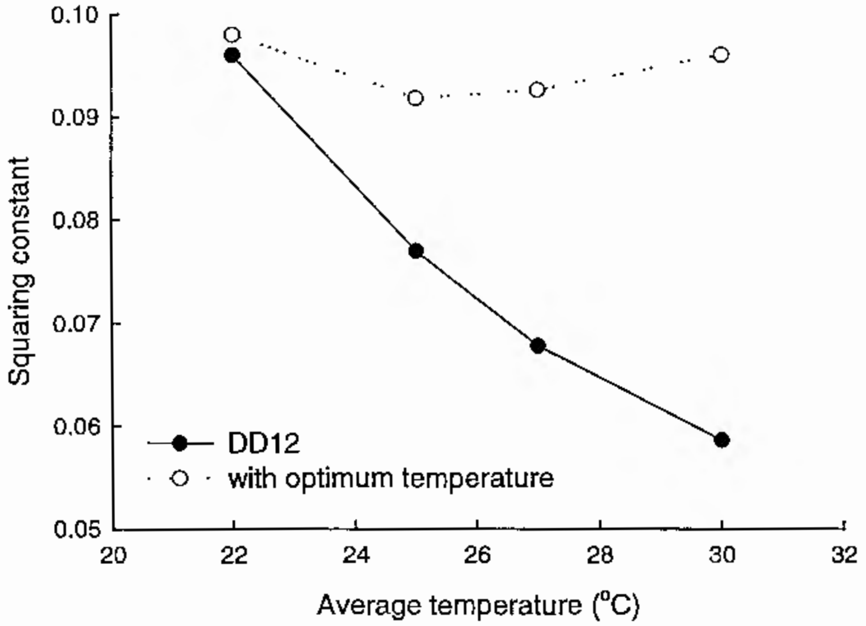

Figure 3. Squaring rate for cultivar S324 versus daily average air temperature (°C) calculated using the present cotton industry function (DD12) as well as a function that includes an optimum temperature.

These results demonstrate that the present function to calculate DD does not account for the effects of high daily temperatures. The addition of an optimum temperature in the DD function, in the same way as a base temperature of 12 °C, may allow for more consistent predictions of developmental rates. Figure 3 shows that a more reliable squaring constant can be estimated when an optimum temperature is included in the DD function. The functions are still being explored, particularly for the development to first square.

Improving the function that calculates DD by including an optimum temperature will enable better prediction of cotton development in a greater range of environments and seasons. Continuing work is concentrating on developing the response over a greater range of temperatures and for different developmental processes in cotton growth, as well allowing for differences between cultivars. The new temperature functions are also being tested using field grown crops.

References

Constable, G.A. (1991). Mapping the production and survival of fruit on field-grown cotton. *Agron. J.* **83**: 374-378.

Constable, G.A. (1976). Temperature effects on early field development of cotton. *Aust. J. Exp. Agric. Anim. Husb.* **16**: 905-910.

Constable, G.A. and Shaw, A.J. (1988). Temperature requirements of cotton. Agfact P5.3.5. New South Wales Agriculture and Fisheries.
Wells, A.T. (1994) Estimating parameters for the OZCOT cotton crop model for a range of cotton cultivars by field measurement. Master of Engineering Thesis, University of Southern Queensland, Toowoomba.

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