Applying cotton crop physiology to production issues.
(CSP123C)

FINAL REPORT

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1. Outline the background to the project.

The cotton simulation model is an important component of a number of current and future projects. It is a key tool for exploring cotton crop responses to environmental stresses or management inputs and for extending the outcomes of science into the industry. The latter may be as publications or as decision support tools where the predictive capacity of OZCOT can be used to test the outcomes of different management options. In this project we aimed to ensure the ongoing maintenance of the model as well as the continued incorporation of new science to improve our capacity to deal with current industry issues.

The project covered three main research components: 1.) exploring varietal differences in determinacy, 2.) exploring the model's capacity to simulate compensatory growth responses to insect damage, and 3.) implementing a new soil water balance in the model. These areas were identified as being of current high importance by a meeting of researchers associated with the project, including Drs Greg Constable, Lewis Wilson, Mike Bange and Brian Hearn. Ensuring the model's capability to simulate compensation is important for specific applications but the issues of growth form and soil water extraction are important for the general performance of the model and hence its application to a range of issues.

1. Plant growth form: earliness / determinacy

In the Mississippi Delta area of the USA, it has been suggested that cultivars with low determinacy are most suitable for raingrown production because they allow continued growth after retardation due to drought stress. However, there is little documented evidence of the efficacy of this approach. The same idea can be suggested for raingrown crops in Australian growing conditions, since we have a similar unpredictable rainfall pattern. In fact, variation in determinacy may be a useful trait in relation to a number of environmental stresses. For example, in irrigated crops, low determinacy may allow a higher degree of recovery from damage by insects later in the season. The value of such an approach has not been assessed. We aim firstly to explore whether varietal (genetic) variation in determinacy exists and how it may be characterised and secondly whether it can be manipulated to advantage. While the level of determinacy may be of value in a number of situations, in particular those which perturb the carbon supply:demand ratio, for logistical reasons we restricted our investigation to the interaction between determinacy and drought stress.

To a large degree, determinacy is linked to vegetative vigour and (inversely) to earliness. This can be the result either of genotype or management. We investigated whether genetic variation in determinacy occurred independent of other growth habit traits and the potential for this to be manipulated to advantage in management.

The growth of a number of cultivars that had been qualitatively assessed as differing in these traits was studied in the field under different resource supply. The degree to which they differed in their ability to continue to produce new organs during increasing boll load was assessed together with degree to which they differ in their ability to reinitiate organ production after a stress has halted growth.

2. Compensation

Cotton's capacity to compensate for damage by insect pests has been recognised for some time. However, variability in the degree of compensation that occurs under different environmental and agronomic conditions restricts the ability of managers to make appropriate allowance for this process. The model provides a tool both to assist in exploring this issue and to assist in using compensation to economic benefit in the industry. The model will be used to supplement and increase the power of the experimental work of Dr Tom Lei into the capacity of cotton to compensate under different circumstances. In the area of extension, Dallas Gibb of NSW Agriculture, aims to post simulation results on the web on a weekly basis as some indication of the capacity of the crop to compensate at various stages of development. This capacity declines with time after sowing. Access to data updated on a weekly basis may provide a way for growers to factor into their management the plants ability to compensate for different types of damage.

Prior to use in either form of application, it will be necessary to carefully evaluate the capacity of the model to reliably simulate the compensation response. The fruiting routines in the model are able to simulate the increase in the rate of fruit production due to fruit removal. This will also cause a response in the leaf area development, similar to that observed in earlier experiments observed by Victor Sadras. Whether the model can successfully mimic the other growth responses that have been observed in the field is not known. It is unclear to what extent these responses contribute to the plant's compensation ability. The degree to which the model is able to capture the variation in compensation with variable resource supply is also unknown.

The planned first phase of the work was to assess the performance of the model in simulating compensation by running it against a collection of data sets which include various manual damage treatments as well as a range of environmental conditions. These are available from the previous studies of Tom Lei, Lewis Wilson and Victor Sadras. It will be necessary to assess the simulation of different plant processes including LAI development, RUE, and resource partitioning as part of how the simulation is responding to damage. The final aim is to link the model to the *Helicoverpa* feeding model developed by Ted Wilson. This will make it possible to assess the compensation response to a specified insect pressure. Data for this step are available from the recent work of Tom Lei. The work will be done in collaboration with Dr Lei.

3. Water balance

The water balance currently used in the cotton simulation model is the first version developed by Ritchie and co-workers at the Blacklands Research Station in the USA. This approach does not allow for differences in the rate of moisture extraction by a crop on different soil types. Two other problems have also arisen with the water balance: (a) the soil water remaining at the end of crop growth is predicted to be greater than observed which causes problems when simulating crop sequencing issues, and (b) Peter Carberry has had difficulty in generating realistic soil moisture extraction patterns for dryland and partially irrigated crops grown on the Darling Downs.

The aim was to implement a new soil moisture extraction routine in the model to overcome the limitations of the version of the Ritchie model currently being used. The routine will use the resource capture approach of Montieth-Passioura. This approach allows for different extraction patterns of different soil types but without the high data requirements and calibration difficulties of the CERES approach and other models based on root growth.

The approach is already being used by the APSRU group for other crops and so will readily allow the use of the cotton model in cropping sequence analysis in combination with the crop models already developed by APSRU. The improvements will be important for Mike Bange and Dirk Richards and others in the cotton industry looking at crop sequence issues. It will also be important for researchers looking at water use issues or doing simulations of dryland cotton production.

As part of a previous project, Phil Goyne has started to collect water extraction data suited to this approach for soils on the Darling Downs. We currently also have a limited amount of data for soils on the Myall Vale research station. In collaboration with Dirk Richards we planned to collect data on moisture extraction by cotton grown on different soil types covering a wide geographic distribution to establish a database of parameters for model application.

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

1. *To explore the potential for utilising the degree of determinacy of a cultivar in management.*

Three field experiments were conducted on the determinacy of cotton cultivars. The analysis of the first two experiments allowed parameters for the assessment of determinacy to be devised and the degree of variation in determinacy to be quantified. The third experiment, which was designed to test the response of cultivars of different determinacy to intermittent drought stress, is still being analysed. This work was interrupted by the departure of the projects key researcher, late in the projects duration.

2. *To continue the development of the cotton simulation model in terms of*

    a. *The response of cotton to insect pests.*

The model has been modified to accommodate both the input of observed fruit numbers and fruit loss numbers. The former is appropriate for using fruit counts made on damaged crops in the field, including experimental data sets. The latter allows the input of numbers from the feeding model of Ted Wilson. Compensation routines developed by Tom Lei and Akio Takenaka have been incorporated into the OZCOT code and are operating correctly. These accommodate both fruit removal and tip damage.

    b. *Soil water extraction.*

Code for the simulation of water uptake using the Montieth-Passioura approach has been re-written from the APSIM pseudo-code. Additional modifications required in the model to accommodate the changes have been made and a fully operative version of the model is now available which incorporates the new water extraction routine. Drought has limited the collection of data on water extraction by dry land crops and thus complete testing of the new model has been hampered.

3. *Ongoing maintenance and development of the model code.*

During this project the model has been extensively rebuilt by David Johnson. OZCOT code has been converted to compile under Compaq Visual Fortran. It has been restructured into modules with appropriate naming conventions, coding styles and constructs applied. Variable names indicate scope of use and type while the code style has been changed from fixed format to free format. This helps to speed up coding and reduces coding errors. The code has also been tidied in a number of ways including removal of obsolete code and the addition of comments to clarify complex pieces of code. As well as being important in their own right, these are functional steps towards implementing the CSIRO Plant Industry "Common Modelling Protocol" which will allow rapid exchange of developments between research groups.

4. *Provide support to researchers using the model.*

David Johnson has provided substantial support to model users. This has included reworking model code to make it appropriate for use in the HydroLOGIC re-development, carried out by

Scott Johnston, as well as training and trouble shooting for scientists using the model both for on-farm application and research.

3. Detail the methodology and justify the methodology used.

Implementation of an improved procedure for soil water extraction:

The soil moisture content beneath one commercial dryland crop and three partially irrigated experimental crops was monitored from shortly after emergence. Data was also collated from two dryland crops grown some six years ago. The crops were chosen to reflect a range of soil types on which cotton is commercially grown (Table 1). All crops were sown on a 1m row spacing with the partially irrigated crops being grown on a ridge/furrow system. The crops were grown following commercial practices, except for the irrigation strategy for the partially irrigated crops. Each crop received between 80 and 100kg of nitrogen per hectare and commercial insect and weed control as required.

Table 1: Listing of crops used to obtain data for the new moisture extraction routine in the OZCOT simulation model.

Site Name	Nearest Town	Sowing Date	Irrigation	Soil Type
ACRI - Leitch	Wee Waa	2001	Partial	Grey vertosol
ACRI - Chicko	Wee Waa	2002	Partial	Grey vertosol
ACRI - Block 18	Wee Waa	2001	Partial	Alluvial clay
Glen Cairn	Bellata	2001	Nil	Brown clay over gravel
Calatoota- Skip	Edgeroi	1996	Nil	Brown clay
Calatoota-Solid	Edgeroi	1996	Nil	Brown clay

Soil water content was measured at regular intervals from early in crop development using a neutron moisture meter. Replicated measurements were made in the middle of the depths ranges of: 0-100mm, 100-200mm, 200-400, 400-500, 500-700, 700-900, 900-1000mm. The neutron moisture meter was calibrated at each site against gravimetric soil moisture content measured during the growing season.

The rate of descent of the extraction front was determined by plotting the depth of a stratum against the time (DAS) at which extraction began in the stratum. This yields a rate in mm/day. The kL parameter, describing the rate of extraction from a stratum, was determined by fitting an exponential decline to the soil water content against the time from when extraction began in that stratum.

Exploring the potential for utilising the degree of determinacy of a cultivar.

Four field experiments were conducted at Narrabri from 1999to 2002. Each experiment included two sowing dates to generate variation in temperature and radiation regimes, which in turn should influence dry matter production and fruiting patterns. Cotton lines with known differences in timing of crop maturity and determinacy, as assessed by the CSIRO cotton breeding team, were used (Table 2). Sowing times and lines were combined factorially. Plots (8 m by 18 m), containing eight rows spaced at 1 m, were sown in October (S1), and November (S2). Randomised complete block designs were used with three replications. Except as specified by drought treatments, the experiments were grown with full irrigation on a grey-clay soil utilising high input management and insect control.

Table 2. Description of lines used in field experiments to assess determinacy (P. Reid, personal communication).

Name	Maturity	Determinacy
Tamcot HQ95	Very early	High
Siokra S-102	Early	Medium-high
89007-33	Early-medium	Medium-high
Siokra V-16	Medium-Late	Low
Selection 118	Late	Low
Sicot 189	Late	Low
CS 8S	Early	Medium
Albar G501	Very late	Low

In the first two experiments, starting just prior to the appearance of the first square, destructive plant samples were taken from 1 m^2 quadrats approximately every two weeks. Total dry weight and dry weight of leaf (laminae), stem (including petioles), squares (flower buds), green bolls (capsules) and open bolls were determined.

In the third experiment, additional measurements were also made. After the plants had reached first flower, the number of nodes above the highest open flower on the plant was counted each week. This number declines due to increasing boll load as the rate of node production slows but the rate at which flowers are exserted (and hence open) at successive nodes up the main stem remains constant.

The final experiment included ± water stress treatments. In the stressed treatment, one irrigation was withheld during flowering and irrigation resumed as normal when the control treatment became due for its next treatment. The two irrigation treatments were combined factorially with the cultivar treatments and a split-plot design used; irrigation management treatments being main plots. Measurements were the same as in the third experiment.

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

Exploring the potential for utilising the degree of determinacy of a cultivar.

The cultivars differed in their pattern of dry matter accumulation and partitioning. Two examples of the variation of crop and fruit growth rate over time are presented in Figure 1. There appeared to be a tendency for cultivars that had been described by the breeder as determinate to approach the point where the fruit biomass accumulation rate matched the total dry matter accumulation rate more rapidly. By ranking the cultivars within each time of sowing according to the degree of abruptness with which they approached this point, that is the angle of intersection of the lines, and averaging this across the sowings and years, a determinacy ranking was derived. This was found to be well correlated with the breeders' ranking (Figure 2a). However, since maturity and determinacy ranking of the breeder were highly correlated, our derived ranking also correlated with maturity (Figure 2b).

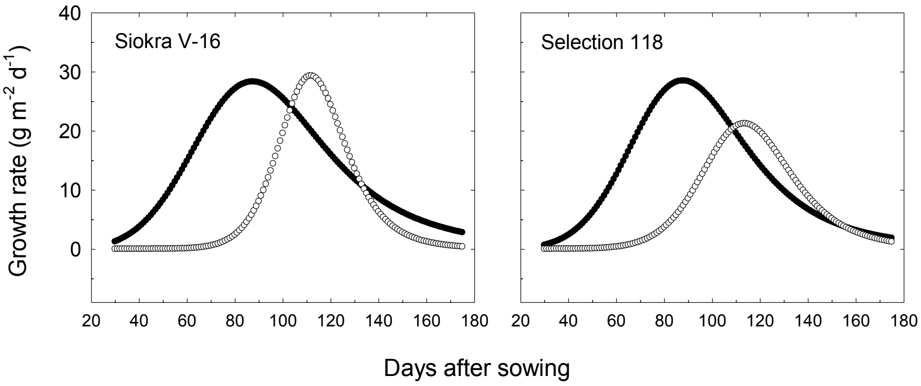


Figure 1. Examples of crop growth rate (closed symbols) and reproductive growth rate (open symbols) used to derive determinacy ranking.

In the third experiment an alternative measure was determined for each cultivar. This was derived from the rate of decline in the number of nodes above the highest open flower. The values ranged from -0.125 nodes per day for Albar G501 to -0.165 nodes per day for Siokra S-102. The rate was weakly associated with the breeders ranking for determinacy but well associated with the physiologically derived determinacy ranking except for the two okra leaf cultivars (Figure 3). The okra leaf cultivars were markedly offset from the regression line for the normal leaf cultivars.

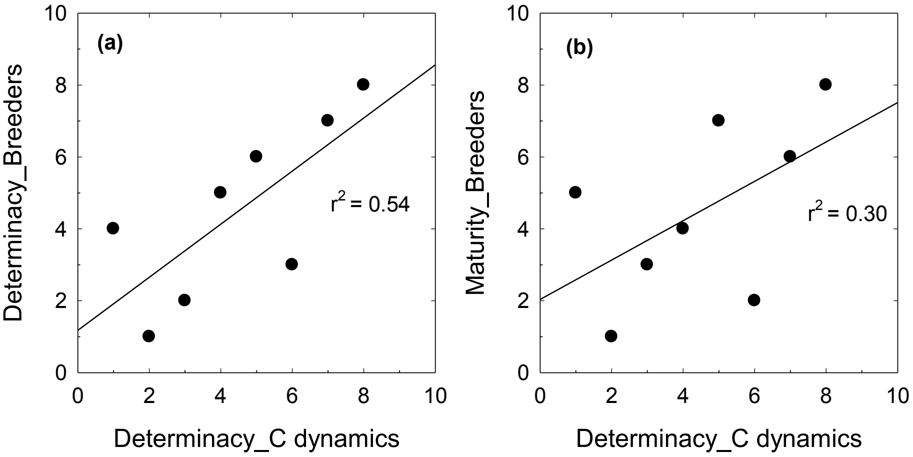
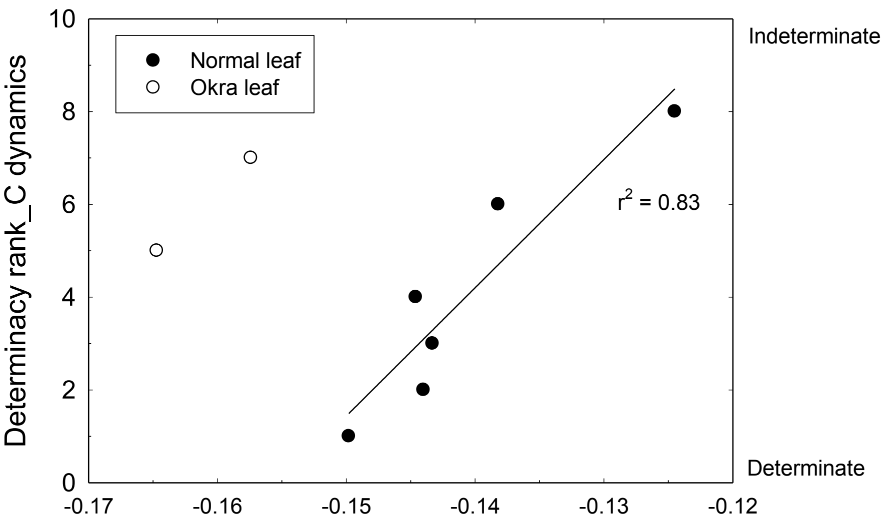


Figure 2. Comparison of rankings of cultivar determinacy (a) and maturity (b) from CSIRO



breeding team (G.A. Constable, personal communication) with determinacy ranking derived from carbon dynamics.

Figure 3. Determinacy ranking of cultivars derived from carbon dynamics versus the rate of change of nodes above highest open flower as an alternative measure of determinacy.

This is the first study that we are aware of to attempt to derive an objective, quantifiable measure associated with determinacy in cotton. That both the biomass accumulation and flowering rate indices were correlated to the breeders' field assessment suggested that they might provide a suitable basis for an index of determinacy. The measure based on rate of decline in nodes above last flower is the simpler of the two for field use. That the two measures were well correlated, even though they were derived from different experiments, indicated a likely link between the putative physiological process and the morphological outcome and thus adds weight to the validity of the more simple approach.

Experiments are currently underway to assess whether those cultivars that were assessed as indeterminate show any greater ability to tolerate drought stress in terms of their ability to continue to produce fruit or reinitiate fruit production after a stress.

Ongoing maintenance and development of the model code.

A range of corrections and enhancements have been made to the code to satisfy the output requirements of a number of users by extending the details reported on a daily basis, to allow Dirk Richards to continue with his research into on-farm irrigation decisions, and also to allow OZCOT to integrate with a redeveloped HydroLOGIC application. The changes made to support HydroLOGIC include supporting INI file formats for input files. INI file formats allow for self documenting input files that are well supported by all modern programming languages. Other enhancements/modifications have been made that were basic to implementing the Common Modelling Protocol.

A bug tracking system is being utilized to register bugs, issues, concerns and suggested enhancements and to document their resolution or status as development proceeds.

Version Control software has been implemented to secure code sets from known historical points and is being used to ensure current development is retraceable. Changes to the model can now be tracked from a central, on-line repository (Visual SourceSafe).

OZCOT can currently run as a single (monolith) component with the Canberra Plant Industry CMP model environment. This has been a major achievement as it involved the melding of mixed programming environments (C and FORTRAN), and disparate modelling approaches. Considerable work is required in migrating the stand-alone highly respected OZCOT model with some 30 years of history in its development, to work in an equivalent way and give its proven outputs in a very different and modern programming and modelling environment. Work is progressing towards seeing this same component run with the APSRU version of the CMP environment which is in itself a major challenge. For while the two versions of the CMP environments do, by definition, achieve the same functionality, they are in practice very different: components working under one will not automatically work under the other. Work is also progressing on breaking the monolith component into the required functional components, again with the overarching complexity of ensuring that OZCOT will continue to have the flexibility and robustness in its results that it currently has.

Modified functionality relating to LAI generation has been incorporated and validated. Two alternative versions of the LAI Generation routine were compared for performance in predicting yield and maximum LAI for the entire validation data set. A small data set was also used to review the routines' performances at simulating daily LAI development.

The skip row functionality developed by Brian Hearn was migrated into the current version of OZCOT and its performance validated. A number of limitations were identified and changes incorporated to ensure robust functioning over a wide spectrum of possible scenarios. Validation data sets were developed from data provided by Brian Hearn and performance in the new modelling environment validated.

5. Provide a conclusion as to research outcomes compared with objectives. What are the “take home messages”?

OZCOT is a primary software research tool for capturing and integrating current cotton crop agronomy knowledge. It allows for the influences of a range of factors acting on the crop simultaneously. It also provides a valuable method of integrating and applying complex research findings to industry issues.

A complete review and restructure of the model has been undertaken. In addition to meeting existing usage requirements, the restructure has allowed considerable advances to be made towards making the science included in the model readily available to a much wider audience through conforming the model components to CSIRO Plant Industry’s Common Modelling Protocol. Project outcomes include:

- Reduced maintenance overheads and improved reliability of model code
- Greater capacity to integrate new science into the model
- Greater capacity to monitor performance of updated versions
- A model structure approaching the “Common Modelling Protocol” of Plant Industry thus allowing greater dissemination of ACRI research results via model components and also allowing greater access by ACRI scientists to computer models developed by other sections of Plant Industry and APSRU.
- Collaboration toward the release of HydroLOGIC

Implementation of an improved procedure for soil water extraction:

Coding for the use of the Montieth-Passioura approach in the OZCOT model has been completed is a version of the model using this approach has been developed. Collection of data for validation and for the development of a database of parameters for different soil types has been impaired by drought and the reduced plantings of dryland crops.

Exploring the potential for utilising the degree of determinacy of a cultivar.

This is the first study that we are aware of to attempt to derive an objective, quantifiable measure associated with determinacy in cotton. That both the biomass accumulation and flowering rate indices were correlated to the breeders’ field assessment suggested that they might provide a suitable basis for an index of determinacy. The measure based on rate of decline in nodes above last flower is the simpler of the two for field use.

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

The OZCOT model is a powerful tool both for research and on-farm applications. It is currently being used in the study of compensation of cotton to insect damage, crop management with reduced water availability and on-farm decision making. In the on-farm situation it has potential to assist in the optimum use of limited resources for maximum economic return. One application to this end is the integration of OZCOT into HydroLOGIC to improve water use of-farm.

7. **Provide a summary of the project ensuring the following areas are addressed:**
   a) **technical advances achieved (eg commercially significant developments, patents applied for or granted licenses, etc.)**

   The OZCOT model has undergone extensive redevelopment to ensure reliable operation, ease of maintenance and efficient incorporation of new science.

   Within this project we have developed the first indices of which we are aware which specifically measure determinacy. Further work is needed to assess the value of the trait in agronomic management.

   b) **other information developed from research (eg discoveries in methodology, equipment design, etc.)**

   c) **are changes to the Intellectual Property register required?**

   No.

8. **Detail a plan for the activities or other steps that may be taken:**
   (a) to further develop or to exploit the project technology.
   (b) for the future presentation and dissemination of the project outcomes.

Mechanisms for the utilization of project outcomes are in place. Ongoing research into cotton compensation and farming systems both benefit from access to the OZCOT model and its continued improvement, as does on-farm modelling activities within CSIRO Plant Industry and in APSRU. In addition, work in this project has contributed to the development of HydroLOGIC which has been launched. Industry development officers have received basic training in the operation of a user-friendly version of OZCOT. This avenue of dissemination should be strongly encouraged.

   (c) for future research.

Work in this project has identified an approach to the quantification of determinacy as a trait. Further work is required to assess the value of the trait in stress conditions such as intermittent drought or conditions which may induce excessive vigour.

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

The articles listed below include those relating to model maintenance and developed as described by Aim No.3 of this project. In addition, two further articles are planned: one on moisture extraction by cotton on different soil types and the second on the response of cotton fruit to temperature.

Journal Articles Under Internal Review:

Milroy,S.P. Thongbai,P. Bange,M.P. and Gibberd,M.R. (20**). Persistent reduction in photosynthesis and radiation use efficiency of cotton (*Gossypium hirsutum*) under repeated transient waterlogging. (For submission to *Field Crops Research*)

Refereed Journal Articles:

Milroy,S.P., Bange,M.P. and Hearn,A.B. (20**). Row configuration in rainfed cotton systems: modification of the OZCOT model. *Agricultural Systems* (Submitted). – **Attachment 1.**

Bange,M.P. Thongbai,P. and Milroy,S.P. (2004). Cotton's response to waterlogging: crop growth and yield. *Field Crops Research* (In press) – **Attachment 2.**

Bange,M.P. and Milroy,S.P. (2004). Growth and dry matter partitioning of diverse cotton genotypes. *Field Crops Research* (In press). – **Attachment 3.**

Milroy,S.P. and Bange,M.P. (2003). Nitrogen and light responses of cotton photosynthesis and implications for crop growth. *Crop Science,* **43**, 904-913. – **Attachment 4.**

Scientific Conference Papers:

Milroy,S.P. and Bange,M.P (2003). Determinacy in cotton: measurement and potential implications. *Proceedings of the 11th Australian Agronomy Conference, Geelong, 2003*. In press. – **Attachment 5.**

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, 2001*, www.regional.org.au/au/asa/2001/.

Industry Articles:

Milroy,S., Bange,M. and Roberts,G. (2002). Is earliness really next to Godliness? *Proceedings of the 11th Australian Cotton Conference, 13-15 August 2002, Brisbane, Qld.* pp. 473-476. [Non-citable]. – **Attachment 6.**

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

The work conducted in this project has potential to significantly improve water use efficiency of the Australian cotton industry through use of OZCOT both in research and in on-farm applications. Effort needs to be focus on increasing grower confidence in the model and increasing support systems for trained users. As mentioned in 8b, Ozcot has already been incorporated into the re-developed HydroLOGIC, which has great potential to encourage objective approaches to water use.

The development of a version of OZCOT that is capable of reliably simulating compensation for pest damage will be valuable in making better pest management decisions and should help to reduce insecticide use.

Part 4 – Final Report Executive Summary

Provide a half to one page Summary of your research that is not commercial in confidence, and that can be published on the World Wide Web. List the main outcomes and contact details for more information.

The cotton simulation model, OZCOT, is an important component of a number of current and future projects. It is a key tool both for exploring cotton crop responses and as a means of extending the outcomes of science into the industry. In this project we aimed to ensure the ongoing maintenance of the model as well as the continued incorporation of new science to improve our capacity to deal with current industry issues.

The project covered three main research components: 1.) exploring varietal differences in determinacy, 2.) exploring the model's capacity to simulate compensatory growth responses to insect damage, and 3.) implementing a new soil water balance in the model. These areas were identified as being of current high importance by a meeting of researchers associated with the project, including Drs Greg Constable, Lewis Wilson, Mike Bange and Brian Hearn. Ensuring the model's capability to simulate compensation is important for specific applications but the issues of growth form and soil water extraction are important for the general performance of the model and hence its application to a range of issues.

A complete review and restructure of the model has been undertaken. In addition to meeting existing usage requirements, the restructure has allowed considerable advances to be made towards making the science included in the model readily available to a much wider audience through conforming the model components to CSIRO Plant Industry's Common Modelling Protocol.

Modifications have been made to the model to allow it to respond to pest damage. Research is underway to refine these modifications with the aim of developing a version of OZCOT that can be linked with EntomoLOGIC to improve pest management decisions and reduce insecticide use.

Coding for the use of the Montieth-Passioura approach in the Ozcot model has been completed is a version of the model using this approach has been developed. Collection of data for validation and for the development of a database of parameters for different soil types has been impared by drought and the reduced plantings of dryland crops.

This is the first study of which we are aware to attempt to derive an objective, quantifiable measure associated with determinacy in cotton. Two indices were developed which were well correlated to the breeders' field assessment of determinacy, suggesting that they might provide a suitable basis for an index of determinacy. The measure based on rate of decline in nodes above last flower is the simpler of the two for field use.

Attachments

The following attachments are the significant publications from the project, including those associated with the ongoing development of the OZCOT model. They form detailed reports on key aspects of the research activities.

Row configuration in rainfed cotton systems: modification of the OZCOT simulation model

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Abstract

Over the last ten years there has been a rapid expansion of rainfed cotton production in Australia. The majority of this area has used “skip row” configurations in which certain rows in the crop are not sown with the aim of providing a slowly available supply of soil moisture during periods of low rainfall. In the past, the OZCOT cotton crop simulation model has been used with long-term climate records to assess the impact of different management strategies for irrigated cotton production and to study the prospects for rainfed cotton production in the major cotton growing regions. In this paper we present modifications made to OZCOT to better accommodate skip row. Firstly, a simple procedure previously used to approximate light interception of row crops was assessed for its ability to enhance the capability of OZCOT to simulate skip row configurations and secondly, a modification to allow for the possibility that water in the skip is not as freely available as the water in the plant row was also explored. Including modifications to allow for differences in soil water extraction significantly improved predictions of crop yield for cotton in skip row configurations across a number of locations in the Eastern Australian cotton producing regions, but modifications to account for light interception in row configurations reduced the ability of the model to simulate skip row cotton yields. The modified model gave reasonable predictions of yield for solid planted and skip row crops. The performance was within the range of results published by Hearn for solid planted crops over a range of nitrogen and irrigation treatments and planting dates. The model’s simulation of skip row yields when compared to solid planted crops grown under the same conditions, reflected the relationships seen in the measured data and those published in the industry literature.

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Additional keywords: Cotton, rain-fed, dryland, row configuration, simulation, model, OZCOT

1. Introduction

The wild ancestors of cotton are found in the arid regions of the world and are naturally adapted to survive long periods of extremely dry weather. They are also able to respond to the occasional storm or flash flood by rapidly producing fruit while conditions are favourable. Modern cultivars have inherited these attributes, making the cotton crop well adapted to the intermittent water supply that occurs with rain-fed (dryland) and irrigated production (Hearn, 1990).

Over the last ten years there has been a rapid expansion of rainfed cotton production in Australia. (Hearn, 1990). In Australia the proportion of area sown to rainfed cotton yearly averages 17% (59 067 ha) of the total cotton area (338 133 ha average) (Dowling, 2002). At times the area has been as much as 31%. The majority of this area has used "skip row" configurations.

In Australia, cotton is generally grown on a 1m row spacing (solid; Fig. 1a), but in the single skip configuration each third row is left unsown (Fig. 1b). In the double skip configuration two rows are sown and then the following two are omitted (Fig. 1c). The intention behind skip row configurations is to provide slowly available soil water to the planted rows to allow continued growth during dry periods between rainfall events. In practice, however, the benefits lie primarily in: (a) a reduced risk of negative effects of water stress on fibre quality, (b) reduced yield variability, and (c) better economic returns due to production costs being reduced more than the yield relative to solid planted cotton (Bange et al., 2002).

The rapid expansion of skip row production has included uptake of cotton production by many new producers and expansion in to new production areas. Simulation modelling presents an opportunity to address the limited experience within the industry in optimizing the management approaches for cotton grown using skip row systems. The OZCOT cotton crop simulation model has been used with long-term climate records to assess the impact of different management strategies for irrigated cotton production (Hearn, 1994; Hearn, 1995; Dudley and Hearn, 1993) and to study the prospects for rainfed cotton production in the major cotton growing regions (Hearn, 1990). More recently the model has been used with growers to explore a range of issues in rainfed cotton production including choice of row configuration in cotton, comparing potential returns with different cropping systems and the impacts of climate variability (Carberry and Bange, 1998; Carberry et al., 2000). In this paper we present modifications that were made to OZCOT to better accommodate skip row. These modifications fall into two categories: water extraction and light interception.

Research (Goyne and Hare, 1999) on the Darling Downs region of Australia has explored the extraction patterns of rainfed cotton under different row configurations. The results showed that in both double and single skip row configurations the crops had water available for a longer time and during critical stages of growth. They also indicated that moisture at all positions across the skip could be depleted to the lower limit of plant available water holding capacity. Similar results have also been found by Bange and Richards (unpublished data) for a range of soil types in northern NSW of Australia. The results of Goyne and Hare also showed the water under the plant line was more readily available and was extracted first. Water extraction then proceeded across into the skip. Based on this, it would appear necessary to modify the relative availability of water to the crop in order to simulate skip row.

In common with many top-down simulation models, OZCOT uses Beer’s law to estimate the amount of solar energy intercepted by a given leaf area index (LAI) (Monsi and Saeki, 1953). However, this assumes that the leaf area distribution across the ground area is approximately uniform. In skip row production systems this is clearly not the case (Routley et al., 2003). Jackson and Palmer (1972) developed a simple model to account for the hedgerow effect in forest systems. The approach was extended and successfully applied to legume row crops by Charles-Edwards and Lawn (1984). The value of this approach for the simulation of skip row configurations in cotton was explored.

2. Methods

2.1 Model overview

The structure and validation of the OZCOT model has been described in detail by Hearn (1994). It was developed using a “top down” approach. That is, only sufficient detail was incorporated for the simulation of each process to provide reliable estimation of the impact of management and environment on growth, development, and yield of cotton. The approaches chosen are broadly mechanistic at the crop and plant level.

The central component of the model is the fruit production and survival subroutine (Hearn and Da Roza, 1985). The rate of fruit production, fruit shedding and growth of the organs are governed by carbon supply. Carbon supply for a given day is estimated from intercepted light and a crop level photosynthetic rate with respiration deducted. Light interception is estimated using Beer's law (Monsi and Saeki, 1953) and leaf area generated using an empirical correlation between fruiting site production and leaf area (Jackson et al., 1988).

The rate of leaf expansion, photosynthesis and fruiting are modulated by the supply of water and nitrogen and by waterlogging. The water balance uses the Ritchie approach with a simple moisture extraction routine based on increasing supply with increasing depth of extraction over time (Ritchie, 1972). The impact of the stressors is imposed using 'stress indices' which scale the rate of a process for a given resource supply.

The modifications explored in this work aim to improve the simulation of light interception by skip row crops through explicitly allowing for: 1. the non uniform distribution of leaf area, and 2. the integration of light interception over the daylight period. The influence of soil water on growth processes was modified to allow for: 1. the non uniform availability of water from the planted and non planted rows in the crop and, 2. the influence of non uniform distribution of saturated zones during waterlogging events. The performance of the OZCOT model in predicting yield with these modifications included was tested using data from crops with different row configurations grown in a number of cotton production regions in Australia.

2.2 Modification of light interception

The procedure of Charles-Edwards and Lawn (1984), developed to approximate light interception of row crops, was assessed for its ability to enhance the capability of OZCOT to simulate skip row configurations. This was done in two steps. The first modification was to approximate light interception of the planted row by multiplying the crop's LAI by the ratio of the total ground area to the planted row area (which we term the hedgerow effect). As no data where available on the dynamics of canopy width, this ratio was based on the total number of rows to the number of rows with plants. That is 1.5 for single skip and 2.0 for double skip. Light interception is calculated using the LAI thus derived but then divided by the ratio of occupied area to total area. As interception is not linearly related to LAI, the result is a reduction in the amount of light intercepted. This approximates the effect of the greater amount of self shading that occurs in row crops compared to having the leaf area uniformly distributed. The result is lower interception and greater transmission to the soil surface for a given crop LAI. This alters the values of evaporation from the soil surface, transpiration and the carbon-based carrying capacity.

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The second step was to incorporate the relationship developed by Charles-Edwards and Lawn (1984) to adjust the proportional light interception for the greater interception when considered on a daily basis compared to the proportion intercepted at noon (the diurnal effect):

$$Q_A = 2Q_{AN}/(1+Q_{AN}) \qquad (1)$$

where Q_A is the proportion of light intercepted by the canopy over the day, and Q_{AN} is the light interception at noon.

2.3 Soil water use in skip row crops

In the Introduction it was suggested that changes to extraction of water from the soil might be needed in OZCOT to simulate skip row configurations reliably. The possibility that water in the skip is not as freely available as the water in the plant row was thus explored.

Based on the experimental results of Goyne and Hare (1999), it was assumed that the water in the skip is not freely available at the start of a drying cycle. Initially water is extracted from under the plant row until water supply limits transpiration. When supply from the plant row becomes limiting, water is drawn from the skip at the limited rate until it is depleted to the same level as the plant row, after which water is drawn from the plant row and skip simultaneously.

A subroutine (SKIPWATER) was developed in OZCOT to implement this pattern of soil water use from the skip row. The proposed pattern of extraction implies a two dimensional soil model, but subroutine SKIPWATER does this implicitly through the modification of the SMI (Soil Moisture Index). SMI is the ratio between current plant available water content (PAW) and plant available water-holding capacity (PAWC) of the soil, and is used to mediate the effect of water stress on a number of processes (Hearn, 1994). This circumvents the need to develop an explicit two-dimensional soil water model.

At the start of a drying cycle, the daily calculation of SMI is based on the plant row only, and termed SMI_ROW (Fig. 2). This is done by adjusting the PAWC of the soil in proportion to the ratio of planted row area to total ground area. At the time in the drying cycle when water supply becomes limiting (i.e. the level of PAW that would normal yield SMI < 1), the value of SMI_ROW is stored and no longer re-calculated. From then on the variable SMI_ALL is calculated each day for all soil water (i.e. water in the plant row plus that in the skip row). The effective SMI is the lesser of SMI_ALL and SMI_ROW.

$$SMI\_ROW = 1 + (SMI - 1) \times RS \qquad (2)$$

$$SMI = \text{Minimum of } (SMI\_ALL, SMI\_ROW)$$

where RS is the average row spacing of the crop. That is, for a single skip crop based on 1 m row spacing RS is 1.5 and 2.0 for a double skip crop.

The result is that during a prolonged drying cycle, SMI initially falls sharply (Fig. 2., Line A-B) until supply is limiting in the plant row, then remains constant until water in the skip is depleted to the level of the plant row (Fig. 2., Line B-C), and finally falls at the usual rate (Fig. 2., Line C-D).

In OZCOT, waterlogging is defined as being when PAW is above PAWC of the soil. Under these conditions photosynthesis and nitrogen uptake are suppressed. To allow us to assess the influence of non-uniform soil moisture under waterlogging independently from that under dry soil conditions, we employed an additional index (waterlogging index, WLI) calculated from SMI. WLI was set to equal SMI prior to SMI being adjusted for skip row to retain the original waterlogging response of the model. However, if the effect of waterlogging was calculated considering the water status of the whole profile the impact of waterlogging would be exaggerated in situations where the skip contains high levels of water and the plant row is relatively dry (since water is extracted from the plant row before the skip). Therefore WLI was set to equal SMI_ROW (Eqn. 2) in subroutine SKIPWATER and the model performance compared to the original approach.

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2.4 Model validation

For validation purposes, yield and agronomic management data were compiled for a number of previous experiments (Table 1). The experiments were conducted in northern New South Wales and southern and central Queensland in regions of existing rainfed cotton production in Australia. Configurations tested were solid plant, single skip and double skip. Except where noted, all configurations were tested at each site, and where there was more than one year, variety or water supply at one site, all factorial combinations with each configuration were applied. There were 100 treatments in all, made up of 34 solid plant, 34 single skip and 32 double skip treatments.

To assess model performance, simulated lint yield was plotted against the measured (observed) yield. This was done either including all the data or for subsets including only one row configuration at a time. Accuracy of the predictions was quantified using the root mean square deviation (RMSD) between a number (n) of predicted (P) and observed (O) paired results:

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$$RMSD = \left[\sum (O-P)^2 / n\right]^{0.5}$$ (Steele and Torrie, 1987)

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RMSD represents a mean weighted difference between predicted and observed data. The linear regression of predicted versus observed yields analysis was used to quantify bias and the coefficient of determination (R^2) of this regression described the degree to which the data clustered around a straight line. Regression analyses were conducted using the functions in the SigmaPlot 2002 package (SPSS Inc. Chicago, IL., 2001).

3. Results

3.1 Model performance prior to modification

Prior to modification, OZCOT simulated the solid planted treatments in the data sets reasonably well. For the regression between the simulated and observed yields RMSD = 310 kg ha^{-1} and R^2 = 0.69. OZCOT was less reliable for the simulation of the skip-row treatments (Fig. 3). There was more dispersion than for the simulation of solid plant treatments: RMSD = 379 and 328 kg ha^{-1} for single and double skip, respectively, and R^2 = 0.53 and 0.59. The lines of best fit showed positive intercepts and slopes less than 1.0 indicating a bias to overestimate yields at the lower end of the range. In these simulations, it was assumed the water in the skip was as freely available as water in the plant row but the resultant bias is consistent with this not being the case.

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3.2 Effect of modifications for the simulation of skip row.

The benefit of including the hedgerow effect for light interception was not clear. While the RMSD was reduced somewhat for the pooled data, in two of the regions it increased. For the pooled data and across the regions the slopes were further from 1.0 but the intercepts were improved for the Darling Downs and central Queensland regions (Table 2). Considering the data for single and double skip separately but pooled across regions also indicated that the modification did not improve the simulation of skip row configurations compared with the original model: RMSD was reduced slightly but both the slope and the intercept were poorer (Table 3 cf. Fig. 3).

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On the other hand, including only the modified calculation of the soil moisture stress indices, SMI and WLI, to allow for the differences in accessibility of soil water in the skip and in the row (Eqn. 2) improved the overall reliability of the predictions with the RMSD falling from 340 to 277 kg ha^{-1} and R^2 increasing from 0.62 to 0.73 (Table 2). It also improved the results for each region except Central Queensland. Across the regions RMSD fell from 379 to 276 kg ha^{-1} for single skip and from 328 to 238 for double skip

(Table 3 cf. Fig. 3). In addition the bias was somewhat reduced with the regression coefficients being closer to unity and the intercepts smaller for both configurations.

Combining the two modifications (hedgerow and soil water) improved the overall simulation of the data sets reducing the RMSD from 340 to 281 kg ha^{-1} and increasing R^2 of 0.62 before modification to 0.70 (Figs. 3 and 4), similar but numerically inferior to SKIPWATER alone, although for the highest yields the simulation was poorer. Simulation of experiments from each of the four regions was also improved (Table 2). For northern NSW the accuracy was less than including soil water effects alone, but for other regions it was improved (Table 2). As expected, the performance for the solid planted simulations was not altered, but for skip row configurations it was improved (Figs. 3 and 4). The intercept was reduced for single skip and more so for double skip, however the slope of the regression was reduced in both cases. The outcome is a suggestion of a bias toward under-estimating high yields, however there is limited data at the higher yield levels.

Given that the hedgerow effect did not improve the model's ability to simulate the crops on skip row configurations, the impact of including the diurnal effect on light interception (Eqn. 1) was assessed. The modification was tested by adding it into the modified model that included both the hedgerow effect and soil water alterations. Again no improvement was achieved. Across all data sets the RMSD increased from 281 to 306 kg ha^{-1} (R^2 fell from 0.70 to 0.67) and the slope was also reduced. Further, the R^2 for both single and double skip configurations was reduced to 0.61 and 0.68 respectively.

The importance of the modification to WLI in OZCOT was also tested. With this modification included the ability of the model to predict the yield of skip row configurations was improved. Overall the RMSD was reduced from 312 to 281 kg ha^{-1} (R^2 increased from 0.66 to 0.70) across all data sets. The slope was not altered. Predictions for each region were also more reliable.

3.3 Relationship between yields for skip row and solid plant crops

Consistent with relationships published in industry literature, the observed yields from the skip row treatments where less than those of solid planted treatments and the difference was greater when there was a higher yield potential (Fig. 5a). This was particularly so for double skip. The simulated yields using the modified model (SKIPWATER and Hedgerow) followed the same relationship (Fig. 5b). There was some indication that the model was underestimating high yielding crops, although again data was limited in this range.

4. Discussion

Modifying OZCOT to allow for differences in soil water extraction significantly improved predictions of crop yield for cotton in skip row configurations across a number of locations in the Eastern Australian cotton producing regions. Surprisingly, modifications to OZCOT to account for light interception in row configurations contributed little to the ability of the model to simulate skip row configurations when considered across all regions. However, given the advantages shown in two of the four locations and recognising the poor applicability of the assumptions behind Beer's Law for the skip row situation, it was considered worthwhile to retain both components. Modification to the stress index for waterlogging was also beneficial.

The modified model gave reasonable predictions of yield for solid planted and skip row crops. The performance was within the range of results published by Hearn for solid planted crops over a range of nitrogen and irrigation treatments and planting dates (Hearn, 1994). The model's prediction of skip row yields when compared to solid planted crops under the same conditions, reflected the relationships seen in the measured data and those published in the industry literature (Bange et al., 2002).

Simulating the impacts on soil moisture dynamics by modifying the stress index has the advantage of requiring significantly less parameterisation than more complex two dimensional models such as RHIZOS (Boone et al., 1995). This is important for on-farm applications where the opportunity to collect detailed data for parameters is limited. It allows scope for the model to be used in a greater range of farming systems and regions. However, the simplicity of the approach does not allow for the possibility of lateral limitations to root exploration, such as in heavy clay soils. McLean et al. (2003)

presented a somewhat more mechanistic model for water extraction under skip row sorghum crops which still retained the advantages of the one-dimensional approach. Based on the experimental results of Routley et al. (2003) the model assumes a uniform rate of radial expansion of the root system from the planted row. From this, the proportional exploration of a particular horizon is estimated and the rate of water extraction from the horizon modified accordingly. Such an approach retains the advantages of minimising the number of parameters required but may allow scope to modify root zone expansion based on soil characteristics. McLean's approach is being incorporated into the APSIM crop simulation environment (McCown et al., 1996; Keating et al., 2003).

A noticeable improvement in the model's capability was seen when the stress index for waterlogging was modified for skip row arrangements. Cotton is known to be sensitive to waterlogging (Hodgson, 1982), however it would appear that a relatively small volume of aerated soil may be adequate for growth (Thongbai et al. unpublished). WLI was modified to follow the pattern of the modified SMI, thus reflecting the fact that as soil water falls more quickly in the row with plant extraction, the chances of waterlogging are less.

Light interception differs markedly between skip row and solid planted situations (Routley et al., 2003; Goyne unpublished data). The clumped distribution of leaves could be expected to increase the amount of self shading and thus lower the amount of light intercepted per unit of LAI. This was the basis for Charles-Edwards and Lawn (1984) developing the approach to account for light interception by row crops. The data were for legumes grown on row spacings of 0.5 and 1.0 m. In our analysis, we were unable to improve the ability of the model to simulate yield of skip row cotton crops with either the hedgerow or diurnal components of the light interception procedure. The reasons for this could relate to the much greater differences in canopy architecture between solid planted cotton and cotton grown in skip rows relative to the row crops of Charles-Edwards and Lawn (1984). The distance between planted rows can be as much as 3m in the double skip arrangement. The wide spacing may in fact lead to improve lateral illumination of lower leaves in the canopy. Assimilate supply by these leaves is important for the growth of fruit set lower in the canopy (Constable and Rawson, 1980), which provide a significant proportion of crop yield (Constable, 1991). In addition because the rows are further apart, the consequences of row orientation are likely to be greater than previously suggested by Charles-Edwards and Lawn. The value of more complex light interception models for clumped canopies, such as that developed by Friday and Fownes (2001), needs to be explored.

There are a number of general limitations to the use of OZCOT to address questions relating to row configuration. As mentioned in the introduction, one of the important considerations in the choice of configuration is the trade-off between yield potential on the one hand and variability in yield and fibre quality on the other. While skip row configurations have lower yield potential they are widely considered because of the risk of low fibre quality in years when rainfall is low. OZCOT does not currently simulate fibre quality. Another issue is the potential differences in nutrient uptake associated with skip row configurations. This is further complicated by skip row systems that vary the placement of fertiliser. There is currently no published information on this area. These aspects are subjects of continuing research.

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Tables

Table 1: Details of experimental data collated to validate the OZCOT cotton simulation model for different row configurations. All experiments included solid, single and double skip row configurations.

Source	Experiment	Year	Regional Designation	Varieties	Water Supply
Pyke (1991)	Biloela - early sowing	1991-92	Biloela	Siokra L22	Rainfed Partial irrigation Full irrigation
	Biloela - late sowing	1991-92		Siokra L22 DP90 Siokra 1-4	Rainfed
	Biloela - plant density x sowing	1991-92		Siokra L22	Rainfed
	Vandeena - rainfed	1991-92	Central Queensland	Siokra L22	Rainfed
	Vandeena - irrigation	1991-92		Sicala V-1	Full irrigation
	Mt Wilkins	1991-92		Siokra S324	Rainfed
Gibb (1998)	Boggabilla	1994-95	Northern New South Wales	DP90	Partial irrigation
Hearn (unpublished)	Australian Cotton Research Institute (Narrabri)	1988-89		DP90	Rainfed
		1989-90		Siokra 1-4	Partial irrigation Full irrigation
Goyne (2000)	Perrinuan	1995-96	Darling Downs	Siokra L22 CS8S Sicot 189	Rainfed
	Hermitage Research Station Warwick	1995-96		Siokra L22 CS8S Sicot 189	Rainfed
	Perrinuan	1996-97		Siokra V15 Siokra S101	Rainfed
	Hermitage Research Station Warwick	1996-97		Siokra V15 Siokra S101	Rainfed

Table 2: The regression coefficient (slope), the coefficient of determination (R^2), intercept, and RMSDs (root mean square deviation) for predicted versus observed data for lint yield for different modifications of the OZCOT cotton simulation model including all data and different regions. Hedgerow and SKIPWATER are modifications to OZCOT for light interception and soil water, respectively, for skip configurations. Ticks indicate inclusion of modification.

Simulation Analysis		Slope	Intercept	R^2	RMSD
Hedgerow	SKIPWATER				
All Data					
X	X	0.77	357	0.62	340
X	✓	0.89	140	0.73	277
✓	X	0.70	384	0.58	335
✓	✓	0.82	169	0.70	281
Northern New South Wales					
X	X	0.81	220	0.76	327
X	✓	0.86	112	0.85	263
✓	X	0.74	252	0.75	343
✓	✓	0.76	160	0.85	287
Biloela					
X	X	0.43	821	0.57	387
X	✓	0.74	361	0.63	269
✓	X	0.43	792	0.55	368
✓	✓	0.77	298	0.63	261
Darling Downs					
X	X	1.07	90	0.49	350
X	✓	1.26	-216	0.61	305
✓	X	1.12	-3	0.53	324
✓	✓	1.29	272	0.63	290
Central Queensland					
X	X	0.98	-217	0.87	223
X	✓	0.97	-167	0.82	418
✓	X	0.72	131	0.77	235
✓	✓	0.98	-218	0.87	272

Table 3: The regression coefficient (slope), the coefficient of determination (R^2), intercept, and RMSD (root mean square deviation) for predicted versus observed data for lint yield for different modifications of the OZCOT cotton simulation model for the single and double skip row configurations. Hedgerow and SKIPWATER are modifications to OZCOT for light interception and soil water, respectively, for skip configurations. Ticks indicate inclusion of modification.

Simulation Analysis	Slope	Intercept	R^2	RMSD
✓ *SKIPWATER;* X *Hedgerow*				
Single Skip	0.79	261	0.69	276
Double Skip	1.04	-41	0.77	238
X *SKIPWATER;* ✓ *Hedgerow*				
Single Skip	0.61	484	0.47	364
Double Skip	0.51	524	0.43	327

Figure Captions

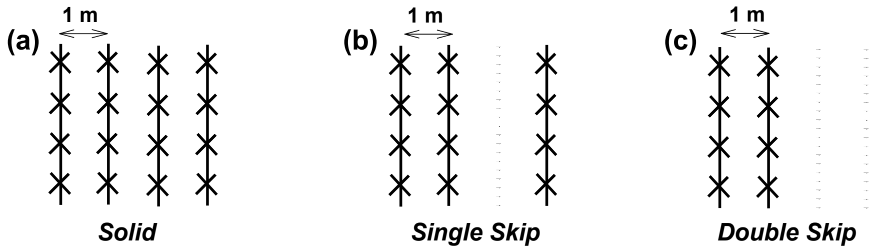
Fig. 1. Diagrammatic representation of (a) solid, (b) single skip, and (c) double skip row configurations as used in rainfed cotton production in Australia. Solid lines represent rows with plants present, while dotted lines represent skipped rows.

Fig. 2. Generalised relationship of SMI (Soil Moisture Index) as a function of the fraction of plant available water-holding capacity (PAWC) as modified for use in simulating skip row crops. Line A-B represents extraction under the planted row. At point B water supply from the row first becomes limiting. Line C-D represents extraction across the whole area.

Fig. 3. Predicted lint yield versus observed lint yield for all data, solid, single, and double skip configurations individually prior to modification of the model. Solid line is the line of best fit. Dotted line is the 1:1 line.

Fig. 4. Predicted lint yield versus observed lint yield for: all data, solid, single, and double skip configurations individually after including the SKIPWATER and Hedgerow modifications in the model. Solid line is the line of best fit. Dotted line is the 1:1 line.

Fig. 5. Comparison of treatment mean yields for skip row versus solid planted crops from experiments used in this study where both configurations were measured: (a) observed yield of skip row versus solid plant configurations, (b) simulated yield of skip row versus solid plant configurations using the OZCOT model including the SKIPWATER and Hedgerow modifications. Solid lines (closed circles) are the regressions for single skip versus solid configurations, broken lines (open circles) are the regression for the double skip. The dotted line is the 1:1 line.



Solid *Single Skip* *Double Skip*

Fig. 1

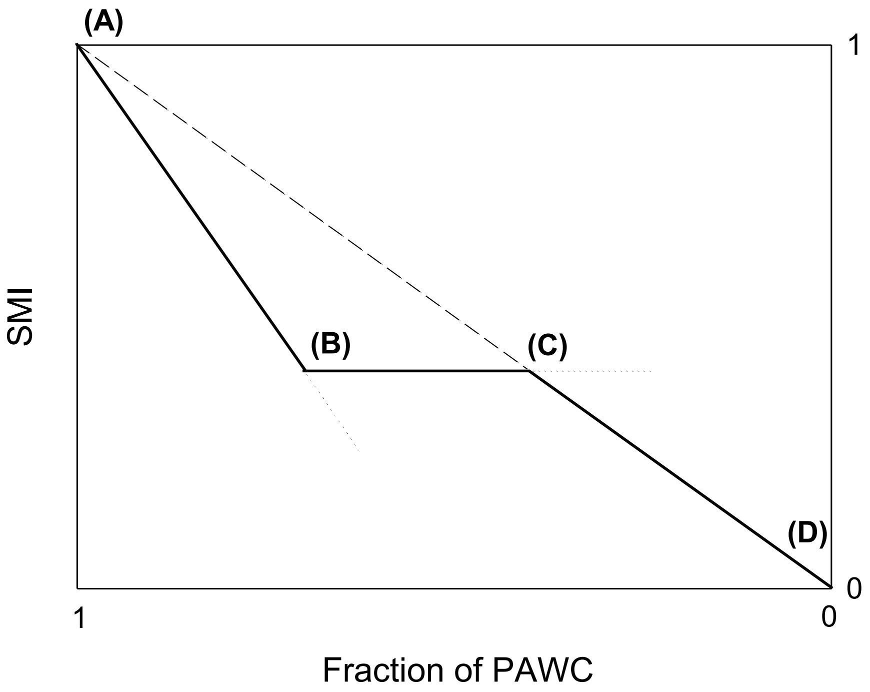


Fig. 2.

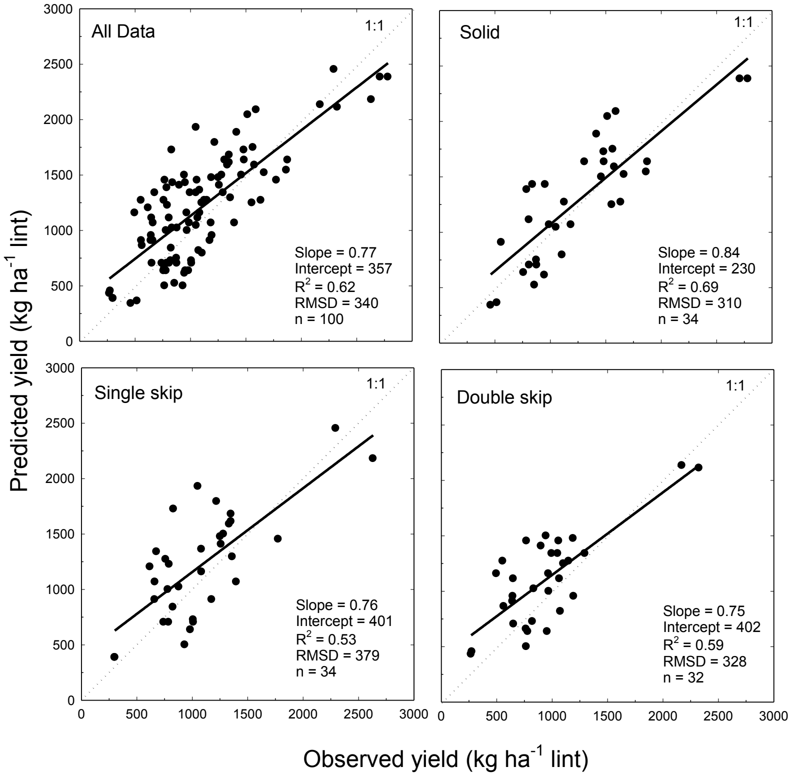
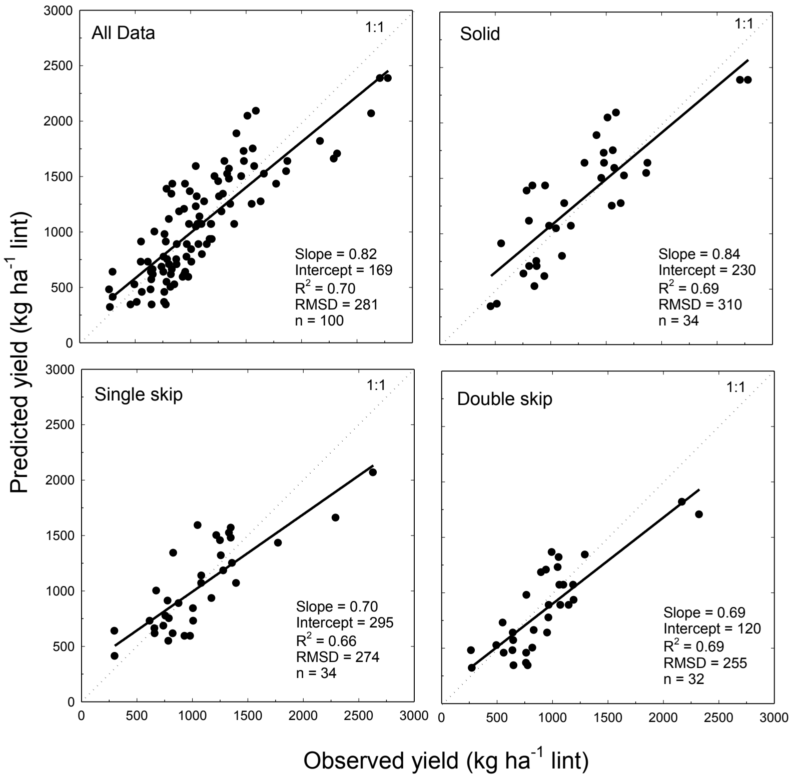

All Data
1:1
Slope = 0.77
Intercept = 357
R^2 = 0.62
RMSD = 340
n = 100
Solid
1:1
Slope = 0.84
Intercept = 230
R^2 = 0.69
RMSD = 310
n = 34
Single skip
1:1
Slope = 0.76
Intercept = 401
R^2 = 0.53
RMSD = 379
n = 34
Double skip
1:1
Slope = 0.75
Intercept = 402
R^2 = 0.59
RMSD = 328
n = 32
Predicted yield (kg ha^{-1} lint)
Observed yield (kg ha^{-1} lint)
0
500
1000
1500
2000
2500
3000

Fig. 3.



Predicted yield (kg ha^{-1} lint)
Observed yield (kg ha^{-1} lint)
All Data
1:1
Slope = 0.82
Intercept = 169
R^2 = 0.70
RMSD = 281
n = 100
Solid
1:1
Slope = 0.84
Intercept = 230
R^2 = 0.69
RMSD = 310
n = 34
Single skip
1:1
Slope = 0.70
Intercept = 295
R^2 = 0.66
RMSD = 274
n = 34
Double skip
1:1
Slope = 0.69
Intercept = 120
R^2 = 0.69
RMSD = 255
n = 32
0
500
1000
1500
2000
2500
3000

Fig. 4.

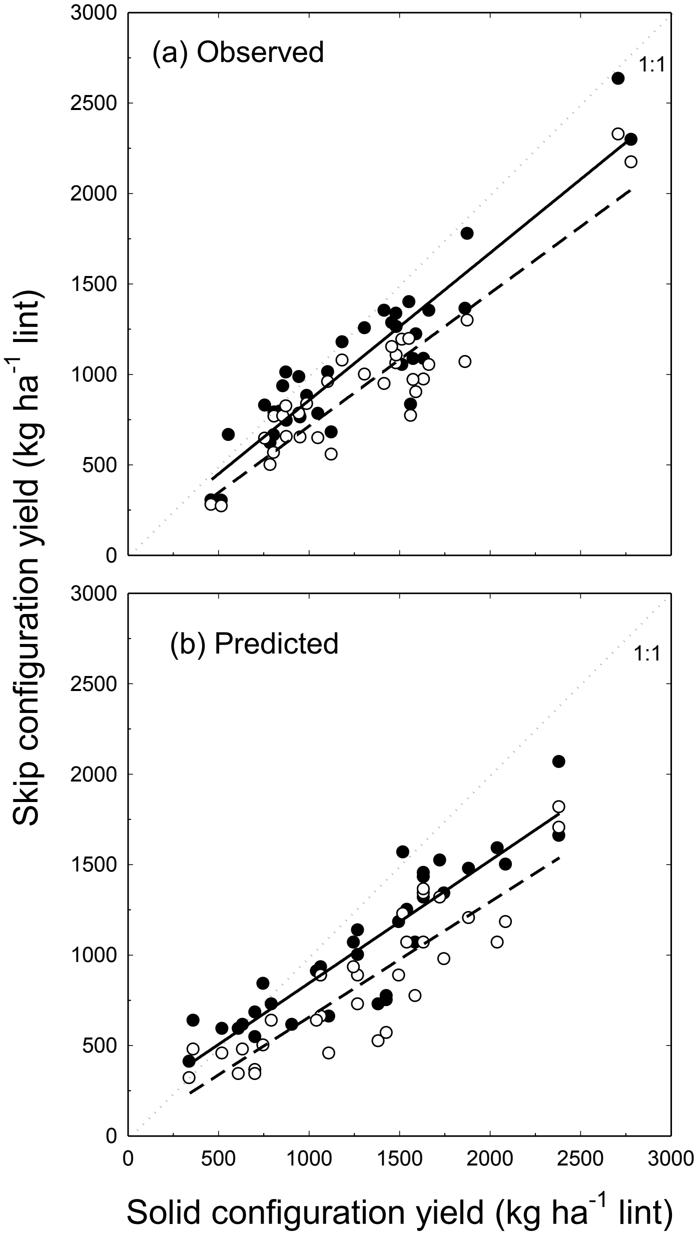

(a) Observed
(b) Predicted
1:1
1:1
Skip configuration yield (kg ha^{-1} lint)
Solid configuration yield (kg ha^{-1} lint)
0
500
1000
1500
2000
2500
3000

Fig. 5.

Growth and yield of cotton in response to waterlogging

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Abstract

Cotton is known to be poorly adapted to waterlogged conditions. In Australia, cotton production is concentrated on soils with inherently low drainage rates, which, combined with the almost exclusive use of furrow irrigation and a summer dominant rainfall pattern, results in a significant risk of intermittent waterlogging. Three field experiments were conducted in which cotton was subjected to intermittent waterlogging by extending the duration of irrigation events. Timing of waterlogging, cultivar and landform were also varied. Treatments required to generate significant impacts on crop growth and yield were more extreme than previously reported. Possible reasons for this are discussed. Consistent with the literature, yield loss was associated with reduced boll number (R^2=0.82). The reduction in boll number was commensurate with the reduction in total plant dry matter: dry matter was reduced by up to 32% with the allometric ratio between boll number and glucose adjusted dry matter being unaltered by the treatments. The reduction in dry matter was due to lower radiation use efficiency (RUE_g), which fell by up to 35%, rather than lower light interception. While leaf area was reduced, the resultant change in cumulative light interception was less than 5%. Thus, yield loss was caused by a reduction in the number of bolls. This reduction was commensurate with the reduced dry matter production from lower RUE_g rather than light interception. A single waterlogging event during early squaring and five events through-out growth of the same cumulative duration gave the same impact on lint yield. However, when the single event was imposed at peak green bolls, it had no significant effect on yield. No impact of waterlogging on fibre quality was detected in any of the experiments.

1. Introduction

Cotton is known to be poorly adapted to waterlogging (Hodgson and Chan, 1982) which is considered to be one of the major problems in global production (Gillham et al. 1995). The root system does not develop functional aerenchyma (Leonard and Pinckard, 1936; Huck, 1970) and endogenous levels of alcohol dehydrogenase, associated with anaerobic metabolism, are low (Dennis et al., 1992). In Australia, production of cotton is concentrated on cracking grey clay soils (vertosols) which have inherently low drainage rates (Hodgson and Chan, 1982; McKenzie et al., 1984; Triantifilis et al., 2003). Combined with the almost exclusive use of furrow irrigation and a summer dominant rainfall pattern, this results in a significant risk of intermittent waterlogging. The problem can be exacerbated by poor land forming such as excessive field length, inadequate slope, by poor soil structure, poor levelling or bed formation, or by substantial rainfall after an irrigation.

In a number of field experiments Hodgson (1982) found that yield declined with duration of inundation at each irrigation event. The relationship between yield and duration of inundation differed between experiments. However, across experiments yield was strongly related to the number of days when air filled porosity of the soil at a depth of 10 to 20 cm was below 0.1 $cm^3 cm^{-3}$. Lint yield was reduced by 4.8 g m^{-2} for every day of low O_2, primarily through a reduction in bolls per metre. Hodgson found that there were no further reductions in yield beyond 96 h of cumulative inundation.

Waterlogging of cotton has been reported to cause a reduction in root growth and nutrient uptake (Letey et al., 1962; Huck, 1970; Hocking et al., 1987), leaf area and photosynthesis (Hodgson, 1982; Meyer et al., 1987; Sahay, 1989) and dry matter accumulation and fruiting (Hodgson, 1982; Hocking et al., 1987). However there has been little work trying to assess the relative importance of these processes in an integrated way. In the work we present here, our objective was to use crop growth analysis to trace physiological mechanisms (at the crop level) by which the various effects of waterlogging impact crop growth and yield. This approach will enable the development of a more functional approach to simulate a cotton crop's response to waterlogging.

2. Materials and methods

2.1. Cultural details

Three field experiments were conducted at the Australian Cotton Research Institute (ACRI) at Narrabri (30.31°S 149.78°E), in a semi-arid environment of north-west New South Wales, Australia. All experiments were sown with a commercial row crop planter and grown with full irrigation on a grey-clay soil (vertosol; Isbell, 1996). The soil has a clay fraction of 60-65%, pH of 8.0 to 8.8, and low organic matter and nitrogen. Northcote classification is Ug 5.25 (Northcote et al., 1975). Crops were grown using high input management and insect control, typical of commercial practice, as described in Hearn and Fitt (1992). Cotton was grown on ridges spaced 1 m apart separated by a furrow in which water was applied as furrow-flood irrigation (Constable & Hearn, 1981). Standard irrigation scheduling practice was used to determine the timing of irrigation.

Nitrogen was applied as anhydrous ammonia before sowing in all experiments at a rate of 100 kg N ha^{-1}.

The first experiment (Exp. 1) was sown to cultivar Sicala V-2*i* on 16 October 1998 with two treatments: non-waterlogged control (–WL) and waterlogged (+WL) in four randomized blocks. Each plot was 20 m long and four rows wide. An additional three rows was included on either side of each –WL plot to provide a buffer against lateral water movement through the soil from the +WL plots. The non-waterlogged treatment received standard irrigations of approximately 8 h. The +WL treatment received an extra two days of 8 h irrigation at each of the 2nd, 3rd and 4th irrigations, on 96, 110 and 119 days after sowing (DAS) respectively (Table 1). Irrigation water was run during daylight hours.

The second experiment (Exp. 2) was sown on 29 September 1999. The experimental design was a split-plot design with four replications. Each plot was 25 m long and 6 rows wide. Again, an additional three rows was included on either side of each –WL plot. Main plots were the +WL and –WL treatments and sub-plots were a factorial combination of two cotton cultivars and two ridge heights. The cultivars were Nucotn 37 developed by the Deltapine Company and Sicala V-2*i* developed by CSIRO Australia. The two ridge heights were low (5 cm) and normal (15 cm).

The waterlogging treatments (+WL) in this experiment differed from those implemented in Exp. 1 in that irrigation was applied continuously for 52 h at the first irrigation and 72 h at each subsequent irrigation. A total of five irrigation events were imposed over the course of the experiment at 47, 74, 87, 101 and 137 DAS (Table 1). The non-waterlogged (–WL) treatments in this experiment had standard irrigations that were typically 8 h in duration similar to Exp. 1.

The third field experiment (Exp. 3) was sown on 29 October 2000, using Sicala V-2*i* and the low ridge treatment (5 cm) used in Exp. 2. The experimental design was a randomized complete block with four treatments and four replications. The treatments were (1) non-waterlogged (–WL); (2) waterlogged at each irrigation (similar to that implemented in Exp. 2; +WL); (3) a single early waterlogging event (second irrigation, 65 DAS; +WL$_{\text{early}}$); and (4) a late waterlogging event (fourth irrigation, 112 DAS; +WL$_{\text{late}}$). The late and early waterlogged treatments (–WL$_{\text{early}}$, +WL$_{\text{late}}$) received 120 h inundation at the single extended irrigation (Table 1). Each plot was 43 m long and six rows wide. Each –WL plot was flanked by an additional buffer of five rows on each side.

Meteorological data for the experimental period were measured 2 km from the site.

2.2. Measurements

Final yield and crop maturity were measured in all treatments of the experiments. Detailed measurements of soil water and crop growth were conducted in Exp. 1 and Exp. 3 and the low ridge treatments of Exp. 2.

2.2.1. Soil water content

Soil water content throughout the profile was measured using a calibrated neutron moisture meter (503DR Hydroprobe, CPN International, Martinez, CA) at depths from 20 to 120cm and gravimetric measurements made in the 0-10 and 10-20 cm layers. In Exp. 1, soil water content was measured every 7-10 days with extra measurements around the waterlogging events. In Exps. 2 and 3, the measurements were taken the day before and 1, 2, 3, 5, 7, 14, and 21 d (if applicable) after each of the waterlogging events.

2.2.2. Light interception

From 50 to 142 DAS in Exp 3, measurements of photosynthetically active radiation (PAR, 0.4-0.7 μm) above (PAR_O) and below (PAR_T) the canopy were taken weekly in each plot. Three measurements were made randomly on each plot using a ceptometer (Delta-T Devices Ltd., Cambridge, UK) between 1100 and 1400 hours (Australian Eastern Standard Time). In Exp. 2, light interception was measured twice, 82 and 101 DAS.

2.2.3. Crop sampling

At 92, 99, 102, 105, and 112 DAS for Exp. 1, and on the day before and 7, 14 and 21 d after the start of each irrigation cycle in Exps. 2 and 3, plant samples were taken to measure dry matter production and partitioning. Plants from 1 m^2 were cut at ground level and partitioned into green leaves (laminae), stem (including petioles), squares, green bolls and open bolls. The number and type of fruit were recorded. A square was defined as being present when the leaf that subtended the square had unfolded. Fruit were defined as green bolls from the day of anthesis and as open bolls once two sutures had split. Leaf area was measured using a planimeter (Licor 3100, Licor, Nebraska, USA), and leaf area index (LAI) calculated. Dry weights were recorded after 48 h drying at 70°C on an oven-dry basis. Specific leaf area (SLA) was calculated as the leaf dry matter per m^{-2} divided by LAI.

2.3.4. Crop maturity and yield

Timing of crop maturity (60% bolls open) was estimated by taking repeated weekly counts of the number of open bolls in 1 m^2 in Exp 2 and 2 m^2 in Exps. 1 and 3, in each plot. The lint collected from these samples was kept to calculate final yield, yield components (final boll number, boll size and lint percentage), and fibre length (mm) and micronaire (a measure of fibre fineness and maturity, no units).

2.3. Data analysis

Biomass of all components was converted to glucose equivalents using production values (g glucose per g dry matter) from Wall et al. (1994) for cotton leaves, stems, squares and fruits. This is necessary to account for the high cost of synthesis of cotton fruit relative to vegetative tissue. A glucose adjusted total above ground dry matter (TDM_g) and reproductive 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 and, from this, the proportion of PAR intercepted over the day (Q_D) was estimated using the relationship of Charles-Edwards and Lawn (1984). Both Q_I and Q_D were regressed on days after sowing (DAS) using an exponential function to allow interpolation between measurement dates.

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

$$Q_I = d\left[1 - \exp\left(-\mathrm{k}LAI\right)\right] + f$$

where *d* and *f* are fitted coefficients. The effects of waterlogging on k were tested using forward stepwise regression analysis (Genstat Version 5; Lawes Agricultural Trust, IACR, Rothamsted, UK).

Using Q_D and the measured incoming PAR for each day, the cumulative intercepted PAR over the period of measurement was derived. Average radiation use efficiency (RUE_g) for the season was derived from the linear regression of TDM_g against cumulative intercepted radiation. Forward stepwise regression analysis was used to test for differences between treatments. In Exp. 2, cumulative light interception and hence RUE_g was estimated from LAI measured over time and k derived from the two measurement dates.

To test whether there was a significant trend for one treatment 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 in Exps. 2 and 3. This was derived as the ratio of the increment in FDM_g to the increment in TDM_g. The DR for the waterlogged treatments was then plotted against DR for non-waterlogged treatments. Distribution ratios can be biased if development or dry matter production differ markedly (Coleman et al. 1994), so reproductive partitioning was also examined using the allometric approach by plotting ln FDW_g against ln TDW_g for the two treatments. The slope of this plot is equivalent to the ratio between the relative growth rate of the fruit and the whole plant. Forward stepwise regression analysis was used to test for differences between all treatments.

3. Results

The two cultivars Nucotn 37 and SicalaV-2*i* behaved similarly; there were no significant differences for any trait. Therefore, data from Exp. 2 will be presented as means across the varieties.

3.1. Soil water

The imposition of the extended inundation resulted in soil moisture content being up to 50mm higher after the irrigation than in the control (Fig. 1). The magnitude of the difference was maintained throughout the subsequent drying cycle, so the rate of soil drying appears to have been little effected by the treatments.

3.2. Crop yield

In Exp. 1, there was no significant difference in lint yield. In Exp. 2, analysis of variance showed a highly significant interaction between waterlogging treatment and ridge height, with neither main effect being significant. Lint yield was significantly lower in the +WL treatment on the low ridges but there was no difference in yields between the irrigation treatments (+WL and –WL) on the high ridge treatments. Overall, +WL on low ridges had the lowest lint yield but was only significantly different from –WL on low ridges. The highest yield was in –WL on low ridges, but this was not significantly different from +WL on the high ridges.

In Exp. 3 lint yield was lowest in the +WL and the +WL$_{early}$ (early squaring) treatment and these treatments were not significantly different from each other. The +WL$_{late}$ treatment (peak green boll number) had no effect on yield when compared with the –WL treatment.

Final boll number was the only yield component that was significantly affected by waterlogging (Table 2). This was well correlated with lint yield in the various treatments (Lint yield g m^{-2} = 1.95(±0.32) x Boll No. -10.9(±35.1); $P < 0.001$, $r^2 = 0.82$). There were no significant effects of waterlogging treatments on any fibre quality trait in any experiment (Table 2).

3.3. Dry matter production

In Exp. 1, TDM$_g$ of the waterlogged plants was not significantly different from the control until 110 DAS when the waterlogged treatment exceeded the control plants (Fig. 2a). In Exp. 2, a significant difference between +WL and –WL treatments developed at 95 DAS (Fig. 2c). The growth rate of the control remained higher until maximum dry matter was achieved, at which point the difference between the treatments was some 400 g m^{-2}.

In Exp. 3, early growth in all treatments was slow (Fig. 2e) due to a prolonged period of high rainfall and low radiation two weeks after planting. A significant difference in TDM$_g$ between –WL and +WL was measured within two weeks of the first waterlogging event, and similar to Exp. 2, this was maintained through to crop maturity. Dry matter accumulation in the +WL$_{early}$ treatment was similar to the full +WL treatment, but with some suggestion of a recovery in the last three weeks of the measurement. The +WL$_{late}$ treatment had only a small effect on total dry matter production resulting in a reduction of some 15% at peak dry matter with no significant effect at maturity.

In all experiments, effects on reproductive dry matter production (Fig. 2b,d,f) followed a similar trend to total dry matter production.

3.4. Dry matter partitioning

The distribution ratio (DR) was calculated as the ratio of the increment in the reproductive dry matter to the increment in the total above ground dry matter between consecutive harvests. Plotting DR for each interval for the +WL against –WL treatments in all experiments gave a significant linear relationship with a slope of 0.90, which was not significantly different from unity ($P < 0.05$) (Fig. 3a). This indicates that there were no significant differences between +WL and –WL treatments in their partitioning of dry matter production to fruit at similar times through the season.

Stepwise regression analysis showed that there was no significant difference ($P < 0.05$) in the DR between the +WL and –WL treatments or between experiments.

As the growth of +WL treatments at a given point of time was lower than the –WL plants (Fig. 2), an allometric analysis was also done to allow for the possibility of differences in growth inducing apparent differences in distribution (Coleman et al, 1994). The relative growth rate of total above ground dry matter and reproductive dry matter showed a constant linear relationship over the whole growing period in both treatments for all experiments (Fig. 3b). Again, stepwise regression analysis showed that there was no difference ($P < 0.05$) in the allometric ratios between the +WL and –WL treatments and between experiments.

Due to the lack of treatment differences found for crop yield and dry matter production in Exp. 1 no further analysis will be presented on data from this experiment.

3.5. Leaf area development and light interception

Waterlogging reduced leaf area development with the treatments following a similar ranking as for total biomass (Figs. 2 and 4). In Exp. 2, LAI of the +WL treatment was significantly lower than for the control from approximately 87 DAS (Fig. 4a). Peak LAI was approximately 3.6 in –WL compared with 2.3 in +WL. In Exp. 3, +WL was again significantly lower than –WL, this time from approximately 60 DAS (Fig. 4c). Peak LAI in –WL was 3.6 compared with 2.0 in +WL. In the +WL_{early} treatment LAI was greater than the +WL treatment but less than both –WL and +WL_{late}, being 10-15% greater than +WL. The LAI of the +WL_{late} treatment was significantly lower than the control following the imposition of the treatment and remained lower until the end of the growing season, being some 20% less at this stage.

SLA of +WL in Exp. 2 was similar to –WL until 109 DAS, after the fourth waterlogging event (Fig. 4b). For the remainder of the season +WL was 25-30% less. In Exp. 3 the SLA was some 20% less in the +WL and +WL_{early} treatments from 64 DAS until later in the season, when the SLA of –WL and +WL_{late} declined to a similar level to +WL (Fig. 4d). The SLA of the +WL_{late} treatment was similar to the control through out the season.

Cumulative PAR_i in both experiments was 5% less in +WL than the control (–WL) (Table 3). In Exp. 3 both the +WL_{early} and +WL_{late} treatments were significantly less than –WL, with +WL being significantly less than +WL_{late}.

In Exp. 3, where a number of light interception measurements were taken throughout the duration of crop growth no significant difference ($P < 0.05$) in extinction coefficient (k) was found between the treatments (k = 1.26 ± 0.05).

3.6. Radiation-use efficiency

Radiation-use efficiency (RUE_g) in the two experiments was 25-35% less in +WL than –WL (Table 3). In Exp. 3 RUE_g in both $+WL_{early}$ and $+WL_{late}$ were also significantly less than –WL. The $+WL_{early}$ treatment was significantly less than $+WL_{late}$ treatment.

3.7. Fruit production

Peak squaring occurred at about 87 DAS for all treatments in Exps. 2 and 3 (Fig. 5a,d). In Exp. 2 total square number in both +WL and control treatments were similar until about 83 DAS (Fig. 5a). The +WL treatment produced about 155 squares m^{-2} at its peak, while the –WL treatment peaked at about 245 squares m^{-2}.

In Exp. 3, square number of the fully waterlogged (+WL) treatment was lower than the control from an early stage (Fig. 5d). The peak production in +WL was 135 squares m^{-2} compared with 225 squares m^{-2} in –WL. In the $+WL_{early}$ treatment square production slowed significantly following the implementation of the waterlogging. At no stage beyond this point did square production recover to reach that of the control with peak square production equivalent to that of the +WL. The $+WL_{late}$ treatment had little effect on square production.

It is important to note that the change in square number potentially incorporates both changes in square production and the crop's ability to retain fruit. In Exp. 3 mainstem node production was also measured as an approximate indicator of the square production rate, as the two are well correlated (Hearn, 1969). At peak squaring there was approximately a 40% reduction in peak square number in +WL and $+WL_{early}$. At the same point, there was a reduction in mainstem node number of up to 15%, with the control and $+WL_{late}$ treatments having 19.3 and 19.5 nodes, the +WL having 16.3 and $+WL_{early}$ having 17.3 nodes.

Treatment differences in square number translated into the number of green bolls and open bolls (Fig. 5). Green boll number in the $+WL_{early}$ treatment in Exp. 3 was similar to +WL until 127 DAS when it was significantly higher than +WL but lower than –WL. In the $+WL_{late}$ treatment of Exp. 3

there was an initial decline in boll number measured at the sampling following the waterlogging but there was no significant difference between +WL$_{late}$ and the control by maturity.

4. Discussion

The primary objective of this research was to quantify the changes in crop level growth processes in response to waterlogging and to trace the mechanisms by which they effect crop yield. In summary, waterlogging reduced yield via a reduction in boll number. The reduction in boll number was commensurate with the reduction in total plant dry matter and the suppressed dry matter production was due to lower radiation use efficiency rather than changes in light interception. This mechanistic description should provide a useful basis for the simulation of cotton's response to waterlogging.

The response of boll number to stress and the relative stability of boll size are consistent with the findings of Hodgson (Hodgson, 1982; Hodgson and Chan, 1982). Hodgson consistently found reductions in boll number in response to waterlogging but boll size was less responsive and in some cases did not change significantly. The lack of response of fruit size to waterlogging in our experiments meant that yield was highly correlated with boll number (R^2 = 0.82). Boll size and lint percentage are generally found to be conservative, with drought or nitrogen stress also showing a greater impact on boll number than size (McMichael and Hesketh 1982; Gerik et al., 1994).

Hearn and co-workers concluded that the impact of nitrogen (Hearn 1975) and drought (Turner et al., 1986) on reducing boll number was primarily via a reduction in assimilate supply. Consistent with this, in our results, the modifications in fruit number due to the various treatments were always closely associated with the changes in glucose adjusted plant dry matter. The result is also consistent with that of Sadras et al. (1997), who found that factors such as sowing date, nitrogen fertilizer and plant density had little effect in changing reproductive allocation of cotton crops. Clearly, our result does not prove the putative mechanism, but the modification of plant size through waterlogging did lead to the expected outcome in terms of fruit number.

While the changes in fruit number were consistent with the changes in total dry matter, it is not possible from this data to pinpoint the cause of the reduction in fruit number. The results of Hearn (1969) suggest that a fall of 15% in mainstem node number, as seen in our results, could result in a 20-30% change in fruiting site production. This is consistent with the size of the change seen in our data. Explicit measurement of site numbers and shedding rates could clarify this point.

Changes in dry matter production due to waterlogging appear to have been caused more through changes in RUE_g than light interception. LAI was considerably reduced and the data for SLA suggest that this was not merely a secondary impact of dry matter accumulation: area was reduced more than leaf dry matter. However, the resultant reductions in cumulative PAR_i were less than 5%. In contrast RUE_g was reduced by up to 35%.

The suppression of RUE_g is consistent with the reduction in leaf and whole plant photosynthesis by waterlogging that has been found by other researchers (Meyer et al., 1987; Sahay, 1989) and the down regulation of photosynthetic enzymes (Pandey et al., 2000); although changes in RUE are not only related to changes in leaf photosynthetic rate (Sinclair and Horie, 1989): self-shading, distribution of leaf angles and the vertical distribution of nitrogen and light within the canopy can all influence the relationship between changes in leaf photosynthesis and canopy photosynthesis (De Pury and Farquhar, 1997; Milroy and Bange, 2003). Further, root growth is particularly sensitive to waterlogging with the growth of cotton roots stopping within minutes of the imposition of anoxia (Huck, 1970). In general, where root:shoot ratios are perturbed, subsequent growth is partitioned in such a way as to redress the balance (Brouwer, 1983). As the calculation of RUE was based on above ground dry matter, a shift in partitioning towards the roots would result in an apparent decline in RUE. However, little data are available to approach this question. Root counts by Meyer et al. (1987) suggest that flooding had a greater impact on leaf growth of cotton than root growth. Further work is required in this area.

The reasons for the reduction in photosynthesis and RUE are still to be clarified. In other species, the initial decline in photosynthesis appears to be induced through reduced stomatal conductivity with longer term effects involving changes in carboxylation enzymes and chlorophyll content (Kozlowski and Pallardy, 1984). Hodgson and MacLeod (1988) showed that while leaf N of cotton was reduced due to waterlogging, applying foliar N in the days prior to waterlogging did not fully alleviate the reductions in growth in all cases nor did it rectify the observed chlorosis. This suggests that other mechanisms, in addition to those acting through the reduced uptake of N, were likely to be acting on leaf performance.

Hocking et al. (1987) showed marked impacts on K and P uptake during flooding and declines in laminar P, K and Mn. In particular, P and K declined to levels that were likely to have been limiting (Reuter et al., 1997). However, Hocking et al. (1987) used a facility the same as that used by Meyer et al. (1987), who found that soil oxygen did not revert to normal levels after the end of the waterlogging treatment. Significant changes in soil pH and the redox state of many mineral nutrients can occur within two weeks of waterlogging which would result in changes in nutrient availability (Ponnamperuma, 1972). This may have exaggerated the impacts on mineral nutrition observed by Hocking et al. (1987). These effects are likely to have been far less important in our shorter inundation periods.

An interesting outcome of our study was the much more severe treatments which were needed to generate yield reductions when compared with the results of Hodgson (Hodgson and Chan, 1982; Hodgson, 1982). They reported a linear reduction in yields with the duration of inundation up to 32 h in two separate experiments without the need to modify ridge formation. In our studies it was difficult to achieve yield losses with periods up to 72 h on five occasions (Exp. 2). To generate marked effects of waterlogging we found it necessary to reduce the ridge height. Cotton has been reported to be susceptible to even mild reductions in soil oxygen (eg. 10% O_2; Leonard and Pinckard, 1936). Combining this with the finding of Hodgson and Chan (1982) that soil oxygen at 10-20 cm depth was far more important than at 0-10 cm, it was expected that the soil oxygen levels in Exp. 1 would have been low enough without overnight inundation to cause negative impacts on growth and yield. It was postulated that the effect may have been due to either redistribution of soil water overnight or the development of tolerance to anoxia due to exposure to significant periods of hypoxia (Drew, 1997). However, in Exp. 2 even with continual irrigation, up to 72 h at each irrigation, there was still no significant reduction in yield without the ridge height being modified.

A number of reasons can be suggested for the contrast to Hodgson's results. It is feasible that oxygen levels were not as severely affected by inundation in our experiments because since the 1980's there has been increased awareness within the Australian cotton industry of management practices aimed to maintain good soil structure (Daniells et al., 1996; Hearn and Bange, 2002). As a result, compaction is less severe and less widespread. Concurrent with this, there has been considerable improvement of water flow in furrow irrigated fields through the use of laser-guided levelling systems. Indirect selection of cultivars more suited to the intermittent waterlogging experienced in the Australian growing environments may also have played a role. The cultivar DP61 used by Hodgson in his studies was developed in the USA and experienced no selection under Australian conditions. In contrast both NuCotn 37 and V-2*i* underwent selection processes in Australia. To clarify whether the difference between our study and that of Hodgson (1982) was due to soil or plant factors, soil oxygen measurements were introduced in Exps. 2 and 3. The results will be presented in a subsequent paper.

In contrast with Hodgson (1982), Exp. 3 showed a marked effect of the timing of waterlogging on its impact on yield. With the same length of waterlogging period, growth and yield were significantly lower when waterlogging occurred at the second irrigation (early squaring) than at the fourth irrigation (peak green boll number). The single early waterlogging event had an impact similar to the five short events, a result consistent with Hodgson (1982) but the late waterlogging had less effect, even though it was applied at the same date and developmental stage as Hodgson's late treatment. To date there has been limited research on the effect of waterlogging on cotton of different developmental stages. Owen-Bartlett (1977; cited in Sojka and Stolzy, 1980) presented results that might suggest that declining oxygen concentrations may have caused a smaller proportional change in stomatal resistance in older plants than young plants, but this has not been confirmed. At the stage when the late stress was applied, there was a much smaller proportion of fruit that were susceptible to shedding (i.e. squares and young bolls less than two weeks old). Since yield was strongly related to fruit number, this could explain the limited yield response to late waterlogging in our experiment but it does not explain the limited impact on dry matter accumulation nor the contrast to Hodgson's (1982) results. The mechanisms for the differences between our results and those of Hodgson need to be explored.

5. Conclusions

In these experiments yield loss was caused by a reduction in the number of bolls. This reduction was commensurate with the reduced dry matter production from lower RUE_g rather than light interception even though leaf area was affected.

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Growth and dry matter partitioning of diverse cotton genotypes

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Abstract

As cotton is an indeterminate species, the timing of crop maturity is largely 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 increases to a point where none remains for the initiation and support of new fruiting sites. Thus dry matter production could impinge both on the timing of crop maturity and yield. The aim of this work was to determine the extent to which cotton genotypes of diverse genetic background varied in their growth determinants and dry matter partitioning and how this related to crop maturity.

Two field experiments were conducted, each involving two sowing times to provide variation in effective season length and growing conditions. Growth analysis showed little difference in growth characteristics of eight genotypes that would affect timing of crop maturity. Allometric plots showed that partitioning to the fruit began earlier in early genotypes but there was little systematic difference in the rate of partitioning after the onset of reproductive growth. The timing of crop maturity (60% bolls open) was related to the time when the growth rate of the fruit per unit area was equal to the crop growth rate. Taken together the results imply that the key trait driving maturity was the timing of the onset of reproductive growth and the subsequent development of the demand for dry matter.

Additional keywords: *Gossypium hirsutum*; development; radiation use efficiency; RUE; light interception; canopy extinction coefficient

1. Introduction

In the study presented in this paper we explored the degree of variation in growth and dry matter partitioning among eight cotton genotypes of diverse growth habit and how these may affect crop maturity.

Because cotton is an indeterminate species, the timing of crop maturity is largely determined by the capacity of the plant to continue the production of new vegetative organs and the associated fruiting sites. As the crop develops, the rate of fruit production and the rate of fruit retention both decline. Following the nutritional hypothesis of Mason (1922) and based on crop level measurements, Hearn (1969; 1972; 1994) proposed that both these processes are related to the ratio between rate of accumulation of boll dry matter and crop growth rate. In support of this Guinn and co-workers suggest that the imbalance between photosynthate supply and demand is a major cause of this process (Mauney et al., 1978; Guinn, 1974; Guinn, 1985); although the involvement of mineral nutrition or plant hormones cannot be excluded (Guinn and Brummett, 1989).

The dynamics of dry matter production and reproductive demand may also have significant impact on yield of different genotypes (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; Stiller, 2000). Thus the capacity of the crop to supply resources to the fruit may impact on yield and the timing of cutout (the cessation of fruiting site production) and thus crop maturity.

Despite this, studies of the growth characters of cotton rarely show significant differences between cultivars. Rosenthal and Gerik (1991) found differences in the apparent above ground radiation use efficiency (RUE, the amount of dry matter produced per unit of photosynthetically active radiation intercepted) among three United States cultivars. However, the difference was attributed to differences in the fruit load of the cultivars, since the high oil content of the seed means there is a higher energy requirement for fruit production than vegetative growth (Wall et al., 1994). When compared over the vegetative period only, Rosenthal and Gerik found no difference between the genotypes. Our earlier work also did not detect a consistent difference between an early and a late Australian genotype (Bange and Milroy, 2000).

Similarly, Sadras (1996) and Heitholt et al. (1992) found no difference in the canopy light extinction coefficient (*k*) of different genotypes. While they found variation in *k* with other treatments, within each set of growing conditions the genotypes had similar extinction coefficients. In terms of dry matter partitioning, a compilation of results from earlier experiments failed to find marked differences in reproductive partitioning between cultivars or with variations in management (Sadras et al., 1997). Bange and Milroy (2000) found a difference in absolute partitioning between an early and full season cultivar but allometric analysis showed this to be related to differences in absolute plant size.

Given the lack of differences found in earlier studies we selected eight genotypes of widely differing growth habit and time to maturity in an attempt to confirm the lack of differences in gross growth characteristics and dry matter partitioning. Where differences occurred, we also aimed to assess whether there was any association between these traits and the timing of crop maturity. Dry matter production was broken down into light interception and radiation use efficiency. Light interception was characterised by differences in leaf area dynamics and the light extinction within the canopy.

2. Materials and methods

2.1. Cultural details

Two field experiments were conducted at the Australian Cotton Research Institute (ACRI) at Narrabri (30° S 150° E), in a semi-arid environment of north-west New South Wales, Australia. Both experiments included two sowing times so as to generate variation in temperature and radiation regimes (Table 1) which in turn would influence development, dry matter production and fruiting patterns. Cotton genotypes with known differences in their time of crop maturity and growth forms were used in both experiments. It has been postulated however, that the genetic base of cultivated *G. hirsutum* as a whole is relatively narrow (Brubaker and Wendel, 2001) and most of this germplasm was relatively elite for its area of adaptation, so the genetic variability in the material may still not necessarily be very wide. The inclusion of the African Albar G501 and the Texan Tamcot HQ95 extended the range of maturity types and also increased the variation in the genetic background. A short description of the genotypes used in these experiments is presented in Table 2.

Both experiments (Exp. 1 and Exp. 2) consisted of two sowing times and the genotypes arranged factorially. Plots (8 m by 18 m), containing eight rows spaced at 1 m, were sown on 16 October 1998 (S1), and 5 November 1998 (S2) for Exp. 1, and 29 October 2000 (S1), and 29 November 2000 (S2) for Exp. 2. In both experiments a randomised complete block design was used with three replications. Both experiments were sown with a commercial row crop planter.

The experiments were established and grown with full irrigation on a grey-clay soil (vertosol) utilising high input management and insect control as described in Hearn and Fitt (1992). Nitrogen was applied as anhydrous ammonia 35 days after the first sowing in Exp. 1 at a rate of 100 kg ha^{-1} (injected below and to the side of the plant line), and 87 days before the first sowing in Exp. 2, at a rate of 90 kg ha^{-1} injected below the plant line. 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 two weeks in both experiments. Sampling started just prior to the appearance of the first square in each sowing and involved taking all plants from within one metre of row, selected randomly from the inner four rows of each plot. Total fresh biomass was measured and a sub-sample of four plants taken. Sub-samples were partitioned into green leaf (laminae), stem (including petioles), squares, green bolls and open bolls. A square was defined as being present when the leaf that subtended the square had unfolded. Fruit 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 (PAR_T) the canopy at approximately weekly intervals. Three measurements were made on each plot using a ceptometer (Delta-T Devices Ltd., Cambridge, UK) between 1100 and 1300 hours (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. The lint collected from these samples was kept to calculate final yield (g m^{-2}).

2.3. Data analysis

LAI (leaf area index) 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. The persistence of the canopy (leaf area duration, LAD (d)) for each treatment was derived by calculating the area under the plot of LAI versus DAS (days after sowing).

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. (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 (Q_I) by the crop was calculated for each date of measurement. This was then regressed against DAS to allow interpolation using an exponential function (Bange and Milroy, 2000). From this relationship Q_I on the day of the biomass samplings was derived. A canopy light extinction coefficient (*k*) was then calculated for each plot from a non-linear regression between Q_I and LAI:

$$Q_I = d\left[1 - \exp\left(-\mathrm{k}LAI\right)\right] + f \qquad (1)$$

where *d* and *f* are fitted coefficients.

Average RUE_g for the season was derived from the linear regression of TDM_g against cumulative intercepted radiation. For this, the proportion of light intercepted at midday was adjusted to approximate daily interception using the approach of (Charles-Edwards and Lawn, 1984). In each sowing, the period over which this could be determined was dictated by the availability of light interception and dry matter data. The measurements used in Exp. 1 were from 55 to 164 DAS in S1, and 35 to 115 DAS in S2; in Exp. 2 the ranges were from 52 to 151 DAS in S1 and, 21 to 113 DAS in S2.

Reproductive partitioning was examined using the allometric approach by plotting *ln* FDW_g against *ln* TDW_g for the genotypes in each experiment. The slope of this plot is equivalent to the ratio between the relative growth rate (RGR) of the fruit and the whole plant (Coleman et al., 1994).

Forward stepwise regression analyses were used to test for differences between genotypes and among times of sowing for *k*, RUE_g and allometric partitioning.

To compare the dynamics of carbon production and its partitioning to reproductive dry matter among the genotypes, we generated the crop growth rate (CGR) from the differential (Eq. 3) of the logistic function (Eq. 2) of TDM_g versus DAS (Landsberg, 1977). Similarly, we generated the rate of accumulation of reproductive dry matter (FGR), again using the differential of the logistic function of FDM_g against DAS. The form of the logistic function was:

$$Growth = g/(1+(DAS/h)^i) \quad (2)$$

where *g* and *h* and *i* are fitted coefficients.

The differential form of this response was:

$$Growth\ Rate = -g.i(DAS/h)^{i-1}/(h(1+(DAS/h)^i)^2) \quad (3)$$

All ANOVA, regressions and stepwise analyses were conducted using the Genstat 5 statistical package (Lawes Agricultural Trust, IACR, Rothamsted, UK). In addition, to remove row and column effects of the experimental designs and thus increase the precision of the analysis, final TDM_g, harvest index (HI), LAD, cumulative LI (Cum LI) and peak LAI were reanalysed using estimated variance components generated using the method of residual maximum likelihood (REML), again using Genstat.

3. Results

As expected, the genotypes varied significantly in the time taken to reach maturity as measured by days to 60% bolls open (Table 3). HQ95 was consistently the earliest genotype. In Exp. 1 this was followed by S-102 and CSX 33. Unfortunately S-102 did not establish in Exp. 2. In this experiment CS8S matured second after HQ95. In Exp. 1, SC189 was latest maturing in S1 but in S2 there was little difference between SC189, V-16 and CSX 118. In Exp. 2, the African G501 was latest to mature and again, there was little difference between V-16 and CSX 118.

Across both experiments, lint yield was loosely but significantly correlated with time to maturity (R^2= 0.41) when all data were included. A stronger relationship (R^2= 0.61; Fig. 1) was derived by excluding G501 for both times of sowing from the regression. Its yields were far less than implied by the regression against maturity.

3.1 Dry matter production

Final TDM_g varied significantly between the genotypes in S2 of Exp. 1 and the S1 of Exp 2 (Table 4). The general trend was for early maturing genotypes to have a lower TDM_g than later maturing ones. However, there was no significant difference in TDM_g between the genotypes up to around the time of first flower (Table 5; Figs. 2 and 3) and TDM_g at this time was not related to time of maturity.

Early maturing genotypes tended to have a lower LAD than later maturing genotypes. While this was associated with a lower cumulative light interception, the relative differences in light interception were small (Table 4). Like dry matter, the lower LAI of early genotypes was not apparent at the time of first flower (Table 5). The differences in LAD appear to be associated more with the duration for which leaf area continued to develop or the degree to which LAI was maintained later in crop growth than with the rate of development of LAI (Figs 4 and 5).

RUE_g only varied significantly among the genotypes in S1 of Exp. 2. The very early genotype HQ95 and the early-medium genotype CSX33 had low RUE_g in this case. HQ95 also had a significantly lower k than the other genotypes in S2 of Exp. 1 and a relatively low k in S2 of Exp. 2. Across sowings and years, RUE_g was loosely but significantly associated with 1/k if HQ95 was excluded (R^2=0.39; $P<0.01$). However their was no association when the sowings were considered individually, except for Exp 2, S1. For this sowing R^2 was 0.86 ($P<0.01$).

3.2 Dry matter partitioning

Final harvest index (HI) was higher for the earlier genotypes. On average in Exp. 1, HQ95 and S-102 had harvest indices of approximately 0.75 (glucose adjusted)

(Table 4). There was no significant difference among the other genotypes which ranged from 0.55 to 0.66. In Exp. 2, HQ95 and CS8S had the highest HI in both sowings, although the distinction was less marked in S2. HI used as a measure of final reproductive partitioning can only be taken as a relative measure in this study, as senesced leaf material was not collected. Within each sowing in each year, HI was negatively correlated with time to 60% maturity (Fig. 6)

The allometric ratio for partitioning to vegetative structures relative to total dry matter differed significantly among the genotypes in Exp. 2 but not Exp. 1 (Table 6). In S1 of Exp. 2, CSX 118 and V-16 had higher rates of partitioning to vegetative organs than HQ95 and in the second sowing CSX 118 and G501 had higher rates.

3.3 Partitioning and maturity

Dry matter partitioning was further explored by comparing the crop growth rate (CGR) over time to the rate of accumulation of reproductive dry matter (FGR). Both these rates were based on glucose adjusted dry matter. The time when the FGR increased to equal the CGR was taken to approximate the point at which the fruit were consuming the total net carbohydrate production. This approximation is based on net change and does not account for loss of material through senescence. Fig. 7 presents two examples comparing an early and late genotype showing approximately 18 d difference in the timing of when FGR = CGR. Crops which reached the point at which FGR was equal to CGR earlier tended to mature earlier. Pooling all the data across the sowings showed a strong linear relationship between the time when FGR = CGR and the time of 60% maturity (Fig. 8; $P < 0.0001$; $R^2 = 0.73$).

4. Discussion

The timing of maturity of the genotypes was well related to the time when the FGR increased to be equal to the CGR (Fig. 8). This is consistent with the nutritional hypothesis of Mason (1922) and the results of Hearn (1969; 1972; 1994). Hearn (1972) demonstrated a relationship between the timing of when FGR = CGR and the time at which new fruiting sites stopped being produced. His experiments involved variation in irrigation and nitrogen application. Our results demonstrate that a similar relationship holds for maturity across the genotypes, despite the wide variation in maturity class and growth form.

The relationship between maturity and when FGR = CGR comprises two components: the relationship between the time when FGR = CGR and when fruiting sites stop being produced, and how long it takes for the last bolls produced to reach maturity. This will be further modified by the response of fruit shedding to carbon status and the possibility of variation between genotypes in the response of boll development to temperature (Yfoulis and Fasoulas, 1973). Significant variation in these four factors could alter the relationship in one of two ways. If the variation between genotypes was correlated to the genotype's maturity class, the slope of the relationship between the time when FGR = CGR and the timing of crop maturity would change. If any differences were unrelated to genotype maturity class, dispersion around the line would be increased. The slope of the regression was 0.81, which was not significantly different from 1.0 ($P = 0.05$). It was further improved to 0.93 by the omission of a single outlier at the left of the range. These results suggest that the influence of any differences between the genotypes in terms of the above mentioned factors are small relative to the primary relationship between the time when FGR = CGR and crop maturity. It has been suggested that later maturing genotypes have longer boll periods (Munro, 1971; Yfoulis and Fasoulas, 1973), so while the slope was not different from 1.0, there is some reason to expect that this could occur.

Considering growth and partitioning as components of this process, little consistent difference was found in the growth components of the genotypes that would explain the differences in maturity. The exception to this was the low k and RUE_g found for the very early genotype HQ95 on some occasions. The lack of difference is consistent with our previous comparison of a late and early genotype of similar genetic background (Bange and Milroy, 2000) and also with previous genotype comparisons of RUE_g and k (Heitholt et al., 1992; Sadras, 1996; Rosenthal and Gerik, 1991) although these studies were not specifically designed to compare genotypes of contrasting maturity. The importance of the differences in k and RUE_g of HQ95 are difficult to assess given the lack of difference in TDM_g up to around the time of first flower. It is worthwhile to note here that the RUE_g and k were calculated over the whole period of measurement and not for specific time intervals. It is possible that the traits differed less between the genotypes early in growth than later.

Sadras (1996) found a significant relationship between RUE and the inverse of *k*. This can be explained on the basis of a more uniform distribution of light in the canopy allowing more leaves to be exposed to high light intensities. While there was a weak relationship across the experiments between RUE_g and the inverse of *k* in our data, this could only be obtained by omitting the most different cultivar, HQ95. Further, HQ95 had both low *k* and RUE_g and when the sowings in the experiments were analysed separately the relationship was only significant once. There is thus little evidence to suggest that the variation in RUE_g was a secondary effect due to variation in *k*.

The differences in allometric partitioning (Table 6) contrasts to our previous findings (Bange and Milroy, 2000). Genotypes CSX 118, G501 and V-16 had high rates of reproductive partitioning in Exp. 2 although they are late or medium-late genotypes. Thus, while earlier genotypes began to partition biomass to fruit when they were smaller than late genotypes, consistent with our earlier findings there was no evidence that early genotypes showed a preferential partitioning of biomass to reproductive structures. Where a higher rate of partitioning was detected, it did not result in early maturity. This contrasts with the conclusions of Pace et al. (1999) who suggested that early genotypes partitioned more to fruit than late genotypes based on partitioning of ^{14}C carbon from the youngest fully expanded leaf. However their measurements were made on both cultivars at the same time after sowing and thus the early cultivar had a larger proportion of its total biomass in fruit at the time of measurement. Comparing the two genotypes, the difference in proportion of dry matter in the fruit was more marked than the difference in partitioning, which is consistent with our results.

It would appear therefore, that the differences in maturity were consistent with the nutritional hypothesis, reflecting when the growing fruit monopolised resources. However, the lack of difference in growth variables in this and other studies, along with the lack of evidence for higher allometric partitioning to fruit in the earlier genotypes, suggests that the key difference was the size of the plant at the beginning of reproductive development. As there was little difference in the size of the plant at 65 days (just prior to the onset of reproductive partitioning) this suggests that the timing of the onset of reproductive development could be the important factor in the eventual carbon balance of the crop and hence the timing of maturity. The negative relationship between HI and time to 60% maturity is consistent with the initial difference in size at the beginning of reproductive development being maintained through to maturity.

This analysis is based on carbon nutrition. The results of Guinn and co-workers suggest that the imbalance between photosynthate supply and demand is a major cause of this process (Mauney et al., 1978; Guinn, 1974; Guinn, 1985). However, neither mineral nutrition nor hormonal action can be categorically excluded. It is feasible for example, that the initiation of new fruiting sites is related to hormone levels produced by developing bolls or that hormonal messages coordinate the plant's response to declining nutritional status (Guinn and Brummett, 1989). The role of mineral nutrition requires further exploration. Declining mineral status may act directly to limit fruit growth or may limit the capacity of leaf tissue to continue to supply photosynthate to the fruit (Wright, 1999). These mechanisms need further exploration.

The dynamics of dry matter production and reproductive demand may also have significant impact on yield of different genotypes (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; Stiller, 2000; Fig. 1). Thus the capacity of the crop to supply resources to the fruit impacts both on yield and timing of cutout and hence subsequent crop maturity. The positive correlation between yield and maturity was evident in our results. We excluded Albar G501 from the response as it is appeared to fit poorly and is known to be poorly adapted to local conditions. The slope of the relationship was the same as that obtained by Stiller (2000) but somewhat more than the 2.0 g m^{-2} d^{-1} obtained by Constable et al. (1976) in their examination of the effect of sowing date on yield. The lack of variation in growth characteristics suggests that the mechanism for this relationship was through the timing of reproductive growth and the subsequent development of the demand for dry matter rather than total capacity to produce dry matter. It would appear that it is the termination of development due to increasing FGR that governs both yield and maturity hence the correlation between the two. The season length at a particular location will dictate the range over which the linear correlation can extend. A genotype with a very long development relative to the length of the growing season will be truncated and penalised in terms of yield. As a result, yield will at some point start to decline with increasing development. This happens at an earlier point in a shorter growing season area.

A better understanding of the relationship of crop growth and maturity of different genotypes will allow opportunities to better tailor production systems for regions varying in season length. In addition, the concept of relating the timing of maturity to when FGR equals CGR has scope for improving simulation of crop maturity. This is a common problem in models where the time of crop maturity is often necessary for the simulation of yield. The rate of increase in the proportion of reproductive biomass is often more readily determined than the duration of the increase. However, the applicability of this relationship would need to be specifically tested in suitable simulation models.

5. Conclusion

The timing of maturity of the different genotypes was related to when the accumulation rate of fruit biomass increased to match the crop growth rate. Little difference was found in the growth characteristics of cotton genotypes which covered a wide range of maturity and growth habits. Genotypes differed in the intercept of the allometric plot when RGR of fruit was plotted against RGR of the whole plant, but there was no consistent pattern of earlier genotypes showing a higher rate of allometric partitioning to fruit. Taken together, these results suggest that the difference in maturity between the genotypes was related more to the timing of the onset of reproductive development than dry matter production or partitioning characteristics

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Tables

Table 1

Monthly average of daily weather data for the duration of the two field experiments. Average daily maximum temperature (Max), minimum temperature (Min), and total incident solar radiation (Radiation MJ m^{-2} d^{-1}) are shown.

Year	Variable	Oct	Nov	Dec	Jan	Feb	Mar	Apr
98-99	Min °C	11.6	14.6	17.6	20.4	18.0	17.2	10.3
	Max °C	25.0	27.6	32.4	32.8	21.2	29.7	23.8
	Radiation	18.9	22.0	25.6	21.9	21.2	16.7	10.9
00-01	Min °C	12.5	16.9	18.8	20.8	20.4	16.5	12.1
	Max °C	26.6	27.0	33.0	35.1	32.1	29.5	27.0
	Radiation	16.6	16.6	23.7	23.9	21.8	17.3	14.5

Photosynthesis of Cotton Leaves in Response to Nitrogen and Light, and Implications for Crop Growth.

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Abbreviations: C_A, leaf CO_2 assimilation rate (μmol CO_2 m^{-2} s^{-1}); C_{Adark} , leaf CO_2 assimilation rate at PAR 0 μmol m^{-2} s^{-1} (i.e. the y-intercept of the light response curve); C_{Amax} , leaf CO_2 assimilation rate measured at PAR 2000 μmol m^{-2} s^{-1}; DAS, days after sowing; k, canopy light extinction coefficient; LAI, leaf area index; LAI_{cum}, cumulative leaf area from the top of the canopy to the level of interest; PAR, photosynthetically active radiation (MJ m^{-2}); PAR_D, proportion of light intercepted by the crop canopy over the day; PAR_I, proportion of radiation intercepted by the crop canopy measured at midday; RUE, radiation use efficiency (g MJ^{-1}, glucose equivalents); SLN, specific leaf nitrogen (g N m^{-2} of leaf); SLN$_{grad}$, vertical SLN gradient within the canopy.

Photosynthesis of Cotton Leaves in Response to Nitrogen and Light, and Implications for Crop Growth.

ABSTRACT

Leaf nitrogen content and light intensity affect leaf photosynthesis. Responses of cotton leaf photosynthesis to nitrogen and light were developed and used in a framework that scales up from leaf photosynthesis to canopy radiation use efficiency (RUE). This was then used to explore the impact of nitrogen and light dynamics on RUE of cotton canopies. Photosynthetic rate and nitrogen concentration of leaves (specific leaf nitrogen, SLN) were measured from two field experiments in which the rate of nitrogen application was varied. The overall shape of the relationship between photosynthesis and SLN of individual leaves was consistent with that for other species, being described well by an exponential rise to a maximum of 32.49 (±1.08) μmol CO_2 m^{-2} s^{-1}. Incorporating the influence of age improved the relationship, showing an impact of leaf age independent of SLN. The photosynthesis relationship developed should be appropriate for use in simulating cotton crops.

The results of this study also indicate that the approach used by Hammer and Wright (1994) to scale from leaf photosynthesis to canopy RUE was effective in capturing the variation in the RUE of cotton as observed in three field experiments. There appeared to be little impact of the ontogenetic changes in light extinction coefficient and vertical gradients of SLN within the canopy on the variation in RUE. For crop simulation purposes, this simplifies the process of modulating RUE in growth models.

INTRODUCTION

Radiation use efficiency (RUE, dry matter produced per unit of intercepted light) is widely used in the analysis of crop growth and to calculate biomass production in crop simulation models (Sinclair and Muchow, 1999). For simulation purposes, the intercepted radiation over a time period is multiplied by the RUE to estimate dry matter production for that period. Because RUE varies with the nitrogen status of the crop, RUE is often modulated using the current specific leaf nitrogen (SLN, g N per m^2 of leaf area) averaged for the canopy (Sinclair and Muchow, 1999). However, it has been shown that N is often concentrated in the upper layers of plant canopies (Sadras et al., 1993; Shiraiwa and Sinclair, 1993; Wright and Hammer, 1994) generating a nitrogen gradient within the canopy. This is a functionally efficient pattern because the leaves with the highest N concentration, and hence highest density of photosynthetic material are placed in the best light environment (Charles-Edwards et al., 1987; Evans, 1989). It has been demonstrated that a nitrogen gradient results in higher total canopy photosynthesis for a given total amount of N in the canopy (Field, 1983; Werger and Hirose, 1991; Chen et al., 1993). As a result of this, the degree to which RUE should be modified for average canopy SLN in simulation models will also depend on the vertical gradient of nitrogen in the canopy. Milroy et al. (2001) have shown that the N gradient in cotton canopies varies during development, becoming more marked with age. Thus the correlation between RUE and average SLN may also vary with development. The importance of this interaction for cotton growth has not been quantified.

To explore the significance of N gradient on the relationship between RUE and average SLN, we used a simple method presented by Hammer and Wright (1994) which scales from photosynthesis at the leaf level to canopy RUE. The approach allows for the vertical N distribution in the canopy, the average canopy SLN and the light extinction coefficient (k) to be manipulated when calculating the net carbon gain of the canopy based on the photosynthetic rates of leaves in various strata within the canopy. Hammer and Wright successfully used this approach to explore the effects of radiation environment and canopy nitrogen dynamics on RUE of peanut. The main objective of the work we present here was to use this method to explore the sensitivity of cotton RUE to changes in SLN, SLN gradient and k and test whether these traits can explain the observed ontogenetic changes in RUE (e.g. Sadras, 1996). The purpose is to assess whether it is necessary to accommodate the developmental changes in N gradient and k in the simulation of biomass production by cotton. The first step will be to assess the capacity of the scaling approach to capture variation in RUE in cotton.

To calculate the whole canopy photosynthetic rate using this approach requires the relationship between photosynthesis and light and the impact of nitrogen on this response. The response of leaf level photosynthesis to leaf nitrogen status has been reported for cotton by Reddy et al. (1997). However, the experiments were conducted under controlled environment conditions and have not been validated against plants grown in the field.

An important consideration in exploring the impacts of leaf nitrogen status on photosynthesis is to determine the relative influence of leaf age. Constable and Rawson (1980) and Wullschleger and Oosterhuis (1990) have studied the influence of leaf age on photosynthesis. However, photosynthesis and nitrogen concentration decline in unison as the leaf ages (Constable and Oosterhuis, In Press). The interaction of nitrogen and age on photosynthesis of cotton leaves has not been assessed. Thus, additional aims of this work were to quantify the influence of leaf N status on the response of photosynthesis to light for field grown cotton plants over a wide range of leaf N; and to assess whether or not the impact of leaf age on photosynthesis can be detected independently of the effect of leaf nitrogen status.

MATERIALS AND METHODS

Photosynthesis Experiments

Cultural Details

Leaf photosynthesis was measured in two nitrogen rate experiments conducted at the Australian Cotton Research Institute near Narrabri (30° S, 150° E) in a semi-arid environment of northwest New South Wales, Australia. The soil was a uniform grey cracking clay (USDA Soil Taxonomy: Typic Haplustert). Experiment P1 was sown on 13 October 1999 and experiment P2 was sown on the 28 October 2000. Both were sown to cultivar Sicala V-2*i* on a 1 m row spacing to give an established density of 10 plants m^{-1}. The crops were grown with full furrow irrigation utilizing high input management and insect control as described in Hearn and Fitt (1992).

There were three nitrogen treatments: 0, 60, 120 kg ha^{-1} in both experiments. Nitrogen was applied as anhydrous ammonia, 54 d before sowing in P1 and 85 d before sowing in P2. The experimental designs were RCBD with four replicates (plots 6 m x 11 m).

Measurements

Starting 36 and 44 DAS after sowing for experiments P1 and P2 respectively, the number of main stem nodes of 10 plants in each plot was counted on a weekly basis. Plotting these numbers against DAS allowed the age of sample leaves to be estimated from the node of insertion on the main stem.

In experiment P1, photosynthesis was measured on 12 occasions at 1-2 week intervals between 30 November (48 DAS) and 23 March (152 DAS). In the second experiment P2, photosynthesis was again measured on 12 occasions at similar intervals between 12 December

(45 DAS) and 23 March (146 DAS). On the first four occasions in both experiments the youngest fully expanded main stem leaf was measured from two plants in each plot. As the plants produced more nodes, one plant per plot was sampled with a main stem leaf from the upper and lower canopy being measured. In experiment P2 an additional leaf was measured from the middle of the canopy.

On the day of sampling, each leaf was first exposed to full sunlight for a minimum of 15 minutes and on most occasions for about 1 to 2 hours. The CO_2 assimilation rate was then measured using an open chamber infrared gas analysis system (LiCor 6400, Lincoln, Nebraska, USA) with a 6 cm^2 chamber. Measurements were recorded when both leaf CO_2 assimilation rate and stomatal conductance were stable. Ambient temperature and humidity were used. An average was taken of five readings spaced evenly over 120 s. Readings were taken using an LED light source which supplied 2000 $\mu mol\ m^{-2}\ s^{-1}$ PAR (660-675 nm). Although a light source was used, heavily overcast days were avoided to minimize the time required for the leaves to adjust to the light intensity used. Readings were taken within three hours of solar noon, for the same reason and to avoid any possible effects of more rapidly changing temperature in the early morning.

After the photosynthesis reading had been taken, the node of insertion of the leaf was recorded and the leaf removed. The area of each leaf was measured using a planimeter (Licor 3100, Lincoln, Nebraska, USA) it was then dried and ground. Nitrogen content was measured using the microKjeldahl technique.

On six occasions in experiment P2, a series of light response measurements were taken on the sample leaves before removal. Photosynthesis was measured at 2000 $\mu mol\ m^{-2}\ s^{-1}$ PAR and then at 1500, 1000, 500, 250, 125 and 0 μmol m^{-2} s^{-1} PAR. Photosynthesis measures at 0 μmol m^{-2} s^{-1} PAR were taken as dark respiration.

Data Analysis

The relationship of photosynthesis (C_{Amax} μmol CO_2 m^{-2} s^{-1}) measured at PAR 2000 μmol m^{-2} s^{-1} to specific leaf nitrogen (SLN g N m^{-2} of leaf) of individual leaves was fitted to the response reported by Sinclair and Horie (1989):

$$C_{A\max} = b \times \left[2 / \left\{ 1 + \exp\left(-c \times (SLN - SLN_0) \right) \right\} - 1 \right] \qquad [1]$$

where *b* represents the limiting value of C_{Amax} at saturating SLN, SLN_0 is the value of SLN at which C_{Amax} becomes zero, and *c* is a fitted coefficient giving the curvature of the response. An analysis of parallelism was used to test for differences in the response between experiments.

The response of photosynthetic rate (C_A) to light intensity (PAR) was fitted using an exponential rise to a maximum function of similar form to that of Constable and Rawson (1980):

$$C_A = C_{A\max} - a \times \exp\left(-Q \times PAR \right) \qquad [2]$$

where *a* and *Q* are fitted coefficients. Dark respiration can be derived as C_{Amax} minus the coefficient *a*. The initial slope of the response curve is $Q \times a$ and indicates the efficiency of light use at low intensity. This gives higher values of the efficiency than when the slope is calculated from the initial data points, so the value was also calculated arithmetically.

The regression analyses and analysis of parallelism were conducted using the procedures in Genstat Version 5 (Lawes Agricultural Trust, IACR, Rothamsted, UK).

Crop Growth Experiments

Cultural Details

Three irrigated crop growth experiments were conducted at the same location as the photosynthesis experiments. The first two, referred to as G1 and G2 have been described previously (Milroy et al. 2001). Briefly, experiment G1 was sown on 11 October 1995 and comprised cultivar Siokra L22 grown with high nitrogen application (150 kg ha^{-1}) and full irrigation. Eight plants m^{-2} were established. There were three replicates. Experiment G2 was sown on 16 October 1996 and comprised cultivar Sicala V-2*i* grown with high (150 kg ha^{-1}) or nil nitrogen application. The experimental design was a RCB with four replicates. A density of 13 plants m^{-2} was established.

Experiment G3 was sown on the 16 October 1998 and comprised cultivar Sicala V-2*i* grown with high (100 kg ha^{-1}), low (50 kg ha^{-1}) or nil nitrogen application. Plots were 25 m by 8 m (8 rows) and the experimental design was an RCB with four replicates. Nitrogen was applied as anhydrous ammonia, 35 DAS. A density of 11 plants m^{-2} was established. In all growth experiments commercial equipment and management practices were used, including full irrigation.

Measurements

Plant samples were taken approximately every two weeks. Prior to first flower, normal samplings involved taking all plants from within one meter of row. Beginning around the time of first flower, destructive stratified samplings were made. All samples were selected randomly from the inner two or four (from eight row plots) rows of each plot. In the normal samplings total fresh biomass per m^2 was measured and a sub-sample of four plants was taken. In the stratified samplings in each plot a 1 m^2 area of the crop canopy was cut in four successive layers of equal vertical thickness. Details of the method have been published previously (Milroy et al., 2001).

All samples were partitioned into leaves (laminae), stem (including petioles), squares, and bolls. A square was defined as being present when the leaf that subtended the square had unfolded. Fruit were defined as bolls from the day of anthesis. The leaf area (and hence leaf area index, LAI) in the sub-sample of normal samplings and in each layer of stratified samplings was then measured using the planimeter. All samples were dried in a forced draught oven at 70 °C for at least 48 h and weighed. Normal biomass samplings were converted back to m^{-2} using a drying ratio. All masses are presented on an oven-dry basis.

The leaf material was ground and analysed for N concentration on a mass basis (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 crops were approaching maturity. A total of seven stratified harvests were made in Exp. G1, six in G2 and five in G3.

Measurements of photosynthetically active radiation (PAR, 0.4-0.7 μm) were taken in each plot above (PAR_O) and below the canopy at ground level (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.

Data Analysis

For each plot, the proportion of radiation intercepted by the crop (PAR_I) was calculated at each day of measurement and PAR_I was then related to DAS using an exponential rise to a maximum function to allow interpolation between measurement dates. Using the interpolated values of $\mathrm{PAR_I}$ for the day of the stratified biomass samplings, a canopy light extinction coefficient (k) was calculated for each plot from a non-linear regression between $\mathrm{PAR_I}$ and the measured leaf area index (LAI):

$$PAR_I = g[1-\exp(-\mathrm{k}\times\mathrm{LAI})]+h \qquad [3]$$

where g and h are fitted coefficients. The calculated k was then converted to a total global radiation basis using the relationship of Szeicz (1974).

Vertical gradients of specific leaf nitrogen (g N $\mathrm{m^{-2}}$ of leaf) within the canopy ($\mathrm{SLN_{grad}}$) and average canopy SLN were calculated for each harvest date using the data collected on leaf weight, leaf area and N concentration for each stratified layer. $\mathrm{SLN_{grad}}$ was calculated from the linear regression of SLN in each layer against cumulative LAI ($\mathrm{LAI_{cum}}$) from the top of the canopy to the mid-point of each layer.

The RUE was calculated for each date when a stratified harvest was taken by using data from three consecutive sampling dates centered on the date of interest. For each set, RUE was calculated from the linear regression of accumulated biomass on cumulative intercepted PAR over the three dates. In calculating biomass, the high synthesis cost of cotton fruit relative to vegetative growth was taken into account by adjusting the reproductive biomass for biosynthetic production costs (g glucose per g dry matter) of reproductive and vegetative tissues using the conversion factors of Wall et al. (1994). The conversion includes the growth respiration component.

The proportion of light intercepted by the crop canopy over the day ($\mathrm{PAR_D}$) was estimated from the proportion of PAR intercepted around noon ($\mathrm{PAR_I}$) using the equation of Charles-Edwards and Lawn (1984):

$$PAR_D = 2\times PAR_I/(1+PAR_I) \qquad [4]$$

The appropriateness of this conversion has been tested for cotton by Sadras and Wilson (1997). Daily values of PAR_D were derived by interpolation as for PAR_I. The cumulative intercepted radiation was then derived from the daily values of PAR_D and the daily radiation (PAR) recorded by a fully serviced weather station at the research institute.

RESULTS

Photosynthesis

Using the function of Sinclair and Horie (1989) (Eq. [1]), leaf photosynthesis at 2000 μmol m^{-2} s^{-1} (C_{Amax}) showed a loose but significant ($P < 0.001$) response to SLN in each season (Fig. 1). No significant improvement in the response was achieved using alternative response types. There was a small but significant ($P < 0.001$) difference between the two seasons in the asymptote of the response of C_{Amax} to leaf SLN. In experiment P1 the asymptote was 35.11 (± 2.03) compared with 31.55 (± 1.38) in experiment P2. For the purposes of inclusion in the scaling framework a combined response across the two seasons was derived (Fig. 1c). The combined response was:

$$C_{A\max} = 32.49[\pm 1.08] \times (2/(1+\exp(-1.48[\pm 0.17] \times (SLN - 0.65[\pm 0.07]))) - 1) \qquad [5]$$

($r^2 = 0.41$; $n = 598$; $P < 0.001$).

To test for the impact of leaf age on the response of C_{Amax} to leaf SLN a multiple regression analysis was conducted on each season. In experiment P1 there was no improvement in the response, however in experiment P2 there was a significant improvement ($r^2 = 0.58$; $P < 0.001$). When the data from both experiments were combined the response of C_{Amax} to leaf SLN and leaf age (d) was:

$$C_{A\max} = Age \times (0.46[\pm 0.16] \times (2/(1+\exp(-0.59[\pm 0.44] \times (SLN - 3.42[\pm 0.35]))) - 1)) + 31.26[\pm 0.69] \quad [6]$$

($r^2 = 0.50$; $n = 533$; $P < 0.0001$).

To explain more of the variation in photosynthesis, a number of other variables were considered. The possibility of water stress was excluded by omitting all measurements taken within four days prior to an irrigation or by omitting all measurements with less than the average stomatal conductivity. In neither case was an improvement in the regression against age and SLN achieved. Similarly, no improvement was found when only leaves from the upper portions of the canopy were considered in an attempt to exclude leaves which had undergone some degree of light acclimation. A weak correlation was found between leaf temperature and photosynthesis, but again, adding temperature to the response after the age and SLN terms did not improve the response.

The influence of SLN on the response of photosynthesis (C_A) to light intensity (PAR) was explored in the second season (experiment P2) on a subset of the leaves. The leaves were categorized into seven groups each spanning 0.5 units of SLN. An analysis of parallelism was conducted using the light response function of Sinclair and Horie (1989) (Eq. [2]) to compare the response of C_A to PAR across the seven different categories of leaf SLN. As expected, the shape of the response varied to reflect the reduction in C_{Amax} with declining SLN (Fig. 2). The analysis showed that this difference was due to changes in C_{Amax} and dark respiration (C_{Adark}) ($P < 0.001$) but not in the parameter Q, implying no change in the initial light use efficiency. Calculating the initial slope arithmetically also showed it to remain constant at around 0.047 mol CO_2 mol^{-1}. The responses of C_{Amax} and C_{Adark} , calculated as the mean of the measurement taken at PAR = 0, to the average leaf SLN (Fig 3.) were:

$$C_{A\max} = 30.86[\pm 1.27] \times (2/(1+\exp(-1.84[\pm 0.50] \times (SLN - 0.94[\pm 0.18]))) - 1) \quad [7]$$

($r^2 = 0.92$; $P < 0.01$) (Fig. 3a),

$$C_{Adark} = -6.88[\pm 1.08] + 16.39[\pm 4.93] \times \exp(-0.70[\pm 0.29] \times SLN) \quad [8]$$

($r^2 = 0.94$; $P < 0.01$) (Fig. 3b).

The change in the response of photosynthesis (C_A) to light intensity (PAR) across a range of leaf SLN levels can therefore be represented by the function:

$$C_A = C_{A\max} - (C_{A\max} - C_{Adark}) \times \exp(0.0016 \times PAR) \quad [9]$$

where ($C_{Amax} - C_{Adark}$) is equivalent to the fitted coefficient *a* described in Eq. [2] and C_{Amax} and C_{Adark} are derived from Eq. [7] and Eq. [8].

Crop Growth

The canopy characteristics which are needed for scaling from leaf photosynthesis to RUE were measured on the growth experiments and presented in Table 1 along with the measured RUE. It can be seen from this table that both the light extinction coefficient (k) and the nitrogen gradient varied during the development of the crop. There was no simple correlation between RUE and average canopy SLN, k or SLN_{grad} ($r^2 < 0.12$). Our aim was to use the approach of Hammer and Wright (1994) to investigate the impact of the variation in the nitrogen gradients and k on the observed RUE.

SCALING FROM LEAF PHOTOSYNTHESIS TO CANOPY RADIATION USE EFFICIENCY

Scaling Methodology

The importance of the observed relationships between nitrogen, light intensity and photosynthesis for resultant crop growth was explored using a simple method to scale from leaf photosynthesis to RUE (Hammer and Wright, 1994). The framework (coded in FORTRAN) accounts for, amongst other factors, both the vertical distribution of N and the light interception characteristics of the canopy. Photosynthesis of sunlit and shaded leaves at each of the specified layers in the canopy is estimated as a function of their light receipt and N status (SLN). The photosynthesis of leaves in all the layers is totaled and adjusted for respiration to calculate a whole-canopy photosynthesis rate. From this value and the calculated light interception, whole canopy RUE can be estimated. Briefly the method follows the procedure:

1. The proportion of light interception by sunlit and shaded leaf area in each stratum in the canopy is estimated from the observed k and the leaf area above the midpoint of the stratum (Table 1).
2. The N content of the leaves in the layer is estimated from the observed average canopy SLN and SLN_{grad} (Table 1).
3. Potential photosynthetic rate of leaves is calculated from the response of C_{Amax} to SLN (Eq. [1]).
4. Photosynthetic rate of the sunlit and shaded leaf area is calculated from the light intensity received at that level (Eq. [2]).
5. The photosynthetic contribution of the layer is calculated by multiplying the photosynthetic rate by the area of the shaded and sunlit leaves.

6. Daily gross photosynthesis is estimated by summing the contribution of each layer and integrating the rates over the day.

7. Net photosynthetic gain is estimated by deducting maintenance respiration for the various organ types from the gross photosynthesis. Maintenance respiration was calculated from values for cotton taken from Hesketh et al. (1971) and Mutsaers (1976).

8. RUE is estimated by dividing the net photosynthetic gain by the integrated light interception for the day.

Further process refinements to the framework explored in this study were to use SLN to estimate the other parameters (which included respiration and the initial slope of the light response curve) defining the light response curve (Eq. [7] to [9]).

No allowance was necessary within the framework for the glucose requirement for the synthesis of different tissue types or growth respiration. This is because RUE calculated from the experimental data has been converted to a glucose equivalent basis (Wall et al., 1994). This circumvents the need to apply an average synthetic efficiency or alter the coefficients within the framework for plants with different partitioning of biomass due to ontogeny.

Scaling Results

Three modifications of the existing method (Hammer and Wright, 1994) to scale from leaf photosynthesis to canopy RUE were assessed. Each was compared with the observed RUE (Fig. 4). The first approach (Fig. 4a) used the functions published in the framework that estimate carbon assimilation (C_A) from light intensity, and uses the response for C_{Amax} versus leaf SLN taken from this study (Eq. [5]). The second approach (Fig. 4b) used Eq. [9] for estimating C_A from light intensity with the relationships of C_{Amax} and C_{Adark} to leaf SLN being derived from the same data (Eq. [7] and [8]). The third approach (Fig. 4c) is the same as the second approach but uses Eq. [5] instead of Eq. [7]. The strength of Eq. [5] is that it is based on much larger sample size, and includes data from both years. In each case actual daylength, light intensity, k, average canopy SLN, SLN_{grad}, and LAI as measured in the growth experiments (Table 1) were used.

The three approaches to incorporate light and nitrogen responses generally gave similar results to each other (Fig. 4). Canopy RUE tended to be over estimated, however using the generalized response for C_{Amax} to leaf SLN (Eq. [5]), the C_{Adark} response from the light response data (Eq. [8]), and C_A versus PAR response again from light response data (Eq. [9]) gave the estimations of RUE with the highest r^2 when the calculated values were regressed against the observations. The slope was not significantly different between the three approaches but the bias was greatest in the first approach. While there was a significant bias, the variation in the calculated RUEs generally reflected that of the observed values. Subsequent analysis is done using the third approach since it has less bias than the first and accounted more of the variation in observed RUEs than the second approach.

Substituting a single overall SLN_{grad} into the calculation instead of the one measured on each sampling date had little impact on the capacity of the method to accurately estimate RUE within the observed range of SLN. Using a uniform vertical nitrogen distribution, that is SLN_{grad} equals zero, for all samplings resulted in little change in the regression equation but slightly increased variability in predicted RUE (Fig. 5). Using a pooled light extinction coefficient (k) caused no change in the estimated RUE.

The sensitivity of the framework to SLN_{grad} and k was tested over a range of average canopy SLN using LAI, photoperiod and radiation for DAS 111 in experiment G1 (Fig. 6). Three different vertical SLN gradients (0.0, 0.4, and 1.2) (Fig. 6a), and two different average light extinction coefficients (0.4 and 0.8) were tested. These represent the higher and lower ends of the observed range of values. We also then explored the interaction of three different canopy LAI (0.76, 2.84 and 5.00) with two different SLN_{grad} (0.31 and 1.30) (Fig. 6c). There was a limited response to the change in SLN_{grad} over the range of average canopy SLN observed in the growth experiments, and only a minimal effect of k. The interaction of LAI and SLN_{grad} showed no effect of the gradient at low LAI but a variation of about 25 to 30 % at LAI 5.

DISCUSSION

Photosynthesis Experiments

Based on the photosynthesis data collected for leaves selected from throughout the canopy, covering a range of ages and conditions, the response of C_{Amax} to SLN was similar to that derived by Reddy et al. (1997) within the range covered by his data (Fig. 1c). The range in our data is very similar to that of Reddall (2000) who reported SLN for leaves of field grown cotton between 0.9 and 4.7, although in an extremely hot season SLN was higher. Over the range of our data, the quadratic equation used by Reddy does not describe the response well at either high or low SLN. At low nitrogen, Reddy's function fell too rapidly compared to the field data. At high nitrogen, although the field data were variable, there was no indication of the photosynthetic response falling as suggested by extrapolation of Reddy's function. The shape of the response was similar to that found for other crops including soybean, rice, maize, peanut, and sunflower (Sinclair and Horie, 1989; Connor et al., 1993; Hammer and Wright, 1994; Bange et al., 1997).

The asymptote of the C_{Amax} curve is comparable to other field based measurements for cotton (Pettigrew and Turley, 1998; Wells, 1988; Stiller, 2000) and the glasshouse trial of Reddy (1997).

However it was approximately 30 percent greater than the highest rates measured by Constable and Rawson (1980) and Wullshleger and Oosterhuis (1990).

The impact of age on leaf photosynthesis has been studied by Constable and Rawson (1980) and Wullschleger and Oosterhuis (1990). Although the latter measured leaves *in situ* within field canopies, thus confounding the influence of leaf age with increasing shading, in both studies C_{Amax} had a strong correlation with leaf age. In this study we also found that leaf SLN and leaf age were strongly correlated (data not shown) however there was still an improvement (9 %) in the ability to account for the variation in C_{Amax} when age was added as a variable after leaf SLN.

The high variation in the relationship between C_{Amax} , age and SLN is surprising. The effects of temperature (El-Sharkawy and Hesketh, 1964; Bednarz and Van Iersel, 2001) and moisture stress (Ackerson et al., 1977; McMichael and Hesketh, 1982; Turner et al., 1986) on photosynthesis of cotton are well documented. However, incorporating these terms provided no improvement in the variability, nor did making allowance for shade acclimation which has been shown to effect C_{Amax} in other species (Evans 1989). It is possible that there were residual effects of age which were not taken into account. Photosynthesis per unit leaf area in cotton usually peaks just prior to full expansion (Constable and Rawson, 1980). However, it is feasible that some of the upper leaves sampled were still in the increasing phase of photosynthesis, thus fitting poorly with the rest of the data which was in the declining phase with leaf age.

The estimates of C_{Amax} derived from the light response functions for the leaves of different SLN classes was consistent with the overall SLN function, showing a similar rise to a maximum (Fig. 2). The concurrent increase of C_{Amax} and C_{Adark} to increasing SLN (Fig. 3) is consistent with the general relationship of C_{Adark} to the preceding rate of C_A (M^{c}Cree, 1974). More specifically, the response of C_{Adark} to SLN (Fig. 3) was consistent with the hypothesis of Barnes and Hole (1978) that respiration rate can be standardised by expressing it on a per unit N basis. The rate of respiration was greater than rates reported by Constable and Rawson (1980), -0.2 to -0.4 μmol CO_2 m^{-2} s^{-1}, as theirs were averaged over the whole night period. Ludwig et al. (1965) reported values of -2 to -2.5 μmol CO_2 m^{-2} s^{-1}, which are closer to those reported here. However, they do not report the N status of the leaves, so direct comparison is not possible. The lack of response in initial light use efficiency to SLN was consistent with the results of Pons et al. (1989) who showed that apparent quantum use efficiency of *Lysimachia* sp. was far less responsive to SLN than C_{Amax} or respiration and those of Connor et al. (1993) who found no response in apparent quantum use efficiency for sunflower.

Thus overall, the response functions for photosynthesis to SLN are of a type consistent with those for other crops and the C_{Amax} values obtained are similar to those previously published for cotton in field and glasshouse studies. The results should provide robust relationships for field grown cotton under favourable conditions, suitable for inclusion in simulation models intended to reflect growth of commercial crops.

Scaling from Leaf to Canopy

The results of this study further demonstrate the robustness of the approach of Hammer and Wright (1994) for scaling from leaf photosynthesis to canopy RUE. The pattern of variation in the calculated RUE was good when compared with the observed data, although there was a significant bias at low RUE. Using more refined responses to account for the effects of nitrogen and light on the photosynthesis of cotton leaves significantly improved our ability to account for the variation in RUE (Fig. 4). We then used the scaling process to explore the relative importance of the dynamics of canopy nitrogen and light on the observed variation in RUE.

The variation in the observations was due to both ontogenetic variation and differences in soil N supply. The values correspond well to those obtained by Sadras (1996). The ability of the method to account for these changes is indicated in Fig. 4. Given this ability, the sensitivity analysis indicates that the calculated RUE is responsive to SLN_{grad} and to a lesser extent to k (Fig. 6). When assessed for their impact on simulating the actual RUEs, however, these parameters had minimal impact. While the importance of these characteristics has been demonstrated in other crops, it has also been shown that they are of most significance at high LAI (Hirose and Werger, 1987). The LAIs measured in our crops were relatively low. When the impact of SLN_{grad} was tested at different LAI, no impact was evident at the lowest LAIs in this experiment but a large impact was evident at an LAI of 5.0 (Fig. 6). The LAI values in the growth experiments are typical of those observed in temperate (Constable and Hearn, 1981; Constable et al., 1990) and well managed tropical crops in Australia (Basinski, 1975; Ockerby et al., 1993) although high N rates can generate much larger canopies (Basinski, 1975; Ockerby et al., 1993). Thus there is no evidence that ontogenetic changes in SLN_{grad} or k generally contribute to the dynamics of RUE for Australian cotton crops.

The approach of Hammer and Wright (1994) was developed from one previously published (Sinclair and Horie, 1989) by including the provision for SLN_{grad}. It appears that there is some value in including the gradient in that it gave a small improvement in the r^2 of the regression against observed RUE values (Fig 5.). However, for simulating cotton growth, a single value for the gradient appears adequate and there is no benefit in varying the gradient for crop development.

The reasons for the bias in the calculated RUE at low values needs to be explored. Possible reasons for the bias are the estimation of maintenance respiration rate, the degree of partitioning to the roots, and the effects of reproductive organs on canopy light interception and distribution. Limited data are available on these aspects of cotton growth. In support of the idea that root partitioning is the cause, most of the points which lie furthest from the 1:1 line are the earliest sampling in each treatment. At these samplings partitioning to the roots would have been highest which would have increased the observed RUEs if it had been taken into account. Excluding these six points from the regression reduced the bias, increased the slope to 0.75, and increased the r^2 to 0.77.

CONCLUSIONS

The central finding of this study is that there appears to be little impact of the ontogenetic changes in k and SLN_{grad} on the variation in RUE. For crop simulation purposes, this simplifies the process of modulating RUE in growth models. The results also indicate that the approach of Hammer and Wright (1994) was effective in capturing the variation in the RUE of cotton as observed in the growth experiments, although further refinement would appear worthwhile.

The overall shape of the relationship between photosynthesis and leaf SLN for cotton was consistent with that for other species. Incorporating the influence of age improved the relationship significantly but by less than 10 percent, in spite of the correlation of leaf SLN and age. The photosynthesis relationship developed should be appropriate for use in simulating cotton crops.

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Table 1: Observed canopy parameters and radiation use efficiency (RUE) for the three growth experiments: Experiment G1 sown 1995, Experiment G2 sown 1996, Experiment G3 sown 1998. (DAS, days after sowing; k, light extinction coefficient; LAI, leaf area index; SLN, average canopy specific leaf nitrogen; SLN_{grad}, vertical SLN gradient within the canopy). Numbers in parentheses are standard error of the mean.

Experiment/Treatment	DAS	LAI	k	SLN ($g\ m^{-2}$)	SLN_{grad}	RUE ($g\ MJ^{-1}$)
G1 (95-96)	83	0.97 (0.09)	0.44 (0.11)	1.93 (0.02)	0.43 (0.13)	1.21 (0.11)
	96	1.71 (0.06)	0.46 (0.07)	1.87 (0.06)	0.50 (0.09)	1.67 (0.13)
	111	1.98 (0.07)	0.44 (0.06)	2.05 (0.06)	0.34 (0.06)	2.04 (0.09)
	124	2.52 (0.22)	0.62 (0.08)	1.71 (0.04)	0.42 (0.05)	1.66 (0.14)
G2 (96-97) High N	77	1.65 (0.13)	0.36 (0.04)	2.46 (0.09)	0.72 (0.09)	1.50 (0.07)
	94	1.89 (0.13)	0.46 (0.04)	2.31 (0.07)	0.82 (0.12)	2.17 (0.13)
	113	2.65 (0.17)	0.42 (0.04)	1.90 (0.04)	0.31 (0.04)	2.69 (0.52)
G2 (96-97) Low N	77	0.76 (0.05)	0.44 (0.04)	1.73 (0.02)	0.58 (0.16)	0.81 (0.06)
	94	0.91 (0.03)	0.47 (0.04)	1.46 (0.04)	1.17 (0.11)	1.06 (0.07)
	113	1.01 (0.03)	0.47 (0.04)	1.29 (0.03)	1.03 (0.18)	1.31 (0.16)
G3 (98-99) High N	87	1.82 (0.31)	0.54 (0.14)	2.66 (0.08)	1.00 (0.20)	1.61 (0.26)
	105	2.54 (0.46)	0.53 (0.10)	1.94 (0.09)	1.78 (0.30)	1.97 (0.41)
	117	2.33 (0.32)	0.69 (0.11)	2.13 (0.18)	1.27 (0.22)	2.74 (0.42)
	132	2.84 (0.22)	0.65 (0.10)	1.68 (0.09)	1.20 (0.38)	3.10 (0.51)
G3 (98-99) Mid N	87	1.09 (0.06)	0.44 (0.08)	1.60 (0.03)	0.96 (0.12)	1.19 (0.05)
	105	1.32 (0.03)	0.45 (0.07)	1.37 (0.07)	1.02 (0.10)	1.64 (0.04)
	117	1.39 (0.04)	0.47 (0.07)	1.54 (0.06)	0.88 (0.06)	1.59 (0.20)
	132	1.28 (0.18)	0.61 (0.09)	1.63 (0.13)	0.79 (0.15)	1.05 (0.40)
G3 (98-99) Low N	87	0.79 (0.15)	0.54 (0.09)	1.64 (0.16)	0.69 (0.16)	0.89 (0.18)
	105	1.17 (0.24)	0.47 (0.09)	1.50 (0.06)	0.43 (0.23)	1.46 (0.07)
	117	1.05 (0.09)	0.56 (0.10)	1.58 (0.10)	0.38 (0.08)	1.45 (0.50)
	132	1.06 (0.10)	0.56 (0.10)	1.36 (0.06)	0.51 (0.11)	1.27 (0.38)

Fig. 1. Relationship between leaf assimilation rate measured at 2000 μmol m^{-2} s^{-1} (C_{Amax}) and specific leaf nitrogen (SLN) of individual leaves for (a) experiment P1 sown 13 October 1999, (b) experiment P2 sown 28 October 2000 and (c) with both experiments combined. For comparison, the fitted curve of Reddy et al. (1997) is also presented in (c).

Fig. 2: Relationships between leaf assimilation rate (C_A) and light intensity (PAR) for three categories of specific leaf nitrogen (SLN) of individual leaves as measured in experiment P2 (2000-2001). The responses are for SLN of 1.45 (●, solid line), 2.76 (▲, dotted line), and 4.32 (□, broken line).

Fig. 3. Relationships of (a) leaf assimilation rate measured at 2000 μmol m^{-2} s^{-1} (C_{Amax}) and (b) leaf CO_2 assimilation rate measured in the dark (C_{Adark}) plotted against specific leaf nitrogen (SLN) of individual leaves. These responses are derived from data of experiment P2 (2000-2001) specifically used to measure the response of leaf assimilation rate to light intensity.

Fig. 4. Calculated radiation use efficiency (RUE) versus observed RUE. Three approaches using the existing method of Hammer and Wright (1994) that scales from leaf photosynthesis to canopy RUE are compared. The first comparison (a) used the published functions in the Hammer and Wright (1994) that estimate carbon assimilation (C_A) from light intensity, and uses the response for C_{Amax} versus leaf SLN taken from this study (Eq. [5]). The second comparison (b) used Eq. [9] for estimating C_A from light intensity with the relationships of C_{Amax} and C_{Adark} to leaf SLN being derived from the same data (Eq. [7] and [8]). The third comparison (c) is the same as the second approach but uses Eq. [5] instead of Eq. [7].

Fig. 5. Calculated radiation use efficiency (RUE) compared to observed RUE. Values were calculated using either (i) a vertical SLN gradient within the canopy (SLN_{grad}), or (ii) a uniform vertical distribution. The method used here utilizes responses taken from this study (Eq. [5], [8], and [9]).

Fig. 6. Sensitivity analysis of the scaling method: The predicted response of radiation use efficiency (RUE) to average canopy specific leaf nitrogen (SLN) for (a) three different vertical SLN gradients within the canopy (SLN_{grad}) (0.0, dotted; 0.4, broken; 1.2, solid line), (b) two different average light extinction coefficients (k) (0.4, broken; 0.8, solid line) and (c) a combination of three different canopy LAI (0.76, 2.84 and 5.00) with two different SLN_{grad} (0.31, dotted; 1.30, solid).

Determinacy in cotton: measurement and potential implications

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Abstract

Cotton is an indeterminate species. However, the term 'determinate' is applied to cultivars that terminate reproductive development comparatively abruptly and do not readily begin a second fruiting cycle. It has been suggested that low determinacy may have agronomic benefit when intermittent stresses interrupt reproductive development. We developed two objective measures of determinacy. The first reflects the speed with which a cultivar approaches the point where dry matter is monopolised by developing fruit. The second reflects the outcome of this process in terms of the declining rate of node production relative to the rate at which flowers are exserted on successive nodes up the main stem. Both were correlated to the breeders' subjective assessment of determinacy but were also strongly correlated to each other. It will be necessary to demonstrate the repeatability of this approach to assessing determinacy and to test its applicability under a range of conditions and with different groups of cultivars. Experiments to use these measures to explore whether low determinacy confers an advantage in conditions of intermittent drought stress, such as dry land cotton production, are underway.

Key words

Development, fruit, partitioning, phenology, reproductive partitioning.

Introduction

Cotton is an indeterminate species. The mainstem does not terminate in a reproductive meristem. The terminal is morphologically capable of continuing to produce new nodes that exert branches on which the fruit are born. The timing of crop maturity is determined by when the plant stops producing new fruit ('cutout') due to the demand on the assimilate supply by growing fruit leaving none for the initiation of new fruiting sites. The concept of cotton crop 'determinacy' is used to describe how abruptly a cultivar tends to cut out and how readily it will start a second cycle of fruit production (1). A so-called determinate cultivar is one that cuts out abruptly and will not readily start a second fruiting cycle.

It has been suggested that cultivars with low determinacy are important for rainfed production because they allow growth to resume more readily after retardation due to drought stress. In irrigated crops, low determinacy may allow a higher degree of recovery from damage by insects later in the season. However, there is little documented evidence of the efficacy of these concepts.

The degree of determinacy is strongly associated with whether a cultivar is a short or long season type. Short season cultivars are widely considered determinate. While cultivars are described as determinate or indeterminate, there is no empirical evidence demonstrating the existence of such a trait independent of maturity type. As a preliminary step toward determining the value of determinacy as an agronomic trait, we explored whether varietal (genetic) variation in determinacy actually exists and how this might be characterised. The growth of eight cultivars, which have been qualitatively assessed as differing in determinacy and maturity, were studied in the field. The degree to which they differed in their ability to continue to produce new organs during increasing boll load was explored.

Materials and methods

Three field experiments were conducted at Narrabri (30.31° S 149.78° E), Australia in the 1999-2000, 2000-2001 and 2001-2002 seasons. Each experiment included two sowing times so as to generate variation in temperature and radiation regimes, which in turn would influence dry matter production and fruiting patterns. Cotton lines with known differences in timing of crop maturity and determinacy, as assessed by the CSIRO cotton breeding team, were used (Table 1).

Sowing times and lines were combined factorially. Plots (8 m by 18 m), containing eight rows spaced at 1 m, were sown in October (S1), and November (S2). Randomised complete block designs were used with three replications. The experiments were grown with full irrigation on a grey-clay soil utilising high input management and insect control as described in Hearn and Fitt (2).

Table 1. Description of lines used in field experiments (P. Reid, personal communication).

Name	Maturity	Determinacy
Tamcot HQ95	Very early	High
Siokra S-102	Early	Medium-high
89007-33	Early-medium	Medium-high
Siokra V-16	Medium-Late	Low
Selection 118	Late	Low
Sicot 189	Late	Low
CS 8S	Early	Medium
Albar G501	Very late	Low

In the first two experiments, starting just prior to the appearance of the first square, destructive plant samples were taken from 1 m^2 quadrats approximately every two weeks. Total dry weight and dry weight of leaf (laminae), stem (including petioles), squares (flower buds), green bolls (capsules) and open bolls were determined.

In the third experiment, after the plants had reached first flower, the number of nodes above the highest open flower on the plant was counted each week. This number declines due to increasing boll load as the rate of node production slows but the rate at which flowers are exserted (and hence open) at successive nodes up the main stem remains constant.

Results

The cultivars differed in their pattern of dry matter accumulation and partitioning. Two examples of the variation of crop and fruit growth rate over time are presented in Figure 1. There appeared to be a tendency for cultivars that had been described by the breeder as determinate to approach the point where the fruit biomass accumulation rate matched the total dry matter accumulation rate more rapidly. By ranking the cultivars within each time of sowing according to the degree of abruptness with which they approached this point, that is the angle of intersection of the lines, and averaging this across the sowings and years, a determinacy ranking was derived. This was found to be well correlated with the breeders' ranking (Figure 2a). However, since maturity and determinacy ranking of the breeder were highly correlated, our derived ranking also correlated with maturity (Figure 2b).

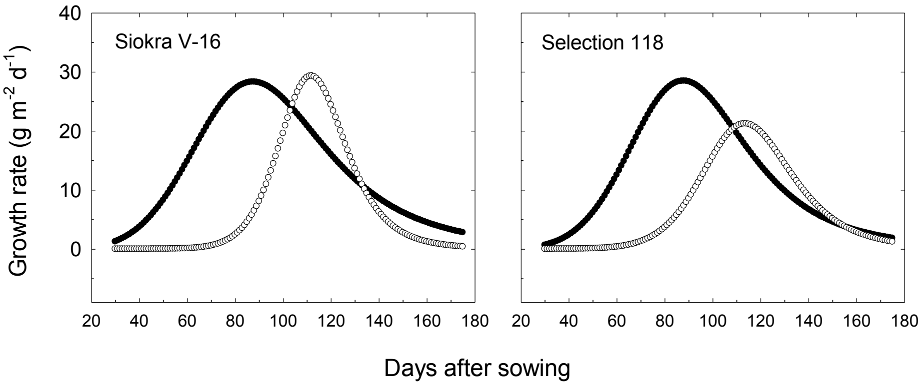

Figure 1. Examples of crop growth rate (closed symbols) and reproductive growth rate (open symbols) used to derive determinacy ranking.

In the third experiment an alternative measure was determined for each cultivar. This was derived from the rate of decline in the number of nodes above the highest open flower. The values ranged from -0.125 nodes per day for Albar G501 to -0.165 nodes per day for Siokra S-102. The rate was weakly associated with the breeders ranking for determinacy but well associated with the physiologically derived determinacy ranking except for the two okra leaf cultivars (Figure 3). The okra leaf cultivars were markedly offset from the regression line for the normal leaf cultivars.

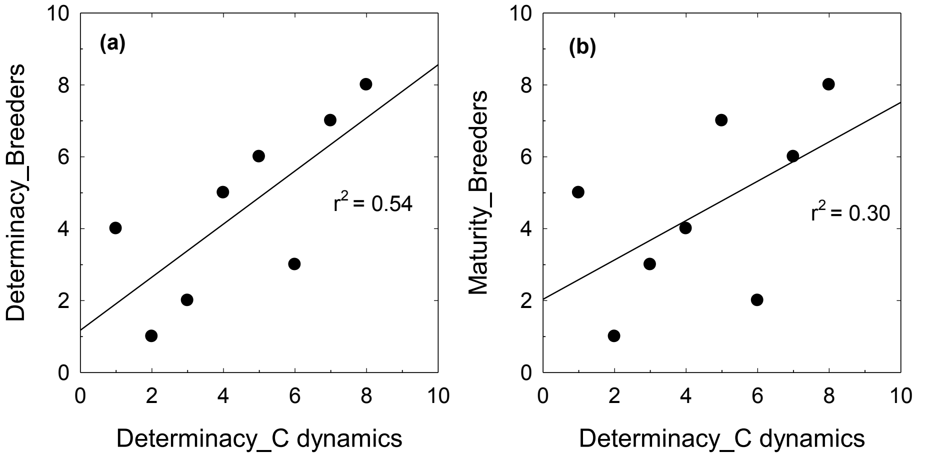

Figure 2. Comparison of rankings of cultivar determinacy (a) and maturity (b) from CSIRO breeding team (G.A. Constable, personal communication) with determinacy ranking derived from carbon dynamics.

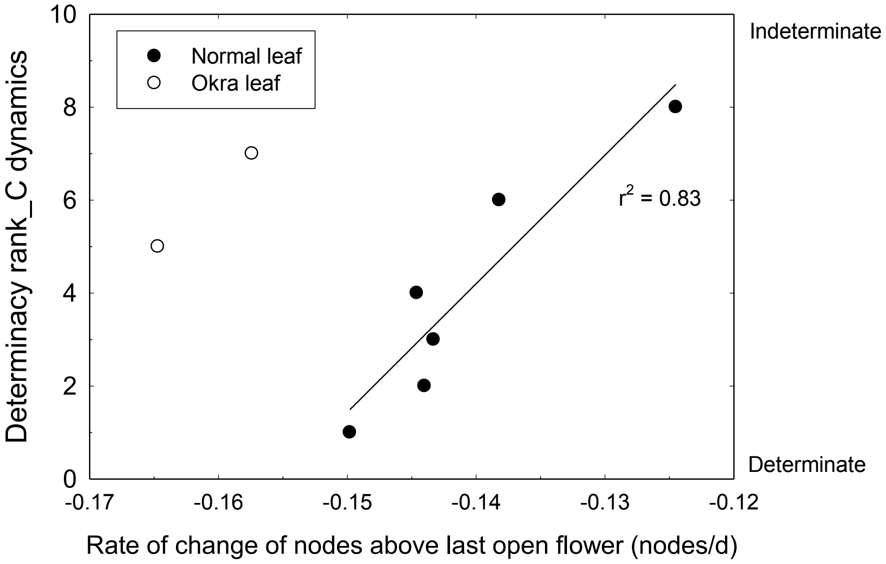

Figure 3. Determinacy ranking of cultivars derived from carbon dynamics versus the rate of change of nodes above highest open flower as an alternative measure of determinacy.

Discussion

This is the first study that we are aware of to attempt to derive an objective, quantifiable measure associated with determinacy in cotton. That both the biomass accumulation and flowering rate indices were correlated to the breeders' field assessment suggested that they might provide a suitable basis for an index of determinacy. The measure based on rate of decline in nodes above last flower is the simpler of the two for field use. That the two measures were well correlated, even though they were derived from different experiments, indicated a likely link between the putative physiological process and the morphological outcome and thus adds weight to the validity of the more simple approach.

The offset of the two okra leaf cultivars in the correlation between the two indices (Figure 3) could relate to leaf-size profiles on okra compared with normal cultivars. Okra leaf cultivars have smaller individual leaves and this is exacerbated at higher node positions by declining temperatures (3). The result is a more rapid decline in canopy photosynthesis as the canopy ages and so, because of competition from the fruit, a more abrupt reduction in node production and hence the more rapid decline in the number of nodes above the highest open flower in the okra cultivars. This mechanism will be explored in more detail in future experiments, which will include more okra leaf cultivars.

Experiments are currently underway to assess whether those cultivars that were assessed as indeterminate show any greater ability to tolerate drought stress in terms of their ability to continue to produce fruit or reinitiate fruit production after a stress.

Acknowledgements

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Is earliness really next to Godliness?

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CSIRO Plant Industry and Australian Cotton CRC. Narrabri, NSW.

Earliness can be manipulated by choice of cultivar, insect management, water or nutrition. Early crop maturity may allow you to pick earlier to avoid quality down grades and perhaps save on late season insect protection. However, this needs to be balanced against the fact that earliness may cost you between 0.6 and 1.0 bales/ha per week in lost yield.

Match your cultivar choice to the desired timing of crop maturity first and tune water and nutrition inputs. This allows appropriate implementation of IPM.

Introduction

At various times, strong interest develops within the industry for early crop maturity. Earliness can allow the manager to harvest the crop in a more timely manner and thus reduce the risk of quality down grades due to weather damage. It can also mean a saving on water and late season spray costs if the period for which protection is required can be reduced. In this paper we will bring together some pieces of ongoing research which are dealing with aspects of the timing of crop maturity.

In this article we use the term 'earliness' to describe the time taken from sowing to crop maturity, defined as 60% of the bolls open. Thus, a crop which is sown ten days later than a normal crop but harvested only five days later, has greater earliness because the growth period is reduced.

The Mechanism of Earliness

It is generally understood that the timing of crop maturity in cotton is not determined solely by temperature and day length as in many other crops, but by the balance of supply and demand of resources to the developing fruit and growing points. When the fruit load develops to the point were the rate of growth monopolises the entire supply rate of resources, the crop cuts out and ceases to produce new fruit. Because of this, the timing of crop maturity can actually be manipulated by altering either the supply of resources to the fruit or the demand by the developing fruit load. In terms of differences between cultivars, the biggest difference is in fruiting patterns, hence the developing demand for resources.

In experiments conducted over the last eight years, we have looked at whether there is much difference between late and early cultivars in their ability to supply resources to the fruit in an attempt to test if this explains why early maturing varieties are early. In terms of capturing light and converting it into growth we found that there was a surprisingly small amount of variation. The cultivars had a similar capacity to intercept light per unit of leaf area. They also had a similar capacity to convert the light they intercepted into photosynthate and hence dry matter. Other researchers who have compared cotton genotypes for other purposes have also found these traits to be fairly stable, although they did not specifically compare early and late cultivars.

As expected, the characteristic that varied most between the cultivars was the way that the fruit load developed. An earlier fruit load development led to an earlier cut out and hence earlier maturity. The analysis of this data is still under way to better understand how we can utilise this principle in crop management.

Manipulating Earliness

The timing of crop maturity can be manipulated by a range of management factors. Fruit retention, and hence insect control, is a key driver. Variety, nitrogen and water are three other factors.

Varying nitrogen rate or water stress modifies the growth rate of the plant and so alters its capacity to support fruit. This means that the time taken for the supply rate to be matched by the increasing fruit demand varies. Brian Hearn and others have demonstrated this, and shown that when other factors are not limiting, it is biologically possible to generate a wide variation in crop maturity time by varying nitrogen rate, for example high nitrogen rates can extend crop maturity. However, when considering the range of inputs typical in commercial systems, the difference is far less; one week at the most.

It is far easier to generate a difference in maturity by modifying retention rates early in the season. It must be born in mind that low action thresholds early in the season work against IPM and may have little economic benefit in terms of increasing yield, however protecting the crop early in fruiting allows a rapid accumulation of boll dry matter and hence forces the crop to cut out sooner. This is seen for example in commercial Ingard® crops. In controlled experiments, early fruit retention rates (through the use of Ingard® varieties and lower action thresholds) were able to induce a variation in earliness that was three to four times greater than that caused by manipulating nitrogen, water and Pix®.

The decision to attempt to manipulate earliness may be based on a number of different factors. One might be to attempt to match harvest time to months with a lower likelihood of rain. In short season environments, early crop maturity is imperative. In these conditions, late maturity can result in high yield variability due to late crops being truncated in cooler years and a reduced average long term yield. However, in full season environments the cost of earliness should be assessed. There is a general relationship between the duration of crop growth and yield. For each day that maturity is brought forward, there is a yield loss of between 20 and 35 kg/ha per day, that is between 0.6 to 1.0 bales/ha per week (Fig. 1).

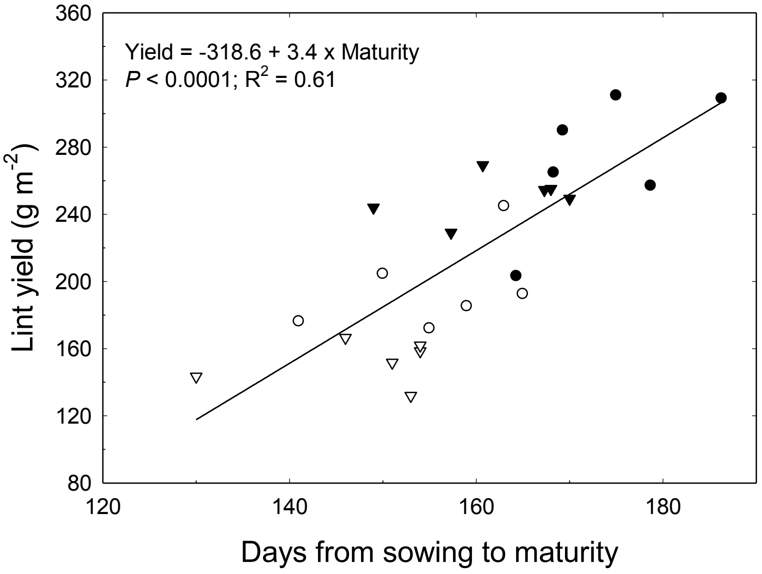

Figure 1. The relationship between yield and crop duration for a range of cultivars, years and sowing dates at Narrabri. For each week that the crop matures earlier yield decreased by about 1 bale/ha. Similar relationships have been found in a number of studies.

On-farm experiments conducted in the Namoi Valley, Bourke and McIntyre Valley, as part of a CRC farming systems study on earliness, showed that on average, reducing the nitrogen rate and increasing Pix® application resulted in crops being three days earlier but yielding 0.3 bales less. By contrast, simply choosing an earlier cultivar resulted in eight days earliness but no significant loss in yield. When examined on a case by case basis, however, the early variety showed a yield advantage at Boggabri (cool area) but a yield penalty at Bourke (warm area) (Fig 2). Clearly it is important to match crop maturity type to season length and use as much of the growing season as possible if you wish to maximise yields.

When cultivar choice is correctly matched to region, then nitrogen and water management need to be optimised to ensure adequate, but not excessive, crop growth. Over supply of either can delay maturity and cause excessive vegetative growth. IPM can then be appropriately applied. Cultivar choice and pest control are the key components of managing earliness (Fig. 3). If the cultivar type is too late for the region, greater emphasis is needed on insect management to ensure high retention rates and hence earliness. However, this is likely to compromise IPM strategies and may sacrifice yield and reduce profitability.

Thus, to avoid losing yield unnecessarily, match variety to season length, whether this is based on temperature or some other parameter, and manipulate other inputs (nitrogen, water, Pix®) to match crop requirements. It is also important to ensure that an appropriate IPM approach is also adopted to achieve sensible levels of retention at flowering.

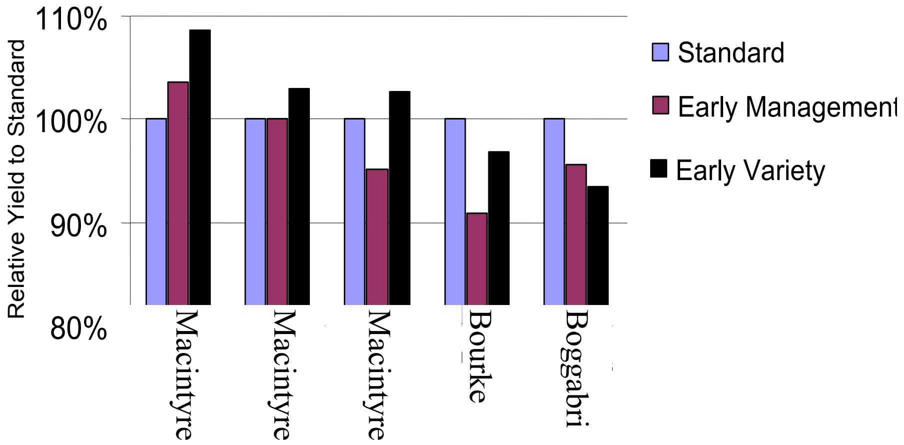

Figure 2. Yield of crops which were managed for early maturity, or for which an early cultivar was used, compared to a standard cultivar grown with standard management.

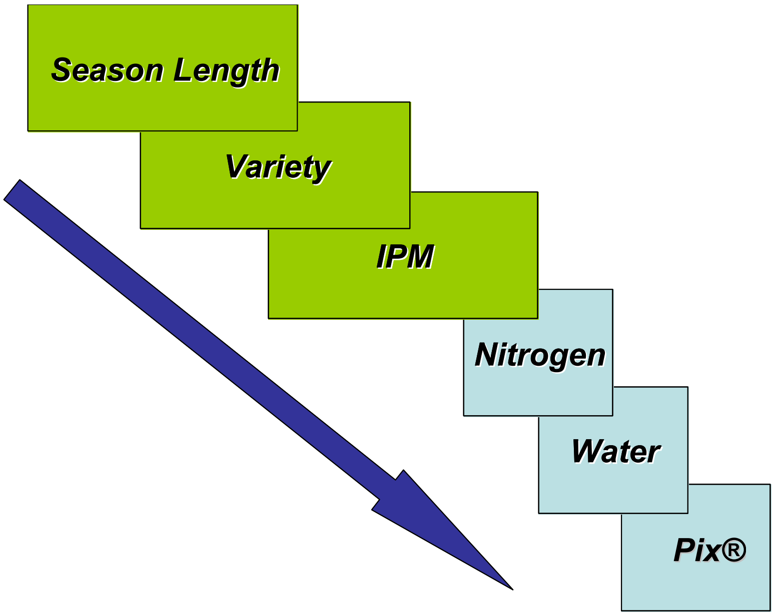

Figure 3. The level of importance of factors in manipulating earliness. Matching cultivar to season length is the first step when targeting correct maturity time without loss of yield. This allows appropriate implementation of IPM rather than striving for high retention to achieve earliness.

Ongoing Research

Research into earliness and the mechanisms that drive the timing of crop maturity is continuing. This includes research at the farming systems scale, crop agronomy and physiology. The capacity of the crop to compensate for insect damage and the concept of determinacy are two components being examined.