TEMPERATURE-TIME THRESHOLDS FOR IRRIGATION SCHEDULING IN DRIP AND DEFICIT FURROW IRRIGATED COTTON

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A thesis submitted for the degree of Doctor of Philosophy
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October, 2010

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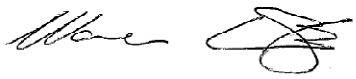

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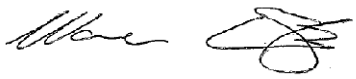

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ABSTRACT

Water is one of the most limiting factors to Australian cotton production. Improved irrigation scheduling efficient water use is central to the sustainability of the Australian irrigated cotton industry. Irrigation scheduling is a two-fold process where-by the amount and frequency of water applied to a plant is determined. Producers must aim to optimise crop water use through timely irrigation scheduling and efficient utilisation of in-crop rainfall. Currently, furrow irrigation is the dominant form of irrigation delivery and cotton farmers use a limited range of methods to make irrigation decisions. A combination of the cost, accuracy and complexity of these methods has limited their effective use in commercial production. In this study a potentially simpler method based on crop canopy temperatures and the thermal optimum concept was investigated.

Compared to well-watered plants, water stressed plants exhibit elevated canopy temperatures. This is a consequence of the closing of stomata, in response to soil water deficits. The closure of stomata results in a decrease in transpiration and consequently a reduction in latent energy flux, leading to a rise in canopy temperatures. However, ambient conditions can have a large influence on canopy temperatures; thus canopy temperatures are a reflection of both plant and environmental factors. In order to develop indicators of the early onset of water and temperature stress, research conducted in the USA developed a theory that defined optimal plant temperatures with respect to the thermal dependence of the Michaelis-Menten constant of an enzyme (K_m). The optimal enzymatic function was restricted to a range of ambient temperatures that was termed the thermal kinetic window (TKW), which is an indicator of the optimal temperature range of

a plant species. Using alternative diagnostic methodologies of chlorophyll fluorescence recovery rates and analysis of plant physiological function under field conditions, the optimal temperature of an Australian cultivar was identified to be ~28 °C. Although this was consistent with values obtained from US cotton cultivars, and average day-time canopy temperatures that were achieved in the field at close to optimal water applications, it was important to verify this as Australian cotton cultivars are genetically different to US cultivars and the combined effect of different genetics and ecological adaptations may potentially influence the optimal temperature of biochemistry.

The TKW theory was used as the basis for the BIOTIC (Biologically Identified Optimal Temperature Interactive Console) protocol. This protocol was developed by researchers at the USDA-ARS, and uses the relationship between canopy temperature (T_c) and plant water status to schedule irrigation using a temperature-time threshold system. Irrigations are commanded when the crop's T_c exceeds an optimal temperature threshold for a pre-determined period of time. Using the BIOTIC system as a basis, this study aims to assess the physiological base and utility of the thermal optimal approach to schedule irrigation, with particular emphasis on its use in precision application and large soil water deficit irrigation systems of the Australian cotton industry. Deficit irrigation is an optimisation strategy where full crop water requirements are not necessarily provided, improving water-use efficiency (WUE). The thermal optimal approach was studied previously; however, its use was limited to irrigation systems that provide full water requirements at high irrigation frequencies and low irrigation volumes. Hence, its application to deficit and furrow irrigation systems was unknown.

The physiological basis of the principles underlying the thermal optimum concept for irrigation scheduling was examined through the monitoring of T_c of the commercial cotton cultivar Sicot 70BRF at 'Myall Vale' Narrabri Australia. Surface drip irrigation experiments were conducted in the 2007/08 and 2008/09 seasons, where irrigation treatments were based on daily crop evapotranspiration (ET_C) rates calculated using the FAO56 protocol with a locally calibrated crop coefficient. A furrow-irrigated experiment was conducted in the 2008/09 season, where irrigation treatments were based on plant available soil water deficits (mm) from field capacity calculated from neutron attenuation data. The objectives of this research were to: (1) confirm that the optimum temperature (T_{opt}) of a current commercial Australian cotton cultivar (Sicot 70BRF) is the same as other measured USA cotton cultivars; (2) determine if T_c can define plant water stress by comparison with soil and atmospheric conditions; and (3) determine the potential of the thermal optimum approach to scheduling irrigation in Australian cotton systems.

The hypothesis that T_c provides sufficient information for irrigation scheduling was investigated in the surface drip and furrow irrigated cotton. Irrigation treatments resulted in differences in lint yield, plant architecture, growth, biomass accumulation and T_c. Canopy temperatures were correlated with crop lint yield and the volume of water applied to the crop. Peak lint yields occurred at average day-time ($R_n > 300$ W m^{-2}) T_c of 26.4 ± 1.7 °C and total water of 108% calculated ET_C under surface drip conditions, and at T_c of 28.6 °C ± 0.6 °C and water supplies of 99% calculated ET_C under furrow irrigated conditions. Acclimation of T_c due to the wetting and drying cycles of furrow irrigation did not occur and the combination of both furrow and drip irrigated data showed a single

relationship where peak lint yields occurred at T_c of 28 °C. This highlights the benefits of maintaining average canopy temperatures close to 28 °C, and supports the potential utility of the thermal optimum concept in Australian drip and furrow irrigated cotton.

Although lint yield is proportional to the thermal optimum, the physiological limitations of a plant can mean that a well-watered plant's T_c can still exceed the thermal optimum. This gives rise to the stress time (ST) concept, where ST represents the average daily period of time that a well-watered crop's T_c can exceed its optimum temperature. The ST concept was tested and adapted to Australian field-based drip and furrow irrigation systems. Peak lint yields and crop WUE (the ratio of lint yield produced per hectare to the cumulative amount of water used by the crop through evapotranspiration) in drip-irrigated cotton occurred at 4.5 h ST, considerably higher than the empirically calculated threshold of 2.8 h. A thermal optimum protocol was developed to schedule furrow irrigation events through a cumulative ST approach, where one ST h represents 0.6 mm plant available soil water depletion, enabling a producer to determine the desired soil water deficit and schedule irrigations based on cumulative ST. An integrated approach to stress detection was also proposed. This approach, the sum of cumulative ST, is theoretically advantageous as it considers both the degree and duration of time T_c exceeding the optimum.

The physiological principle underlying a thermal optimal approach to irrigation scheduling were analysed in this thesis. An independently estimated optimal temperature was determined to be 28 °C. This optimal temperature was correlated with peak lint

yields, and T_c was responsive to irrigation. A stress time threshold producing peak lint yield was developed in surface drip irrigation systems, and a cumulative stress time threshold for soil water deficits was outlined for furrow irrigation systems. These modified stress time thresholds provided the information required to detect water stress for irrigation scheduling. The practical implication of this research is that temperature-time thresholds in a thermal optimal irrigation scheduling system have utility in the irrigated Australian cotton industry. However, the time thresholds that were determined in this study were developed by monitoring cotton crops with infra red thermometers, and irrigations were not scheduled with a thermal optimum protocol in this study. With field validation, these irrigation protocols could be used as the basis for a modified BIOTIC system and be adopted by the commercial cotton industry, as it is a simple, cost effective irrigation scheduling system.

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ABBREVIATIONS

A	Photosynthetic rate (μmol (CO_2) m^2 s^{-1})
ABA	Abscisic acid
ABARE	Australian Bureau of Agricultural Resource Economics
ABS	Australian Bureau of Statistics
ACRI	Australian Cotton Research Institute
ATP	Adenosine triphosphate
BIOTIC	Biologically Identified Optimal Temperature Interactive Console
BOM	Bureau of Meteorology
BRF	Bollgard Round-up ready Flex
Bt	*Bacillus thuringiensis*
CSD	Cotton Seed Distributors
CSIRO	Commonwealth Scientific and Industrial Research Organisation
CTD	Canopy Temperature Depression
CWSI	Crop Water Stress Index
DAS	Days After Sowing
DD	Degree Days
ET	Evapotranspiration
ET_C	Crop Evapotranspiration
ET_O	Reference Evapotranspiration
F_m	Dark adapted maximal fluorescence
F_o	Dark adapted initial fluorescence
F_v	Dark adapted variable fluorescence
g_c	Stomatal conductance to water vapour (mol (H_2O) m^2 s^{-1})
HSP	Heat Shock Protein
HVI	High Volume Instrument
IRGA	Infra-Red Gas Analyser
IRT	Infra-Red Thermometer
K_c	Crop co-efficient
K_m	Michaelis-Menten constant
LAI	Leaf Area Index
LHCPSII	Light Harvesting Complex of Photosystem II
l.s.d.	Least significant difference
NMM	Neutron Moisture meter
NSW	New South Wales
PAR	Photosynthetically Active Radiation
PAWC	Plant Available Water Capacity
PRD	Partial Root-zone Drying
PEP	Phosphoenopyruvate
pH	Concentration of hydrogen ions (H^+) in solution, measured on log scale from 0 to 14
PSII	Photosystem II

QLD	Queensland
RCBD	Randomised Complete Block Design
RDI	Regulated Deficit Irrigation
R_n	Net radiation
R_g	Short-wave irradiance
Rubisco	Ribulose-1,5-biphosphate carboxylase-oxygenase
ST	Stress time (hours)
STT	Stress time threshold for irrigation scheduling (hours)
T_a	Air temperature (°C)
T_c	Canopy Temperature (°C)
T_l	Leaf temperature (°C)
T_n	Normative plant temperature (°C)
T_{opt}	Optimal plant temperature (°C)
T_s	Soil temperature (°C)
TDM	Total Dry Matter
TKW	Thermal Kinetic Window
TT	Temperature Threshold
USDA-ARS	United States Department of Agriculture-Agriculture Research Service
VPD	Vapour Pressure Deficit (kPa)
WUE	Crop water-use efficiency (kg (lint) mm^{-1} ha^{-1})
Ψ_l	Leaf water potential

PUBLICATIONS BY THE CANDIDATE RELEVANT TO THE THESIS

Yeates, S., Neilsen, J., Conaty, W., and Roberts, J. (2008) Irrigation scheduling and cotton productivity during the drought. In *'Cotton in a climate of change. Proceedings 14th Australian Cotton Conference'* Gold Coast, Australia, 12-14 August 2008

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Mahan, J.R., Conaty, W., Neilsen, J., Payton, P. and Cox, S.B. (2010) Field performance in agricultural settings of a wireless temperature monitoring system based on a low-cost infrared sensor. *Computer and Electronics in Agriculture*, **71**, 176-181.

ACKNOWLEDGEMENTS

I would like to thank and acknowledge the support and advice from the following people: My supervisors, Prof Bruce Sutton, Dr James Neilsen, Dr James Mahan and Dr Daniel Tan, who have all made generous investments of time and expertise into this thesis. In particular, thanks Bruce for your support and guidance throughout and your valued comments on the thesis. Jimmy, thanks for your sustained support, guidance and friendship throughout the entire Ph.D. process from the research proposal to submission. James, I have enjoyed working with you and appreciate your continued effort and interest from across the Pacific. I hope that the "general vibe" of this thesis directs it "straight to the pool room". Dan, I am so grateful for the timely guidance, openness and help you have provided to me, both before and during my Ph.D. candidature.

I would also like to thank Dr Michael Bange for his continued support and direction throughout my candidature. I appreciate the selfless help and guidance you have given me, your name should be in the paragraph above.

I gratefully acknowledge the advice and feedback provided by Dr Greg Constable, Dr Warwick Stiller, Stephen Yeates, Dr Nicola Cottee, Dr Paxton Payton, Dr Lewis Wilson, Dr Rose Brodrick and Dr Michael Braunack, all of whom provided valuable help, discussion and comment during the planning and reviewing of experiments and during the writing of the thesis.

Sincere thanks to the staff of ACRI, Myall Vale, especially Jonathan Cuell, Jenny Roberts, Mitchell Cuell, Martyn Tann, Norm Winters, Peter Bell, Des Magaan, Jo Price, Darin Hodgson, Rebecca Warnock, Jane Caton and Loretta Clancy as well as Guy and Ingrid Roth in Narrabri, and Julia Brown, Andrew Young, Tommy Martin and Jeff McNeill in Lubbock, for technical support and advice throughout my candidature. I would also like to extend my immense gratitude to John Burke and Jacob Sanchez for advice and conducting some laboratory work on optimal temperatures.

The financial support of The University of Sydney, the Cotton Catchment Communities Cooperative Research Centre, and the Cooperative Research Centre for Irrigation Futures is gratefully acknowledged. The provision of field and laboratory resources by The University of Sydney, CSIRO Plant Industry and USDA-ARS Lubbock is also gratefully appreciated.

I would like to acknowledge the support and encouragement from my friends and family, particularly Mum, Dad, Simon, Justine, Cassie, and Non and Pa.

Finally, I would like to thank Merry. Thanks for all your sustained and selfless support, love, understanding and tireless assistance, without which this would have not been possible.

1. GENERAL INTRODUCTION

1.1 Background

The cotton genus (*Gossypium* sp.) consists of more than 50 species of perennial xerophytic shrubs (Hearn, 1994; Hearn and Constable, 1984). The genus is pan-tropical and characterised by short-day plants of the arid tropics and sub-tropics, occurring along dry stream beds with some hardier species extending to plains and slopes (Hearn and Constable, 1984). Of these 50 species in the genus, only four are cultivated: *Gossypium hirsutum* (Upland cotton), *G. barbadense* (Pima cotton), *G. arboreum* (Asian cotton) and *G. herbaceum* (Levant cotton). These true cotton species possess lint, convoluted and flatted seed hairs made from cellulose with a thin coating of wax, which can be spun into yarn. Only one wild species of cotton, *G. herbaceum* race africanum, has lint and is generally regarded as the ancestor of modern cotton species (Hearn and Constable, 1984). Most commercially grown cotton is the upland cotton species (~90%), which was first developed by the Mayan civilisation in Central America.

Modern cotton production in Australia started in the 1960s following the construction of major inland water storages, enabling irrigated cotton production. The Australian cotton industry is an intensive production system, based on high inputs of irrigation water, fertiliser, and in conventional crops, pesticides (Fitt, 1994). Cotton is a long season crop, taking ~180 d from sowing to reach maturity when defoliation occurs (60% open bolls). In Australia the growing season starts in September/ October (planting) and ends in March/April (picking). Heat and low humidity combined with high levels of irradiance

are favourable for cotton production, with temperature being the primary driver for cotton growth and development. Although cotton is a xerophytic plant, it requires substantial amounts of water in different quantities throughout the growing season to produce commercially sustainable lint yields, with peak yields occurring at ~700 mm evapotranspiration (Tennakoon and Milroy, 2003) (Figure 1.1).

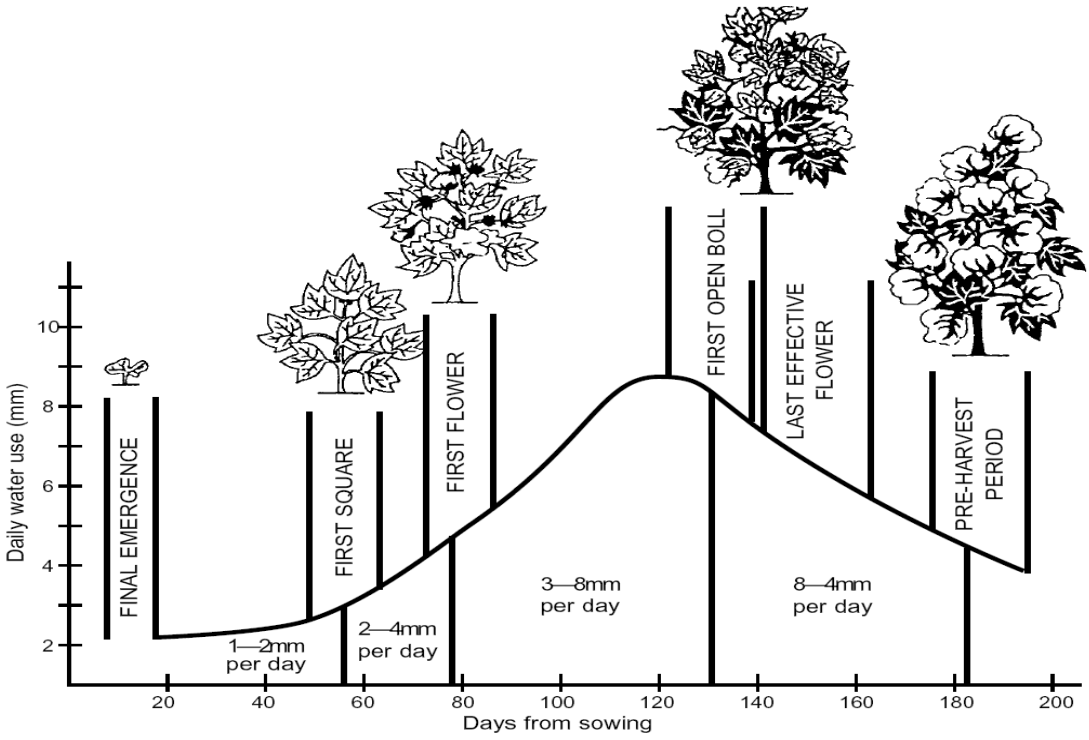


Figure 1.1. The seasonal pattern of daily cotton water use (Source: NSW department of Agriculture).

Approximately two thirds of the Australian cotton crop is grown in New South Wales in regions stretching from the Macintyre River on the Queensland border extending south through the Gwydir, Namoi, and Macquarie river valleys. Cotton is also grown along the Darling and Barwon rivers in the west and the Lachlan and Murrumbidgee rivers in the south. The remaining third of the crop is grown in Queensland, mostly in the Darling

Downs, St George and Macintyre valleys as well as Emerald and other central Queensland regions (Figure 1.2) (Cotton Australia 2008). The industry is heavily dependent on world cotton prices, only producing ~3% of the world cotton crop, but in non-drought years represents the third largest cotton exporter and generates in excess of AUD$1 billion in revenue (Writeability, 2006). Cotton production in Australia steadily increased to a maximum area of 562 000 ha in 1998/1999, producing over 716 thousand tonnes of cotton lint that year (ABARE, 2000). However, for the past six seasons, cotton production in Australia was affected by one of the worst recorded droughts in history. Production area fell to as low as 63 000 ha in the 2007/08 season, but has since more than doubled to 164 000 ha in the 2008/09 season and continues to rise in the 2009/10 season with an estimated planting area of 195 000 ha (ABARE, 2009). This highlights the dependence of the Australian cotton industry on the availability of irrigation water, and the need for simple, cost effective and accurate scheduling and water management tools.

In the past decade (2000-2010) the Australian industry has achieved a 126% increase in lint production, whilst the production area has only increased by 50%, and the industry has faced reduced water availability and drought (Cotton Australia 2008). The fibre quality and average lint yield for irrigated Australian cotton is the highest in the world, producing yields two and a half times that of the global average. The high fibre quality and lint yields can be attributed to improvements in crop management systems, breeding and the cotton industry's willingness to adopt new technologies such as transgenic cotton cultivars. Furthermore, the majority of the crop is irrigated, i.e., ~85%. Although a high proportion of the crop is irrigated, cotton growers have achieved significantly higher lint

yield without using more water. In recent years growers have doubled their water-use efficiency (WUE) from one to two bales per mega litre (Writeability, 2006).

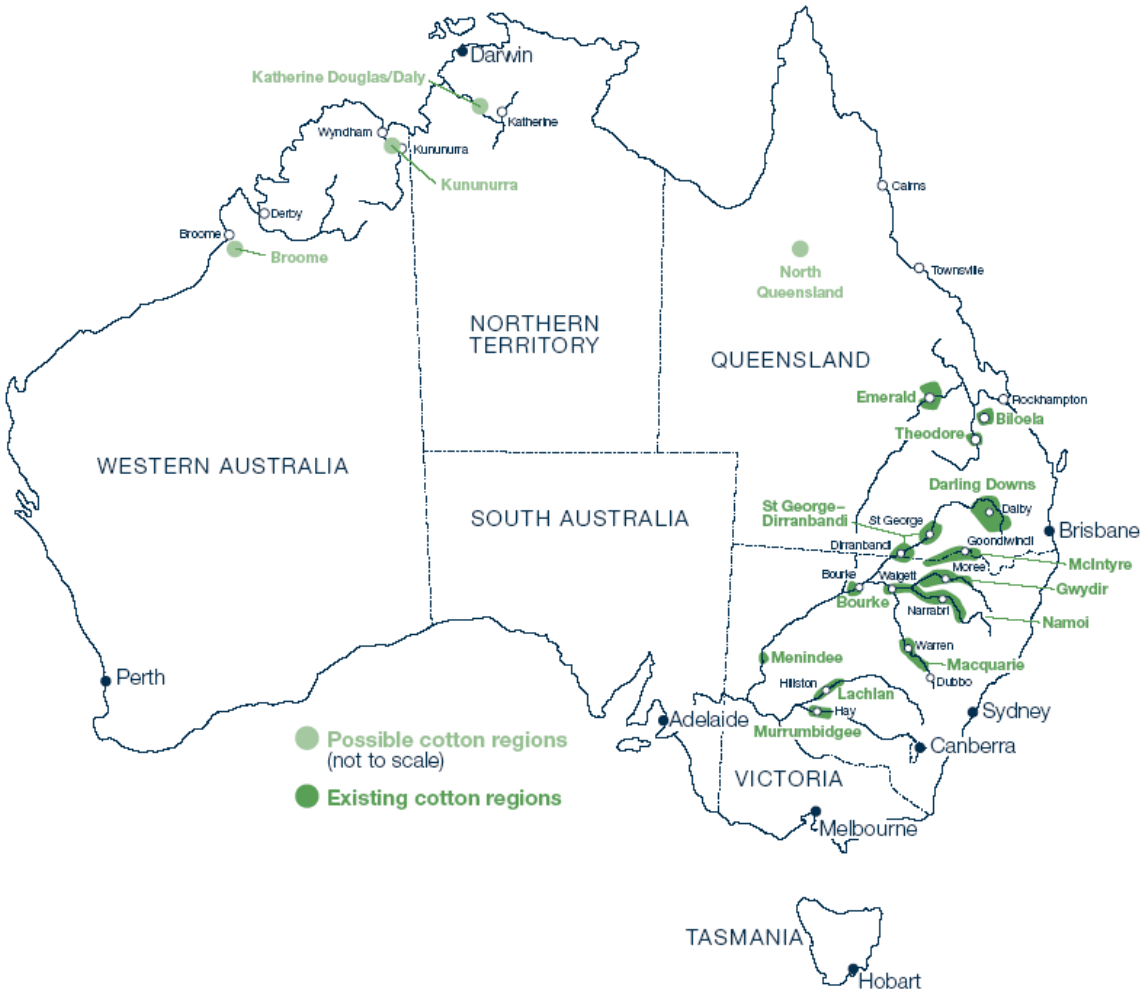


Figure 1.2. The major cotton growing regions of Australia (Source: Lovett *et al.* (2003)).

Upland cotton is a tropical, indeterminate, perennial, xerophytic shrub. When discussing the water relations of cotton, cultivated as an irrigated, broadacre, annual crop, it is essential to recognise these growth habits and origins. Cotton production is affected by

water supply, and the relationship between water application and physiological response and cotton lint yield has been studied extensively (Constable and Hearn, 1981; Cull *et al.*, 1981; DeTar, 2008; Grimes and El-Zik, 1990; Hearn, 1994; Pettigrew, 2004b; Pettigrew, 2004a), with publications documenting lint yield water relations as far back as 1934 (Crowther, 1934). These studies show that the response of cotton to water is complex and involves many processes. In summary, under-watering results in reduced number of fruiting positions, fruit loss, poor boll development and decrease lint yield, whilst over-watering can lead to rank growth and fruit shedding. The challenge for irrigation scheduling is two-fold: to find the optimum application regime, which responds accurately to conditions over a range of seasonal pressures, and determine the volume of water required.

1.2 Biologically Identified Optimal Temperature Interactive Console (BIOTIC)

BIOTIC is an irrigation scheduling tool, developed in 1996 as a result of several years of research at the USDA-ARS in the semi-arid climate of Lubbock, Texas (Upchurch *et al.*, 1996). The BIOTIC protocol is based on plant temperatures and the temperature optimum of the crop species of interest (Mahan *et al.*, 2005). BIOTIC works on the assumption that as a plant's soil available water is reduced, transpiration must also be reduced to avoid plant desiccation. This reduction in transpiration reduces evaporative cooling, and results in a corresponding rise in plant T_c. The BIOTIC protocol also utilises the theory that plant species have a preferred range of plant temperatures for growth and development, known as the thermal kinetic window (TKW), as well as an optimal *in vivo* temperature for metabolism and enzyme function. BIOTIC differs from other temperature-based

irrigation scheduling methods as it compares T_c with a biologically based estimate of the optimum temperature of the plant using a three step threshold system. The first threshold is the species-specific optimum temperature. This optimum temperature or threshold temperature is based on the observation of the thermal dependence of plant metabolic activity (Peeler and Naylor, 1988; Terri and Peet, 1978; Mahan, 2000) and represents the plant's ideal temperature for metabolic and enzymatic function. The second threshold is a time threshold. This time threshold represents the amount of time that the temperature of a well-watered crop canopy can exceed the temperature threshold, regardless of plant available soil water capacity (Wanjura *et al.*, 1995). This is important, especially in irrigation systems where irrigation cannot be applied at short intervals and large soil water deficits are inevitable. The final threshold is a limiting relative humidity threshold. The relative humidity threshold is important as under certain environmental conditions relative humidity can limit transpirational cooling to the point that T_c may exceed the optimum, regardless of soil water. Therefore, temperatures above the optimum under these conditions are not considered in the irrigation scheduling decision-making process. Under the BIOTIC irrigation scheduling protocol, irrigation is considered appropriate when T_C exceeds the threshold temperature for a period of time in excess of the time threshold when relative humidity is not limiting transpirational cooling (Mahan *et al.*, 2005).

The primary advantage of BIOTIC is that it utilises a plant based biological basis for scheduling irrigation, its simplicity and provision of reliable irrigation scheduling (Mahan *et al.*, 2000). It does not provide information on the amount of water applied in response

to an irrigation signal and is designed to provide full irrigation. It can provide irrigation signals at any frequency, however as the interval between detection of water stress and the irrigation event increases, the irrigation signal becomes increasingly complex (Mahan *et al.*, 2000). This is especially important in the context of evaluating the utility and adaptability of BIOTIC to large deficit irrigation scheduling systems such as furrow irrigation.

The BIOTIC protocol has been demonstrated to be an effective irrigation scheduling method for several crop species (cotton, peanut, corn, soybean, sunflower, millet and sorghum) using surface and sub-surface drip, linear and centre pivot irrigation in both humid and arid environments in the U.S.A (Texas, Mississippi, and California) (Mahan, 2000; Mahan *et al.*, 2005). In each case BIOTIC provided irrigation scheduling equivalent to that achieved by soil water balance or evapotranspirational methods (Mahan *et al.*, 2005). However, BIOTIC has not been evaluated outside the USA or in large deficit irrigation systems, such as furrow irrigation, and the response and utility of the system to these conditions are unknown.

1.3 Objectives

The aim of this study was to evaluate the potential utility of a thermal optimal approach to irrigation scheduling, using BIOTIC irrigation scheduling system as a basis, in Australian cotton production systems, with particular emphasis on an Australian cotton cultivar and large deficit irrigation systems. The specific objectives were to:

(i) Define the thermal optima for one Australian cotton cultivar, in order to compare this cultivar with those grown and studied in the USA (Chapter 4).

(ii) Determine whether T_c can adequately detect plant stress. This was achieved through:

(a) Experiments conducted under surface drip (Chapter 5) and fixed soil water deficit furrow irrigation (Chapter 6) in order to evaluate the effect of soil water on plant growth and T_c;

(b) Investigation of the ability of T_c to capture plant water stress in comparison with soil and atmospheric environmental conditions (Chapter 5 and 6).

(c) Determine the potential effect of plant adaptation of T_c to the wetting and drying cycles of furrow irrigation (Chapter 6).

(iii) Determine if the thermal optimal approach to irrigation scheduling system can be effectively used for irrigation scheduling in drip and large deficit furrow irrigation systems. Particular reference was made to the temperature threshold (Chapter 4), the stress time threshold (Chapter 7), and any modifications to the BIOTIC protocol that may be required to schedule irrigation in Australian drip and deficit irrigation systems.

2. LITERATURE REVIEW

2.1 Introduction

The complex effects of water supply on the physiological and growth responses of cotton (*Gossypium hirsutum* L.) are the result of xerophytic adaptations and an indeterminate growth pattern that modern cultivated cotton inherited from its wild ancestors. Generally, an excess in water leads to rank growth, leading to reduced boll set that can aggravate peat and disease problems. Water stress adversely affects the production of flower buds, reduces boll set, and can reduce lint yield by reducing boll size (Hearn, 1979). Ambient temperature and soil water availability are two of the most important drivers of cotton growth and development. The cotton plant is morphogenically indeterminate, producing a new node every two to four days depending on temperature and water availability. The morphogenic relationship with temperature is described by the accumulation of degree days over a base temperature of 12 °C, where a new node is produced every 40 degree days provided other factors are not limiting (Hearn and Constable, 1984). The relationship between morphogenesis and water supply in cotton is that once the crop germinates, morphogenesis is unaffected by water supply until approximately two-thirds of available water has been depleted. At this point, the production of squares ceases, and if water supply is not replenished crop growth terminates and the set fruit is matured (Hearn and Constable, 1984). Therefore, the aim of irrigation management of cotton in temperate regions is to avoid the cessation of morphogenic development to produce peak yields, which are ultimately governed by temperature limitations. However, in tropical

regions, the role of water supply ultimately affects morphogenesis as temperature is no longer a limitation in crop growth and development.

The negative effects of water and thermal stress on crop yield are both cosmopolitan and substantial, reducing yields in all cropping systems and regions world-wide. Irrigation scheduling has conventionally aimed to achieve an optimum water application, maintaining soil water around field capacity to produce peak yields. However, in recent years research has recognised the advantages of providing a small degree of water stress, reducing water use and optimising crop quality (Jones, 2008). Irrigation water is necessary to satisfy crop water requirements in both arid and semi arid regions. Therefore, adequate methods of irrigation scheduling are required and are especially important in the context of increasing competition between end users of water resources (Jones, 2004b).

The methods of irrigation scheduling can generally be divided into three classes, soil water based measurements, meteorologically calculated crop demands and plant based measurements of water stress. Direct measurements of the plant's water status would appear to be superior to soil and meteorological methods as the plant responds to both its aerial and soil environments (Jones 2008; Wanjura *et al.* 2006). One method of assessing crop water stress conditions is the use of T_c, that has been shown to reflect subtle changes in physiological processes such as cell growth and biochemical reactions associated with the damaging effects of super-optimal temperature.

The measured canopy-air temperature differential (CTD) of a crop is in some way related to plant water stress (Widmoser, 2010). The CTD was first studied by Ehrler (1973), who found that CTD decreased after irrigation, reaching a minimum several days following irrigation, and then increased as soil water became increasingly depleted. After showing a linear relationship between CTD and vapour pressure deficit (VPD), Ehrler (1973) concluded that CTD has potential for informing irrigation scheduling tools. Following the findings of Ehrler (1973), theoretical research carried out by Jackson *et al.* (1981) and experimental work by Idso *et al.* (1981a) developed a crop water stress index (CWSI), which is a measure of the relative transpiration rate of a plant at the time of measurement using a measure of plant temperature and the vapour pressure deficit. As surface canopy temperatures can be estimated by infrared thermometry, many efforts have been made to understand and formalise this relationship (Guilioni *et al.*, 2008; Wanjura *et al.*, 2006; Jones, 1999; Alderfasi and Nielsen, 2001; Mahan *et al.*, 2005; Gonzalez-Dugo *et al.*, 2006; Qiu *et al.*, 2009; Widmoser, 2010; Balota *et al.*, 2008; Baker *et al.*, 2007; Cohen *et al.*, 2005; Leinonen *et al.*, 2006).

One of these methods, developed by Upchurch *et al.* (1996), is the temperature-time-humidity threshold system known as BIOTIC. The BIOTIC system views plants as natural integrators of their environment, using T_c as an indicator of crop water stress. The specific amount of time that a T_c of a given crop exceeds its species-specific optimum temperature threshold (TT) determines the need for irrigation scheduling (Mahan *et al.*, 2000). The daily amount of time that a crop's T_c exceeds this threshold value directly produces an irrigation signal, and thus controls the sequence of irrigation events (Wanjura

et al., 2006). The BIOTIC system results in the precise maintenance of a crop at a controlled water status in precision application irrigation systems.

This review aims to outline the physiological consequences of water and thermal stress, as well as some of the contemporary irrigation scheduling and delivery methods used by the Australian cotton industry. This review outlines the historic use and physiological basis of using T_c for water stress detection, with a special focus on the BIOTIC irrigation scheduling system.

2.2 Irrigation and irrigation scheduling

2.2.1 Irrigation delivery

(a) Furrow irrigation

Furrow irrigation is the dominant method of irrigation delivery in Australian cotton industry, accounting for 90% to 95% of all irrigated cotton (Purcell, 2006). Furrow irrigation, where water is transferred from a head ditch to crop furrows via siphons, is one of the most simple and ancient forms of irrigation delivery (Hansen *et al.*, 1980). It can achieve reasonable crop WUE; but is very variable and is limited. Furrow irrigation involves a balance between field slope and length, water infiltration rates, and the rate of irrigation application for uniformity of applied water in the profile and reduction of drainage beyond the root zone (Hansen *et al.*, 1980). Due to the nature of the system (inundation of furrows), waterlogging is common. Furthermore, a greater amount of water will be supplied to the upper end of the field, thus increasing deep drainage beyond the root zone in this region or depriving plants at the lower end of the field from a fully

recharged root zone. A high rate of application and a long run time can result in excessive runoff, whilst low rates of application results in slow water advance, cause poor water distribution and deep drainage losses. Soil type, heterogeneity and associated infiltration rates both across and down the field will also affect the efficiency of furrow irrigation. Therefore, hard setting (crusting) soils can be problematic in furrow irrigation systems, as soil slaking can result in bed deformation and slumping. Tail water losses, deep drainage, evaporative and drainage losses from irrigation channels constitute the predominant water losses from furrow irrigation systems. Furrow irrigation, although inherently limited, is a very reliable and flexible system that can be managed to achieve reasonable WUE. Furthermore, such a system encourages deeper crop rooting depths in order to utilise water from the whole profile.

(b) Bankless channel irrigation

Bankless channel irrigation is not commonly used in the Australian cotton industry, however, it has received increased attention due to successful implementation on properties in central Queensland as well as the Murrumbidgee Irrigation Area (Grabham and Williams, 2005). Bankless channel systems use raised beds and a series of terraced bays running laterally across the field gradient which, while irrigated separately, are connected by a bankless channel. Each bay is irrigated by backing-up water behind a closed gate in the bankless channel, causing water to spill into the adjacent bay. Once the bay has been sufficiently inundated, the gate in the bankless channel is opened allowing both supply water from the channel and drainage water from the bay to flow into the next bay in the series. This process is repeated until all bays are irrigated. The bankless

channel delivers the water to the bay, distributes water across the inlet width of the bay and also acts as a drain for the bay. This irrigation system's major advantages are its labour savings, simplicity, increased ability to facilitate drainage following irrigation and rainfall and improved timeliness of operations (Grabham and Williams, 2005; Grabham *et al.*, 2009). This system is however limited in that like all surface inundation irrigation techniques, there is a distinct possibility for non-uniform depths of water infiltration, and due to the nature of the system there is also a possibility for non-uniform distribution of water flow into furrows (Grabham *et al.*, 2009). Furthermore, bankless channel irrigated fields tend to suffer from increased compaction, lowering water infiltration rates and thus increasing the potential for waterlogging. This increased compaction is thought to be responsible for the reduction in water used (~0.1 ML ha^{-1}) as well as a slower maturing and lower yielding crop (Hood and Carrigan, 2006).

(c) Drip irrigation

Drip irrigation has developed rapidly since the early 1960s with the advent of the modern plastics industry, and represents 5% of the total irrigated area in the United States (Ayars *et al.*, 1999). Drip irrigation is one of the most efficient application methods of irrigation water. Currently, the use of drip irrigation systems is limited in the Australian cotton industry and broadacre irrigated cropping as a whole, however internationally in countries such as the USA and Israel, drip irrigation has been successfully implemented in cotton and other row crops (Rourke, 2004). Drip irrigation systems consist of lines of drip tape that run along the length of each furrow, either on the surface or sub-surface. Water is pumped into the system and supplied to the crop from emitters spaced at the

desired interval along the drip tape. This creates a wetted zone in a three dimensional 'tear-drop' shape, where the root zone is simultaneously exposed to both wet and dry soil conditions. This can discourage the production and exploration of roots throughout the full extent of the soil profile. This can result in implications regarding to water and nutrient uptake from the whole profile, limited rooting patterns which has associated implications for plant support.

The main disadvantage of drip irrigation systems is the cost of drip tape and its installation. However, drip irrigation may play a role in satisfying the demands associated with increased pressures of growers to increase WUE and maximise production (Rourke, 2004). Historically, irrigation scheduling in drip irrigation systems has proved to be slightly more difficult than other irrigation delivery methods (Hansen *et al.*, 1980). Furthermore, once installed, the surface or sub-surface drip tape can limit agronomic practices such as cultivation and deep ripping. Therefore most drip irrigation occurs on permanent plantings such as trees and vines with limited field crop application (Ayars *et al.*, 1999). This difficulty is partially alleviated through the use of sub-surface drip irrigation. Although burying the tubing adds additional initial cost to the system, it eliminates the need to install and remove tubing at the beginning and end of each growing season. Root intrusion, distribution uniformity, tubing damage from equipment and burrowing animals are all concerns with the operation of drip irrigation systems, this is especially important in sub-surface drip irrigation as the system is underground and no longer in view.

Drip irrigation can substantially improve WUE by minimizing evaporative loss of water and maximizing capture of in-season rainfall by the soil profile (Bhattarai *et al.*, 2008). Drip irrigation is advantageous as precise amounts of water can be applied directly to the root zone at almost any irrigation frequency. This has great potential to improve water management for crop yield and quality optimisation, making drip irrigation one of the most water use efficient irrigation application methods. Furthermore, due to the nature of the system, less water and nutrients are lost through deep percolation, total water requirements are reduced, evaporation and deep drainage losses are minimal, rainfall is captured and used more effectively and it is less likely to create waterlogged conditions as plant roots are exposed to both dry air-filled soil and wetted air-reduced soil. Despite this, hypoxia of the rhizosphere can be created by a sustained wetting front, which is detrimental to effective plant functioning. Oxygenation of irrigation water, particularly in soil with high clay contents, can help ameliorate the effects of this wetted zone in drip irrigated crops, allowing drip irrigation systems to achieve their full benefit (Bhattarai *et al.*, 2008; Bhattarai *et al.*, 2006). It also provides a simple and precise method of fertilisation and insect management, through fertigation of soluble nutrients and application of systemic insecticides. Cotton lint yields and net profits, as well as WUE, have been improved using drip irrigation (Ayars *et al.*, 1998; Smith *et al.*, 1991; Collins, 2004; Hodgson *et al.*, 1990; Radin *et al.*, 1992).

(d) Centre pivot and lateral move irrigation

Centre pivot and lateral move irrigation are forms of overhead or sprinkler irrigation. They consist of several segments of pipe joined together and mounted on wheeled towers

with sprinklers positioned along its length (Hansen *et al.*, 1980). Centre pivots move in a circular pattern and are fed with water from the pivot point at the centre of the circle. Lateral move irrigation systems move in a straight line and water is supplied by an irrigation channel positioned either at one side or midway across the field width and running the length of the field. The motor and pump equipment is mounted on a cart adjacent to the supply channel and travels with the machine. Centre pivot and lateral move machines are becoming more appealing to growers as their benefits become more widely understood. These benefits include more efficient application of water, the possibility of variable application regimes, reduced soil movements and no need for head ditches and tail drains, which have advantages for machinery access (Collins, 2004). However, there are potential problems for irrigation uniformity (especially in regard to runoff), evaporation losses from sprinkler droplets and soil surface crusting (as sprinkler droplets can cause dispersion of soils). Furthermore, it is very difficult to replenish soil water once critical levels are reached, and due to the technical nature of the system machinery can be problematic (Collins, 2004). Rather than spraying water into the air at moderate to high pressures, low energy precision application (LEPA) systems distribute water directly to the furrow at very low pressure through drop tubes and controlled emitters, reducing water losses from droplet evaporation. LEPA is best used in conjunction with micro-damming land preparations, which also increase rainfall capture and minimise runoff. Significant savings in both water and energy resources can be made with LEPA systems (Lyle and Bordovsky, 1981; Collins, 2004).

2.2.2 Irrigation scheduling

In arid and semi arid regions, where water for irrigation of crops is vital for complete or partial substitution of crop water requirements, adequate methods of irrigation scheduling are necessary to improve WUE. This is especially important in the context of increasing competition between the environment and the various end users of water resources (Jones, 2004b). There have been numerous reviews on the methods of irrigation scheduling, which in general divide scheduling techniques into four categories, soil based water measurements such as neutron attenuation and capacitance probes (Dane and Topp, 2002; Hansen *et al.*, 1980; Smith and Mullins, 2001), water balance calculations based on meteorological data (Allen *et al.*, 1998), plant based scheduling from on-the-ground (Jones, 2004b) or remotely sensed data (Bastiaanssen and Bos, 1999), and a combination of several of the above. In theory, direct measurements of the plant's water status would appear to be superior to soil and meteorological methods as the plant responds to both its aerial and soil environments (Jones, 2008; Wanjura *et al.*, 2006). These methods include visual observation and scoring of plants for leaf rolling and tissue wilting and the measurement of parameters such as leaf, stem or plant water potentials (Scholander *et al.*, 1965), leaf relative water content (Longenecker and Lyerly, 1969), leaf diffusion porometry (Kanemasu *et al.*, 1969) and gas exchange rates. However, such methods are either ineffective in early stress detection or time-consuming and require numerous measurements in order to characterise a field on the basis of single leaf or plant.

Two irrigation scheduling strategies of interest are partial root zone drying (PRD) and regulated deficit irrigation (RDI). The PRD is an irrigation strategy that aims to maintain

plant water status and create favourable physiological response due to biochemical signalling (Bravdo, 2005). It uses alternate wetting and drying of sections of the root zone, attempting to maintain water availability and plant water status, whilst elevating biochemical signalling, such as increased abscisic acid (ABA) levels and alkalisation of sap pH. These biochemical signals result in a decrease in vegetative growth and stomatal conductance, which leads to improved crop WUE (Bravdo, 2005). The RDI is another irrigation scheduling technique that aims to reduce the water availability through the plant root zone. It aims to increase crop WUE by maintaining plant water status within a limit of deficit, thus limiting vegetative vigour (Kreidemann and Goodwin, 2003). The key differences between PRD and RDI are that RDI does not maintain plant water status, and RDI is characterised by an absence (or at least reduction) of biochemical signalling in comparison to PRD. There is an ongoing debate as to whether PRD can be effectively implemented in commercial field situations and whether the WUE benefits of PRD are actually due to PRD or a form of RDI (White and Raine, 2009). Both PRD and RDI are commonly used in high value, perennial crops such as grapevines and fruit trees; however, interest is beginning to emerge in the physiological response of cotton to these root zone water gradients (White and Raine, 2009).

2.3 Water and temperature relations of cotton

Water and temperature relations of cotton are often discussed in terms of stress levels above and below a species-specific optimal range. In the agronomic context stress can be defined as a deficit that leads to a reduction in the economic return of the crop through physical reductions in yield or reductions in yield quality. However, stress can also be

defined in a physiological context, where the induction of stress is seen as when a particular physiological process is affected, or ecological context, where survival within or between generations is important.

Cotton is indeterminate and produces a new main stem node every two to three days. Squares are produced on lateral fruiting branches every five to seven days. Node and square initiation continue as long as environmental conditions are favourable, thus their number increases exponentially throughout the season. The demand for carbohydrates and N, which are ultimately limiting, also places inevitable restraints on production (Hearn, 1979). This internal competition for assimilates allows the number of bolls to influence the rate of square production. If a number of young bolls and squares are shed, the production of squares increases, allowing for the lint yield potential to compensate. Thus, crops can potentially yield the same through several development routes, where the time taken may be limited by water supply or temperature (Hearn, 1979).

Water stress is one of the most common types of plant stress and is often associated with deficit soil water and during periods of high irradiance and heat (Cothren, 1999). The area of cotton under water-limited conditions is estimated to be around 47% (Hearn, 1994). The agronomic effects of water stress in cotton include reduced biomass, loss of fruit and decreased lint quality. The physiological effects of water supply are well recognised and have significant effects on the time taken for a crop to reach maturity. Excess water leads to rank growth, increasing the prevalence of pests and disease, while water deficits affect the production of squares, boll setting and can further reduce lint

yield by reducing boll size. Despite the associated physiological effects of water stress, cotton may be considered a drought-tolerant plant with low tissue water potential (Turner, 1979). This is observed through the fact that under dryland farming conditions leaf water potential can be reduced to as low as -4.0 MPa at noon, while profitable levels of lint yield are still obtained in the face of reduced photosynthesis and growth due to water deficit (Moreshet *et al.*, 1979).

Ambient temperature is considered to be the primary driver for cotton growth and development (Hodges *et al.*, 1993). Outside the tropics, temperature limits the cropping cycle, where sub-optimal temperatures govern planting and crop maturation (Hearn, 1994). Although the detrimental effects of sub and supra-optimal diurnal temperatures on various physiological processes impacting crop yield are complex, low temperature stress is characterised by reduced growth and development rates. High temperature stress is characterised by reduced growth and carbon assimilation, reduced boll development and increased fruit shedding (especially during flowering which is most sensitive to temperature stress), in both field and glasshouse grown cotton (Cottee, 2009). These impacts result in reduced yields, where high temperatures (> 35 °C) have a strong negative correlation with crop yield, with lint yields decreasing by 110 kg ha^{-1} for each 1 °C increase in maximum day temperature (Singh *et al.*, 2007).

2.3.1 Water stress

(a) Wild cotton and water deficits

The cotton genus (*Gossypium*) is characterised by xerophytic, perennial shrubs containing some 50 species, of which only four are cultivated (Bielorai *et al.*, 1983). The genus is pan-tropical; however, individual species have limited distributions and are of relict status with little genetic diversity, suggesting an ancient and declining genus (Hearn and Constable, 1984). The wild species of cotton originated from arid and semi arid regions of the tropics and sub tropics and were the source of germplasm for the modern, high yielding, cultivated species. Therefore, when discussing the water relations of modern cotton genotypes, it is essential to discuss these xerophytic origins as sources of drought tolerance and the consequential water relations of cotton (Hearn, 1994; Ray *et al.*, 1974).

Drought survival in wild cotton species is achieved through three broad non exclusive strategies. The first group has lifecycles adapted to vegetative growth when water is abundant, deferring fruiting until the start of the dry season, followed by dormancy until the wet season (Hearn, 1994). The second group grows preferentially in dry stream beds where ample water would only be available during flood events of the rainy season, but where long periods of drought also occur (Ray *et al.*, 1974). As soon as the water recharges the root zone, development and growth occurs. As the stored soil water is depleted, morphogenesis stops and existing fruit are matured. The plant becomes dormant aging until the next flood event where the next cycle of morphogenesis is commenced and seed is dispersed (Hearn, 1994). The third grouping displays morphological adaptations such as compact habits and leaf structure to minimise water loss, however, in

these species vegetative and reproductive growth occurs simultaneously (Hearn, 1994). These species commonly inhabit regions with a higher water potential than the second group that are adapted to extreme fluctuations in water potential. In its natural habitat, wild cotton species produce vegetative growth in the wet summer season and mature their fruit in the dry winter. However, in contrast cultivated cotton, grown under dry summer conditions, adapts to atmospheric and soil water deficits, which can be detrimental to crop yield (Bielorai *et al.*, 1983).

The drought adaptation strategies of wild cotton are to some extent exhibited in modern cultivars and influence some of the general characteristics of the commercial cotton crop and its water relations. Cotton root systems are extensive and penetrate to relatively large depths. Fruiting periods can be flexible and are modulated by both the environment and genetic factors and leaves and fruit can be shed in response to water relations and the broader environment. Leaves and fruit are abscised not only during water deficits, but also under waterlogged and excessive water conditions. During waterlogging, the plant abscises floral buds and immature fruit (Conaty *et al.*, 2008), whilst during luxurious water conditions vegetative growth dominates reproductive growth until water becomes limiting and fruiting is reinitiated (Hearn, 1994).

(b) Morphological and lint yield traits

(i) Seedling and root growth

Water is imbibed by the seed due to a gradient of water potential between the seed exterior and the potential of the seed (Bielorai *et al.*, 1983). The rate is not affected by

soil water potentials between -0.03 MPa and -1.0 MPa and occurs within 36 to 48 hours (Hearn and Constable, 1984; Wanjura and Buxton, 1972). Soil aeration, temperature (> 18 °C) and water all play important roles in germination and early growth and must all be sufficient for germination and emergence. Cotton will not develop a radicle in dry soil, where radicle production is inhibited in partially imbibed seed until higher seed water potentials are reached. The rate of radicle and hypocotyl elongation is temperature and soil water potential dependent, with emergence occurring in 5 days at soil water potentials of -0.03 MPa, 7 d at -0.3 MPa and no emergence at -1.0 MPa (Wanjura and Buxton, 1972).

Cotton has a taproot that can reach depths of up to 3 m, depending on the soil type, soil bulk density and soil water content (Hearn and Constable, 1984). The range of root growth rate is usually 8 mm d^{-1} to 90 mm d^{-1} (Hearn and Constable, 1984); however, under favourable conditions this can be increased to 100 mm d^{-1} to 150 mm d^{-1} (Bielorai *et al.*, 1983). At optimum soil temperatures and osmotic potentials of -0.08, -0.66 and -1.24 MPa, maximum root elongation averaged 3.3, 1.8 and 0.8 mm h^{-1} (Gerard, 1971). During water deficits leaf growth is reduced as photosynthates are translocated primarily to the roots. This highlights the preference of root dry matter accumulation to that of leaf dry matter under soil water deficits (Bielorai *et al.*, 1983). However, a large boll load may result in reductions in root growth as bolls are stronger carbohydrate sinks than roots. This is seen through the inhibition of root growth through competition for sugar and N from developing bolls (Bielorai *et al.*, 1983). The depletion of water in the upper soil profile can lead to proliferation of roots at greater depths resulting in increased extraction

of water. However, if water resources are not limited in the upper portion of the upper soil profile, root proliferation at greater depths is reduced (Bielorai *et al.*, 1983; Hearn and Constable, 1984).

(ii) Vegetative growth

The growth and expansion of leaves only occurs when internal water balance is favourable, such conditions usually correspond to periods of high water potential (Bielorai *et al.*, 1983; Boyer, 1968). The initial response of cotton to soil water deficits is vegetative, where a reduction in leaf expansion, inhibition of growth rate and reductions in height, LAI and the number of fruiting branches occurs. Under glasshouse conditions, height, leaf area and fresh weight of cotton seedlings was inhibited at plant water potential > -0.8 MPa (Bielorai *et al.*, 1983). The growth of stems decreases with time following an irrigation event; however, soil water deficits can affect leaf growth more than stem growth, partly due to the influence of water relations on cell turgor (Cutler and Rains, 1977).

Despite the effect of water stress on leaf growth, recovery from mild and moderate water stress events is rapid; however, prolonged water stress can have permanent damaging effects. Bielorai and Hopmans (1975) found that following prolonged periods of water deficit, the leaf area in water stressed cotton was 17% less than those that were fully irrigated, furthermore this reduction in leaf area did not recover fully after irrigation. Leaf abscission increases linearly as Ψ_l decreases from -1.0 MPa to -2.4 MPa and depends on leaf age. Mature leaves abscised after relatively mild water stress events and juvenile

leaves did not abscise even after severe water deficits. Significant leaf abscission only occurs once predawn leaf water potentials are lower than -0.8 MPa (McMichael *et al.*, 1972).

(iii) Flower production and boll setting

The production of flowers and their development into mature bolls is influenced by soil water availability as well as other environmental factors. Furthermore, it should also be highlighted that the reduction in vegetative growth under water deficits has lasting effects for reproductive growth in the form of a reduction in the total number of fruiting sites due to reduced vegetative growth and smaller plants. This is observed through the negative relationship between the number of squares and soil water, and a corresponding positive relationship between the number of squares and plant height (Bruce and Römkens, 1965). The development of the flower depends on vegetative growth, where new flowering sites are formed through the formation of additional main-stem and branch nodes, which is primarily thermal dependent. Shortly after floral initiation, the rate of flower opening exceeds leaf formation (crop cutout), resulting in flowers opening closer to the stem apex (Bielorai *et al.*, 1983), closer to the most productive sites of carbon assimilation. Therefore, as soil water deficits reduce vegetative growth, the number of flowering and fruiting sites is also affected through competition for carbon assimilates (Grimes *et al.*, 1970).

The importance of water relations on cotton production is emphasised by the reduction in the number of bolls, which is affected by water stress during the early flowering phase of

plant growth. Irrigation prior to flowering prevents soil water stress and results in a higher cotton seed yield of higher lint quality (Bielorai *et al.*, 1983). Water deficits during floral initiation considerably reduce lint yield, however, during peak flowering the effect is less pronounced. This is because soil water stress at a particular time is associated with a reduction in the number of flowers 20 to 30 d later (Shimshi and Marani, 1971). Thus soil water deficits during early flowering result in a reduction in flowers, and hence potential bolls, during peak flowering, corresponding to a reduction in bolls during the peak boll setting stage. However, Grimes *et al.* (1970) reported that a severe plant water deficit during peak flowering reduced lint yield more significantly than an equivalent water deficit earlier and later in the flowering period. This result is due to the fact that water stress during the early flowering period resulted in increased square shedding, whereas later water deficits reduced flowering rates and boll retention.

Floral buds, or squares, and their growth are highly affected by water stress, where the rate of square initiation is associated with soil water (Bielorai *et al.*, 1983). Using soil water as a surrogate for plant water status, Bruce and Römkens (1965) found that the rate of initiation of squares was associated with a soil water tension of -0.03 MPa for four weeks following the first flower developing and an increase in tension to -0.38 MPa increased the abscission of squares. From five weeks prior to the development of the first flower, a soil water tension of -0.07 MPa increased the abscission of squares.

(iv) Boll and fibre development

Boll and fibre development is generally observed as less sensitive to water deficits than vegetative growth (Grimes and El-Zik, 1990). Stockton *et al.* (1961) showed that water stress in cotton resulted in the shedding of squares and bolls. In addition, if water stress is absent during early square production, a subsequent stress will increase the shedding of bolls and squares. This is due to a reduction in photosynthetic rates and the associated increase in competition for the now limited carbohydrates under water stress (Grimes *et al.,* 1970). However, boll growth is maintained during water stress for longer than vegetative growth. This is because bolls have fewer stomata than leaves and therefore lose water less rapidly, maintaining a higher water potential and thus have a greater potential for growth under water stress (Hearn and Constable, 1984). Like leaf abscission, boll abscission increases linearly with Ψ_l between -1.0 MPa and -2.4 MPa where young bolls were most sensitive to water stress, but those that were 14 d or older were retained even after exposure to severe water deficits (McMichael *et al.*, 1972). However, boll growth is not affected until Ψ_l reaches -2.7 MPa to -2.8 MPa (Hearn and Constable, 1984). The abscission of bolls is not only caused by water stress but also the number of bolls set per day and the resultant competition for carbohydrates. Vegetative and reproductive tissues compete for carbohydrates, hence a large number of bolls creates a carbon sink, reducing overall carbohydrate levels, stimulating a high level of boll abortion (Saleem and Buxton, 1976).

Water stress also alters the time taken for a boll to reach maturity. Water deficits result in the hastening of maturity, whilst excessive soil water tends to slow maturity (Hearn,

1994; Hearn, 1979; Marani and Amirav, 1971b; Marani and Amirav, 1971a). This occurs as a result of the inherent plant water relations fixed within commercial cotton cultivars derived from its wild xerophytic ancestors. As a result, when two thirds of the soil water is used, vegetative growth ceases, boll setting and square production cease and the retained bolls mature. Boll setting and square production can resume, if conditions are favourable, when mature bolls open, leading to a second fruiting flush (Hearn, 1979).

Soil water deficits also alter the rate of supply of phytohormones to the abscission zone (Eaton, 1955). Observed changes in the concentrations of auxin and ethylene, which are known to induce abscission rates of leaves and bolls, have been correlated with water stress (McMichael *et al.*, 1972). Therefore, the final retention rate and lint yield of a cotton crop is a function of the balance between vegetative growth and reproductive growth, boll set, abscission affects and the size of the mature bolls.

(v) Levels of water stress and cotton production

Cotton requires some mild water stress for maximum lint production. Cotton maintained at Ψ_l of -1.5 MPa to -2.0 MPa maximises the setting of bolls and hence the upper limit of production is limited by boll load and the sufficient production of carbohydrates. This is because vegetative growth is curbed but boll growth and photosynthesis are unaffected. This maximises the amount of surplus assimilates for boll production and is hence the most agronomically viable option. It is important to have some minor water stress on the crop as minimal stress (> 1.5 MPa Ψ_l) sees an increase in vegetative growth with reduces surplus assimilates decreasing boll carrying capacity. Such minimal stress leads to rank

growth and its associated problems such as excessively large and vegetative plants, boll rot, delayed production and insect damage.

Plants under moderate stress (Ψ_l of -2.0 MPa to -2.5 MPa) are primarily affected by reduced square production. Boll production and setting is slightly affected due to reduced excess assimilates and carrying capacity. Lint yield will be reduced if there is insufficient time to the end of the season for the plants to compensate for reduced square production. Severe water stress (Ψ_l < -2.5 MPa) prevents square production and greatly reduces boll production.

(c) Physiological traits

(i) Leaf water potential

Leaf water potential is the measurement of the negative hydrostatic pressure of a leaf and was developed by Scholander *et al.* (1965). Soil water potential declines with soil water availability, which in turn influences the water potential of aerial plant parts. Therefore, measurement of Ψ_l may be indicative of soil and canopy water conditions, particularly when taken during the pre-dawn period when soil water is more likely to be in equilibrium with canopy moisture potential (Ritchie, 1981). However, Ψ_l can also be measured during solar noon as variation in incident solar irradiance is reduced and Ψ_l becomes a product of soil water availability, environmental conditions driving evaporative demand (air temperature, wind speed and humidity) and the subsequent leaf stomatal aperture (Loveys *et al.*, 2005). Using Ψ_l as a means of detecting physiological stress is limited, as Ψ_l is not a direct measurement of plant water stress physiology. There

is doubt as to the physiological significance of Ψ_l (Passioura, 1988; Hearn, 1994), as correlations between Ψ_l and stomatal conductance, photosynthesis and growth rate have not been proven as cause and effect. Turgor was thought to be a controlling mechanism for stomatal conductance and cell expansion, however evidence suggests that reductions in leaf growth rate and stomatal conductance occur before detectable changes in Ψ_l (Hearn, 1994). Rather, root to shoot signalling in response to drying soils results in changes in Ψ_l. Despite this, Ψ_l is important because, although turgor can be over ridden by root signalling, it powers cell expansion (Hearn, 1994). Furthermore, Ψ_l is a well established method for the assessment of plant water status and, agronomic guidelines for the interpretation of Ψ_l values have been developed. However, since the measurement of Ψ_l is relatively slow and it varies spatially, multiple measurements are often necessary to reduce error, especially in variable soil water conditions.

(ii) Gas exchange

Gas exchange measurements have been used to quantify and detect water stress. Generally, transpiration rates proceed at a maximum according to environmental demand until ~ 0.3 to 0.4 of the fraction of transpirable water is remaining (Ray *et al.*, 2002; Ritchie, 1981). At this point plant growth (Hearn, 1979) and gas exchange (Ritchie, 1981; Ray *et al.*, 2002; Sinclair, 2005; Sinclair and Ludlow, 1986) decline until the remainder of transpirable water is used or soil water is replenished. A linear decline in photosynthesis has been observed in cotton at Ψ_l below -2.0 MPa (Karami *et al.*, 1980; Ackerson *et al.*, 1977; Sung and Krieg, 1979; Hearn and Constable, 1984). Gas exchange is less responsive than cell expansion and more responsive than boll growth to water

deficits (Hearn and Constable, 1984). Medrano *et al.* (2002) showed that drought regulation of parameters related to photosynthesis were more dependent on stomatal conductance than measured leaf water status (relative water content or Ψ_l). They showed that the relationship between stomatal response and water stress is similar in different plant species, and concluded that during water stress conditions, the down regulation of photosynthetic processes depended more on CO_2 availability in the mesophyll (stomatal conductance) than leaf water status. Baker *et al.* (2007) showed that stomatal conductance is more sensitive than carbon assimilation to the onset of soil water deficits. However, when water stress becomes more severe carbon assimilation is rapidly reduced.

Despite this, it is well established that cell expansion rates are more sensitive to water stress than stomatal conductance (Ritchie, 1981; Hearn, 1979; Jordan, 1986). However, it is generally accepted that gas exchange rates are an adequate indicator of the degree of water stress as changes in leaf level gas exchange immediately follow cell expansion rate reductions under water stress (Baker *et al.*, 2007; Hearn, 1994). However, it must be highlighted that any process dependent on cell expansion, such as increase in leaf area or plant height, would be more sensitive to water stress than gas exchange (Puech-Suanzes *et al.*, 1989; Turner *et al.*, 1986). There are several routes that result in lint yield reduction in response to water deficits, where the most sensitive routes (cell expansion, leaf growth rate, LAI expansion, light interception and canopy photosynthesis) are first affected, and in some circumstances without affecting the photosynthetic rate of a single leaf (Hearn, 1994). This is because there are two paths associated with reductions in leaf photosynthetic rates: stomatal control and non-stomatal effects (Hearn, 1994).

Although the effects of water stress on photosynthesis and gas exchange have been extensively studied (Boyer, 1982) there has been some conflict surrounding the interpretation of changes in gas exchange rates. Originally, studies were polarised with some research attributing stomatal closure as the dominant reason for declines in carbon assimilation (Hall and Hoffman, 1976; Sharkey and Seemann, 1989), whilst others ascribed these reductions to non-stomatal effects (Boyer, 1971; von Caemmerer and Farquhar, 1981; Gimenez *et al.*, 1992; Krieg and Hutmacher, 1986). Krieg (1986) cited six papers where stomatal closure in cotton induced by soil water deficits resulted in reductions in gas exchange. However, Ephrath *et al.* (1990) and Radin *et al.* (1992) confirmed that stomata can remain open under soil water deficit conditions resulting in zero leaf turgor and reduced photosynthesis. Presently, research has identified both stomatal and non-stomatal limitations to photosynthetic rates (Du *et al.*, 1996; Martin and Ruiztorres, 1992; Wise *et al.*, 1990; Shangguan *et al.*, 1999) where non-stomatal effects are generally considered more prevalent in long-term or increasingly extreme water deficits or hot arid environmental conditions (Pankovic *et al.*, 1999; Flexas and Medrano, 2002; Hearn, 1994). The potential non-stomatal limitations to photosynthesis include inhibition of CO_2 uptake as a result of conformational changes in the thylakoid membrane, reduced carboxylation efficiency through deactivation of Calvin cycle enzymes and an increase in photorespiration due to heat stress (Sailsbury and Ross, 1992). Furthermore, interactions between plant hormones, such as abscisic acid (ABA), and regulation of stomatal aperture have added more complexity to the debate surrounding the mechanisms of stomatal conductance. It is also important to note other limitations in the use of gas exchange and photosynthetic rates as indicators of water

stress. Photosynthetic rates are not exclusively affected by water stress and can differ among genotypes (Constable, 1981) and be affected by other abiotic stresses such as nutritional factors, temperature stress, the amount of photosynthetically active radiation (Sailsbury and Ross, 1992), as well as physiological and plant factors such as leaf age, leaf position, sink effects and mutual shading (Constable, 1981; Constable and Rawson, 1980).

The response of transpiration to the drying of soils is well documented and, is relatively stable according to environmental demand and plant species (Sadras and Milroy, 1996; Weisz *et al.*, 1994). This response is generally suitable for water stress detection and is characterised by the maintenance of a constant transpiration rate under certain environmental conditions, until a threshold soil-water content is reached (usually about 0.3 to 0.4 of transpirable soil water content). After this point transpiration rate is decreased linearly (Sadras and Milroy, 1996; Weisz *et al.*, 1994; Ray *et al.*, 2002). This is because as the soil dries, the corresponding reduction of soil hydraulic conductivity limits the transport of water to plant roots, which must result in a reduction in transpiration or the plant will desiccate. Hence, plant stomata are closed when water supply cannot match transpiration rates under uninhibited stomatal conductance (Ray *et al.*, 2002). This reduction in transpiration theoretically leads to a rise in leaf temperature as incoming radiant energy can no longer be dissipated by transpiration, and the latent heat flux of the leaf is reduced and sensible heating of the leaf ensues.

(d) Water stress and adaptation

Under rainfall limited conditions, dryland and partially irrigated crops must be able to avoid, tolerate or adapt to soil water deficit conditions. Adaptive mechanisms in relation to drought resistance include:

1. Drought escape- the ability of a plant to complete its lifecycle before serious soil and plant water deficits occur. This includes rapid phenological development and developmental plasticity;
2. Drought tolerance with high tissue water potentials- the ability of a plant to endure periods of significant water stress while maintaining high tissue water potential. This includes the maintenance of turgor through continued root development and water uptake, the reduction of water loss through reduced vegetative growth (leaf area), the increase in stomatal and cuticular resistance, increased shedding of solar irradiance by leaf rolling, leaf movement and increased reflection, and osmotic adjustment; and
3. Drought tolerance with low tissue water potentials- the ability of a plant to endure periods of significant water stress and low tissue water potentials, for example, protoplasmic tolerance.

This review will further discuss the dehydration postponement adaptive responses to water stress of osmotic adjustment, stomatal response, and photosynthesis and gas exchange.

(i) Osmotic adjustment

Following studies by Hsiao (1973) and Turner and Jones (1980) proposed the use of the term osmotic adjustment for the accumulation of cell solutes and increase in osmotic pressure in plants. It is important to note the difference between osmotic adjustment and osmoregulation, where osmoregulation is the passive concentration of solutes as a consequence of decreasing water content of cells, commonly occurring in algal calls and microorganisms (Turner, 1986). Furthermore, the lowering of osmotic potential alone is insufficient evidence of osmotic adjustment as a decrease in the water content of a cell will cause a passive increase in cellular solute concentrations and an increase in elasticity at constant water potential will lower osmotic potential without increasing cell solute concentrations (Turner *et al.*, 1978). Osmotic adjustment is an adaptive mechanism that maintains positive turgor pressure at low values of Ψ_l, in response to water deficits (Grimes and El-Zik, 1990). This provides a degree of continued growth under water stressed conditions, where as much as 1 MPa adjustment of osmotic potential for whole cotton leaves is commonly reported (Brown *et al.*, 1976). Adaptive mechanisms include osmotic adjustment (the accumulation of cell solutes), small cell size (where more cell walls per unit of volume exist), and greater cell wall elasticity. Turgor maintenance in cotton is due to both the accumulation of sugars and malate as well as high cell-wall elasticity (Cutler *et al.*, 1977), as well as solely solute accumulation (Oliveira, 1982). Different cotton cultivars have differing abilities to osmotically adjust. Karami *et al.* (1980) found that under severe water stress super-okra genotypes consistently had the lowest level of osmoregulation, which resulted in Ψ_l -0.2 MPa to -0.3 MPa higher than normal leaf genotypes. Osmotic adjustment is considered to have a wide range of

physiological effects including maintenance of stomatal conductance and photosynthesis at lower Ψ_l; however, osmotic adjustment does not always confer maintenance of photosynthesis under at low Ψ_l (Turner, 1986). Osmotic adjustment can also maintain root growth at higher soil water potential and mechanical impediments, where plants that undergo osmotic adjustment have been shown to achieve higher crop yield under stress, which are associated with larger root densities and water extraction (Turner, 1986). Another advantage of osmotic adjustment is the delayed leaf rolling and leaf death by maintenance of Ψ_l.

(ii) Stomatal and gas exchange response

Stomatal closure provides a mechanism for the reduction of water loss. The response of stomata to Ψ_l is well established and has been extensively studied (Turner, 1986). Osmotic adjustment of cotton leaves in response to soil water deficits, results in the differential sensitivity of stomata for plants with and without previous water stress conditioning. Thomas *et al.* (1976) showed that stomata from field grown cotton plants preconditioned to water stress remained open at Ψ_l (-2.8 MPa) lower than those required to close stomata of well-watered plants (Ψ_l -1.8 MPa). Brown *et al.* (1976) observed similar results in growth chamber grown cotton.

Stomatal resistance on the adaxial surface of cotton leaves is greater than that of the abaxial surface, partly because of the higher stomatal density for the abaxial epidermis (McMichael and Hesketh, 1982). However, the stomata located on the adaxial surface of the leaf have a greater sensitivity to lowering of Ψ_l, and have a reduced response to water

stress conditioning (Grimes and El-Zik, 1990). Brown *et al.* (1976) found the osmotic potential of abaxial guard cells to be 0.7 MPa lower than those of the adaxial surface of the leaf. Differentials in stomatal sensitivity are also observed between young and old leaves, where Jordan *et al.* (1975) observed stomatal closure, independent of irradiance effects, of older leaves before younger leaves. Low N status has also been reported to change osmoregulation, where stomatal closure was observed at higher Ψ_l under low N conditions and plants that deplete their N supply throughout the season lose their ability to osmoregulate (Grimes and El-Zik, 1990). This suggests a physiological response to increase WUE under N and water limited conditions. The Ψ_l that result in stomatal closure is dynamic, being different at contrasting leaf positions in the canopy, upper and lower leaf surfaces, and water and N stress histories.

As water stress develops, photosynthesis is reduced from its maximum rate of 40 to 45 μmol (CO_2) m^2 s^{-1}. For non-osmotically adjusted plants, a reduction in Ψ_l is accompanied by a reduction of transpiration, which is under stomatal control. However, in osmotically adjusted plants (which have prior exposure to water stress conditions) photosynthesis still declines linearly with Ψ_l, but diffusive resistance may remain low over the range of declining Ψ_l (Grimes and El-Zik, 1990). This supports the theory that photosynthesis is under both stomatal and non-stomatal control.

2.3.2 Temperature stress

Both extreme low and high ambient temperatures are routinely observed in many cotton-producing regions. These sub-optimal T_a place limitations on cotton production due to

associated morphological, yield, physiological and biochemical temperature constraints. Low T_a is often observed in thermally marginal areas where crops may experience lower than optimal temperatures during the start and the end of the season due to short cropping seasons. High T_a is often observed in hotter growing climates during mid-season heat-waves. It is also important to note that all assertions of high and low temperatures must be relative to a standard.

(a) Morphological and lint yield traits

(i) Seedling and root growth

The base soil temperature (T_s) (lower limit) for seed germination is 12 °C and for seedling growth it is ~ 15.5 °C (Singh *et al.*, 2007). Similarly, Wanjura and Buxton (1972) found the temperature limits for germination were 14.4 °C and 41.9 °C with a optimum of 34.4 °C. Burke (2001) found that when seedling temperatures exceeded this optimal range, acquired thermotolerance systems were induced, with maximum protection levels reached at 37.7 °C to 40 °C. However, at higher plant temperatures, the protection gained from acquired thermotolerance rapidly declined.

The optimal range of day/ night T_a for root development in cotton are 30/22 °C to 35/27 °C (Singh *et al.*, 2007; Reddy *et al.*, 1997a). Higher T_a of 40/32 °C altered the dynamics of root growth, even under optimal water and nutrient environments. These effects were seen through a reduction in the depth of the root systems (Reddy *et al.*, 1997a). Many of the fundamental functions of root systems are sensitive and altered due to temperature. These include hydraulic conductivity, the uptake of water and nutrients, hormone

synthesis, assimilation and synthesis of metabolites and translocation (Singh *et al.*, 2007). Nielsen (1974) proposed that root temperature may be fundamentally more critical than shoot temperature for plant growth and development as roots have lower temperature optima and are more sensitive to extreme temperature fluctuations (Singh *et al.*, 2007). The synthesis of cytokinins in the root is among the most temperature sensitive processes (Paulsen, 1994).

(ii) Vegetative growth

Vegetative growth and leaf area development are highly sensitive to T_a (Singh *et al.*, 2007). Reddy *et al.* (1992c) reported the optimal temperature for leaf area development as 26 °C, and that 20 d after emergence the leaf area of plants grown at 28 °C was six times greater than those grown at 21 °C. The T_a also plays a major role in main stem elongation, leaf area expansion, and biomass accumulation (Singh *et al.*, 2007), with optimal day/ night T_a of 30/22 °C for these parameters (Reddy *et al.*, 1992c). In pima cotton, main stem extension rates were only highly sensitive to temperature post 21 d after emergence (Reddy *et al.*, 1992a). Although growth rates were highly affected by T_a in excess of 30/22 °C, the developmental rates of nodes, fruiting branches and fruiting branch nodes were not as sensitive. Main stem node addition rates and vegetative branch length increased as T_a increased from 20/12 °C to 40/34 °C. However, the optimal T_a for fruiting branch growth, square and boll production and retention was 30/22 °C. Temperatures above this resulted in reduced fruiting branch length while day/ night temperatures of 40/32 °C completely inhibited square production (Reddy *et al.*, 1992b; Reddy *et al.*, 1992c). Sikka and Dastur (1960) suggested the optimum range of growth for

Asian cotton (*Gossypium arboreum*) as 21 °C to 27 °C, where cool nights are needed for best growth rates. However, plants are also able to withstand T_a as high as 43 °C to 46 °C, provided adequate soil water is provided (Singh *et al.*, 2007).

In Reddy *et al.*'s (1992c) experiment, almost eight times more leaf area was produced at 30/22 °C compared with 20/12 °C. Furthermore, ~ 50% more leaf area was produced at 40/32 °C than 30/22 °C, and leaf growth rates were 20% lower in the 20/12 °C and 50% lower at 40/30 °C compared with growth rates at 30/22 °C.

(iii) Flower production and boll setting

Flowering, fruit production and setting is highly dependent on T_a (Reddy *et al.*, 1992b; Singh *et al.*, 2007). High T_a stress before and during flowering has significant effects on several reproductive processes leading to decreased fruit set and hence yield (Singh *et al.*, 2007). Ehlig and LeMert (1973) observed that the number of flowers per m was reduced three wks after a d where T_a exceeded 42 °C (Singh *et al.*, 2007). High T_a ~ 17 d before flowering can lead to decreased pollen viability and fertilisation (Oosterhuis, 1999). Similarly, Meyer (1969) observed that daily maximum T_a 15 to 16 d before anthesis affected pollen sterility more than any other aspect of the external environment. At T_a of 32 °C almost 100% pollen sterility occurred in temperature sensitive homozygous sterile plants, whilst heterozygous sterile lines with cytoplasm from diploid species became completely sterile at 38 °C. As maximum air temperatures > 38 °C an increasing number of sterile anthers were observed on both the sterile lines studied as well as the fertile plants. Burke *et al.* (2004; Burke, 2001) reported optimal pollen germination and pollen

tube elongation in cotton at 28 °C, where both are reduced as T_a exceed 32 °C. Suy (1979) found the rate of pollen tube elongation was reduced to almost zero as temperatures reached lows of 19 °C and highs of 45 °C (Singh *et al.*, 2007). This relatively moderate optimal temperature for pollen viability has an effect on flower pollination, especially those exposed to direct sunlight that often exhibit T_a > 32 °C. Pollen harvested in the afternoon from flowers at the top of the canopy showed significant reductions in viability compared with that from flowers within the canopy (Burke, 2001).

Heat stress during flowering results in square and flower shedding when day T_a > 30 °C (Reddy *et al.*, 1992b), whilst at T_a > 40 °C all squares and flowers were shed in a range of upland cotton cultivars (Reddy *et al.*, 1991b). Similarly, an increase in T_a from 28 °C to 32 °C resulted in increased abortion of bolls < 10 d old after anthesis in chronological order (Zeiher *et al.*, 1995). If this increased T_a was coupled with increased night temperatures, further increases in boll abortion were observed. Reddy *et al.* (1995a; Reddy *et al.*, 1997b; Reddy *et al.*, 2004) found that pima cotton was generally more susceptible to high T_a than upland cotton, where some pima cotton cultivars failed to produce fruiting branches and reproductive sites when average T_a were 36 °C. However, although upland cotton was able to produce fruiting branches and sites at high temperature, it did not successfully produce bolls.

Powell (1969) showed that night T_a are important for fruit set and boll development. In an growth chamber experiment with constant air temperature of 29.4 °C plants did not

produce fertile pollen, whilst plants grown at a constant air temperature of 32.2 °C did not even set fruit when pollinated with viable pollen. This effect on flowers and fruit set was not brought on by indirect response to vegetative damage as vegetative effects were noticed prior to floral effects. Furthermore, decreased T_a during part of the diurnal cycle also increases boll retention (Powell, 1969), however decreased boll retention at constant temperatures may be due to plants reaching a maximum number of bolls to be supported under the conditions. Converse results were observed by Zeiher *et al.* (1995), concluding that poor boll set associated with elevated night temperatures was due to heat stress rather than a specific night temperature effect. However, high night temperatures can reduce boll set through effects on square development, either by suppressing the development of the reproductive meristem or by increased shedding and abortion of young squares (Singh *et al.*, 2007).

(iv) Boll development

In general, higher average air temperatures accelerate crop growth, thus reducing the developmental time for bolls, resulting in smaller bolls, lower lint quality and reduced yield. At high air temperatures, crop development rates proceed at a much faster rate. The time required to produce squares, flowers and mature bolls was reduced by an average of 1.6, 3.1 and 6.9 degree days, respectively, per 1 °C increase in air temperature (Reddy *et al.*, 1997b). Boll growth was more susceptible to temperature than vegetative growth, with boll weight at its peak at approximately 32 °C, and was reduced either side of this temperature (Reddy *et al.*, 1992b). Reddy *et al.* (1992a; Reddy *et al.*, 1992b; Reddy *et al.*, 1992c) showed that air temperatures above this optimum resulted in boll abortion. Only ~

50% of the squares and bolls produced at 33 °C were retained, whilst none were retained at 36 °C.

(v) Lint yield and fibre quality

Air temperature effects on lint yield are somewhat complex as yield is the summation of the crop's response to changes in T_a in terms of growth rates, photosynthetic rates and fruiting, all of which display different thermal optima (Conroy *et al.*, 1994; Polley, 2002). For example, when the T_a is below the optimum for net photosynthesis, a small increase in T_a can stimulate crop growth. However the converse is also true where a small increase in T_a above the optima can dramatically reduce lint yield (Singh *et al.*, 2007). Oosterhuis (1999) showed a gradual decline in boll development from 32 °C, where increased T_a reduced carbohydrate production. Thus the carbohydrate demand of the plant could not be met, resulting in boll abortion, smaller and malformed bolls, decreased lint percentage and lower lint yields. As cotton lint is predominantly carbohydrate, a reduction in carbohydrates for the plant inevitably results in reduced fibre production and lower lint yields.

The evidence suggests that there is an optimal T_a for cotton growth, and plant growth and lint yield is reduced on either side of this optima. However, this optimum is ill-defined and may vary across species and genotypes of cotton as well as growth stages.

(b) Physiological and biochemical traits

(i) Membrane disruption

Cell membranes are selectively permeable phospholipid bilayers that separate the intracellular components from the extracellular environment. Temperature stress on these cell membranes leads to membrane disruption and changes in membrane fluidity (Singh *et al.*, 2007). Membrane fluidity plays a major role in the sensing of both high and low T_a conditions. Increased thylakoid membrane ionic conductance and ribulose-1,5-biphosphate carboxylase-oxygenase (Rubisco) deactivation is believed to be the primary cause for the associated reduction in photosynthesis following heat stress (Singh *et al.*, 2007). Schrader *et al*. (2004) found that heating dark adapted cotton leaves to 36 °C resulted in an increase in thylakoid permeability; however, during steady state heating this increase in permeability did not affect ATP production. Under rapid heating a decline in ribulose-1,5-biphosphate is observed without a corresponding decrease in Rubisco activation, whilst under sustained heat, not only a decline in Rubisco activation was observed, but also oxidation of the stroma, the thick fluid found in between the thylakoid disk stacks of the chloroplasts. It is hypothesised that this is due to an increase in cyclic photophosphorylation, which would explain the maintenance of ATP while thylakoid membrane permeability is increased (Schrader *et al.*, 2004).

(ii) Photosynthesis, gas exchange and carbon assimilation

Photosynthesis is considered as one of the plant functions most sensitive to high temperatures (Kim and Portis, 2005; Salvucci and Crafts-Brandner, 2004). Many measured crop species have a broad optimal T_a range between 20 °C and 35 °C, with

peak photosynthetic rates at 30 °C. An increase in T_a above range is detrimental to carbon assimilation as high T_a reduce photosynthetic respiration through the stimulation of photorespiration and damage to photosynthetic apparatus (Sailsbury and Ross, 1992). Prolonged exposure to high T_a (> 40 °C) generally results in irreversible damage to photosynthetic pathways due to disruptions in thylakoid membranes and damage to photosystem II (PSII). Inhibition of photosynthesis < 40 °C is distinguished by its rapid reversibility (Kim and Portis, 2005). Although the primary mechanisms responsible for inhibition are unclear, a reduction in the activation state of Rubisco accompanies the reduction in carbon assimilation (Kim and Portis, 2005).

The photosynthetic rate of cotton was found to peak at 28 °C, the T_a optima determined by Reddy *et al.* (1995b). Heat stress decreases the maximum quantum yield of photochemistry of PSII and inhibits CO_2-exchange rates by decreasing the activation states of Rubisco through Rubisco activase inactivation (Law and Crafts-Brandner, 1999). Essentially, the inability of Rubisco activase (required for regulation of enzymatic activity of Rubisco) to offset faster deactivation of Rubisco constrains photosynthesis at elevated temperatures (Kim and Portis, 2005). In addition, high T_a increases the rate of photorespiration, reducing carbon assimilation in cotton. When leaf temperature was rapidly (30 s) increased from 30 °C to 42 °C photosynthesis declined instantaneously by 17% and a progressive decay in photosynthetic rates of 8% min^{-1} (Schrader *et al.*, 2004). The slow decline in carbon assimilation was temperature dependent, showing progressively reduced rates from 39 °C to 45 °C. Perry *et al.* (1983) observed that at 22 °C photorespiration in cotton accounted for 15% of the net photosynthesis, while at 40 °C

photorespiration comprised ~ 50% net photosynthesis. Heat stress can have a profound effect on photosynthesis and photorespiration rates. Leaf stomatal conductance increased to T_a of 21/ 23 °C and following this temperature had no effect on stomatal conductance. Transpiration rates also increase with T_a, and a linear trend was observed from 26/ 18 °C to 36/ 28 °C (Reddy *et al.*, 1998).

Advanced pima cotton was bred for high yielding irrigated production in relatively high temperature environments, and thus has a higher g_c and smaller leaf area than the obsolete lines (Lu *et al.*, 1994). Lu and Zeiger (1994) found photosynthetic rates in pima cotton had low sensitivity to T_a in the 23 °C to 36 °C range, whilst g_c increased linearly within this range. Similarly, photosynthetic rates between 24 °C and 36 °C remained constant in a moderately heat-tolerant line of pima cotton (Pima S-6), however an associated increase in g_c was observed (Radin *et al.*, 1994). Although this increase in g_c did not result in increased photosynthesis and carbon assimilation, it is important for canopy cooling to avoid temperature stress. However, it is unlikely that photosynthetic rates, a biochemical reaction, would be insensitive to temperature over a 13 °C temperature range. As g_c increased with T_a, leaf temperature may have been more stable than expected and therefore the variation in photosynthesis may have been reduced.

(iii) Heat shock protein induction

Heat shock proteins (HSP) are a group of proteins whose expression is increased following the exposure of plant (and animal) cells to elevated temperatures. The HSPs are intracellular, cytoplasmic proteins and are one method of plant response to heat stress,

and are molecular chaperones for protein molecules. They form an integral part of the intercellular protein-protein interactions such as protein folding, preventing unwanted protein aggregation, stabilising partly unfolded proteins, and establishment of correct protein conformation. Therefore, their role in plants are implicated in acquired thermotolerance, maintenance of cell integrity, prevention of protein denaturation and protection of PSII (Singh *et al.*, 2007). Burke *et al.* (1985) found the T_a range for the induction of HSPs was 38 °C to 41 °C in laboratory grown cotton. Therefore, heat shock response is of little significance in agricultural settings as it is initiated at such high T_a.

Water and heat stress often occur in unison, and are often accompanied by high solar irradiance and other environmental factors such as wind, which exacerbate plant injury due to water stress. Saranga *et al.* (2001) highlighted the co-existence of water and high temperature stress in field conditions of arid regions. This emphasises the need for a balance between heat and drought tolerance, and the need for coupled changes in crop water use and thermotolerance to improve crop productivity in high temperature and water limited environments.

2.4 Water stress detection and irrigation scheduling from leaf and canopy temperature measurements

The increase in availability of more affordable, portable and reliable infra red thermometers has occurred steadily since the 1970s (Jackson *et al.*, 1981). This has allowed for real time, remote monitoring of plant T_c. The significance of monitoring plant T_c is that through the opening and closing of stomata (in response to soil water deficits)

T_c are altered. The closure of stomata results in a decrease in transpiration and consequently reduction in latent energy flux, leading to a rise in T_c. However, ambient conditions can have a large influence on T_c, thus T_c are a reflection of plant and environmental factors (Fuchs, 1990). Furthermore, T_c measured with a radiometer only measures the surface temperature of all objects within its field of view. Therefore, T_c can ignore the lower portion of the plant and include sun-lit and shaded leaves, stems and fruiting bodies, as well as background soil in crops without full canopy closure. Although T_c ignores the lower portion of the plant, this limitation is usually overlooked as the majority of carbon assimilation occurs in the upper portion of the plant, the sun-lit leaves.

2.4.1 Canopy temperature depression (CTD)

The value of T_c measurements in agriculture has been established since the early 1980s (Idso, 1982; Jackson, 1982). The importance of T_c measurements is that under well-watered conditions T_c can be significantly lower than ambient air temperatures. The converse of this is also true and patterns of the differential between T_c and T_a temperature occur as a result of transpiration rates and the effect these rates have on the evaporative cooling of a leaf. Therefore, when soil water availability declines, transpirational cooling of a leaf is reduced and T_c rise (Mahan *et al.*, 2005).

One of the simplest methods for detecting water stress through T_c is the use of canopy temperature depression (CTD). CTD is the difference between canopy and air temperatures and is calculated by:

Equation 1: Canopy temperature depression

$$CTD = T_c - T_a$$

The CTD is negative when the T_c is cooler than T_a and has been used in numerous applications. Early work on the difference between canopy and air temperatures was conducted by Pallas *et al.* (1967). They found that at high soil water, leaf temperatures ranged from a fraction to a few degrees C above ambient temperature, except at medium and low light intensities and high VPD, when they were below ambient temperature due to increased transpirational cooling. Conversely, during low soil water leaf temperatures were as high as 3.4 °C above ambient temperatures. Other early work on CTD was studied with thermocouples embedded into cotton leaves (Ehrler, 1973). Ehrler found that CTD decreased after irrigation, reaching a minimum value several days following irrigation, and then increased as soil water became increasingly depleted. After showing a linear relationship between CTD and VPD, Ehrler (1973) concluded that CTD has potential for informing irrigation scheduling tools. The application of CTD has been used in plant response to environmental stress (Ehrler *et al.*, 1978; Idso, 1982; Howell *et al.*, 1984; Jackson *et al.*, 1981; Baker *et al.*, 2007), irrigation scheduling (Hatfield, 1983; Wanjura *et al.*, 1995; Evett *et al.*, 1996), and to evaluate cultivar water use (Pinter *et al.*, 1990; Hatfield *et al.*, 1987b), heat tolerance (Amani *et al.*, 1996; Reynolds *et al.*, 1994) and, drought tolerance (Blum *et al.*, 1989; Rashid *et al.*, 1999; Hirayama *et al.*, 2006). Baker *et al.* (2007) found that by including the influence of ambient temperatures on leaf temperature, through the calculation of CTD, the relationship between leaf temperature and the corresponding rates of photosynthesis and g_c was improved. The CTD was used to assess plant water status as it is a product of the leaf's energy balance, including both

environmental and physiological responses to water and high temperature stress (Balota *et al.*, 2007; Balota *et al.*, 2008). However, the suitability of CTD as an indicator of stress tolerance, and hence crop yield, must be determined for individual environments as, for example, its use is restricted when grain yield is limited by the amount of stored soil water (Balota *et al.*, 2007).

2.4.2 The Crop Water Stress Index (CWSI)

Following the findings of Ehrler (1973), theoretical research carried out by Jackson *et al.* (1981) and experimental work by Idso *et al.* (1981a) developed a water stress index known as the crop water stress index (CWSI), which is a measure of the relative transpiration rate occurring from a plant at the time of measurement using a measure of plant temperature and the vapour pressure deficit. The CWSI requires a non-water stress base line from a crop that is transpiring at its potential rate, which is essentially the linear relationship between the difference in T_c and T_a vs. air VPD under non-limiting soil water conditions. The CWSI can be represented as:

Equation 2: Crop Water Stress Index

$$CWSI = \frac{(T_c - T_a) - D_2}{D_1 - D_2}$$

where D_1 is the maximum water stressed baseline and D_2 is the non-water stressed baseline. The CWSI can be represented graphically, as shown in Figure 2.1, where CWSI is the ratio of a to b.

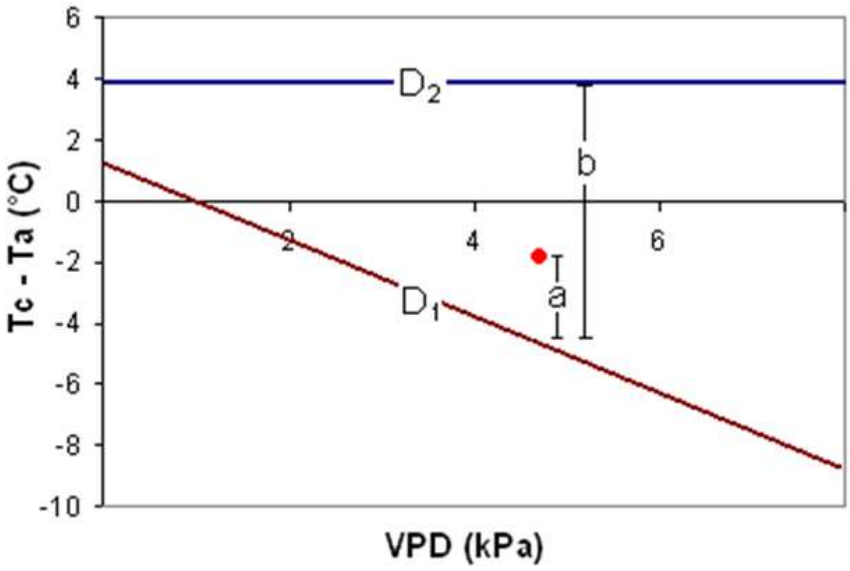


Figure 2.1. A graphical representation of the crop water stress index (CWSI) which can be calculated as the ratio of the difference between a and b where a= the measured CTD and corresponding VPD and the maximum water stressed baseline, and b= the difference between the non-water stressed baseline and the maximum water stress base line, i.e. CWSI = a/b. The red dot represents the measured CTD and VPD which are used to calculate CWSI. T_a is measured at a screen-height of 2.0 m.

Jackson *et al.* (1981) presented the theory behind the energy balance that separates net irradiance from the sun into sensible heat that heats the air and latent heat that is used for transpiration. The value of the CWSI ranges from 0 to 1, where non-stressed plants exhibit a value near zero. As the crop undergoes water stress the stomata close, transpiration decreases and leaf temperature increases. When a plant is transpiring fully the leaf temperature is 1 to 4 degrees < T_a and the CWSI is 0. As the transpiration decreases, the leaf temperature rises and can reach to 4 to 6 degrees > T_a to the point where transpiration ceases and CWSI is 1. Jackson *et al.* (1981), showed that CWSI can also be calculated empirically through knowledge of weather and crop factors using the following equation:

Equation 3: Crop Water Stress Index

$$CWSI = 1 - \frac{E}{E_p} = \frac{\gamma(1 + r_c / r_a) - \gamma^*}{\Delta + \gamma(1 + r_c / r_a)}$$

where E is the latent heat flux to the air (W m^{-2}), E_p is the potential latent heat flux to the air, γ is psychrometric coefficient, which depends on surface temperature and atmospheric pressure (Pa $°C^{-1}$), r_c actual canopy resistance (s m^{-1}), r_a is the aerodynamic resistance (s m^{-1}), γ^* (psychrometric coefficient in a well-watered crop) is equal to $\gamma(1+ r_{cp}/ r_a)$, and Δ is the slope of the saturation vapour pressure-temperature curve (Pa $°C^{-1}$).

Numerous studies have been conducted on irrigation scheduling using CWSI (Garrot *et al.*, 1994; Erdem *et al.*, 2005; Erdem *et al.*, 2006; Cremona *et al.*, 2004; Alderfasi and Nielsen, 2001; Irmak *et al.*, 2000; Shae *et al.*, 1999; Nielsen, 1990; Garrot *et al.*, 1993). In most studies irrigating when CWSI reaches a value of 0.1 to 0.2 will produce maximum crop yields. Gardner *et al.* (1987) developed a device for monitoring CWSI from measurements of T_a, RH and sunlight intensity (Upchurch *et al.*, 1996).

2.4.3 Canopy temperatures and water stress physiology

Numerous studies have correlated T_c with soil water content, environmental conditions and plant physiological responses. Jackson *et al.* (1981) showed that durum wheat (*Triticum durum* Desf.) T_c (in the form of the CWSI) closely paralleled the extractable soil water to 1.1 m in a variety of flood irrigation regimes. The relationships between Ψ_l and plant water potential with respect to T_c have also been outlined (Cohen *et al.*, 2004; Howell *et al.*, 1984; Idso *et al.*, 1981b; Idso *et al.*, 1981c). These relationships are

especially evident when plant water potentials or T_c are normalised with air vapour pressure deficit (VPD) (Cohen *et al.*, 2004; Idso *et al.*, 1981b; Idso *et al.*, 1981c). VPD is used as a result of the success of Idso *et al.* (1981a) in normalising the stress degree day concept (which led to the development of the CWSI) for environmental variability with VPD. The improvement in the relationship between leaf temperatures and Ψ_l by calculating CWSI shows that the use of T_c for stress detection can be adapted to various meteorological conditions (Cohen *et al.*, 2004), and that T_c combined with meteorological data can adequately detect water stress.

Previous research has also described the relationship between gas exchange parameters and foliage temperatures, which is generally also strengthened with the inclusion of air VPD data. Idso *et al.* (1982) observed this relationship in cotton and concluded that any water stress severe enough to reduce transpiration below potential rates also results in a similar reduction in photosynthesis. Thus, it is beneficial to apply irrigation water when CWSI rises significantly above zero (non-stressed). Similarly, O'Toole *et al.* (1984) found that mean daily net photosynthetic rates were correlated with CWSI ($r = 0.84$) in rice (*Oryza sativa* L.), and concluded that the CWSI is an advancement in non-destructive, non-disruptive crop level water stress detection and measurement. There were similar net reductions in photosynthesis in both O'Toole *et al.* (1984) and Idso *et al.* (1982) across a similar CWSI range, which attests to the theoretical soundness and practicality of the CWSI. Leidi *et al.* (1993) also observed reductions in net photosynthesis and stomatal conductance of cotton with rising leaf temperatures. They concluded that leaf temperatures probably rose due to reduced evaporative cooling as a

result of reduced g_c, but also noted that potential non-stomatal effects were not measured. However, the strong relationship between photosynthesis and g_c with leaf temperatures observed by Leidi *et al.* (1993) may be limited. This is because all photosynthesis measurements were taken when leaf temperatures were above the optimal for metabolic performance (Burke, 1990) and over a 8 ºC window of leaf temperatures (30 ºC to 38 ºC).

More recently, Hirayama *et al.* (2006) showed that rice cultivars with lower leaf temperatures can maintain high transpiration and photosynthetic rates, resulting in higher grain yields under upland conditions. This is a cause and effect phenomena, as higher transpiration rates result in lower leaf temperatures, which may enable higher photosynthetic rates. Baker *et al.* (2007) used numerous gas exchange parameters as indicators of plant water stress and compared these to simultaneously measured T_c. They concluded that T_l, and by extension T_c, was not a relevant predictor of drought stress in cotton in terms of gas exchange (A r^2= 0.24, g_c r^2= 0.13). However, the use of canopy temperature depression (CTD), the difference in leaf or canopy and air temperatures, especially when used in combination with VPD, provided greater predictive utility (A r^2= 0.79, g_c r^2= 0.80). This body of research suggests that there is potential utility in T_c as an indicator of physiological water stress, which needs to be further explored (with particular reference to the effects of VPD) for the use of T_c in irrigation scheduling systems.

2.5 Biologically Identified Optimal Temperature Interactive Console (BIOTIC)

Most current irrigation scheduling techniques involve the measurement of soil water, atmospheric parameters, and other plant measurements such as T_c, stomatal aperture, leaf colour and Ψ_l. This data is then used in decision processes ranging from simple rules to complex mathematical formulae, in an attempt to determine the necessity of irrigation (Upchurch *et al.*, 1996). Although varying in technique, all these irrigation scheduling tools have one aspect in common; they all indirectly measure the plants water requirement. The BIOTIC utilises direct plant measurements for irrigation scheduling, through the use of infrared thermometers (IRT) to measure plant T_c. The knowledge of plant T_c is a valuable tool for irrigation scheduling as all plant species have an optimal *in vivo* temperature for metabolism. Once this threshold is exceeded as a result of reduced access to water, transpiration and thus evaporative cooling is reduced. A reduction in evaporative cooling results in a corresponding rise in leaf and T_c and is thus used as a signal for irrigation scheduling. The BIOTIC is an irrigation management tool based on optimal temperatures for plant metabolism and integration of the environment derived from the plant's T_c (Upchurch *et al.*, 1996).

2.5.1 The development of BIOTIC

Canopy temperatures has been used as an indicator of plant water stress since the 1980s (Jackson *et al.*, 1981; Idso, 1982). As a result, thermal stress, through the measurement of T_c, in plants has been used for the detection of water stress to determine the necessity of irrigation. In order to develop indicators of the early onset of water and temperature stress, Mahan *et al.* (1987), Mahan and Upchurch (1988), and Burke *et al.* (1988) defined

optimal plant temperatures with respect to the thermal dependence of the Michaelis-Menten constant of an enzyme (K_m). They found that optimal enzymatic function was restricted to a range of temperatures that they termed the thermal kinetic window (TKW), which is an estimate of the optimal temperature range of a plant species. The period of time that a crop's T_c remains within its TKW was found to correlate with above ground biomass (Burke *et al.*, 1988). Therefore, plants exhibit homoeothermic behaviour where they will preferentially maintain their *in vivo* temperature at a specific temperature, known as the normative plant temperature (T_n) (Burke and Upchurch, 1989; Mahan and Upchurch, 1988). However, this concept is not universally accepted and is limited by sufficient energy input to rise this temperature; sufficient water for transpirational cooling; and humidity conditions that would allow for transpirational cooling to the normative plant temperature (Mahan and Upchurch, 1988). Following this, automated irrigation scheduling using continuous T_c measurements was studied by Wanjura *et al.* (1988; 1990; 1992). In these studies cotton was irrigated when the average T_c during a 15 min time period exceeded a predetermined TT of 26, 28, 30 or 32 °C. The hypothesis behind these experiments was that by attempting to maximise the amount of time T_c were within the TKW, lint yield should be maximised. Lint yield was determined to be consistently highest for the 28 °C TT, and decreased for higher or lower TT. A 28 °C TT provided maximum lint yield where water and season length were not limiting. These experiments compared T_c to a biologically based optimum temperature, and irrigated in response to canopy temperatures exceeding the threshold temperature. The use of a biologically based estimate of optimum T_c provided the departure from previous irrigation scheduling methods using T_c (Mahan *et al.*, 2005).

The initial studies by Wanjura *et al.* (1988; 1990; 1992) used a 15 min interval for irrigation signals. Although this provided rapid alleviation of water stress, and precise control of plant water status, the approach needed to be modified for use in irrigation systems with longer irrigation intervals. This was conducted in order to meet the demand of drip irrigated, and centre-pivot irrigated cotton, which require an irrigation interval of 3 to 7 d (Mahan *et al.*, 2005). These requirements lead to the development of a time threshold. Wanjura *et al.* (1992) demonstrated the feasibility of a temperature-time threshold system, where daily time thresholds calibrated to local environments, for use in longer interval irrigation events. Irrigating with temperature-time thresholds was then tested across a range of geographical areas within the USA, including Mississippi, Texas and California, in environments ranging from humid to arid, in both research and commercial production settings. The irrigation protocol has been shown to be robust over numerous production environments and provides irrigation management that is competitive with existing scheduling techniques (Mahan *et al.*, 2005).

2.5.2 How does BIOTIC work?

The BIOTIC was developed in 1996 as an irrigation scheduling tool (Mahan *et al.*, 2005). It manages crop irrigation using T_c measurements and a specific time threshold (Upchurch *et al.*, 1996). The BIOTIC continually measures the T_c of the target crop with an IRT. After each measurement, the T_c is compared with a predetermined threshold of water stress T_c, where if the crop's T_c is above this value it is thermally stressed. This TT is based on the observation of the thermal dependence of plant metabolic activity (Teeri and Peet, 1978; Peeler and Naylor, 1988). If the measured T_c is $\leq$ to the threshold

temperature, irrigation is not initiated and T_c measurements continue. However, if both the T_c > the threshold temperature and the humidity is not restrictive to plant cooling, an increment of time is added to a time register (Upchurch *et al.*, 1996). The accumulated "stress time" is thereafter compared to the time threshold, i.e., predetermined constant defined as the species-specific mean length of time per day that a well-watered non-stressed plant will naturally exceed its T_c threshold in the target geographical area (Upchurch *et al.*, 1996). As long as the accumulated time is < the time threshold, irrigation is either unnecessary or inefficient to achieve transpirational cooling, and the process is again repeated with T_c, humidity and accumulated time measurements. However, once the accumulated time exceeds the time threshold, an irrigation signal is generated, and crop transpirational cooling is induced. Once a signal to irrigate is initiated the BIOTIC protocol advises sufficient application of water to meet the calculated evaporative demand until the next possible irrigation event. If the applied water is not fully used by the crop before the next possible irrigation, it is delayed until the water is consumed and T_c is elevated.

The quantity of applied water (irrigation and rainfall) was compared in cotton grown at Lubbock, Texas, by Wanjura *et al.* (1990) in three BIOTIC irrigation systems based on canopy threshold temperatures of 28, 30 and 32 °C, a water balance method that replaced depleted soil water on a weekly basis, an irrigation schedule based on an approximate two week cycle and a dryland system that received only a pre-planting irrigation (119 mm water). The results of the study are shown in Table 2.1. Maximum yield was produced using a TT of 28 °C or two week soil water balance, and yield-water relations were

described with a quadratic polynomial function ($y = -0.002x^2 + 3.8x - 2.4$; $R^2 = 0.99$). This study shows that irrigation management of cotton with threshold T_c based on enzyme thermal stability produced lint yields equal to, if not greater than those obtained from tradition irrigation scheduling techniques (Wanjura *et al.*, 1990). However, specific threshold T_c that induce comparative levels of water stress may depend on climatic factors.

Table 2.1. Results from a study by Wanjura *et al.* (1990) comparing water-use and yield under BIOTIC irrigation regimes and soil water balance methods. Super-scrip letters show different levels of significance (P=0.05).

Irrigation treatment	Water (mm)	Lint yield (kg ha^{-1})	WUE (kg (lint) ha^{-1} mm^{-1}
Dryland	180a	353^{e}	2.0
Soil water balance (1 wk cycle)	1380^{d}	1147^{b}	0.8
Soil water balance (2 wk cycle)	700^{c}	1430^{a}	2.0
BIOTIC 28	750^{c}	1431^{a}	1.9
BIOTIC 30	460^{b}	1073^{c}	2.3
BIOTIC 32	360^{b}	902^{d}	2.5

2.5.3 Temperature threshold: Biochemically based optimal plant thermal environments

The effects of thermal stress on plants are substantial and often have significant world-wide effects on crop production. However, one of the difficulties in studying thermal stress is the definition and quantification of stress levels. Generally stress levels are compared with an estimate of the optimal thermal range characteristic of that species or genotype of plant. There are numerous definitions of thermal stress, however it is generally agreed that the optimal thermal range, or thermal kinetic window, of cotton is

23.5 °C - 32 °C (Burke *et al.*, 1988) and high temperatures (> 36 °C) will adversely affect the growth and development potential, and ultimately lint yield of a cotton crop (Hodges *et al.*, 1993). Hale and Orcutt (1987) hypothesised that a zero stress condition must be known in order to discuss thermal stress. Consequently they defined the optimal thermal environment as the thermal range where zero stress conditions are observed. Knowledge of the optimal range of thermal environments is crucial for the reduction of the adverse effects of temperature stress as well as the development of stress avoidance technologies through altering the optimal thermal range of the plant of the plant temperature.

The BIOTIC TT is an estimate of the thermal optimum of metabolism of the plant. Historically, a stress temperature threshold of 28 °C has been used for irrigation scheduling with BIOTIC in cotton. This TT is calculated by estimating the thermal optimum of the metabolism of the plant determined from the temperature dependence of a selected metabolic indicator (Mahan *et al.*, 2005). Three methods have been developed to determine the temperature threshold: enzyme kinetic analysis, the temperature dependence of the reappearance of photosystem II variable chlorophyll following illumination and chlorophyll development in etiolated seedlings.

(a) Enzyme kinetic analysis

Enzyme kinetic analysis has been used to determine plant optimal temperatures on the basis of the thermal dependence of the apparent K_m of the enzyme of the plant species of interest. The minimum apparent K_m approach to determining optimum temperature is based on the concept of the TKW. The TKW for optimum enzyme function is the thermal

range over which the apparent K_m of an enzyme is within the range of ± 200% of the observed minimum value (Mahan *et al.*, 1987). The relevance of 200% was based on earlier work that suggested that enzymes could function optimally within ± 200% of the minimum K_m value (Teeri, 1980; Teeri and Peet, 1978; Somero and Low, 1976). The temperature dependence of enzyme function has been used to explain the ecological niche and limitations of organisms to thermal environments (Somero and Low, 1976; Teeri and Peet, 1978; Burke, 1994). As plant enzymes evolved for optimal function within the normative temperature range of the organism, the TKW concept can be used as a means of determining an optimal plant T_c. The practical utility of this method is limited as it involves complex enzyme assays over a range of temperature controlled conditions (Mahan *et al.*, 2005).

(b) Recovery of variable fluorescence

When a quantum of light is absorbed by a molecule of chlorophyll, the energy of the quantum is transferred to the valence electron of the chlorophyll, raising them to an excited state. The electrons rapidly return to their ground state releasing energy by three possible pathways. Chlorophyll fluorescence is one of these three possible pathways that light energy absorbed by chlorophyll molecules in a leaf can endure. Light energy can be used to drive the photochemical reactions of photosynthesis, dissipated as heat, or re-emitted as light. The latter of these three outcomes is described as chlorophyll fluorescence (Maxwell and Johnson, 2000). These three processes are strongly related and are hence in competition with one another. Therefore an increase in photosynthetic efficiency will result in the decrease of dissipated heat energy and chlorophyll

fluorescence. Such changes in chlorophyll fluorescence can be used to monitor changes in photosynthetic metabolism and heat dissipation (Peeler and Naylor, 1988).

The maximum amount of fluorescence yield is observed when all reaction centres of photosystem II (PSII) are closed, and is only ~ 3% of the absorbed light. When photosynthesis is at its peak and all photochemical reaction centres are operating fluorescence yield is much lower (~ 0.6%) due to the completion of photochemistry (Krause and Weis, 1991). The theory behind the measurement of fluorescence is that the spectrum of fluorescence is different to that of the absorbed light, where the peak of fluorescence emission has a characteristically longer wavelength than the absorbed light. Essentially this means that fluorescence can be measured by exposing a leaf to a known wavelength of light and measuring the amount of re-emitted light of higher wavelengths (Maxwell and Johnson, 2000). Fluorescence measurements are however relative measurements, as some light energy is inevitably lost from the system.

Kautsky *et al.* (1960) were the first to observe changes in chlorophyll fluorescence yield. They found that upon removing a dark-adapted plant from dark to light conditions an increase in the yield of chlorophyll fluorescence occurred for a period of one second. This rise in fluorescence has been explained due to a reduction in photochemistry (Maxwell and Johnson, 2000). A reduction of electron acceptors downstream of PSII results in the rise in chlorophyll fluorescence. This is because once PSII absorbs light and the electron acceptor has accepted an electron, it is not able to accept another electron until it has passed the first onto the subsequent electron carrier. During this time the reaction centre

is said to be closed, and hence a rise in light absorption will lead to a reduction in the overall efficiency of photosynthesis as more light energy is lost as chlorophyll fluorescence of dissipated as heat (Maxwell and Johnson, 2000). Therefore, when a leaf is transferred from a dark-adapted state into light the PSII reaction centres are progressively closed. This results in an increase in chlorophyll fluorescence for approximately the first second of illumination until the fluorescence falls again over a few minutes (Maxwell and Johnson, 2000; Peeler and Naylor, 1988; Burke, 1990). This phenomenon is referred to as fluorescence quenching and can be explained through, photochemical quenching and non-photochemical quenching. Photochemical quenching is an increase in the rate at which electrons are transported from PSII, due to light induced activation of photochemical enzymes and the opening of stomata (Maxwell and Johnson, 2000). This results in the delay in the restoration of the dark adapted variable fluorescence (F_v) due to the slowing of metabolic processes and effects on membrane fluidity (Burke, 1990). Non-photochemical quenching can be described as the increase in the efficiency at which light energy is transferred to heat (Maxwell and Johnson, 2000).

Fluorescence can give insights into the ability of plants to tolerate environmental stresses and the extent to which these stresses have damaged the photosynthetic pathways (Maxwell and Johnson, 2000). Measurements of fluorescence over a diurnal period can provide information on non-photochemical quenching, electron transport rates, quantum efficiency and the extent of photo inhibition as a result of temperature, light and other environmental stresses (Maxwell and Johnson, 2000). Gamon and Pearcy (1989) used measurements of dark-adapted F_v/F_m and F_o to indicate the occurrence of photo inhibitory

damage in response to temperature, whilst Epron *et al.* (1992) studied photo inhibitory damage in the same way in response to water stress. The observation of changes in F_v/F_m and F_o are widely accepted as diagnostic tools for the detection of photo inhibition caused by environmental stresses.

As PSII is sensitive to stress, chlorophyll fluorescence can be used to reflect the temperature sensitivity of PSII, and hence be used to identify the plant temperature optima, at the leaf level (Burke, 1990). The temperature where the minimal dark adapted fluorescence begins to rise suggest the thermo-tolerance of a plant (Burke, 1990). Peeler and Naylor (1988) reported an inhibition of the recovery of F_v in the dark following illumination of cold sensitive cucumber at 5 °C, while no inhibition was observed in resistant peas. Burke (1990) determined species-specific temperature optima for wheat (*Triticum aestivum*), cotton (*Gossypium hirsutum*), tomato (*Lycopersicon esculentum*), bell pepper (*Capsicum annuum* cv. California Wonder) and petunia (*Petunia hybrida* cv. Red Sail) from the recovery of F_v following illumination. Burke designated the temperature that provided the maximum variable fluorescence (F_v/F_o) as the species optimum temperature. These values corresponded to the temperature sensitivity of apparent K_m of hydroxypyruvate reductase for NADH.

Peeler and Naylor (1988) reported that the recovery of variable fluorescence was thermally dependent. Burke (1990) and Ferguson and Burke (1991) used this method to determine the thermal optima of numerous plant species. The principle underlying chlorophyll fluorescence is that light energy absorbed by chlorophyll molecules in a leaf

can be either used to drive photochemistry, dissipated as heat or re-emitted as light-chlorophyll fluorescence (Maxwell and Johnson, 2000). These three processes occur in competition, where an increase in efficiency of one process will result in a decrease in yield of the other two (Maxwell and Johnson, 2000). Chlorophyll fluorescence has been increasingly used in plant physiological studies, as it yields information about the changes in the efficiency of photochemistry, heat dissipation, and is an indicator of the *in vivo* temperature characteristics of a plant. The optimum temperature for F_v reappearance (expressed as the ratio of F_v/F_o where F_o is the initial fluorescence) is defined as the temperature that yields the maximum F_v/F_o ratio, and the minimum time in darkness required to achieve this ratio (Burke, 1990). Correlations between enzyme kinetic analysis and the recovery of variable fluorescence have been reported in bell pepper, cotton, cucumber, petunia, potato, soybean, tomato and wheat (Burke, 1990; Ferguson and Burke, 1991; Burke and Oliver, 1993).

(c) Chlorophyll development in etiolated seedlings

The final method that has been used to calculate the optimal temperature of plant species is chlorophyll development in seedlings. Burke and Oliver (1993) determined the optimum temperature for the development of chlorophyll a/b light harvesting complex of photosystem II (LHCP II) in cucumber (*Cucumis sativus* L. cv. Ashley). Maximum synthesis of LHCP II occurred at 30 °C. Burke and Oliver (1993) compared the three methods for determining optimal temperatures, finding similar thermal dependencies for each method. Using Peeler and Naylor's (1988) method the optimum temperature for photosystem II variable fluorescence reappearance following illumination was measured

to be between 30 and 35 °C (Burke and Oliver, 1993). Similarly, using the enzyme kinetics methodology as described by Burke *et al.* (1988), the TKW for cucumber, based on a minimum apparent K_m of 32.5 °C, was determined to be between 23.5 and 39 °C (Burke and Oliver, 1993). They determined that these values were all similar to the optimum temperature calculated by chlorophyll development, and based on simplicity of procedure, the reappearance of PSII variable fluorescence is the preferred method for calculating the BIOTIC temperature threshold (Burke and Oliver, 1993). These findings are supported by field based application of the temperature threshold where scheduling using a threshold canopy temperature of 28 °C has consistently produced the highest lint yields in cotton (Wanjura *et al.*, 1992). However, if water supply and season length are limiting crop production, the 30 °C threshold temperature produced the higher average lint yield, profit and WUE (Wanjura *et al.*, 1992).

2.5.4 Time threshold: The amount of time a well-watered crop can exceed optimal plant temperature

The time threshold defines the daily amount of time that a well-watered crop's T_c can exceed the temperature threshold, in the absence of a water deficit. In the BIOTIC protocol, irrigation is considered appropriate when the T_c > TT for a period of time in excess of the time threshold. Wanjura *et al.* (1995) described three methods for calculating time thresholds: empirical analysis of historical crop T_c grown under well-watered conditions, empirical field testing of multiple time thresholds that optimise crop yield, and an energy balance approach that calculates the amount of time a well-watered crop will be expected to exceed the temperature stress threshold.

The empirical analysis of historical well-watered crop T_c is the simplest method of determining the time threshold. This method averages the daily amount of time that the T_c > TT, and is only suitable where data has been previously collected. The empirical analysis based on field testing involves the use of multiple time thresholds for the irrigation of a crop (Wanjura *et al.*, 1995). The time threshold that results in optimal crop performance (yield, water use, quality) is considered to be the appropriate time threshold for the desired outcome (Wanjura *et al.*, 1995). However, this approach requires a significant economic and time investment as the time threshold should be calculated over numerous seasons.

The energy balance approach calculates T_c for a well-watered crop using historic weather station and plant height data for the environmental site of interest. The time threshold determined from this method is the arithmetic mean of the daily length of time that the calculated temperature of a well-watered canopy will exceed the TT (Mahan *et al.*, 2005; Wanjura *et al.*, 1995). The energy balance of a crop canopy is described by Monteith (1973) as:

Equation 4: Net irradiance

$$R_n = G + H + \lambda E$$

where R_n is net irradiance, G is the soil heat flux, H is the sensible heat flux from the canopy and E is the latent heat flux to the air. By substituting the fundamental equations for G, H and λE into the above equation the following equation is obtained:

Equation 5: Canopy-air temperature differential

$$T_c - T_a = \left(\frac{r_a R_n}{\rho c_p}\right)\left(\frac{\gamma^*}{\Delta + \gamma^*}\right) - \left(\frac{e_A^* - e_A}{\Delta + \gamma^*}\right)$$

where T_c and T_a is canopy and air temperature (°C at 2.0 m), r_a is the aerodynamic resistance (s m^{-1}), R_n is the net irradiance (W m^{-2} at 2.0 m), ρ is the density of air (kg m^{-3}), c_p is the heat capacity of the air (J kg^{-1}), Δ is the slope of the saturation vapour pressure-temperature curve (Pa $°C^{-1}$), e^*_A - e_A is the vapour pressure deficit of the air (kPa), and γ^* is the apparent psychrometric constant (Pa $°C^{-1}$) in a well-watered crop. In a well-watered crop transpiring at its potential rate the γ^* is:

Equation 6: The apparent psychrometric constant

$$\gamma^* = \gamma\left(\frac{1 + r_{cp}}{r_a}\right)$$

where r_{cp} is the resistance of a well-watered crop and γ is the pure psychrometric constant. The difference between γ and γ^* is that γ^* is adjusted for non-ideal evaporation that occurs in leaves and surfaces where there are boundary resistances that have to be approximated whereas γ relates to idealised conditions in the psychrometer. Canopy temperature of a well-watered, non-stressed plant can be calculated using the crop water stress index (CWSI) developed by Jackson *et al.* (1981). The value of the CWSI ranges from 0 to 1, where non-stressed plants exhibit a value near zero. In this equation, r_{cp} is replaced by r_c, actual canopy resistance:

Equation 7: Crop Water Stress Index

$$CWSI = 1 - \frac{E}{E_p} = \frac{\gamma(1 + r_c / r_a) - \gamma^*}{\Delta + \gamma(1 + r_c / r_a)}$$

The ratio of r_c/r_a can be defined by substituting Equation 6 into Equation 5 and rearranging as:

Equation 8: Instantaneous canopy to aerodynamic resistance

$$\frac{r_c}{r_a} = \frac{\gamma r_a R_n /(\rho c_p) - (T_c - T_a)(\Delta + \gamma) - (e_A^* - e_A)}{\gamma\left[(T_c - T_a) - r_a R_n /(\rho c_p)\right]}$$

All parameters in Equation 8 are measured or derived with the exception of T_c. Therefore, by calculating the value of T_c that results in a canopy with a CWSI between 0 and 0.5, well-watered crop T_c are determined (Mahan *et al.*, 2005). The analysis is further filtered by excluding times when T_a < TT the R_n is negative and relative humidity is sufficiently high to limit transpirational cooling. This filtering enables the analysis to be limited to times when there is sufficient energy to increase T_c to the biologically calculated temperature threshold and transpirational cooling to temperatures below the TT is possible.

2.5.5 Limiting relative humidity threshold

High humidity can limit transpirational cooling, to the point where T_c > TT, regardless of water availability. Under these conditions T_c are not reliable indicators of water stress, and T_c will not respond to irrigation. The BIOTIC method continuously corrects plant stress through comparisons of T_c values with relative humidity measurements.

2.5.6 Advantages and limitations of BIOTIC

The BIOTIC protocol has been demonstrated to be an effective irrigation scheduling method for several crop species (cotton, peanut, corn, soybean, sunflower, millet and sorghum) using surface and sub-surface drip, linear and centre pivot irrigation in both

humid and arid environments in the USA (Texas, Mississippi, and California) (Mahan, 2000; Mahan *et al.*, 2005). In each case BIOTIC provided irrigation scheduling equivalent to that achieved by soil water balance or evapotranspirational methods (Mahan *et al.*, 2005) and produced yields of cotton that were high in comparison to long term averages (Wanjura *et al.*, 1995). The BIOTIC is one of a small number of biologically based irrigation scheduling tools. Its primary advantages are its physiological foundation, its simplicity and its proven ability to provide reliable irrigation scheduling (Mahan *et al.*, 2000).

However, BIOTIC does not provide information on the amount of water required in response to an irrigation signal and is designed to provide full irrigation. Although it can provide irrigation signals at any frequency, as the interval between detection of water stress and induction of irrigation increases the plant response to the irrigation signal becomes increasingly complex (Mahan *et al.*, 2000). The BIOTIC is best suited to controlling crop water stress levels in regions with low rainfall and high precision in irrigation water application (Wanjura *et al.*, 1992). Currently, only one TT is applied to a crop throughout the total growing cycle. Therefore, the accuracy of water stress control is limited in the sense that optimal temperatures may change during various crop development stages; this is obviously an area for further refinement. Furthermore, the biological basis of applying a whole plant optimal temperature on the optimal temperature of enzymatic function of a limited number of enzymes may be questionable.

Infrared canopy temperature must be rigorously measured in order to ensure repeatable and accurate depiction of crop T_c. Measured variations in T_c will result depending on the part of the canopy measured, and as a result of the angle from where the infrared thermometer views the canopy (Wanjura *et al.*, 1992). Furthermore, the optimum canopy temperature threshold value may vary across environments due to alterations in microclimatic factors and input energy fluxes (Wanjura *et al.*, 1992). Finally IRTs need to be accurately calibrated and used within their recommended environmental ranges.

2.6 Synthesis

The major opportunities for research that emerge from this literature review are listed below. They provide a framework for evaluating the implementation of the BIOTIC irrigation scheduling system in Australian deficit irrigation cotton production systems. The BIOTIC irrigation system may potentially be used as a plant-based irrigation scheduling tool, enabling producers to better manage irrigation application for increased WUE, yield or peace of mind.

Although the BIOTIC irrigation scheduling system has evolved over numerous years and is supported by much research, its use, response and performance in deficit irrigation systems has not been previously studied in detail. Historically, research has been focussed on its use in precision application irrigation systems with short irrigation intervals such as surface drip and centre-pivot irrigation systems. Limited research has been conducted in large deficit irrigation systems, and it has not been studied in furrow irrigation systems.

The response of the BIOTIC irrigation system to irrigation regimes used in Australian agriculture has not been described. Australian cotton systems differ from the studied US systems in terms of environment, crop management and germplasm. Hence, the BIOTIC response to water stress in Australian cotton cultivars needs to be studied in Australian production systems. Linking this response with higher crop measurements, such as plant growth and yield, in soil water deficit and furrow irrigation systems will help to determine the utility of the BIOTIC irrigation scheduling system.

Little is known about cultivar specific optimal temperatures for cotton cultivars, particularly Australian commercial cotton cultivars. This is significant as the BIOTIC irrigation scheduling system uses a plant threshold temperature in order to maintain plant T_c at or below the thermal optimum. The hypothesis that the T_{opt} of an Australian cotton cultivar, with different genetic and ecotype adaptations, will be similar to other cultivars of the same species should be tested.

In addition to the response of the BIOTIC irrigation scheduling system to the TT in Australian production systems, the stress time concept needs to be investigated. This will enable the determination of adequate time thresholds for use in the BIOTIC protocol in deficit irrigation systems. This is important as a differential between the calculated average daily stress time and the measured stress time is expected to routinely occur in deficit irrigation systems. The interval between irrigation events and the extent of the imposed soil water deficit is larger in these systems compared with the previously studied drip and centre-pivot irrigation systems.

3. GENERAL MATERIALS AND METHODS

3.1 Site and climate descriptions

Irrigated cotton (*Gossypium hirsutum* L.) field experiments were conducted over two growing seasons at the Australian Cotton Research Institute (ACRI), "Myall Vale". The ACRI is located on the Wee Waa Road ~ 30 km west of Narrabri, NSW (149°35'E, 30°12'S) (Figure 3.1) and is situated in north-west New South Wales on the flood plains of the Namoi River. This semi-arid region is dominated by low lying, flat topographies extending east to the Nandewar Ranges. The climate of this region is characterised by hot summers (daily maximum 35.3 °C, minimum 19.4 °C) and mild winters (daily maximum 17.0 °C, minimum 3.4 °C). The region experiences summer-dominant rainfall patterns, with an annual average of 642 mm (BOM, 2009). The experiments were conducted on a laser-levelled endocalcareous, self-mulching, medium grey Vertosol (Isbell, 1996) with a surface of young alluvium and aeolian clays over old alluvium (Ward *et al.*, 1999). These soils are alkaline and have a high clay fraction.

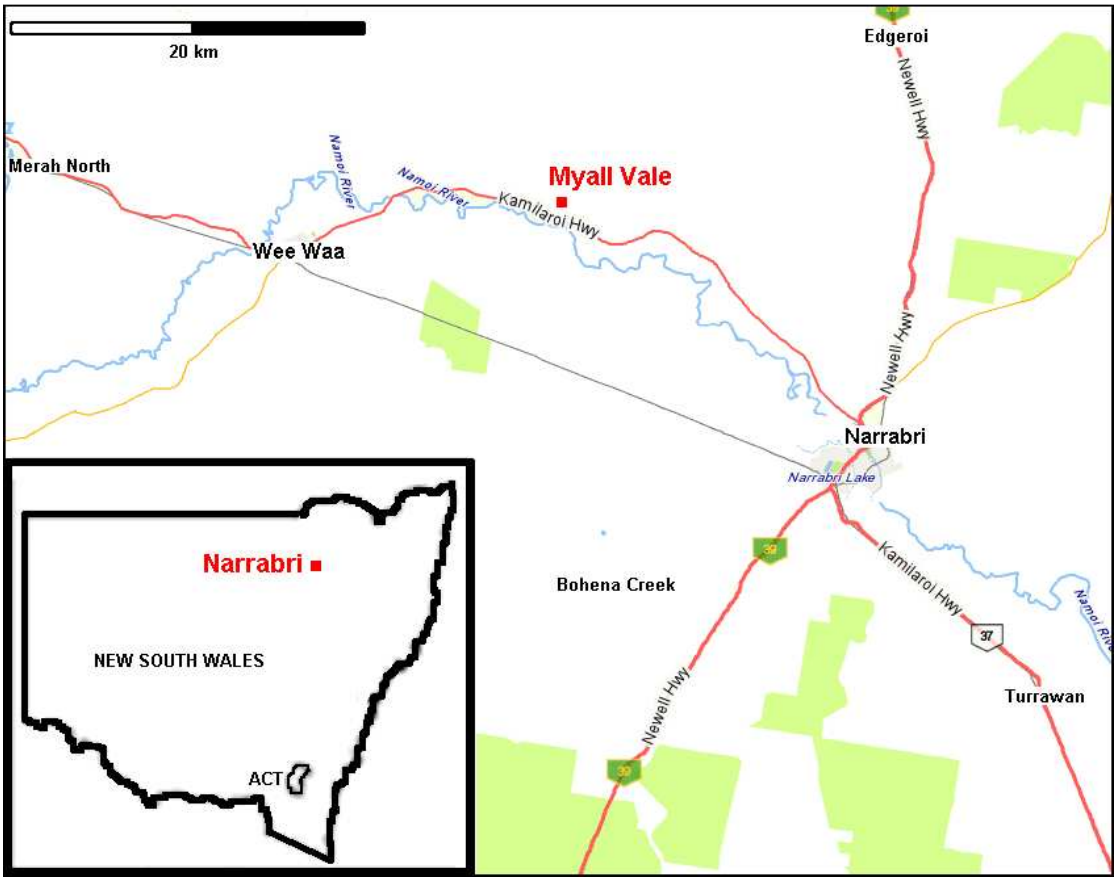


Figure 3.1. Regional map of experimental site showing the location of "Myall Vale".

3.2 Cultivar

All experiments used the CSIRO-developed cultivar Sicot 70BRF. This cultivar is a full season cultivar with compact growth habit suited to Australian production systems (CSD, 2008). It performs well in all Australian production regions, maintaining high lint yield potentials, good disease resistance and good fibre quality. It is the current Australian industry standard cultivar, and in its first year of full release (2008/09), an excess of 70% of the total Australian cotton production area was sown to this cultivar (CSD, *Pers. Comm*). Sicot 70BRF is a transgenic cotton cultivar containing the Monsanto Company's second generation insect resistance technology, Bollgard II®. Bollgard II® cotton contains

the *Bacillus thuringiensis* (*Bt*) insecticidal protein stack of the Cry 1 Ac and Cry 2 Ab genes, for the control of lepidopteron species feeding on vegetative and reproductive plant parts. Sicot 70BRF also contains the second generation technology of vegetative and reproductive plant part tolerance to glyphosate spray application. The Roundup Ready Flex® technology utilises two copies of the CP4-EPSPS coding sequence from *Agrobacterium* sp. to confer tolerance to glyphosate (Monsanto, St. Louis, MO).

3.3 Experiments

A glasshouse experiment was conducted in 2008 at the Cropping Systems Research Laboratory of the United States Department of Agriculture, Agriculture Research Service in Lubbock, Texas. Three field experiments were conducted in the 2007/08 and 2008/09 growing seasons (Table 3.1). Experiment 2 was conducted in the 2007/08 growing season, whilst Experiment 3 and Experiment 4 were conducted in the 2008/09 season. Experiment 2 and Experiment 3 were surface drip-irrigated experiments, and Experiment 4 was a fixed deficit furrow irrigation experiment.

Table 3.1. Growing season, irrigation delivery method and location of experiments conducted in this study.

Experiment	Growing season	Irrigation delivery	Location
Experiment 1	2008	Glasshouse	USDA-ARS, Texas
Experiment 2	2007/08	Surface drip	ACRI, Narrabri
Experiment 3	2008/09	Surface drip	ACRI, Narrabri
Experiment 4	2008/09	Furrow	ACRI, Narrabri

3.3.1 Thermal optima for an Australian cotton cultivar materials and methods

Chlorophyll fluorescence recovery rates (Experiment 1)

Plants were grown under glasshouse conditions (fluorescent and incandescent lights with 16 h photoperiod at 25 °C ± 5 °C). Plant leaf tissue was harvested on four week old plants. Experimental procedure was conducted using the methodology described by Peeler and Naylor (1988), with modifications made by Burke (1990). Leaf discs were excised from plants and placed on moistened 3 mm filter paper on top of a wet sponge in a glass dish and covered with CO_2 permeable plastic film (Gladwrap^{TM}), to avoid desiccation. Leaf discs were illuminated at 25 °C under a high pressure sodium lamp, emitting a light intensity of 650 μmol μm^2 s^{-1}. An illumination period of 1 min was used; however, this period was adjusted if the normalised Fv/Fo ratio taken immediately after the illumination period was > 0.15. A constant illumination period was then used for all treatments within an experiment. Following the illumination period the filter paper containing the leaf disc was transferred to a temperature-controlled thermocouple block, preset to the desired temperature. Temperature treatments ranged from 15 °C to 35 °C at 5 °C intervals in the broad temperature range assay. Following a 10 s excitation period of light intensity of 22 μmol μm^2 s^{-1}, fluorescence measurements were recorded at 0 min and then at 5 min intervals throughout the dark adaption period to 20 min following illumination. Fluorescence measurements were taken on three leaf discs with the Brancker SF-30 (Richard Branckner Research, Ottawa, Canada). To more accurately determine the optimal temperature for chlorophyll fluorescence recovery rates, a fine temperature assay was also conducted from 24 °C to 32 °C at 2 °C intervals. The method

was the same for this assay as the broad temperature range assay, except measurement intervals were reduced to one minute and the measurement period was reduced to six minutes following the excitation illumination.

Results are expressed as the dark adapted variable to minimal fluorescence (Fv/Fo), and were normalised in order to observe trends in dark adapted fluorescence recovery. Data was normalised by subtracting the measured Fv/Fo from the initial Fv/Fo measured at zero time from excitation illumination. The optimum plant temperature for the recovery of PSII fluorescence is characterised by a combination of the maximum Fv/Fo ratio and the minimum time in darkness to reach the maximum Fv/Fo ratio (Burke, 1990).

Gas exchange at discrete leaf temperatures (Experiment 2, 3 and 4)

Leaf photosynthetic rate and g_c at discrete leaf temperatures were measured using an infra-red gas analyser (IRGA), Portable Photosynthesis System; Li-COR® model 6400-40. Measurements were conducted in field grown drip irrigated and furrow irrigated cotton from Experiments 2, 3 and 4. Measurements in Experiment 2 and 3 were taken during the peak period for photosynthesis (10:30am to 11:30am) (see Appendix 1) on the youngest fully expanded leaf in all plots of the well-watered (control) (Treatment 4), excessive (Treatment 5) and the largest soil water deficit (Treatment 1) irrigation treatments. These measurement days were when differential water stress effects were visible between treatments. Measurements were taken on four days throughout the growing season in Experiment 2 (95, 119, 133 and 134 DAS) and five days during Experiment 3 (83, 90, 97, 107 and 114 DAS). Gas exchange was also conducted between

10:30am and 11:30am in all treatments of Experiment 4. Measurements were taken on 69, 81, 91, 100, 113, 120 and 139 DAS. Two measurements were taken on two of the youngest fully expanded leaves in all measured plots.

As gas exchange rate is affected by light intensity, humidity, temperature, CO_2 and time of day, the Li-COR® was matched to ambient conditions and held constant during each period of measurement. This resulted in cuvette relative humidity controlled at 50% to 70%, CO_2 maintained at 360 μmol (CO_2) mol^{-1} air, photosynthetically active radiation (PAR) set to 1800 μmol m^{-2} s^{-1} to 2000 μmol m^{-2} s^{-1} and T_a ranging from 23 °C to 42 °C. Equations used in the instrument for calculating photosynthetic rate or net carbon assimilation (A, in μmol (CO_2) m^{-2} s^{-1}) and g_c (mol (H_2O) m^{-2} s^{-1}) are given in the Li-COR Biosciences manual (Li-COR Biosciences, 2004b).

3.3.2 Surface drip irrigation materials and methods (Experiments 2 and 3)

(a) Irrigation treatments and experimental design

Experiment 2 and Experiment 3 consisted of five irrigation treatments based on daily reference evapotranspiration (ET_O) rates. These five irrigation treatments included a control or theoretical optimal (100% daily water requirement of control applied- Treatment 4), an excessive (125% of control daily water requirement of control applied- Treatment 5) and three deficit (75%, 50% and 25% of control daily water requirement of control applied- Treatments 3, 2 and 1) irrigation regimes. Daily water requirement (ET_C) was calculated according to Allen *et al.* (1998) where:

Equation 9: Daily water requirement

$$ET_C = ET_O * K_C$$

ET_O was calculated using on site weather station data measured over a grass reference crop at a screen height of 2.0 m and the Penman-Monteith equation (Allen *et al.*, 1998):

Equation 10: The Penman-Monteith evapotranspiration equation

$$\lambda ET = \frac{\Delta(R_n - G) + \rho_a c_p \frac{(e_s - e_a)}{r_a}}{\Delta + \gamma(1 + \frac{r_s}{r_a})}$$

Where, R_n is net radiation calculated from observed short-wave radiation measured with a pyranometer at 2.0 m using the methodology of the American Society of Civil Engineers (2005), vapour pressure and air temperature, G is the daily soil heat flux measured with a heat flux sensor, (e_s -e_a) represents the calculated vapour pressure deficit of the air using measured T_a and relative humidity (measured at 2.0 m), ρ_a is the mean air density at constant pressure, c_p is the specific heat of the air, Δ represents the calculated slope of the saturation vapor pressure temperature relationship, γ is the psychrometric constant for 200 m above sea-level (0.066), and r_s and r_a are the (bulk) surface and aerodynamic resistances, calculated from wind speed at 2.0 m measured above well watered clipped grass.

A locally calibrated (Narrabri, NSW) and tested K_C was calculated for the experiments using Equation 11 and light interception data (Yeates, *Pers. Comm.*), where K_C = Crop coefficient and *LI* = Light interception (between the values of zero and one).

Equation 11: Locally calibrated crop co-efficient

$$K_C = 1.2719(LI - 0.0779)$$

Light interception was measured with the Decagon Devices AccuPAR PAR/LAI ceptometer (model LP-80) within one hour of solar noon. Measurements were taken above and below the crop at 5 locations in each of the control (Treatment 4) plots. The initial frequency of measurements was weekly; however, this period was reduced depending on the rate of crop growth, from 1st square to early flowering, then every two weeks until canopy closure. Light interception ratios fell at the end of the season as the crop matured and vegetative growth ceased. This was important as LI was used to calculate *Kc*, which was used in the calculation of crop water requirements.

Irrigation treatments with the drip irrigation system were not imposed until 67 DAS (Experiment 2) and 50 DAS (Experiment 3) when the crop had reached first square. This was because the surface drip-irrigation system had to be installed post-planting to ensure adequate emergence and allow inter-row cultivation for weed control. The experimental design was a randomised complete block design (RCBD) with five replicates (blocks). Each block consisted of six rows of cotton, with five 13 m long plots in Experiment 2, and 10 m long plots in Experiment 3 for each treatment (Figure 3.2 and Figure 3.3). Each plot had an irrigated buffer row followed by a dryland buffer row, which was necessary to enable wheel-track-rows crop management. A row spacing of 1 m was used in all experiments with a planting density of ~ 10 to 12 plants m^{-1}.

The rate of water application in the surface drip irrigation system was determined by measuring the water collected in containers in 30 min periods. A container was placed at two randomly allocated drip emitters in each plot. The irrigation rate was determined to

be a uniform 2.4 mm hr^{-1}, at an operating pressure of 103 kPa (15 psi). The cotton crop was surface drip-irrigated ~ every 2 to 3 d, depending on daily ET_O and in-season rainfall. Irrigation in Experiment 2, Treatments 1 and 2 ceased at 165 DAS and following 165 DAS, for their final three irrigations, Treatments 3, 4 and 5 received only 50% of their calculated ET_C. This was conducted in an attempt to impose a small degree of water stress on these treatments in order to encourage crop maturity, especially in treatments with rank vegetative growth. In Experiment 3, irrigation was terminated following crop maturation at 128, 135, 152, 160 and 161 DAS for the respective Treatments 1, 2, 3, 4 and 5. This reduction in irrigation was to enable the correct maturity of the crop and discourage rank growth at the end of the season, and was aligned with industry practice in this regard.

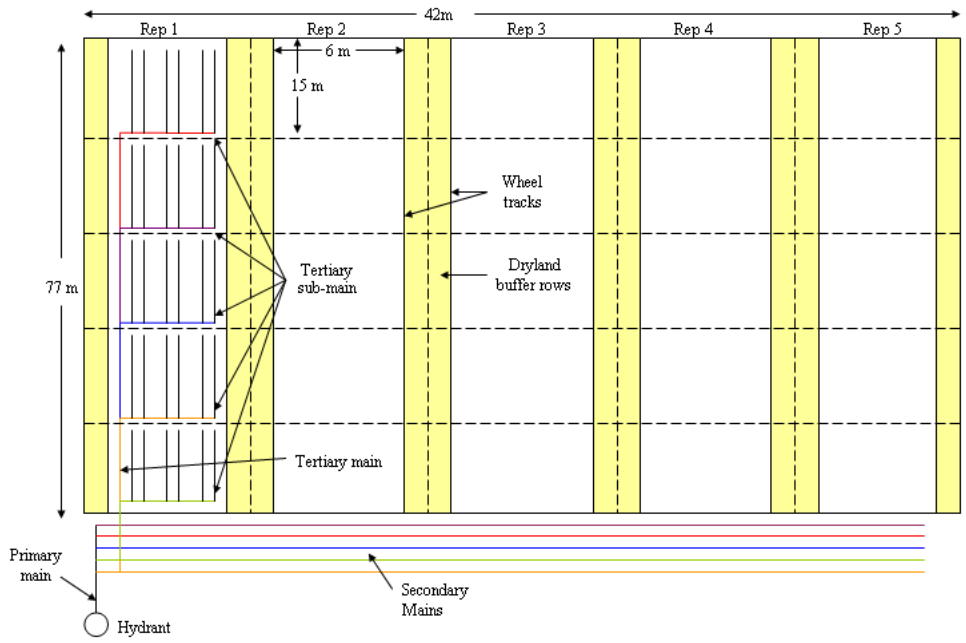


Figure 3.2. The experimental plan showing the layout of the drip irrigation system

Figure 3.3. Layout of the irrigation system. a) Primary main (front) and secondary mains; b) irrigation system looking down one replicate; c) The junction between secondary, tertiary and tertiary sub-mains.

(b) Crop management

Management for all experiments followed current high-input commercial practices outlined by Hearn and Fitt (1992). Each experiment was managed according to its individual requirements (e.g. with respect to pest control), with all replicates of all treatments receiving the same management regime.

Experiment 2 (2007/08 growing season)

Experiment 2 was pre-irrigated via furrow irrigation on 28 September 2007 and was planted one week later on 5 October 2007. Emergence occurred six days after sowing (DAS). The site was furrow-irrigated 19 DAS to ensure consistent germination and an even soil water content across the experiment. Due to complications in setting up the surface drip irrigation system, the first 60 mm of irrigation water was applied via furrow irrigation 47 DAS. Nitrogen was applied as anhydrous ammonia at the required rate of 160 kg N ha^{-1} prior to planting. The crop was defoliated three times following crop maturity. This number of defoliations was necessary due to the combined effect of rank

vegetative growth resulting in the reduced efficacy of the hormone application, as well as rainfall following the second application on 199 DAS. Table 3.2 outlines the detailed crop management history for Experiment 2.

Table 3.2. Agronomic management including fertiliser, herbicide, pesticide and defoliant application in Experiment 2

Experiment 2	Application date	Rate
Fertiliser history		
Anhydrous ammonia	14 Sep 2007	160 kg N ha^{-1}
Herbicide application		
Fluometuron (Cotoran SC)	5 Oct 2007	5.0 L ha^{-1}
Glyphosate (Roundup) (Spot spray)	6 Oct 2007	0.8 L ha^{-1}
Glyphosate (Roundup Ready Herbicide)	16 Oct 2007	1.5 kg ha^{-1}
Glyphosate (Roundup) (Spot spray)	6 Dec 2007	0.8 L ha^{-1}
Pesticide management		
Indoxacarb (Steward) +	29 Jan 2008	0.850 L $ha^{-}1$
Petrolium oil (D-C-Tron canopy oil)		2.0 L ha^{-1}
Defoliant application		
Thidiazuron (Dropp Liquid) +	9 Apr 2008	0.2 L ha^{-1}
Ethephon (Prep 720) +		2.0 L ha^{-1}
Petrolium oil (D-C-Tron canopy oil)		2.0 L ha^{-1}
Thidiazuron (Dropp Liquid) +	21 Apr 2008	0.2 L ha^{-1}
Petrolium oil (D-C-Tron canopy oil)		2.0 L ha^{-1}
Thidiazuron (Dropp Liquid) +	22 Apr 2008	0.2 L ha^{-1}
Petrolium oil (D-C-Tron canopy oil)		2.0 L ha^{-1}

Experiment 3 (2007/08 growing season)

Experiment 3 was planted on 14 October 2008 into moisture following rainfall. Emergence occurred six days post-planting. The site was furrow-irrigated 13 DAS to fill and ensure an even profile. Experiment 3 was planted following an irrigated vetch crop which was estimated to fix ~ 60 kg N ha^{-1}. Nitrogen was supplemented as required via fertigation as dissolved urea at the rate of 25 kg N ha^{-1} 81, 86, 90 and 94 DAS. Again, two defoliations were required to prepare the crop for harvest. This is because the

application had reduced efficacy in the well-watered plots as vegetative growth was still occurring. Table 3.3 outlines the detailed crop management history for Experiment 3.

Table 3.3. Agronomic management including fertiliser, herbicide, pesticide and defoliant application in Experiment 3.

Experiment 3	Application date	Rate
Fertiliser history		
Ammonia (NH_3) via nitrogen fixation-Purple vetch (*Vicia sativa ssp. nigra*)	May to Sep 2008	60 kg N ha^{-1}
Urea (Fertigation)	3 Jan 2009	25 kg N ha^{-1}
Urea (Fertigation)	8 Jan 2009	25 kg N ha^{-1}
Urea (Fertigation)	12 Jan 2009	25 kg N ha^{-1}
Urea (Fertigation)	16 Jan 2009	25 kg N ha^{-1}
Herbicide application		
Pendimethalin (Stomp*Xtra)	30 Sep 2008	3.0 L ha^{-1}
Fluometuron (Cotoran SC)	14 Oct 2008	5.0 L ha^{-1}
Glyphosate (Roundup) (Spot spray)	20 Oct 2008	0.8 L ha^{-1}
Glyphosate (Roundup) (Spot spray)	24 Nov 2008	0.8 L ha^{-1}
Pesticide management		
Diafenthiuron (Pegasus 500EC)	24 Feb 2009	0.800 L ha^{-1}
Defoliant application		
Thidiazuron (Dropp Liquid) +	3 Apr 2009	0.2 L ha^{-1}
Ethephon (Prep 720) +		2.0 L ha^{-1}
Petrolium oil (D-C-Tron canopy oil)		2.0 L ha^{-1}
Thidiazuron (Dropp Liquid) +	7 Apr 2009	0.2 L ha^{-1}
Ethephon (Prep 720) +		2.0 L ha^{-1}
Petrolium oil (D-C-Tron canopy oil)		2.0 L ha^{-1}

(c) Data collection

Biologically Identified Optimal Temperature Interactive Console (BIOTIC)

Wireless, battery-operated "SmartCrop™" IRT (Smartfield Inc., Lubbock, TX, U.S.A.) were placed in four replicates of the experiment (Figure 3.4). The SmartCrop system is an automated crop stress monitoring system, using a Zytemp model TN901 IRT (Zytemp, Hsinchu, Taiwan R.O.C.). The remote IRTs consist of a consumer quality IRT sensor, as well as the electronics necessary for acquiring, storing, processing and transmitting

temperature measurements. The remote IRTs measure average output temperature within the field of view at a one minute interval, and transmit a 15 min average temperature to the base/ controller via a low power radio link. The base/ controller stores temperature data in an on-board memory system, for subsequent retrieval. The system was installed in an open area with no interfering structures or topography that could affect transmission range. The remote IRTs were powered by four AAA batteries that are user replicable. However, these batteries were not replaced, providing adequate operational power for the duration of the measurement period (~ 80 d).

Data was collected throughout the season through to crop maturity, from 80 DAS through 178 DAS (Experiment 2) and 34 DAS to 155 DAS (Experiment 3). This collection period included periods, in some treatments, after irrigation ceased. Sensors were positioned and maintained periodically at 10 cm above the canopy pointing south (to reduce the effects of secular reflectance) at an angle of 70° for the duration of the measurement period. Corresponding ambient T_a and relative humidity were also logged (Smartfield Inc., Lubbock, TX, USA) every 15 min, at times coinciding with the BIOTIC canopy temperature data.

Figure 3.4. The installed BIOTIC equipment. a) receiver aerial and temperature and humidity sensor (inside Stevenson's screen) mounted on the edge of a building adjacent to the experimental field; b) BIOTIC sensors installed in field experiment; c) computerised base station data loggers.

Soil water content

Soil water to 100 cm in depth at 10 cm intervals was calculated every 2 to 3 d from four replicates in all treatments from the experiment using the Gopher® Soil Moisture Profiling System capacitance probe. Probe tubes were located in the middle of the centre row of each plot in all replicates. The Gopher® measures the dielectric constant (ratio of electric flux density produced in the soil and water matrix to that in a vacuum by the same electric force) of the soil and water to determine the water content of the soil. Therefore, the measured dielectric constant increases as the water content of the soil increases. The sensor was used with the factory calibration for medium-heavy clay soils and correlated with NAM measurements from a previously calibrated NAM to determine soil water (mm).

The soil water to 120 mm in 15 cm intervals was also measured on a weekly basis using the CPN Corporation Hydroprobe®, model 503DR, neutron attenuation meter (NAM) in the control (Treatment 4) plots only. This was conducted in order to provide a reference for the Gopher® probe measurements. The NAM was calibrated using the methodology of Tennakoon and Hulugalle (2006).

Water-use efficiency (WUE)

The WUE quantifies the efficiency with which economic yield is produced as a function of water applied to the crop. The WUE (kg ha^{-1} mm^{-1}) was calculated as the lint yield (kg ha^{-1}) produced per mm of water applied to each treatment.

Above ground biomass accumulation

Above ground biomass was measured at five harvests throughout Experiment 2. These harvests represented times when the plant had reached a specific physiological growth stage. Biomass was sampled during squaring (68 DAS), during flowering (96 DAS), peak vegetative growth (cutout) (111 DAS), first open boll (138 DAS) and during the pre-harvest period (173 DAS). Biomass was measured six times during Experiment 3. Biomass was sampled at squaring (64 DAS), first flower (77 DAS), during flowering (93 DAS), peak vegetative growth (cutout) (111 DAS), first open boll (125 DAS) and during the pre-harvest period (162 DAS).

One randomly allocated m^2 of each plot with a uniform plant stand (> 8 plants m^{-2}) per sample date was cut at ground level from each of the experimental plots. The number of plants and sample fresh weight were recorded. Four representative plants of the sample were then sub-sampled for partitioning of stem, leaf, squares, green and open bolls for dry matter (g/m^2) and the count of reproductive plant parts (square, flower, green boll and open boll). All values were then converted to an area (m^2) basis from the sub-sample and initial sample fresh weight. A secondary sub-sample of two of the sub-sampled plants was analysed for leaf area on the Li-COR LA-3100 area meter and converted to the specific leaf area (m^2/g) and LAI.

Heights and numbers of nodes above cotyledon of five representative un-tipped plants from each plot were measured weekly. Cutout, the physiological point when competition

for assimilates exceeds supply and results in the cessation of both vegetative growth and the production of reproductive sites that influence crop yield (Hearn and Constable, 1984) was also determined. This was achieved by counting the number of nodes above a one-day-old flower at the first position of a fruiting branch to the apical bud of the plant (Figure 3.5b). One-day-old flowers were identified as cotton flowers are only white for one day. Cut out was determined to take place when four nodes above a one-day-old flower to the plant apex occurred.

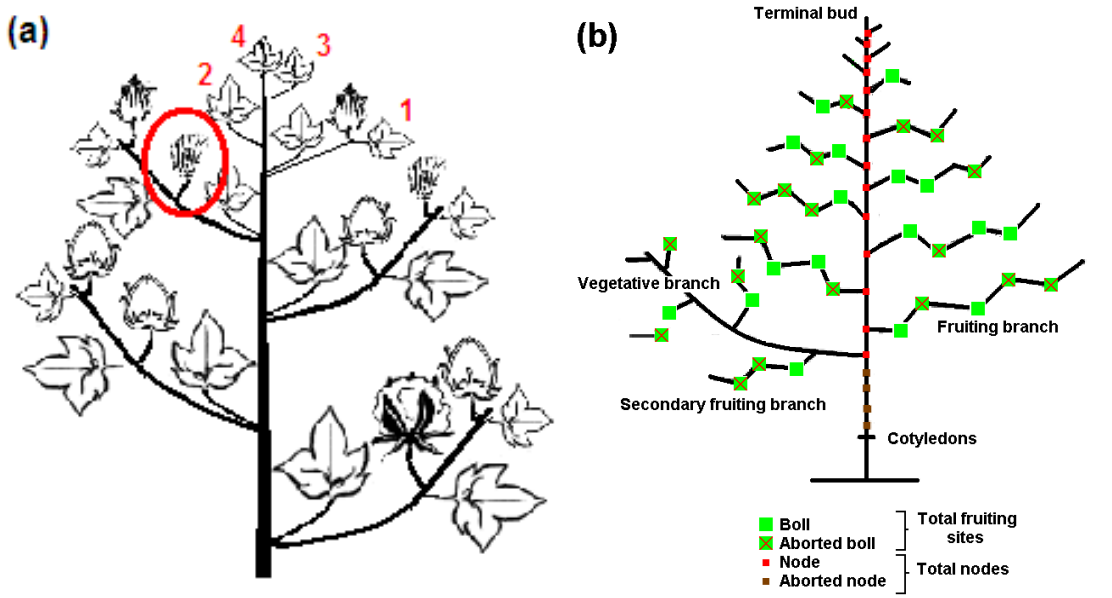


Figure 3.5. (a) Diagram showing a plant that has reached cut out. Cut out has occurred when the number of nodes above a first position one-day-old flower (in the red circle) is four; (b) Schematic diagram of a cotton plant showing the number of nodes and fruiting sites.

Plant mapping and lint yield

Plant mapping was carried out during the pre-harvest period, 179 DAS in Experiment 2 and 162 DAS in Experiment 3. One randomly allocated m^2 of each plot with a uniform plant stand (> 8 plants m^{-2}) was cut at ground level from each block of the experiment. The number of nodes, vegetative branches and bolls, fruiting branches and positions of

both bolls and abortions and non-harvestable bolls at the plant apex was recorded (Figure 3.5a). The number of fruiting branches, vegetative branches and bolls, nodes above harvestable boll and per cent bolls per fruiting branch and fruiting branch position were calculated. Total boll retention rates were calculated by dividing the total mature bolls by the number of potential boll sites.

Mechanically-picked seed cotton weight data was recorded from one row of each plot. The gin turn-out (% lint of seed cotton) and fibre quality was then calculated from a sub sample of the picked lint yield. Fibre quality (fibre length, strength, uniformity and micronaire) was measured on a high volume instrument (HVI).

Weather conditions

Weather conditions at 15 and 60 min, and 24 h intervals were calculated directly adjacent to the crop with a customised weather station (Campbell Scientific, Logan, UT). The weather station measured average, maximum and minimum air temperature (°C) and relative humidity (%) with the HMP50-ET air temperature and relative humidity probe, average, maximum and minimum wind speeds (m s^{-1}) and direction with the 034B-ETM wind set, and short-wave radiation (KW m^{-2}) with the CS305-ETM pyranometer sensor. Temperature, humidity, radiation and wind speed were measured at a screen height of 2.0 m. Total rainfall (mm) with the TE525-ET tipping bucket rain gauge, as well as calculated ET_O (mm hr^{-1}) and vapour pressure deficits (kPa).

Rainfall (mm) was also manually measured with a rain gauge (Rainmaxx 150 mm) due to concerns for the accuracy of the rainfall measured by the weather station. In the event of a discrepancy between rainfall measured by the weather station and the manual rain gauge, the manual rain gauge measurement was used. Effective rainfall was calculated in the control plots of Experiment 2 and Experiment 3 based on the difference between the cumulative crop requirement (ET_C) (minus water supplied by irrigation) and the water supplied by the rainfall event. The crop requirement is considered to be the total amount of water, after taking into account irrigation application, required to return soil water to field capacity, the starting soil water following the initial furrow irrigation. The effects of deep drainage and runoff were ignored as these parameters were not measured.

Degree day was calculated with the CottASSIST day degree calculator (CSIRO, 2008), as follows:

Equation 12: Cotton degree-day equation

$$DD_i = \frac{(T_{max_i} - 12) + (T_{min_i} - 12)}{2}$$

where DD_i is the degree day for day_i in the sum, T_{max_i} is the maximum daily air temperature, and T_{min_i} is the minimum daily air temperature. The significance of 12 is that 12 °C is considered the base temperature for cotton growth and development, and thus temperatures < 12 °C do not contribute to DD. Low and high temperature stress days are those days where ambient temperatures < 11 °C, or > 36 °C. These temperatures represent detrimental ambient conditions on cotton growth and development (Bange and Milroy, 2004; Hodges *et al.*, 1993).

3.3.3 Deficit furrow irrigation materials and methods (Experiment 4)

(a) Irrigation treatments and experimental design

The transgenic cotton (*Gossypium hirsutum*) cultivar Sicot 70BRF was irrigated in a randomised complete block design (RCBD) with four replicates (blocks). The experiment consisted of four irrigation treatments based on daily soil water deficits (mm) calculated from neutron attenuation meter (Table 3.4). These four irrigation treatments included a control or theoretical optimum (40 mm to 50 mm deficit), a frequently irrigated (30 mm to 40 mm deficit) and two extended deficit irrigation treatments: a moderately extended (65 mm to 75 mm deficit) and fully extended (105 mm to 110 mm deficit) treatment. Once the desired soil water deficit below the drained upper limit of the soil was measured, treatments were furrow irrigated, returning the soil to field capacity.

Table 3.4. Deficit irrigation treatments and deficit range.

Treatment	Colour	Deficit	Deficit Range (mm)
Frequent	Blue	35	30 to 40
Control	Green	45	40 to 50
Moderate	Red	70	65 to 75
Extended	Grey	105	100 to 110

Each experimental block consisted of four randomly allocated 164 m long plots under different irrigation regimes. The field was laser levelled to achieve a slope of 1:1500, with crop row and furrow spacing of 1 m. Irrigation plots varied in width according to treatment, with the frequently irrigated plot being 12 rows wide, the control and medium extended plots 16 rows wide and the extended plots 20 rows wide. The large plot width and variation in plot width was necessary to reduce the effect of lateral movement of irrigation water. The more frequently irrigated plots were smaller as the soil remained

wetter and hence fewer cracks formed, reducing irrigation times and the lateral movement of water, whereas the extended irrigation plots were larger for the converse of this reason. Each plot had a single measurement row at the centre of the plot and lint yield was calculated from four 13 m strips up the field in this same row (Figure 3.6).

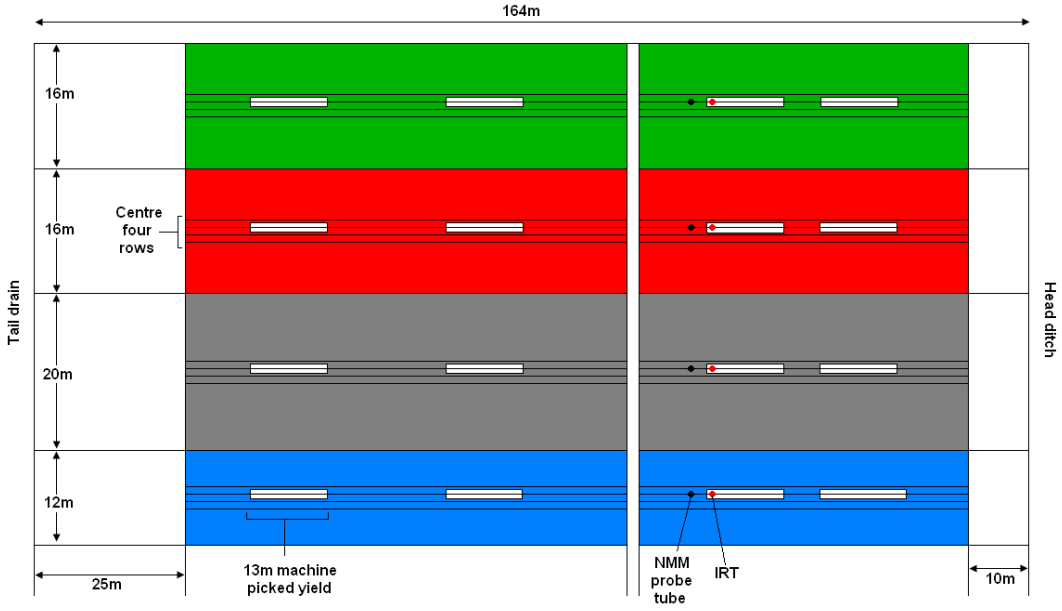


Figure 3.6. The experimental plot showing the layout of one treatment block including the location of neutron attenuation meter probe tubes, infra-red thermometers, and the area machine picked for lint yield analysis. The bottom 25 m and top 10 m of the field are discounted from measurements due to waterlogging from the backing up of water in the tail drain and compaction from previous rotorbuck formations at the head ditch.

The irrigation treatments received varying numbers of irrigations according to their desired deficits. The frequently irrigated plots received eleven irrigations, control plots nine irrigations, moderately extended plots four irrigations and the fully extended irrigation plots only two irrigations (Table 3.5). Rainfall throughout the growing season totalled 327 mm.

Table 3.5. Irrigation dates for each deficit irrigation treatment and corresponding number of days after sowing and cumulative degree days.

Treatment	Irrigation date	Days after sowing	Cumulative degree days
Frequent	9 December 2008	55	550
(≈ 35 mm)	22 December 2008	68	708
	2 January 2009	79	866
	9 January 2009	86	976
	15 January 2009	92	1068
	23 January 2009	100	1189
	30 January 2009	107	1309
	5 February 2009	113	1414
	11 February 2009	119	1526
	27 February 2009	135	1721
	13 March 2009	149	1957
Control	12 December 2008	58	597
(≈ 45 mm)	24 December 2008	70	739
	7 January 2009	84	944
	15 January 2009	92	1068
	25 January 2009	102	1225
	2 February 2009	110	1361
	10 February 2009	118	1512
	3 March 2009	139	1777
	16 March 2009	152	1993
Moderate	11 January 2009	88	1001
(≈ 70 mm)	28 January 2009	105	1276
	8 February 2009	116	1471
	6 March 2009	142	1808
Extended	16 January 2009	93	1087
(≈ 105 mm)	6 February 2009	114	1434

(b) Crop management

The experimental site was pre-irrigated on 2 October 2008 and was planted two weeks later on 15 October 2008 (planting was delayed by a week due to rain). Emergence occurred six days post-planting. Nitrogen was applied as anhydrous ammonia at a rate of 200 kg N ha^{-1}. Two defoliations were required to prepare the crop for harvest. This is because the application had reduced efficacy in the well-watered plots as vegetative

growth was still occurring. Table 3.6 outlines the detailed crop management history for Experiment 4.

Table 3.6. Agronomic management including fertiliser, herbicide, pesticide and defoliant application in Experiment 4

Experiment 4	Application date	Rate
Fertiliser history		
Anhydrous ammonia	12 Sep 2008	200 kg N ha^{-1}
Superphosphate	28 Sep 2008	100 kg ha^{-1}
Herbicide application		
Pendimethalin (Stomp*Xtra)	28 Sep 2008	2.2 L ha^{-1}
Fluometuron (Cotoran SC)	15 Oct 2008	5.0 L ha^{-1}
Glyphosate (Roundup Ready Herbicide)	26 Nov 2008	1.5 kg ha^{-1}
Pesticide management		
Fipronil (Regent)	14 Nov 2008	0.125 L ha^{-1}
Indoxacarb (Steward) + salt	27 Jan 2009	0.850 L ha^{-1}, 1kg ha^{-1}
Diafenthiuron (Pegasus 500EC)	18 Feb 2009	0.800 L ha^{-1}
Pyriproxyfen (Admiral) +	28 Feb 2009	0.500 L ha^{-1}
Organosilicone surfactant (Maxx) +		0.060 L ha^{-1}
Clothianidin (Sumitomo Shield systemic)		0.250 L ha^{-1}
Indoxacarb (Pegasus 500EC)	28 Mar 2009	0.800 L ha^{-1}
Defoliant application		
Thidiazuron (Dropp Liquid) +	3 Apr 2009	0.2 L ha^{-1}
Ethephon (Prep 720) +		2.0 L ha^{-1}
Petrolium oil (D-C-Tron canopy oil)		2.0 L ha^{-1}
Thidiazuron (Dropp Liquid) +	9 Apr 2009	0.2 L ha^{-1}
Ethephon (Prep 720) +		2.0 L ha^{-1}
Petrolium oil (D-C-Tron canopy oil)		2.0 L ha^{-1}

(c) Data collection

Biologically Identified Optimal Temperature Interactive Console (BIOTIC)

Data was collected in the same fashion as for the drip irrigation experiments; however, the system was solar powered due to its remote location (Figure 3.7). The BIOTIC sensors were running from 57 DAS through to crop maturity (60% open bolls) at 154 DAS. This occurred two days after the final irrigation treatment in the control plots. Ten

consecutive days of data from 74 DAS was lost due to system failure during an electrical storm.

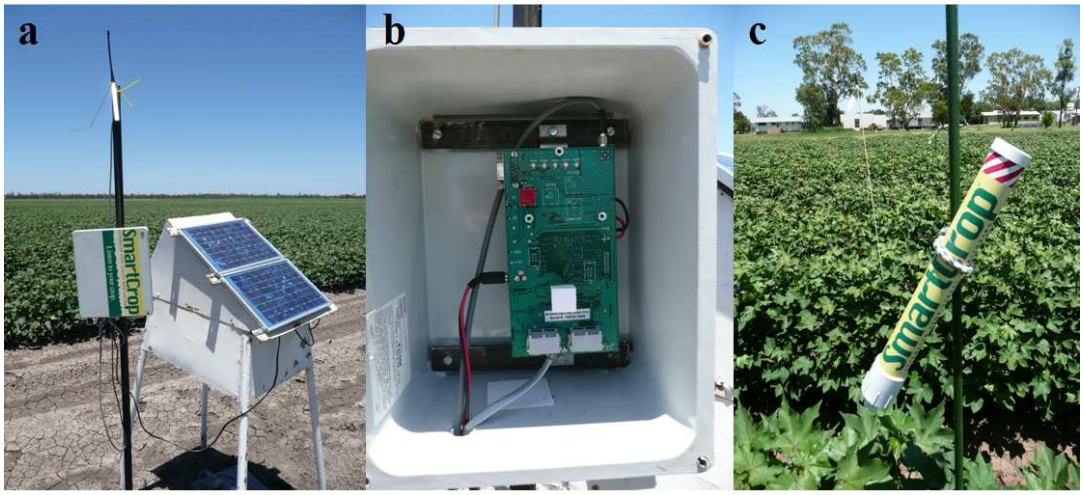


Figure 3.7. The installed BIOTIC equipment. a) receiver aerial, base station (in weather proof box) and solar panels (power source) located at the centre of the experimental field; b) The base station and data logger mounted inside the weather proof box; c) BIOTIC sensors installed in field experiment.

Soil water content

The soil water to 1.2 m at 0.1 m intervals in the top 0.6 m of soil and at 0.2 m intervals below 0.6 m was measured using the CPN Corporation Hydroprobe®, model 503DR, neutron attenuation meter. Using a calibration developed for the same field (Yeates, *Pers. Comm.*) for the NAM probe, the soil water was monitored throughout the season between 28 and 168 DAS. Irrigation was managed through soil water monitoring with the NAM. Irrigation was initiated when soil water content reached the desired soil water deficit range (Table 3.4). Soil water was measured again 48 h prior to an irrigation event, and again during the dry down cycle.

Above ground biomass accumulation

Above ground biomass was measured at five harvests throughout the growing season. These harvests represented times when the plant had reached a specific physiological growth stage. Biomass was sampled at first flower (77 DAS), peak vegetative growth and water use (91 DAS), cut out (120 DAS), during boll filling (138 DAS) and during the pre-harvest period (166 DAS). Biomass accumulation was calculated in the same manner as for the drip irrigation experiments.

Heights and numbers of nodes above cotyledon of five representative un-tipped plants from each plot were measured weekly.

Lint yield

Mechanically picked seed cotton weight data was recorded from four 13 m sections of the measurement row of cotton. It is important to note that the bottom 25 m and the top 10 m of the field, as well as the area surrounding the neutron probe and the access path were excluded from yield and other measurements. Due to waterlogging from back up water from the tail drain the bottom of the field was excluded from measurements. Also, the top of the field was excluded because it receives the most irrigation water and is subject to compaction from the formation of previous season's rotorbucks, i.e., the furrows formed between the head-ditch and crop to direct furrow irrigation water. These are areas of high compaction potential as rotorbucks are continually removed and re-formed throughout the season to enable ground based management practices to occur. The area surrounding the neutron probe and access path was excluded as the cotton there was damaged due to

excessive foot traffic. The gin turn-out and fibre quality was then calculated from a sub sample of the picked lint yield.

Weather conditions

Weather conditions were monitored in Experiment 4 on a weather station adjacent to the experiment in the same fashion as Experiment 2 and 3.

3.4 Data analysis

All data was analysed in Genstat v11.0 and assessed at a P=0.05 level of significance. Specific details are provided in the following chapters.

4. THERMAL OPTIMA FOR AN AUSTRALIAN COTTON CULTIVAR

4.1 Introduction

Temperature affects almost all aspects of plant growth and development and, in a field based setting, is dynamic, with both diurnal and seasonal influences (Mahan and Yeater, 2008). The ancestors of modern cotton cultivars originated in tropical regions and were thus adapted to growth at high temperatures. Today's commercial cotton cultivars have retained this high optimal temperature for growth and metabolism (Burke and Wanjura, 2010). Despite the fact that a significant amount of research evaluating the optimal temperature or temperature range for cotton has occurred, a clear picture on the optimum for cotton metabolism has not emerged. The range in observed results occurs as a consequence of determining optimal air temperature or plant temperature, the method used to measure temperature, and reported differences in optimal temperatures within different anatomical structures or periods of physiological development (Burke and Wanjura, 2010).

It is important to note that T_a and plant temperatures cannot be used interchangeably. Although T_a has been used as a surrogate for plant temperature, plant temperature is rarely equal to that of the air temperature. As differences between air and plant temperature regularly exist it is often important to measure both (Burke and Wanjura, 2010). Differences between canopy and air temperatures exist due to many factors, including the diurnal cycle of irradiance, crop size, wind speed, the water content of the air and plant water status (Burke and Wanjura, 2010). The value of measuring plant T_c

for water stress detection has been recognised since the 1980s (Idso, 1982; Jackson, 1982; Jackson *et al.*, 1981). The significance of monitoring plant T_c is that through the opening and closing of stomata (in response to soil water deficits) changes to the leaf energy balance occur and T_c are altered. The closure of stomata results in a decrease in transpiration and consequently a reduction in latent energy flux, leading to a rise in T_c as a thermal gradient to increase sensible heat loss is established. This has been used to indicate water stress in plants for use in irrigation scheduling. However, it is important to reiterate that ambient conditions influence T_c, thus T_c are a combination of plant and environmental factors (Fuchs, 1990).

The increase in availability of more affordable, portable and reliable IRTs has occurred steadily since the 1970s (Jackson *et al.*, 1981; Mahan and Yeater, 2008). This has allowed for real time, non-contact, remote monitoring of plant, leaf, and canopy temperatures with IRTs, which measure the surface radiometric temperature, giving an average temperature of the field of view (Fuchs, 1990). Canopy temperatures are altered through changes in the leaf energy balance, as a result of altered transpiration rates. Transpiration rates generally proceed at a maximum according to environmental demand until ~ 0.3 to 0.4 of the fraction of plant available soil water is remaining (Ray *et al.*, 2002; Ritchie, 1981). At this point plant growth (Hearn, 1979) and gas exchange (Ritchie, 1981; Ray *et al.*, 2002; Sinclair, 2005; Sinclair and Ludlow, 1986) decline until the remainder of transpirable water is used or soil water is replenished. As soil water availability can influence T_c, species-specific, stress threshold T_c that signal the onset of

water stress have been established for numerous plant species, including cotton (Burke *et al.*, 1988).

The determination of the optimal T_c for cotton developed from the finding by Hatfield *et al.* (1987a) where T_c of well-watered cotton crops became cooler than T_a at $T_c > 27.5$ °C, whilst night T_c of field grown cotton tracked T_a. At the same time Mahan *et al.* (1987) used the concept of the thermal dependence of enzyme parameters to delineate optimal temperatures in plants. Analysis of the thermal dependence of the apparent Michaelis-Menten constant (K_m) of cotton glyoxylate reductase, led to the development of the TKW approach to quantify thermal stress. The TKW for optimum enzyme function is the thermal range over which the apparent K_m of an enzyme is within the range of ± 200% of the observed minimum value (Mahan *et al.*, 1987). The relevance of 200% was based on earlier work which showed that enzymes could function optimally within ± 200% of the minimum K_m value (Teeri, 1980; Teeri and Peet, 1978; Somero and Low, 1976). The temperature dependence of enzyme function has been used to explain the ecological niche and limitations of organisms to thermal environments (Burke, 1995; Somero and Low, 1976; Teeri and Peet, 1978). As plant enzymes evolved for optimal function within the normative temperature range of the organism, the TKW concept can be used as a means of determining an optimal plant T_c. This is especially important as most agriculturally significant crop species are now also grown outside the ecological niche in which they evolved, and hence may be exposed to an increase in both supra and sub-optimal ambient and plant temperatures.

The TKW for cotton was identified as 23.5 °C to 32 °C, with the minimum observed K_m of cotton glyoxylate reductase at 27.5 °C (Burke *et al.*, 1988; Mahan *et al.*, 1987). These observations were supported by Upchurch and Mahan (1988), where cotton T_l grown under glasshouse conditions tracked T_a (to within 1 °C) when T_a was below minimum K_m for cotton enzyme function. They also showed that leaf temperatures under well-watered conditions were maintained to 27 °C ± 2 °C when air temperatures > 30 °C. They concluded that when energy input is insufficient to warm leaf temperature to the TKW, leaf temperatures track air temperatures. Burke and Upchurch (1989) supported this theory, finding that transpiration is minimal at leaf temperatures < 24 °C, the lower limit of cotton's TWK. Upchurch and Mahan (1988) also noted that during daylight hours, incoming radiant energy must be dissipated by transpiration to avoid a rise in T_l above the TKW. This is achieved through stomatal control, which has been shown to be responsive to T_l within the TKW (Burke and Upchurch, 1989). This suggests that cotton has at least some capacity to maintain its T_c at its preferred thermal range (TKW), and more specifically its optimum temperature for metabolism, through transpiration.

The preferred T_a for high cotton yields is generally considered to be ~ 30/20 °C day/night temperature (Singh *et al.*, 2007), where exposure to temperatures above this tend to decrease total biomass and result in a high rate of fruit abscission, while lower temperatures result in slower growth and development (Reddy *et al.*, 1991a). The optimum plant temperature or thermal stress threshold for cotton has been determined through a variety of means including the thermal stability of various enzymes (Mahan, 2000; Mahan and Gitz, 2007; Burke, 1995), the recovery rate of the Chlorophyll *a*/*b* light

harvesting complex of PSII (Burke, 1990), plant growth, development and productivity (Burke *et al.*, 1988), growing crops to avoid T_c exceeding a specific threshold temperature (Wanjura *et al.*, 1990; Upchurch *et al.*, 1996; Wanjura *et al.*, 1992), and pollen germination rates (Burke *et al.*, 2004). These methods all concur that the thermal optimum of cotton is ~ 28 °C ± 3 °C (Burke and Wanjura, 2010). However, it is important to note that all of these studies were conducted on Texan Paymaster cotton cultivars (Paymaster HS26, 958, 145, 404 and 2326RR) and were confined to the Texas High Plains.

The principle underlying chlorophyll fluorescence is that light energy absorbed by chlorophyll molecules in a leaf can be used to drive photochemistry, dissipated as heat or re-emitted as light- chlorophyll fluorescence (Maxwell and Johnson, 2000). These three processes occur in competition, where an increase in efficiency of one process will result in a decrease in yield of the other two (Maxwell and Johnson, 2000). Chlorophyll fluorescence has been increasingly used in plant physiological studies, as it yields information about the changes in the efficiency of photochemistry and heat dissipation. Fluorescence parameters that were measured in this study were the dark adapted zero fluorescence level (F_o) and the dark adapted maximal fluorescence (F_m), which are used to calculate the dark adapted variable fluorescence (F_v, where $F_v = F_m - F_o$) (Figure 4.1). The fluorescence parameter used in this study was F_v/F_o, which represents the reappearance of dark adapted chlorophyll variable fluorescence following illumination, and has been used by Burke (1990) to determine species-specific optimal temperatures.

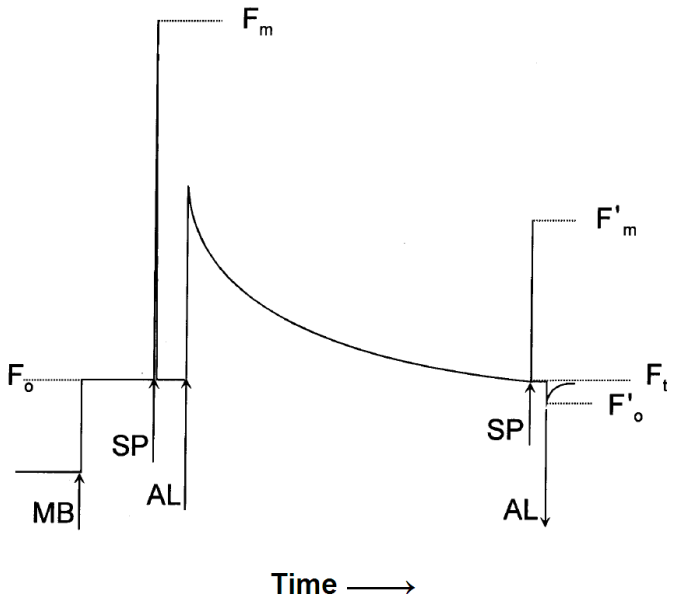


Figure 4.1. Sequence of a typical fluorescence trace. A measuring light is switched on (↑MB) and the zero fluorescence level is measured (F_o). Application of a saturating flash of light (↑SP) allows for the measurement of the maximum fluorescence level (F_m). A light to drive photosynthesis (↑AL) is then applied. After a period of time another saturating light flash (↑SP) allows for the maximum fluorescence in the light (F'_m) to be measured. The level of fluorescence immediately before the saturating flash is termed F_t. Turning off the actinic light (↓AL), in the presence of far-red light, allows for the zero level fluorescence in the light (F'_o) to be *estimated*. Source: (Maxwell and Johnson, 2000).

Optimum temperatures for plant metabolism were determined in this study using the temperature dependence of the reappearance of variable chlorophyll fluorescence following illumination. This method was developed by Burke (1990), and differs from enzyme thermal stability in that it can be used in rapid screening of plant tissue, avoiding the difficulties associated with protein purification and enzyme temperature assays. The temperature dependence of the recovery of PSII F_v following illumination was originally studied by Peeler and Naylor (1988), who found that the recovery of F_v at 5 °C was inhibited in chilling-sensitive cucumber seedlings compared with chilling-resistant pea seedlings. Burke (1990) extended these results to demonstrate the species-specific temperature optima for the recovery of F_v/F_o following illumination. Burke (1990) compared the novel F_v/F_o temperature assay to the thermal sensitivity of apparent K_m of

the enzyme hydroxypyruvate reductase for NADH. This comparison showed consistent calculations of thermal optima using the F_v/F_o recovery temperature assay and the established enzyme thermal stability method (Burke, 1990; Burke and Oliver, 1993). Later, it was also established that while absolute values of F_v/F_o varied following previous stress, the thermal dependence of these values were stable over the life of the plant and unaltered by water or thermal stress (Mahan *et al.*, 1995; Ferguson and Burke, 1991).

Although much research has been conducted on the thermal optimum of cotton, it is important determine the optimal temperature threshold for the Australian cotton cultivar used in this study. This is especially important as the studied USA cultivars are limited in diversity (all Paymaster lines). The accuracy of this optimum is essential as threshold stress temperatures, based on optimal plant function, are central to the water stress detection of the BIOTIC irrigation scheduling system. The purpose of this chapter is to verify that the optimal temperature of the current industry standard commercial Australian cotton cultivar, Sicot 70BRF, is similar to the values measured in the US cultivars of the same species. Using the method developed by Burke (1990) as well as physiological gas exchange responses to leaf temperature in field grown cotton, the optimal temperature of Sicot 70BRF was studied. A sensitivity analysis of the BIOTIC irrigation scheduling system (see Chapter 2 for further details) to temperature thresholds was also conducted in order to determine the accuracy of the temperature threshold and the effect of altering this threshold.

4.2 Materials and methods

4.2.1 Temperature dependence of the reappearance of variable chlorophyll fluorescence following illumination

The Australian cotton cultivar (*Gossypium hirsutum* L.) Sicot 70BRF (CSIRO, Australia) was used to compare the optimal temperature of historically studied US cultivars, Paymaster 145 and Paymaster HS26, which were developed in Texas. Sicot 70BRF was selected to represent a standard commercial Australian cultivar as in its first year of release (2008/09) > 70% of the total area of cotton production in Australia was sown to this cultivar (Cotton Seed Distributors, *Pers. Comm.* 2009). Sicot 70BRF is the result of a cross between Sicala V-1 (seed parent) and the CSIRO breeding line 84009-47 (pollen parent) at ACRI, Narrabri (Reid, 2001). These parental lines were bred from US cotton germplasm from Texas (Tamcot SP37H and Paymaster 101-A lines) and Arizona (Delta Pine 90), as well as a Russian line (King Karajoski 1534), emphasising the strong US background of Australian cotton breeding programs.

Plants were grown under glasshouse conditions (fluorescent and incandescent lights with 16 hour photoperiod at 25 °C ± 5 °C) at the United States Department of Agriculture's Cropping Systems Research Laboratory in Lubbock, Texas. Plant leaf tissue was harvested for analysis on four week old plants. Experimental procedures followed the methodology described by Peeler and Naylor (1988), with modifications made by Burke (1990). A broad temperature assay between 15 °C and 35 °C at 5 °C intervals was initially conducted to roughly gauge the optimal temperature for the reappearance of

chlorophyll fluorescence. The optimum temperature was refined in a fine temperature assay conducted between 24 °C and 32 °C at 2 °C intervals.

Leaf discs were excised from plants and placed on moistened 3 mm filter paper on top of a wet sponge in a glass dish and covered with CO_2 permeable plastic film (Gladwrap^{TM}), to avoid desiccation. Leaf discs were illuminated at 25 °C (the same temperature as growing conditions) under a high pressure sodium lamp, emitting a light intensity of 650 μmol μm^2 s^{-1}. An illumination period of one minute was used to ensure light adaption had occurred; however, this period was adjusted if the normalised F_v/F_o ratio taken immediately after the illumination period was > 0.15. This adjustment was necessary because chlorophyll fluorescence measurements were conducted throughout the dark adaptation period from light adapted conditions. Therefore, an initial saturating light exposure was required to ensure leaf material was light adapted. A constant illumination period was then used for all treatments within an experiment. Following the illumination period, the filter paper containing the leaf disc was transferred to a temperature-controlled thermocouple block, preset to the desired temperature. Temperature treatments ranged from 15 °C to 35 °C at 5 °C intervals in the broad temperature range assay. Following a ten second excitation period of light intensity of 22 μmol μm^2 s^{-1}, fluorescence measurements were recorded at zero minutes and then at five minute intervals throughout the dark adaption period to 20 minutes following illumination. Fluorescence measurements were taken on three leaf discs per temperature and time period with the Brancker SF-30 (Richard Branckner Research, Ottawa, Canada). The fine temperature assay was conducted between 24 °C and 32 °C at 2 °C intervals. The fine temperature

assay was conducted at temperatures within the thermal kinetic window of 23.5 °C to 32 °C, described by Burke *et al.* (1988). The method was the same for this assay as the broad temperature range assay, except measurement intervals were reduced to one minute and the measurement period was reduced to six minutes following the excitation illumination.

Results are expressed as the dark adapted variable to minimal fluorescence (F_v/F_o), and were normalised in order to observe trends in dark adapted fluorescence recovery. Data were normalised by subtracting the measured F_v/F_o from the initial F_v/F_o measured at zero time from excitation illumination. The optimum temperature for the recovery of PSII fluorescence was characterised by a combination of the maximum F_v/F_o ratio and the minimum time in darkness to reach the maximum F_v/F_o ratio. The maximum F_v/F_o achieved is used as the initial predictor of optimal temperature, and the rate to maximum F_v/F_o is used to differentiate between similar maximum F_v/F_o (Burke, 1990). An analysis of variance (P=0.05) was conducted to determine differences in maximum F_v/F_o and rates to maximum F_v/F_o on the fine temperature assay.

4.2.2 Optimal temperature for gas exchange in field grown cotton

Leaf photosynthetic rate and conductance were measured using an IRGA, Portable Photosynthesis System; Li-COR® model 6400-40 (Li-COR Biosciences, Lincoln, Nebraska, USA) in Experiments 2, 3 and 4. Measurements in Experiment 2 and 3 were taken during the peak period for photosynthesis (10:30 am to 11:30 am) (see Appendix 1) on the youngest fully expanded leaf in all plots of the theoretical optimal (control) (Treatment 4), excessive (Treatment 5) and the largest soil water deficit (Treatment 1)

irrigation treatments. Measurements were taken on four days throughout the growing season in Experiment 2 (95, 119, 133 and 134 DAS) and five days during Experiment 3 (83, 90, 97, 107 and 114 DAS). Gas exchange was also conducted between 10:30 am and 11:30 am in all treatments of Experiment 4 (69, 81, 91, 100, 113, 120 and 139 DAS). A range in irrigation treatments considered, ensuring an array of studied leaf temperatures and corresponding gas exchange rates. Leaf temperatures were measured with a chromel-constantan thermocouple junction located within the sensor head of the Li-6400 (Li-COR Biosciences, 2004a). The accuracy of these leaf temperatures was corroborated with a Fluke Ti20 Thermal imager (Fluke, Everett, Washington, USA).

As gas exchange is affected by light intensity, humidity, temperature, CO_2 and time of day, the Li-COR® was matched to ambient conditions and held constant for the time period of measurements. This resulted in cuvette relative humidity controlled at 50% to 70%, CO_2 maintained at 360 μmol (CO_2) mol^{-1} air, PAR set to 1800 μmol m^{-2} s^{-1} to 2000 μmol m^{-2} s^{-1} and air temperatures ranging from 23 to 42 °C. Equations for calculating photosynthetic rate or net carbon assimilation (A, in μmol (CO_2) m^{-2} s^{-1}) and stomatal conductance (g, in mol (H_2O) m^{-2} s^{-1}) are given in the Li-COR Biosciences manual (Li-COR Biosciences, 2004b).

Using GenStat 11th edition, a second order polynomial regression was fitted to the combined photosynthetic rate (A) and corresponding leaf temperatures of Experiments 2, 3 and 4. Regressions were tested for significance and then the peak, or axis of symmetry,

of the quadratic was calculated by finding the mid-point between the roots (*x* intercepts) of the fitted quadratic equation. The roots were calculated using the equation:

Equation 13: The quadratic equation

$$x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

where *a* is the quadratic term and *b* is the linear term and *c* is the constant term of the equation of the fitted line. The range of leaf temperatures that resulted in similar A as the peak value was calculated by substituting the peak value of A ± the standard error of observed A. These values for A were substituted into the fitted equation, which was then solved for *x*, using the above equation, providing the range of leaf temperatures producing photosynthetic rates similar to that of the peak photosynthetic rate. The leaf temperature that produced the peak g_c and the range of leaf temperatures that produced similar g_c rates was calculated in the same fashion as photosynthetic rate calculations above.

4.2.3 Sensitivity analysis of BIOTIC irrigation calls to temperature thresholds

The BIOTIC irrigation scheduling system uses a temperature-time stress threshold system to schedule irrigations. The ST concept used by the BIOTIC irrigation scheduling system is the cumulative amount of time that a crop canopy exceeds both the temperature and the time thresholds. Historically, a stress temperature threshold of 28 °C has been used for irrigation scheduling with BIOTIC in cotton. This threshold is calculated by estimating the thermal optimum of the metabolism of the plant determined from the temperature dependence of a selected metabolic indicator (Mahan *et al.*, 2005). The time threshold is calculated using an energy balance approach. This approach calculates the canopy

temperature of a well-watered, non-stressed plant at specific site. The calculation of this stress time uses historic weather data collected over the growing season for the crop and site of interest to produce an arithmetic mean of the length of time per day that the *calculated* temperature of a well-watered crop canopy is in excess of the threshold temperature of the crop of interest (for more detail see Chapter 2). Using this stress time calculator developed by Mahan *et al.* (2005), a calculated average stress time threshold of 165 min (2.75 hr) was determined for ACRI (Myall Vale), Narrabri (Mahan, *Pers. Comm.* 2010).

The sensitivity of the BIOTIC irrigation scheduling system to temperature thresholds was determined from data collected from Experiments 2 and Experiments 3, where details on the general materials and methods of these experiments are described in Chapter 3. Stress temperature thresholds of 26 °C, 28 °C and 30 °C were studied on cotton monitored with the BIOTIC irrigation scheduling system. The average daily stress time, cumulative stress time for the measurement period, and the number of BIOTIC irrigation calls were calculated from the canopy temperature data collected in Experiments 2 and 3. The number of BIOTIC irrigation calls was calculated by summing the number of days that the crop's canopy temperature exceeded its temperature and time thresholds, or when the ST exceeded the site specific time threshold, which was calculated as 165 min for Narrabri.

The measurement period for the sensitivity analysis was conducted between 85 and 155 DAS. This 70 d period was selected as it was the longest period of time that T_c in both

Experiment 2 and 3 was monitored, and encompasses diverse periods of crop development from flowering through to maturity. This period was between 30th December to 8th March in Experiment 2 (representing an accumulation of 978 degree days) and 7th January to 18th March in Experiment 3 (998 degree days). The analysis was conducted over the same number of days in both Experiments 2 and 3. This is important because irrigation signals are calculated on a daily basis, and therefore, for direct comparisons of irrigation calls across seasons, the number of days studied must be kept constant. If the number of days studied were different across experiments trends in the number of irrigation calls may arise due to differences in measurement periods.

Average stress time T_c were also calculated for each studied temperature threshold. The average stress time canopy temperature was calculated by averaging the measured T_c, during the period when T_c exceeded the temperature threshold of interest. Differences in average ST T_c, within each temperature threshold, were determined by conducting an analysis of variance (P=0.05) in GenStat 11th edition.

4.3 Results

4.3.1 Temperature dependence of the reappearance of variable chlorophyll fluorescence following illumination

The temperature response of the chlorophyll *a*/*b* light harvesting complex of PSII over a broad range of temperatures (15 °C to 35 °C) as determined by the recovery rate of F_v over the dark adaptation period is shown in Figure 4.2. The maximum and rate of F_v recovery of the maximum of Sicot 70BRF were the highest over the 25 °C to 30 °C

temperature range, with normalised F_v/F_o maxima of 1.06 and 0.98 and rates to maximum of 0.21 and 0.20, respectively. F_v/F_o maximums and rates to maximum declined on either side of this temperature range.

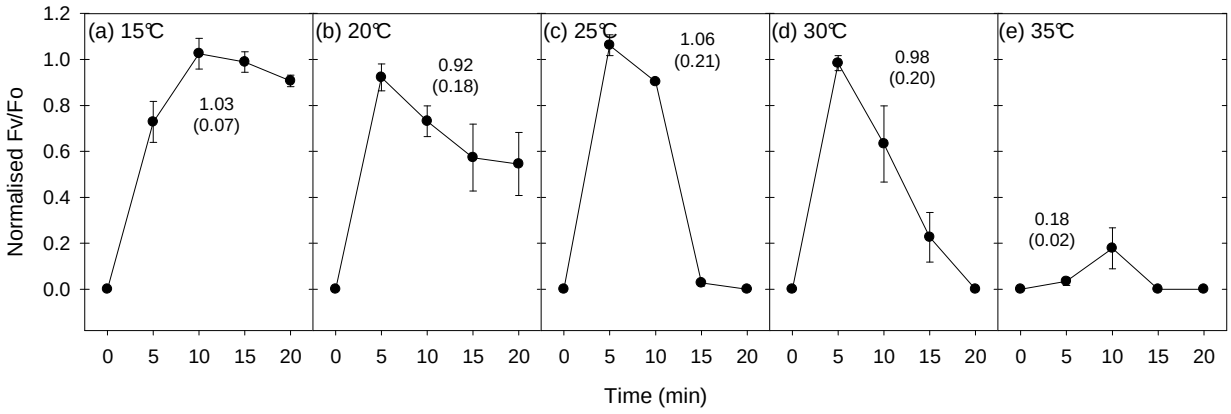


Figure 4.2. Temperature response curves of the recovery of the Australian cotton cultivar Sicot 70BRF's PSII F_v in the dark following illumination at 25 °C. Graphs show the normalised F_v/F_o over time at (a) 15 °C, (b) 20 °C, (c) 25 °C, (d) 30 °C and, (e) 35 °C. The optimal temperature is determined by assessing both the maximum normalised F_v/F_o and the rate to maximum F_v/F_o. The maximum normalised F_v/F_o is shown on each temperature graph, as well as the rate to maximum (shown in brackets). Vertical bars represent standard error of normalised F_v/F_o measurements.

Measurements were then repeated over a smaller range of temperatures (24 °C to 32 °C) at 2 °C intervals. The temperature response of PSII F_v recovery over this refined range of temperatures at one minute intervals is shown in Figure 4.3. Visual assessment of the maximum F_v/F_o and fastest rate to maximum were observed at 28 °C, with maximum normalised F_v/F_o of 0.46 and a rate to maximum of 0.23. The maximum and rate to maximum F_v/F_o declined on either side of the 28 °C, with the exception of the rate to maximum at 32 °C. However, as the maximum F_v/F_o achieved was more than 1.5 times greater at 28 °C than 32 °C, this higher rate to maximum F_v/F_o was disregarded. This is because, as noted earlier, the maximum F_v/F_o achieved is used as the initial predictor of

optimal temperature, and the rate to maximum F_v/F_o is used to differentiate between similar maximum F_v/F_o.

Analysis of variance (P=0.05) was conducted on the fine temperature fluorescence recovery temperature assay. A maximum F_v/F_o of 0.457 with a least significant difference of ± 0.052 was observed at 28 °C. This resulted in no difference observed between the 24, 26, 28 and 30 °C maximum F_v/F_o (P>0.05). The highest slope to maximum F_v/F_o was also observed at 28 °C, with a slope of 0.228 ± 0.027. No difference in slope was observed between the 28 and 30 °C treatments (P>0.05). As the recovery rate of variable fluorescence during the dark adaption period was similar at these two temperatures (with respect to maximum and rate to maximum F_v/F_o), the observed optimal temperature for the cotton cultivar Sicot 70BRF was therefore judged to lie between 28 and 30 °C.

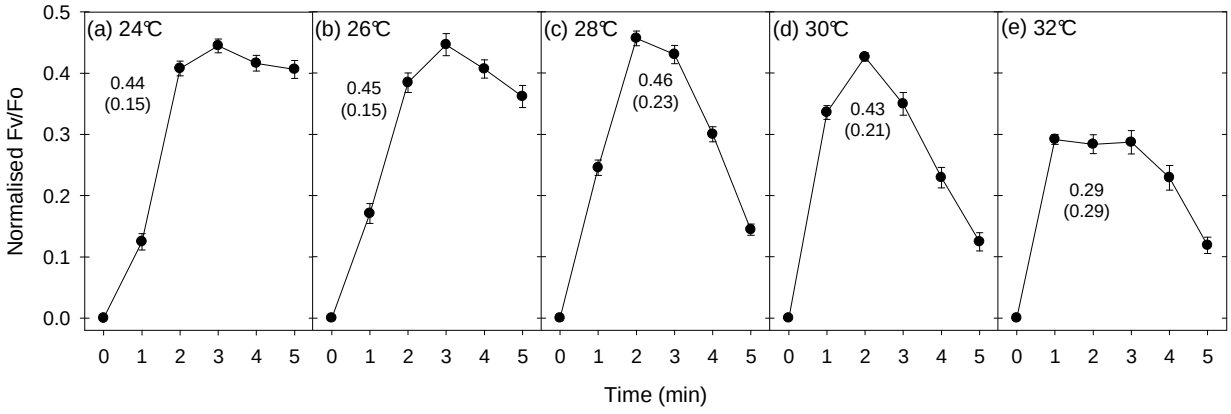


Figure 4.3. Fluorescence optimal temperature assay of the Australian cotton cultivar Sicot 70BRF showing the normalised F_v/F_o over time at (a) 24 °C, (b) 26 °C, (c) 28 °C, (d) 30 °C and, (e) 32 °C. The optimal temperature is determined by assessing both the maximum normalised F_v/F_o and the rate to maximum F_v/F_o. The maximum normalised F_v/F_o is shown on each temperature graph, as well as the rate to maximum (shown in brackets). Vertical bars represent standard error of normalised F_v/F_o measurements.

4.3.2 Optimal temperature for gas exchange in field grown cotton

Gas exchange has been shown to provide a measure of the degree of drought stress imposed on a crop and the response of leaf gas exchange measurements have been used to detect and quantify water stress (Baker *et al.*, 2007). Therefore, leaf A and g_c were used as surrogates for plant performance at a given leaf temperature. These gas exchange parameters exhibited a second order polynomial response to temperature (P<0.001). Forty-one per cent of the variation in carbon assimilation data was accounted for within a regression with T_l. This model saw peak carbon assimilation occurring at 29.3 °C, with an observed standard error of 3.61 μmol (CO_2) m^2 s^{-1} (Figure 4.4a). Fifty per cent of the variation in g_c was accounted for in the regression with T_l (Figure 4.4b). This model saw a peak in g_c at 29.1 °C, with an observed standard error of 0.124 mol (H_2O) m^2 s^{-1}. Although the fit of these regressions was not particularly strong, obvious trends in gas exchange were observed with peak A and g_c occurring at ~ 29 °C. Using the standard error of observations generated from the regressions, ranges of leaf temperatures which represent statistically similar A and g_c were calculated. The range of T_l that represent carbon assimilation rates equal to that of the calculated peak assimilation (29.3 °C) occurred between 27.5 and 31.2 °C, whilst the range for peak stomatal conductance rates (29.1 °C) occurred between 26.8 and 30.5 °C. The combination of these preferred thermal ranges associated with peak gas exchange resulted in a range of leaf temperatures of 26.8 to 31.2 °C.

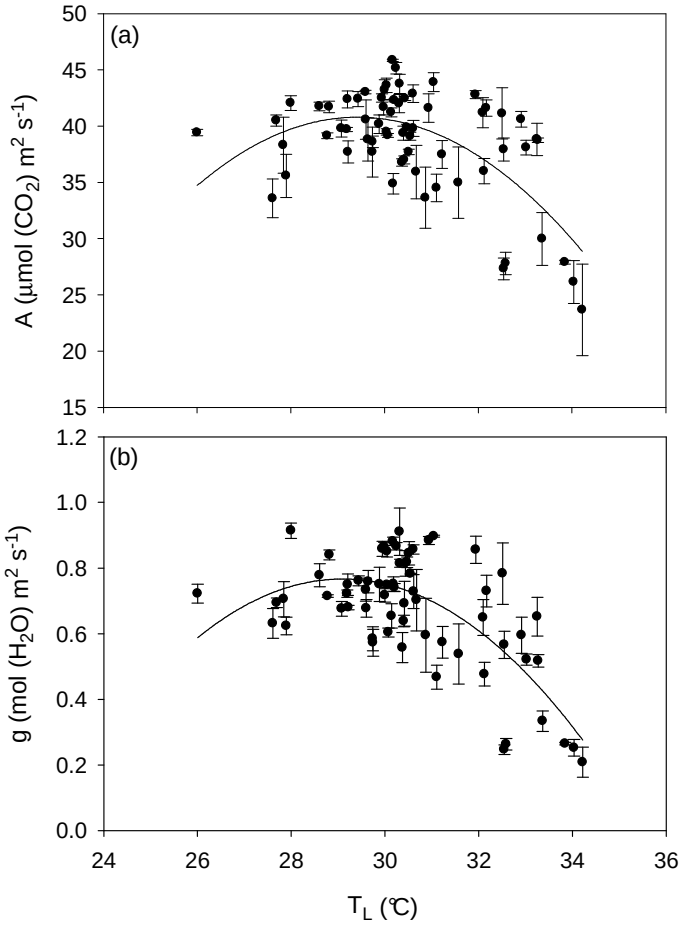


Figure 4.4. (a) Polynomial regression (P<0.001) of leaf net assimilation (A) peaking at 29.3 °C (y= -0.52x^2 + 30.50x -407.83, R^2=0.41); and (b) polynomial regression (P<0.001) of stomatal conductance (g) peaking at 29.1 °C (y= -0.019x^2 + 1.09x -15.07, R^2=0.48). Vertical bars represent standard error of mean.

4.3.3 Sensitivity analysis of BIOTIC irrigation calls to temperature thresholds

The sensitivity of the stress T_c threshold to the calculation of stress time and BIOTIC irrigation calls is shown in Table 4.1. This analysis was conducted to determine the effect of temperature threshold on stress time, irrigation calls and the canopy temperature during the stress time accumulation period. The analysis showed that the number of irrigation calls and stress time for the measurement period were T_c influenced by the temperature threshold used to calculate these parameters, where a higher temperature threshold resulted in lower stress time accumulation and number of irrigation calls. This suggests that stress time canopy temperatures can not consistently be characterised as significantly above the temperature threshold. Although this was expected, the implication for this is that the accuracy of the temperature threshold is important, as stress time canopy temperatures are not always significantly above temperature thresholds.

In order to infer an optimal temperature threshold, the response of average stress time T_c was compared to water application. The response of T_c measured during the stress time accumulation period at temperature thresholds of 26, 28 and 30 °C to water application is shown in Figure 4.5. This regression was significant (P<0.001) and accounted for 93% of the variation in the data with a standard error of observed stress time T_c of 0.36 °C. It was hypothesised that average stress time T_c will not deviate significantly from the temperature threshold at an optimal temperature threshold. Furthermore, at water application rates above optimal (ET_C> 100%), stress time T_c should not increase.

Table 4.1. Sensitivity analysis of the BIOTIC irrigation scheduling system to temperature thresholds and the average canopy temperature during stress time (ST) accumulation (T_c > 28 °C) in Experiment 2 and Experiment 3. Figures followed by the same letters (in superscript) are not significantly different at *P*<0.05, within the same temperature threshold.

Experiment 2	Temp. Threshold	Treatment 1 (75% ETc) WUE=4.6	Treatment 2 (93% ETc) WUE=4.9	Treatment 3 (107% ETc) WUE=4.3	Treatment 4 (123% ETc) WUE=3.2	Treatment 5 (140% ETc) WUE=2.7
Irrigation calls	26	57	53	47	43	40
	28	46	36	27	22	18
	30	28	16	7	5	2
Average daily ST (hours)	26	6.9	6.3	5.3	5.0	4.6
	28	5.0	3.8	2.7	2.2	1.9
	30	2.8	1.5	0.7	0.5	0.3
Cumulative ST for 70 days (hours)	26	483	438	377	353	322
	28	349	265	189	157	135
	30	194	107	50	33	21
Average ST canopy temperature	26	29.9 ^{e}	28.8 ^{c}	28.2 ^{b}	27.9 ^{a}	27.9 ^{a}
	28	30.3 ^{c}	29.5 ^{b}	29.0 ^{a}	28.9 ^{a}	28.8 ^{a}
	30	32.7 ^{f}	31.7 ^{d}	31.2 ^{bc}	31.0 ^{ab}	30.8 ^{a}
Experiment 3	**Temp. Threshold**	**Treatment 1 (57% ETc) WUE=1.8**	**Treatment 2 (67% ETc) WUE=2.8**	**Treatment 3 (77% ETc) WUE=3.2**	**Treatment 4 (92% ETc) WUE=3.0**	**Treatment 5 (104% ETc) WUE=2.8**
Irrigation calls	26	69	68	66	66	64
	28	63	64	59	57	55
	30	55	57	48	39	26
Average daily ST (hours)	26	10.4	10.4	9.9	9.5	9.1
	28	8.0	8.0	7.1	6.4	5.8
	30	5.9	5.8	4.6	3.5	2.4
Cumulative ST for 70 days (hours)	26	738	738	701	675	648
	28	568	570	503	457	411
	30	422	413	329	252	174
Average ST canopy temperature	26	31.5 ^{g}	31.1 ^{f}	30.1 ^{e}	29.5 ^{d}	28.9 ^{c}
	28	32.2 ^{e}	31.9 ^{e}	30.9 ^{d}	30.3 ^{c}	29.8 ^{b}
	30	34.3 ^{h}	33.6 ^{g}	32.6 ^{f}	32.0 ^{e}	31.4 ^{bc}

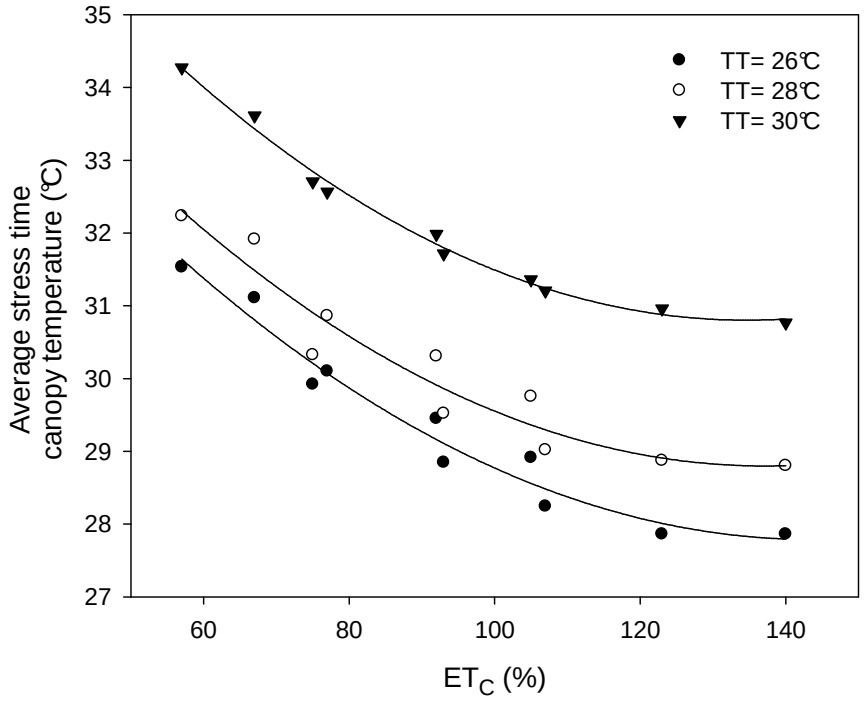


Figure 4.5. Calculated ETc vs. average canopy temperature during the stress time (ST) period at temperature thresholds (TT) of 26 (●), 28 (○), and 30 °C (▼). Note the reduced response of canopy temperature to an increase in ET_C above 100% ET_C application.

The response of stress time T_c to water application was characterised by the reduction of stress time T_c as water application increased. This occurred until crop water requirements were satisfied, where additional application of water after this point did not alter stress time T_c. At a temperature threshold of 26 and 30 °C applications of water > 123% ET_C did not result in an increase in average stress time T_c; however, at 28 °C this occurred at water application of 107% ET_C. The deviation of average stress time T_c from the stress time threshold above water application was characterised by 1.9, 0.9 and 0.9 °C for the 26, 28 and 30 °C thresholds, respectively. This indicates that at sufficient water application, average stress time canopy temperatures were not significantly higher than the temperature threshold in the 28 and 30 °C temperature thresholds. This is supported by the fact that average daily ST accumulation in the 28 °C temperature threshold was

less than the calculated time threshold of 2.75 h in these treatments, suggesting no further increase in stress levels above sufficient water application. This suggests that well-watered plants attempt to keep their T_c at 28 °C to 30 °C through transpiration. However, the average stress time canopy temperature values could be skewed by the decreasing amount of T_c readings above the threshold as the temperature threshold is increased.

4.4 Discussion

The thermal response of the reappearance ratio of dark adapted chlorophyll fluorescence in the cotton cultivar Sicot 70BRF exhibited an optimal temperature in the range from 28 °C to 30 °C. This is consistent with existing research, predominantly conducted on US cotton cultivars (Burke, 1990; Upchurch and Mahan, 1988; Wanjura *et al.*, 1990; Wanjura *et al.*, 1992; Mahan, 2000). The consistency of the optimum value is not surprising as although the *Gossypium* sp. genus has a wide distribution (pan-tropical), individual species have limited distributions and are of relict status with little genetic diversity, suggesting an ancient and declining genus (Hearn and Constable, 1984). Furthermore, many of the cultivars developed in Australia for commercial production were originally bred from US cotton cultivars.

Australian-bred cotton cultivars have historically been selected for phenotypes displaying desirable lint yield, plant habit, disease resistance and fibre quality characteristics. Thermo-tolerance and associated plant metabolic functions have not been used as selection tools in breeding programs. Unless thermo-tolerance has been indirectly selected for through yield and performance indicators, the diversity in the response to

thermal environments may be expected to be retained in germplasm. However, the *Gossypium* genus has very little diversity, and thermo-tolerance traits are controlled by numerous genes and potential plant adaptations. Therefore, the fact that observed differences in plant performance associated with temperature were not observed is not particularly surprising. Furthermore, differences in optimal temperatures, calculated from biochemical metabolic functionality, were not expected as the biochemical metabolic functions are generally reflective of the ecological niche of the native habitat of the species (Mahan *et al.*, 1995).

Enzyme adaptations to temperature occur constantly as plants are exposed to temperature modulations on diurnal and seasonal timescales, as well as over the centuries of evolution (Burke, 1995). These adaptations entail quantitative and qualitative metabolic changes providing competitive advantages, impact on species migration and survival niche, and effect the survival of the species as a whole. The strategies for enzyme adaptation to temperature change include changes in enzyme concentration and cytoplasmic pH, modification of substrate and effectors, changes in isozymes or allozymes, and metabolic regulation of enzyme function without changing enzyme composition (Burke, 1995). Most reported adaptations of enzymes to temperature regime involve genetic diversity in the temperature dependence of the apparent K_m of enzymes, which is highly correlated to the environmental niche the organism evolved in. One of the first examples of this was reported by Somero and Low (1976), in the Antarctic fish *Trematomas*, which is found in nearly constant 0 °C waters. They found that as environmental waters are heated from 5 °C to 20 °C an increase in the apparent K_m of phosphoenopyruvate (PEP), and a

corresponding decrease in the affinity of pyruvate kinase for PEP, is observed. Other examples of the relationship between the temperature dependence of the apparent K_m of enzymes and the adaptation of organisms to unique thermal environments have been observed in numerous other studies (Dahlhoff and Somero, 1993; Graves and Somero, 1982; Hall, 1985; Place and Powers, 1984; Teeri and Peet, 1978; Yancey and Somero, 1978).

Some reports show modification of the thermal dependence of metabolism by changes in pH, or the concentration of existing enzymes. Changes in pH can effectively negate the effect of temperature on protein function. When cytoplasmic pH *in vivo* co-varies with temperature, the apparent K_m of an enzyme does not change (Yancey and Somero, 1978; Burke, 1995), and under experimental conditions will better reflect the physiological response within the cells to temperature (Burke, 1990). A change in enzyme concentration is another way of achieving temperature adaptive changes in metabolic systems. These changes are considered to be particularly important on seasonal scales (Hochachka and Somero, 1984), and can allow species to function at a higher temperature (Burke, 1995; Davidson and Simon, 1983). However, the listed adaptations of enzymes to temperature variations only allow enzyme function to maintain its apparent K_m and a proper catalytic rate within a thermal range, and do not change the optimal thermal environment for these enzymes.

Another way the thermal dependence of metabolism can be altered is through the synthesis of isozymes, enzymes that differ in amino acid sequence, but catalyse the same

chemical reaction. These enzymes usually display different apparent K_m or regulatory properties, and allow for the fine-tuning of metabolism. There is a significant body of literature showing examples of the lack of isozyme changes, or changes in isozymes and their relationship to acclimation of the apparent K_m to temperature stress. In an extensive review on the thermostability and kinetic properties of enzymes during temperature adaptation, Lutova (1995) concluded that despite the fact that species can potentially shift their thermal stability and kinetic characteristics of enzymes, this occurs much less frequently during intraspecific adaptations and acclimations. However, one notable example of intraspecific adaptation was observed in a study conducted by Guy and Carter (1984). They studied the increase in concentration and production of isozymes of glutathione reductase in spinach that had been cold hardened or non-hardened. They found that enzymes from warm grown plants functioned better at moderate temperatures, and enzymes from cold grown plants functioned better at low temperatures. Guy and Carter (1984) point to similar changes in enzyme kinetics from cold tolerant or hardened potato (Huner *et al.*, 1981), rye (Huner and Macdowall, 1979) and wheat (Graham *et al.*, 1979). However, it is important to note that only Huner and Macdowall (1979) actually studied changes in enzyme kinetics during adaptation as Huner *et al.* (1981) and Graham *et al.* (1979) studied differences in enzyme activity in chilling-resistant and non-resistant genotypes.

The discovery that the accompanied corresponding changes in thermostability of enzymes during adaptation of plants to temperature had been regarded as evidence for the conformational flexibility of enzyme macromolecules (Lutova, 1995). This led to the

concept of a dynamic thermal optimum, reflecting acclimation of plant metabolism to thermal experiences and growing environment. This would mean that the thermal optimum of a plant would reflect its growing temperature. However, this was not observed in my experiment as the growing temperature was 25 °C ± 5 °C, and the optimum temperature was observed to be 28 °C to 30 °C. Despite this result, this concept should be further investigated in order to test whether optimal plant temperatures are constant irrespective of growing temperature.

In numerous experiments, Ferguson and Burke (1991) investigated the potential effects of plant adaptation and exposure to previous thermal and water stress on the optimal temperature of cotton. They did not observe differences in thermal optimum environments following thermal or moisture stress, and attribute this to the fact that optimal temperatures were calculated from the thermal dependence of biochemical reactions and plant adaptation to previous temperature or water stress does not affect the optimal temperature of these reactions (Ferguson and Burke, 1991). It is however important to note that although the field grown plants was certainly exposed to different water and thermal stress levels, the experiments conducted in the glasshouse were only allowed to acclimate to thermal treatments for 8 d, which may not be sufficient to induce acclimation responses, if they were to occur.

Lutova's (1995) review supports the lack of changes in optimal temperature as a result of prior stress. Lutova (1995) concluded that alterations in kinetic properties due to changed thermostability of enzymes were mostly observed in experiments comparing plants with

different heat sensitivities. However, some studies have shown exceptions to this rule where plants from different ecotypes and different plant cultivars displayed altered kinetic properties. However, most studies show that the response of enzyme kinetics to growth temperature (acclimation) do not occur (Björkman *et al.*, 1978; Simon *et al.*, 1984; Davidson and Simon, 1981), with only a few rare exceptions (Bhadula *et al.*, 1985; Guy and Carter, 1984). Furthermore, as heat hardening can lead to protein stabilisation, and changes in protein properties were not observed (or studied), changes in enzyme kinetics can usually be attributed to differences in the primary structure of proteins (Lutova, 1995). This is supported by the fact that adaptive changes in the thermostability of enzymes of acclimated plants are observed by heating the whole leaves, rather than purified enzymes (Simon *et al.*, 1984; Lutova *et al.*, 1987) and can be supported by allowing protein properties to be monitored within an intact cell, through differential scanning calorimetry (Lutova, 1995).

In response to the reported effects of pH, activators and inhibitors of enzymes activity on the temperature dependence of the apparent K_m, Burke (1990; Burke, 1995) suggested that the best evidence that optimal temperatures and optimal temperature ranges reflect *in vivo* metabolic responses is the determination of the reappearance of photosystem II variable chlorophyll fluorescence following illumination. This is because chlorophyll fluorescence is a natural indicator of the *in vivo* temperature characteristics of a plant, and correlations between temperatures providing maximum reappearance of variable fluorescence and temperatures providing the minimum apparent K_m of an enzyme have been observed (Burke, 1990; Burke, 1995; Ferguson and Burke, 1991). Correlations

between the temperature dependence of enzyme function and variable fluorescence recovery have been reported for cotton as well as cucumber, tomato, wheat, soybean, tomato, petunia and bell pepper (Burke, 1990; Burke and Oliver, 1993; Ferguson and Burke, 1991).

Chlorophyll fluorescence reappearance ratios have been extensively used to calculate optimal plant temperatures across different species (Steiner *et al.*, 2001; Burke, 1990; Burke, 1995). However, little research has been conducted reporting intra-specific germplasm differences in chlorophyll fluorescence reappearance ratios, and none has been conducted in cotton. However, using the methodology of Burke (1990), Karlsen and Steiner (2007) report genotypic variation in the temperature of peak chlorophyll fluorescence reappearance ratios of colonial bentgrass (*Agrostis capillaris* L.). This result displays the very real possibility of genotypic variation in optimal plant temperature. However, the reported variability in germplasm affecting plant physiological function (fluorescence reappearance ratios) in this study (Karlsen and Steiner, 2007) is present in genotypes from expansive ecological distributions, with distributions ranging from temperate through to sub-arctic regions. These regions include latitudes ranging from 42.4°N to 67.8°N and elevations ranging from 72 m to 1869 m, encompassing humid temperate grasslands in Italy, England and Southern Russia, through to humid temperate Boreal and sub-arctic continental Boreal in Scandinavia and Northern Russia. As the cotton genus evolved over a much smaller ecological distribution (arid tropics) and individual species have limited distribution, similar diversity in genotypic variation in optimal plant temperature is not expected. Furthermore, the same germplasm was used to

breed the Australian genotype studied and the historically studied US cultivars. Therefore, although genotypic variation in chlorophyll fluorescence reappearance ratios can be observed, differences between the commercial Australian cultivar Sicot 70BRF and the historically studied USA cultivars Paymaster 145 and Paymaster HS26 were not observed in this study. This is because the *Gossypium* genus itself encompasses little genetic diversity, which was further reduced by the genetic similarity of the cultivars studied. Despite the fact that no difference in optimal temperature was expected, it is imperative that the correct optimal temperature is determined as the BIOTIC protocol is highly sensitive to changes in temperature threshold (Table 4.1).

The peak in gas exchange parameters, both A and g_s, occurred at leaf temperatures of ~ 29 °C. This initially suggests that when measured in the same cultivar the optimum for gas exchange in field grown Australian cotton may be slightly higher than the optimal temperature for the recovery rate of the chlorophyll light harvesting complex of PSII as measured by the temperature dependence of the reappearance of dark adapted variable fluorescence following illumination. However, the range of leaf temperatures that produced optimal gas exchange rates equal to that of the peak at 29 °C occurred between 26.8 °C and 31.2 °C. This range in optimal temperatures was similar to the TKW for cotton (23.5 °C to 32 °C) and encompassed the optimum temperature for cotton metabolism (28 °C) as outlined by Burke *et al.* (1988) and Mahan *et al.* (1987). This supports the laboratory based calculation of the thermal based optima of cotton at 28 °C with field based observations.

Although the results of this study show consistency between the optimal or stress threshold temperature for an Australian cotton cultivar, and the historically studied cotton cultivar, the significance of this threshold temperature needs to be evaluated using the BIOTIC protocol under field conditions. This was achieved through conducting a sensitivity analysis of the temperature threshold for cotton monitored with the BIOTIC protocol (Experiment 2 and 3). The BIOTIC response to soil water deficits (number of irrigation calls) is sensitive to the temperature threshold used to determine thermal stress (Table 4.1). This was also observed by Wanjura *et al.* (1990), where small temperature threshold differences (2 °C) resulted in vastly different quantities of water applied, average T_c and subsequent lint yields. The sensitivity of BIOTIC to T_c thresholds suggests that BIOTIC is very responsive to changes in temperature thresholds. It also suggests that stress time T_c were not always significantly above the threshold, if this was the case stress times would be common across treatments. Therefore, when there is enough plant available water for transpiration to occur at rates enabling leaf cooling, T_c remains at ~ 28 °C. However, these T_c may rise slightly above this threshold value, regardless of water availability.

A site-specific stress time calculator using on site weather station data and seasonal plant growth parameters was developed to determine the site specific amount of time a well-watered canopy temperature will exceed 28 °C. Using this stress time calculator, a stress time threshold of 165 min (2.75 h) was determined for ACRI (Myall Vale), Narrabri (Mahan, *Pers. Comm.* 2010). When applied to the data observed from Experiments 2 and 3 and a temperature threshold of 28 °C was used, treatments receiving in excess of 107%

ET_C displayed similar average T_c during the stress time accumulation period and average daily stress times less than the calculated stress threshold. In water stressed plants, average stress time T_c of up to 2.3 °C above the threshold (28 °C) were observed, with corresponding average daily stress times of up to 480 min (8 hr). This suggests that these cotton plants, with sufficient access to water, respond to maintain T_c to 28 °C ± 2 °C.

Under fully irrigated conditions, 28 °C is considered the optimum value for the stress threshold. Using the BIOTIC protocol, a temperature threshold of 28 °C and a daily stress time of ~ 165 min produced the highest lint yielding cotton in both Experiment 2 and 3. Changing the temperature threshold had a significant impact on the resultant irrigation scheduling advice provided by the BIOTIC protocol. This response was also observed by Wanjura *et al.* (1990), where small threshold differences of 2 °C (between 28 to 32 °C) resulted in different quantities of irrigation water, biomass accumulation and lint yield. The highest yields were recorded in the treatments receiving 107 and 104% of ET_C in Experiments 2 and 3, respectively. These treatments resulted in average stress time canopy temperatures of 29 °C and 29.8 °C and water use efficiencies of 4.3 and 2.8 kg (lint) mm^{-1} ha^{-1}. However, higher WUE (4.9 and 3.2 kg (lint) mm^{-1} ha^{-1}) was recorded in the treatments of Experiments 2 and 3 that received 93 and 77% ET_C, resulting in average stress time T_c of 29.5 °C and 30.9 °C, respectively. Similarly, Wanjura *et al.* (1992) noted that although a 28 °C stress threshold consistently produced the highest yield, the 30 °C treatment produced slightly lower yields but at a higher WUE.

Therefore, in water limited or environments with high irrigation water costs, a higher threshold (30 °C) may produce a higher profit through reducing the number of irrigations, water applied and increasing WUE. This is especially important in the context where a 2 °C increase in threshold temperature can result in 200 mm less irrigation water applied (Wanjura *et al.*, 1992) or ~ 20 fewer BIOTIC irrigation calls (Table 4.1). Furthermore, water use may be optimised through withholding early or late season irrigation water, which may result in a variable temperature threshold across the season. Such a dynamic temperature threshold would need to take into account the periods where water stress has less impact on agronomic yield and quality. This could include physiological periods when cotton is most susceptible to water stress, such as flowering, or agronomic management practices such as late season reductions in water application to enhance crop maturity rates.

4.5 Conclusion

The optimum temperature range for cotton metabolism has been extensively studied, with evolutionary, physiological, enzymatic and lint yield responses all indicating an optimal plant temperature of ~ 28 °C. Enzymatically, the minimum observed stable K_m of a studied enzyme has been used to determine optimal temperatures for plant metabolism and enzyme function. Mahan *et al.* (1987) and Burke *et al.* (1988) observed the stable K_m of cotton glyoxylate reductase at 27.5 °C, which resulted in a thermal kinetic window of 23.5 °C to 32 °C. Enzyme thermal stabilities are a robust method of determining optimal plant temperatures, as these are not subject to adaptive changes (Mahan *et al.*, 1995). It has also been observed that cotton foliage temperatures separate from air temperature at

28 °C, maintaining temperatures within the TKW (Hatfield *et al.*, 1987a). This suggests an evolutionary adaptive mechanism, which attempts to keep T_c at a preferred or optimal T_c. This is supported by the fact that seasonal biomass accumulation has been shown to express a linear relationship with the amount of time plants are within the TKW (Burke *et al.*, 1988). Furthermore, cotton irrigated when T_c > 28 °C has consistently shown peak lint yields when compared to irrigation regimes based on higher or lower threshold canopy temperatures (Wanjura *et al.*, 1990; Wanjura *et al.*, 1992).

The optimal plant temperature of the commercial Australian cotton cultivar Sicot 70BRF was determined through physiological methods to be in the range of 28 °C to 30 °C using chlorophyll fluorescence recovery rates and between the range of 27 °C to 31 °C using photosynthetic and stomatal rates at discrete leaf temperatures. This value is within the TKW for cotton, 23.5 °C to 32 °C. The thermal optima of Sicot 70BRF is similar to that of cotton cultivars studied by Burke (1990), Burke *et al.* (1988), Upchurch *et al.* (1996) and Mahan (2000), which use both similar physiological methods and divergent enzymatic and plant performance indicators to determine a thermal optimum of cotton at ~ 28 °C ± 3 °C.

5. SOIL WATER DEFICITS AND THEIR INFLUENCE ON CANOPY TEMPERATURES IN SURFACE DRIP IRRIGATED COTTON

5.1 Introduction

Cotton production is affected significantly by water supply, and the relationship between water application, plant physiological response and cotton lint yield has been extensively studied (Constable and Hearn, 1981; Cull *et al.*, 1981; DeTar, 2008; Grimes and El-Zik, 1990; Hearn, 1994; Pettigrew, 2004b), with publications documenting yield-water relations since 1934 (Crowther, 1934). These studies show that the response of the cotton plant to water is complex and involves many processes. It goes without saying that water is essential for the growth of cotton, however the xerophytic adaptations of cotton confer a complex response of cotton to water application (Hearn, 1994). In summary, under-watering results in a reduced number of fruiting positions, fruit loss, poor boll development and decreased lint yield, and over-watering can lead to rank growth resulting in fruit shedding. Extreme over application of water over an extended period can result in waterlogged conditions. Waterlogging increases leaf, reproductive and root senescence and reduces dry matter accumulation and crop yield (Bange *et al.*, 2004). Physiological consequences of waterlogged conditions include altered shoot and root hormonal status, reduced nutrient availability, uptake and translocation, decreased g_c, Ψ_l, and photosynthesis (Conaty *et al.*, 2008).

The key to understanding the water relations of cotton is in its xerophytic origins, and its subsequent sensitivity to both wet and dry soil water conditions (Hearn, 1994). Hence, it

is important to note the divergence between an optimal agronomic and evolutionary water application. Evolutionarily, water supply had a profound effect on the balance between vegetative and reproductive growth. Wet conditions trigger facultative shedding of fruit while vegetative growth continues; however, when about three quarters of available soil water has been used vegetative growth abruptly ceases, and remaining water is used to mature fruit. This response to soil water, along with its indeterminate growth habit, confers reproductive flexibility in the face of variable and unpredictable water supply (Hearn, 1994). Optimal agronomic water application must walk this fine line between sub and supra-optimal water application, increasing vegetative growth to support more fruiting positions, without inducing fruit shedding or early maturation. The challenge for irrigation scheduling is to find an optimum agronomic application regime, which responds accurately to conditions over a range of seasonal pressures, whilst making efficient use of water resources.

Leaf temperature is a result of the balance between leaf energy and water. Thus, if water availability and transpiration are reduced, the latent heat flux from the leaf surface decreases and leaf temperature rises as sensible heat flux increases to shed incident energy. However, irradiance, ambient temperature, humidity, wind speed and the position of the leaf surface in relation to the incident solar irradiance will also modify leaf temperature, and may mask the effects of water stress (Fuchs, 1990). Leaf temperatures have long been recognised as having potential to provide information about plant water stress (Tanner, 1963; Gates, 1964; Wiegand and Namken, 1966). Early studies of CTD involved thermocouples embedded into cotton leaves (Ehrler, 1973). Ehrler found that

CTD decreased after irrigation, reaching a minimum several days following irrigation, and then increased as soil water became increasingly depleted. After showing a linear relationship between CTD and vapour pressure deficit (VPD), Ehrler (1973) concluded that CTD has potential for informing irrigation scheduling tools. Idso *et al.* (1977) and Jackson *et al.* (1977) further refined CTD, developing the stress-degree-day concept which used CTD as an index for crop water status, which was correlated with crop yield and water requirements. They assumed that environmental factors such as VPD, irradiance and wind would manifest in $T_{c;}$ however, this does not always hold true (Jackson *et al.*, 1981). This is because T_c can be profoundly influenced by VPD, irradiance and wind speed, depending on the level of their intensity. Idso *et al.* (1981a) then showed that the relationship between CTD and VPD, in well-watered crops under clear skies, was linear. This was used to create an upper and lower crop-specific limit for transpiration. The Crop Water Stress Index (CWSI) utilised these limits and is a reasonably quantitative evaluation of crop moisture deficits in situations where corresponding VPD data is available (Idso *et al.*, 1981a). Jackson *et al.* (1981) further developed the CWSI by incorporating the Penman-Monteith equation for evapotranspiration, and concluded that, for the quantification of crop water stress, the CWSI was adequate in certain environments, especially under hot and dry conditions. However, further work needed to be conducted before CWSI could be used in universal environments as an irrigation scheduling tool.

Another approach to irrigation scheduling using T_c is the stress time (ST) index developed by Wanjura *et al.* (1992). The stress time index accumulates the amount of

daily time a T_c exceeds its species-specific optimum temperature. Using IRT and a stress time (ST) index, Upchurch *et al.* (1996) developed an irrigation scheduling system known as Biologically-Identified Optimal Temperature Interactive Console (BIOTIC). The foundation of this system is the theory that plant productivity is proportional to the amount of time plant temperatures were observed to be within their thermal kinetic window (TKW) (Burke *et al.*, 1988; Mahan *et al.*, 1987). Burke *et al.* (1988) found that although cotton foliage can only be expected to be within its TKW 30% of the season, biomass accumulation principally occurred during this period. This was observed through a linear relationship between the times that foliage temperature was within the TKW and when plant biomass accumulation occurred. The BIOTIC uses IRT and a three step threshold system (temperature, time and humidity) to determine if and when to irrigate (See Chapter 2). The species-specific temperature threshold is based on the optimal temperature for enzyme function (enzyme thermal stability) or the optimal temperature for stress recovery following dark adaptation (measured by variable fluorescence). The daily time threshold, which represents the period of time a fully irrigated crop canopy temperature is theoretically likely to exceed the optimal temperature in that environment, is based on environmental variables (temperature, relative humidity, wind speed and irradiance), and is specific to a particular region. A more detailed explanation of the BIOTIC irrigation scheduling system can be found in Chapter 2.

This study was conducted to determine the effect of various rates of crop evapotranspiration (ET_C) replacement via surface drip irrigation on the growth and development, yield and canopy temperatures of cotton grown on a grey Vertosol (Isbell,

1996) at Narrabri, NSW Australia. This information was used to evaluate the ET_C method of irrigation scheduling in order to determine the potential utility of the BIOTIC irrigation scheduling system in Australian environmental and production conditions. The BIOTIC system's performance was scrutinised over two growing seasons, with analysis of the interaction between measured canopy temperatures and yield, crop development, biomass accumulation, water relations and weather conditions which influence a crop's stress potential.

5.2 Materials and methods

Two surface drip-irrigated cotton (*Gossypium hirsutum* L.) field experiments were conducted at the Australian Cotton Research Institute (ACRI) at Narrabri during the 2007/08 (Experiment 2) and 2008/09 (Experiment 3) seasons. Five irrigation treatments based on daily crop evapotranspiration (ET_C) rates were imposed. This included a theoretical optimal (100% daily water requirement of control applied- Treatment 4), an excessive (125% of control daily water requirement of control applied- Treatment 5) and three deficit (75%, 50% and 25% of control daily water requirement of control applied- Treatments 3, 2, and 1) irrigation regimes. Daily water requirements (ET_C) were calculated according to (Allen *et al.*, 1998), see section 3.3.2. Weather conditions, soil water, crop growth and development, lint yield and T_c were monitored throughout the experiments. Detailed materials and methods of these experiments can be found in Chapter 3.

5.3 Results

5.3.1 Weather

The experimental site has a long-term average rainfall of 657 mm per annum, and 391 mm for the cotton growing season (October to March) (BOM, 2009). Rainfall throughout Experiment 2 totalled 361 mm and 353 mm in Experiment 3. Although both seasons received similar amounts of rain, the distribution and intensity of rainfall events varied. Experiment 2 tended to be characterised by more numerous, smaller rain events, whilst Experiment 3 saw fewer rain events, but with a greater intensity (Table 5.1 and Figure 5.1a). Rainfall during the period of peak evaporative demand (December to February) was above the long term average in both seasons, except for January 2009 of Experiment 3, which saw rainfall well below the monthly average and February 2008 of Experiment 2, which saw rainfall slightly below the monthly average (Figure 5.1a). According to the daily water requirement calculations (crop ET) in the control plots, only 66 mm and 137 mm of the total rainfall in Experiment 2 and Experiment 3 was effective in the respective years (Figure 5.2). Effective rainfall represents the difference between the cumulative crop requirement (ET_C) (minus water supplied by irrigation) and the water supplied by the rainfall event.

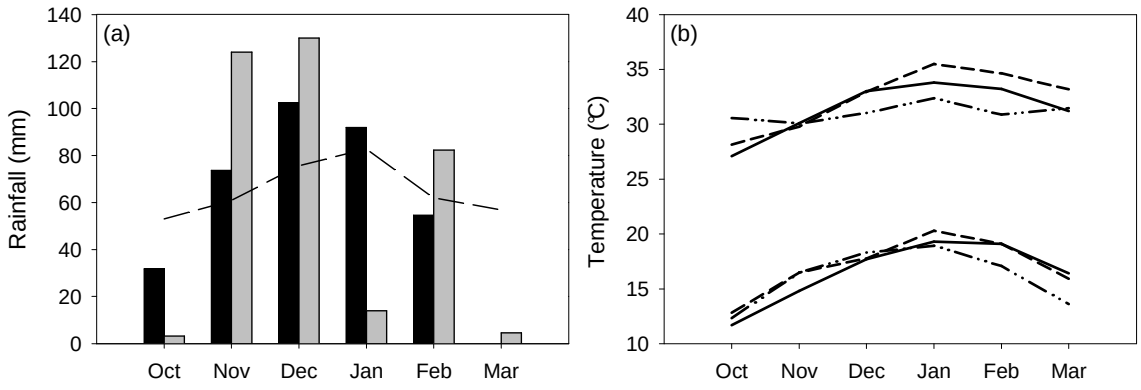


Figure 5.1. (a) Monthly rainfall (mm) in Experiment 2 ( ) and Experiment 3 ( ) and the long term average monthly rainfall ( ). Average maximum and minimum monthly air temperatures (°C) in Experiment 2( ), Experiment 3 ( ); and long term averages ( ).

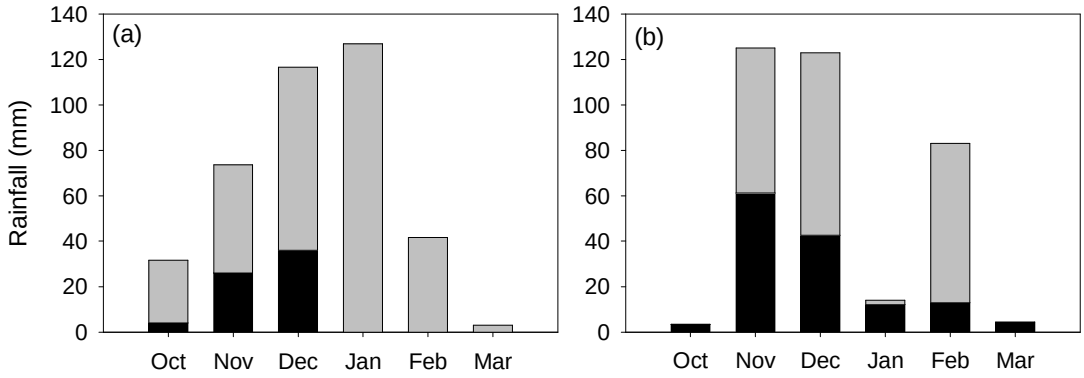


Figure 5.2. Effective ( ) and ineffective ( ) rainfall (in relation to the target amount of total water) in the control plots (Treatment 4) in Experiment 2 (a) and Experiment 3 (b). Values were calculated from locally adapted FAO 56 crop evapotranspiration equations.

Table 5.1. Comparative rainfall, temperature and evaporative demand and other environmental factors that affect the energy balance of a leaf and water stress conditions in Experiment 2 and Experiment 3.

	Experiment 2	Experiment 3
Rainfall		
Total rainfall (mm)	361	353
Effective rainfall in control plots (%)	18	39
Effective rainfall in control plots (mm)	65	138
Days with rain	53	27
Proportion of days with rain > 15 mm (%)	13	37
Air temperature (at 2 m height)		
Average maximum temperature (°C)	30.5	32.1
Average minimum temperature (°C)	15.9	16.7
High temperature stress days* (> 36 °C)	13	43
Low temperature stress days* (< 11 °C)	13	10
Solar irradiance		
Average daily (MJ m^{2-1})	23.6	25.0
Air wind speed		
Average daily (m s^{-1})	4.1	4.3
Air vapour pressure deficit (VPD)		
Average maximum VPD (kPa)	3.1	3.8
Average minimum VPD (kPa)	0.3	0.4
Evaporative demand		
Cumulative ET_C to 90% Open bolls (mm)	755	820
Average daily ET_O (mm)	5.2	5.7
Sowing – 1st Square	5.4	5.3
1st Square – 1st Flower	4.9	5.9
1st Flower – Cutout	5.4	6.4
Cutout – 60% Open bolls	4.9	5.6

* High and low temperature stress days are terms used by the Australian cotton industry to characterise extreme low and high temperature days where crop growth may be compromised (Hodges *et al.*, 1993; Bange and Milroy, 2004).

Air temperatures in Experiment 3 were consistently higher than those experienced in Experiment 2 (Figure 5.1b). Not only were average temperatures higher in Experiment 3, but a larger number of high temperatures stress days were experienced (Table 5.1). Higher ambient temperatures in Experiment 3 resulted in faster thermal time accumulation. Thus, the crop experienced a shorter season length of 145 d to 60% open bolls and 161 d to defoliation in Experiment 3, compared to 160 d and 178 d, respectively

in Experiment 2. Crop water requirements and evaporative demand also followed the same seasonal trends with Experiment 3 exhibiting a higher cumulative crop water demand and higher average daily ET from the development of the first square through to maturity (Table 5.1). Interestingly, during the crop establishment phase from planting to first square, water demand (ET_O) was lower in Experiment 3. Average daily irradiance, wind speed and vapour pressure deficit, three environmental factors affecting the energy balance of a leaf and hence T_c, were also on average slightly higher in Experiment 3 compared with Experiment 2 (Table 5.1). The combination of higher air temperatures, average solar irradiance, average wind speed and average evaporative demand resulted in an increased stress potential in Experiment 3 compared to Experiment 2.

5.3.2 Soil water and irrigation

Every effort was made to keep treatments at the desired per cent ET_C: however, untimely rainfall altered the deficit levels of all treatments (Figure 5.3 and Table 5.2). The extreme of this effect was observed in the Treatment 1 plots in Experiment 2. This treatment actually received 75% of the control treatment's total seasonal ET_C, 50% more than intended (Table 5.2). Despite the effect of rain, a significant range in irrigation treatments was achieved. Experiment 2's treatments ranged by 65% of ET_C from 75% to 140%. Despite this range, deficits were only observed in Treatments 1 and 2 (Figure 5.3), and these were only observed late in the season during boll maturation (132 DAS) in Treatment 1 and post crop maturity (162 DAS) in Treatment 2. Experiment 3's treatments ranged by 61% ET_C in Experiment 3 from 57% to 104%. Although a larger range of per cent daily ET_C was observed in Experiment 2, it is important to note that this experiment

received a higher total amount of irrigation and rainfall. This resulted in more pronounced water stress and soil water deficits in Experiment 3 compared with Experiment 2 (Figure 5.3).

Table 5.2. Irrigation treatment, rainfall, and the actual per cent of ET_C applied to each treatment in Experiment 2 and Experiment 3.

Treatment:	**Experiment 2 (ET_C= 755 mm)**	**Experiment 3 (ET_C= 820 mm)**
1 - Irrigation applied (mm)	187	25
- Stored soil water used (mm)	21	89
- Total water (rain, irrigation & stored) (mm)	569	467
- Desired ET_C	25	25
- Actual ET_C	75	57
2 - Irrigation applied (mm)	314	111
- Stored soil water used (mm)	18	85
- Total water (rain, irrigation & stored) (mm)	699	549
- Desired ET_C	50	50
- Actual ET_C	93	67
3 - Irrigation applied (mm)	460	205
- Stored soil water used* (mm)	-16	73
- Total water (rain, irrigation & stored) (mm)	804	631
- Desired ET_C	75	75
- Actual ET_C	107	77
4 - Irrigation applied (mm)	593	352
- Stored soil water used* (mm)	-22	49
- Total water (rain, irrigation & stored) (mm)	931	754
- Desired ET_C	100	100
- Actual ET_C	123	92
5 - Irrigation applied (mm)	726	470
- Stored soil water used* (mm)	-30	30
- Total water (rain, irrigation & stored) (mm)	1056	853
- Desired ET_C	125	125
- Actual ET_C	140	104

* Represents treatments where the net soil water at crop maturity > at planting.

Experiment 3 saw earlier soil water deficits, with Treatments 1, 2, 3 and 4 reaching a soil water deficit. Deficits occurred in Treatment 1 during flowering (90 DAS), Treatment 2 around cutout (96 DAS), Treatment 3 post cut out (108 DAS) and Treatment 4 post crop maturity (161 DAS). Water stress is a result of the combination of both the soil water deficit itself as well as the duration and timing of the deficit. Therefore, Treatment 2 in Experiment 2 and Treatment 4 in Experiment 3 did not experience significant soil water deficits as these deficits only occurred post crop maturity. Therefore, Treatment 1 of Experiment 2 and Treatment 1, 2, and 3 of Experiment 3 were the only irrigation treatments that were exposed to soil water deficits (Figure 5.3).

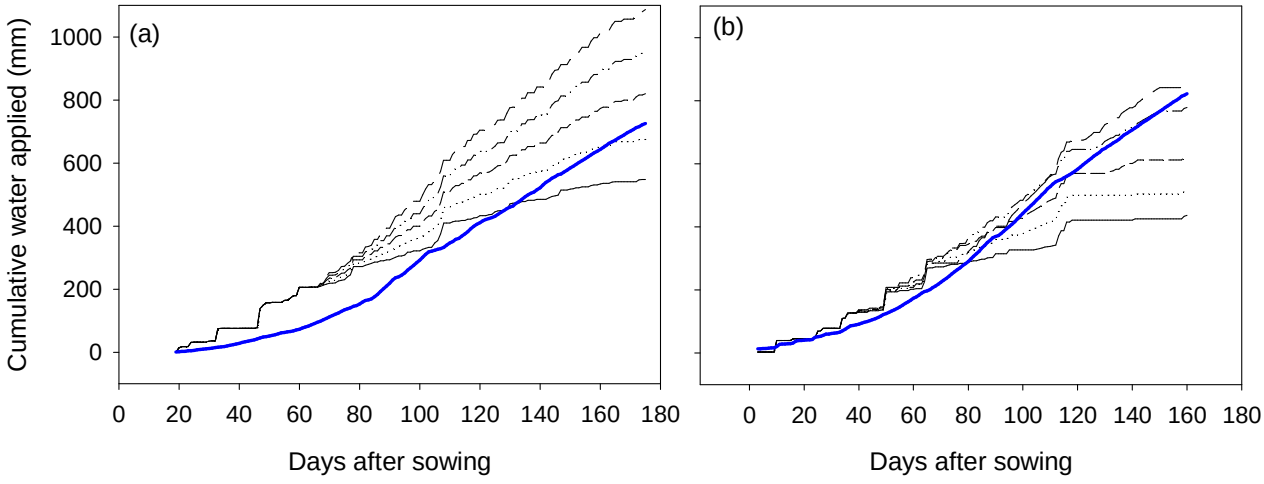


Figure 5.3. Cumulative water applied (rainfall + irrigation) (excluding initial furrow irrigation in both experiments) across all irrigation treatments in (a) Experiment 2 and (b) Experiment 3; ——— Treatment 1, ····· Treatment 2, – – – – Treatment 3, —·—·· Treatment 4, — — Treatment 5 and cumulative 100% ET_C.

Soil water curves measured using a Gopher^{TM} capacitance probe and calibrated with corresponding soil water measurements using a neutron moisture meter over the growing season are shown in Figure 5.4. Soil water curves in Experiment 2 are characterised by minor soil water depletion to 100 DAS, a significant increase in soil water between approximately 100 and 120 DAS, followed by minor soil water depletions for the remainder of the season (Figure 5.4a). This increase is due to high amounts of rainfall, and corresponds to the large amounts of rainfall resulting in excessive water application (Figure 5.2a). This ineffective rainfall (rainfall following irrigation application) resulted in minimal net soil water depletion over the growing season. Soil water depletions of 21 mm and 18 mm occurred in Treatments 1 and 2, whilst net gains of soil water of 16, 22 and 30 mm were recorded in Treatments 3, 4 and 5. The pattern of soil water depletion over Experiment 3 was different to that of Experiment 2. Although similar starting soil water of ~190 mm were observed, Experiment 3 was characterised by sustained soil water depletion over the entire season, with the exception of a significant rainfall event around 125 DAS (Figure 5.4b). Regardless of this rainfall event, net soil water depletions of 89, 85, 73, 49 and 30 mm were recorded across the season in Treatments 1, 2, 3, 4 and 5.

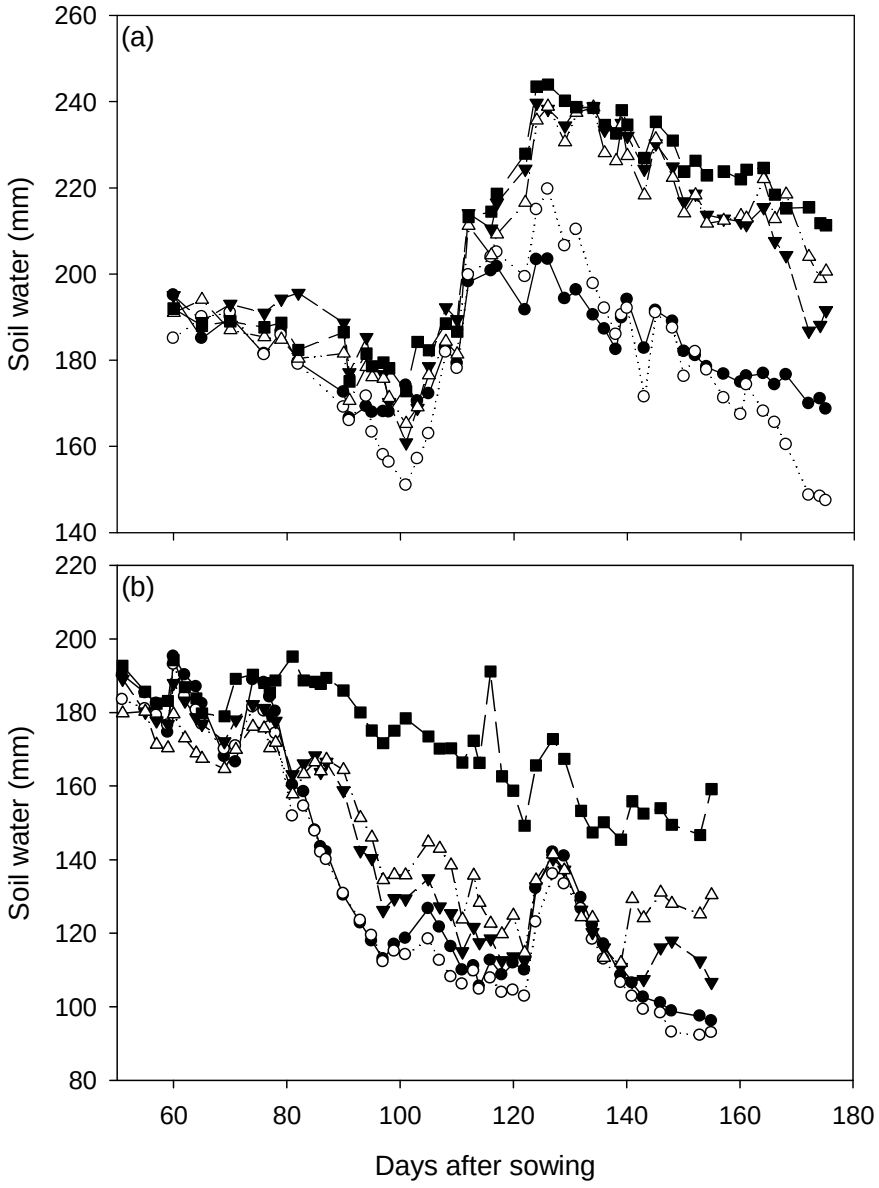


Figure 5.4. Total soil water (mm) throughout the season in (a) Experiment 2 and (b) Experiment 3; Treatment 1 (—●—), Treatment 2 (·····○·····), Treatment 3 (- —▼— -), Treatment 4 (···—△— ···) and Treatment 5 (· —■- -). Note that Experiment 2 used little stored water in comparison to Experiment 3, and the soils of Experiment 3 were consistently drier over the entire season. Dotted lines are included to assist comparison between treatments.

5.3.3 Crop development

In Experiment 2, treatment variation in crop yield was manifest in two statistically significant groups (P<0.001) (Figure 5.5a). The highest yielding treatments were Treatment 2 and Treatment 3, producing approximately 3400 kg ha^{-1}. These higher yielding treatments received a combined total of irrigation and rainfall very close to 100% of the cumulative seasonal water demand (actually receiving 93% and 107% of ET_C) (Table 5.2), without being subjected to excessive conditions. The lower yielding treatments were treatments 1, 4 and 5 which all yielded approximately 2850 kg ha^{-1}, despite receiving different water regimes. Treatments 4 and 5 received excessive water with 123% and 140% of ET_C applied to the respective treatments, while Treatment 1 actually received only 75% of ET_C, resulting in a deficit of water supply.

Treatment effects were more pronounced in Experiment 3, with the observation of four distinct treatment groups and an increased range of yields (P<0.001) (Figure 5.5b). Treatment 1 was the lowest yielding treatment producing approximately 900 kg ha^{-1}, followed by Treatment 2 and 3, yielding 1700 and 2600 kg ha^{-1}, respectively. The control and excessive irrigation treatments yields were the highest and statistically equivalent at 2850 kg ha^{-1}. In a similar fashion to Experiment 2, the highest yielding treatments in Experiment 3 received irrigation water closest to 100% of ET_C, where Treatment 5 received 104% of ET_C and Treatment 4 received 92% of ET_C. The lower yielding treatments received significant deficits in total seasonal ET_C replacement of 57% (Treatment 1), 67% (Treatment 2) and 77% (Treatment 3) of ET_C, resulting in yield reductions with corresponding moisture deficits (Figure 5.5b, Figure 5.6b and Table 5.2).

The yield trends across both Experiment 2 and 3, especially where peak yields were observed in treatments with applied water closest to 100% ET_C, validate the choice of *Kc* and calculation of ET_C.

Despite the similarities in yield, the growth, development and subsequent plant architecture of treatments in Experiment 2 were different (Table 5.3 and Figure 5.7a). Although treatments 1, 4 and 5 produced statistically similar yields, the plants in Treatment 1 produced significantly fewer nodes. The extra node production in Treatments 4 and 5 did not result in an increase in yield as the crop development was vegetative from the 15^{th} node. The average number of bolls per plant followed the same trend as yields, where an increase in water application did not necessarily produce extra bolls (Figure 5.7a). The highest yielding treatment (Treatment 3) had the highest number of bolls at maturity, and a high number of bolls on vegetative branches. The crop growth and plant architecture of Experiment 3 was different among treatments, and did not follow the same patterns as Experiment 2 (Figure 5.7b and Table 5.3). In contrast to Experiment 2, no treatment in Experiment 3 produced excessive vegetative or rank growth. Furthermore, as water application increased so too did the number of vegetative bolls and total number of bolls to reach maturity, enabling well-watered treatments to produce the highest yields.

Yield-water relations in Experiment 2 and Experiment 3 exhibited a polynomial function where yield rose to a peak at 822 mm of applied water, and then fell as water application increased (Figure 5.6a). This peak was calculated by finding the mid-point between the

roots (*x* intercepts) of the equation fitted to the data in the regression analysis. The pattern of yield-water relations across Experiment 2 and Experiment 3 was different. The regression of the two seasons could not be combined as the constant term varied between seasons (the intercepts of the regressions were different), although the linear and quadratic coefficients were not significantly different (*P*=0.007). Similar results were observed in the yield-ET_C regression, where yield rose to a peak at approximately 108% ET_C (Figure 5.6b). This peak was calculated by finding the mid-point between the roots (*x* intercepts) of the equation fitted to the data in the regression analysis. Again, the pattern of yield-ET_C relations was different across Experiment 2 and 3, as although the linear and quadratic terms of the regression were similar (*P*=0.012), the constant term varied across seasons (*P*=0.60). These regression models both accounted for 95 per cent of the variance, with an estimated standard error of yield of 170 kg lint ha^{-1}. The range of ET_C supplied which resulted in similar yields as the peak value was calculated by substituting the peak yield value ± the standard error of observed yield (170 kg lint ha^{-1}). These yield values were substituted into the fitted equation, which was then solved for *x*, providing an ET_C range producing similar yield to that of the peak. This ET_C range was calculated to be 97 to 118% ET_C.

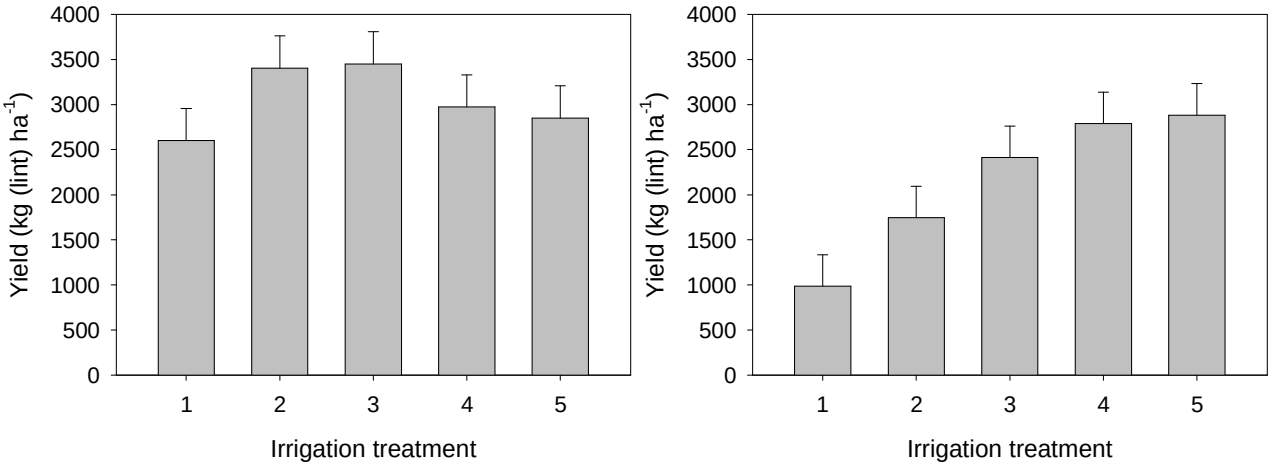


Figure 5.5. Machine picked lint yield (kg ha^{-1}) for Experiment 2 (a) and Experiment 3. Vertical bars represent l.s.d.

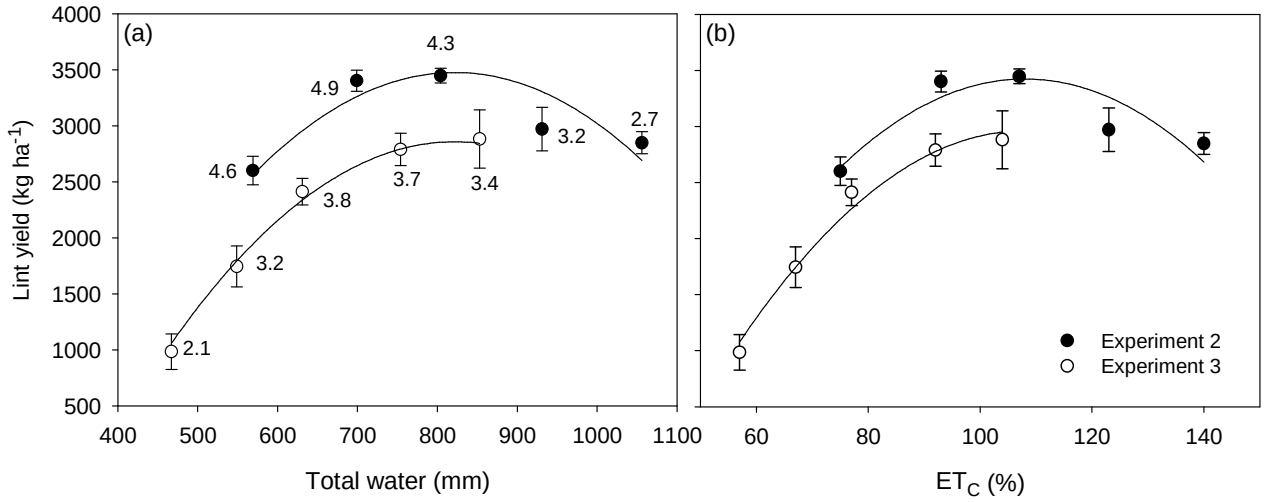


Figure 5.6. (a) Yield-water relations regression in Experiment 2 (y = -0.0143x^2 + 23.5x -6179) and Experiment 3 (y = -0.0143x^2 + 23.5x -6797) (regression R^2= 0.9). Numbers beside each data point show the water-use efficiency (WUE) in kg mm^{-1} ha^{-1} for each treatment. Total water applied includes rainfall, surface drip irrigation and furrow irrigation events. (b) Yield-ET_C relations regression in Experiment 2 (y = -0.7239x^2 + 156.4x -5023) and Experiment 3 (y = -0.7239x^2 + 156.4x -5485) (regression $R2$= 0.9). Vertical bars represent standard error of mean.

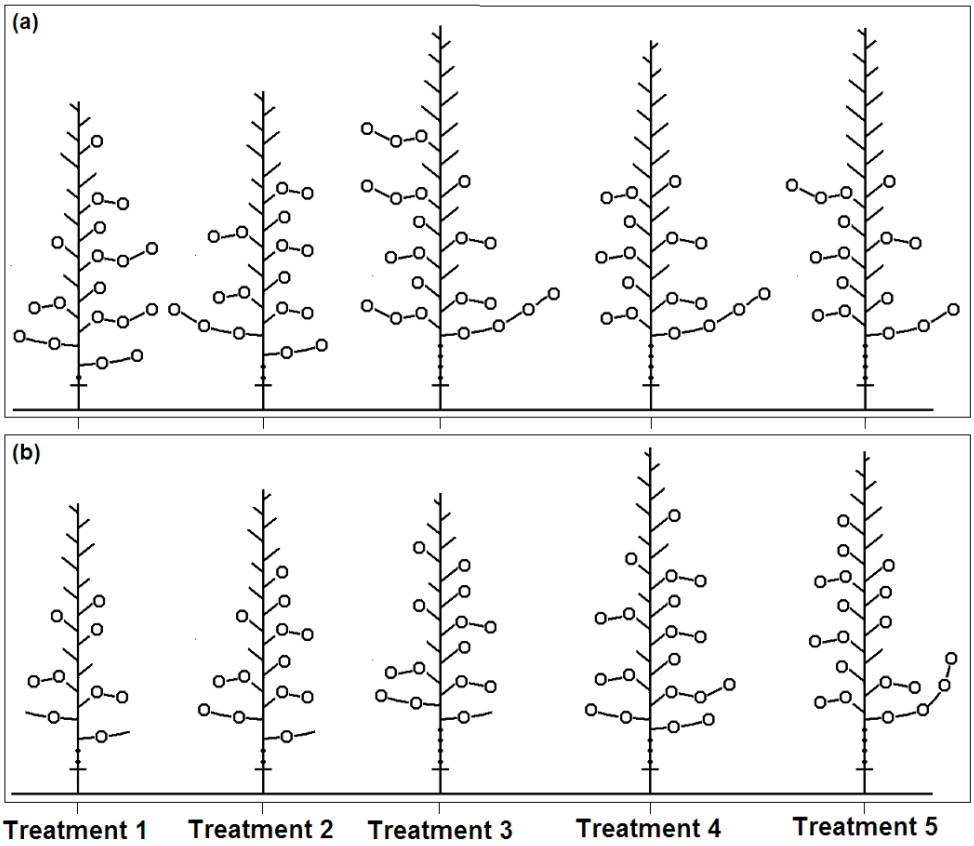


Figure 5.7. Schematic diagram of plant architecture showing the average number of nodes, bolls and boll position for all treatments in (a) Experiment 2 and, (b) Experiment 3.

Table 5.3. Average number and position of bolls and number of nodes, vegetative bolls and branches in all treatments in Experiment 2 and Experiment 3. * represents *P*<0.05, ** represents *P*<0.001, ns represents no significant difference

		Treatment					Significance	l.s.d.
		1	**2**	**3**	**4**	**5**		
Experiment 2								
Nodes		19	20	25	24	25	**	1.6
Vegetative bolls		4	4	3	3	2	ns	2.0
Vegetative branches		1	1	1	1	1	*	0.5
Bolls - Position 1	1-4	3	3	3	3	3	ns	0.5
	5-8	3	3	3	3	3	**	0.4
	9-12	1	1	2	2	2	*	0.5
	13-16+	1	0	1	0	0	*	0.3
Position 2	1-4	2	2	2	2	1	*	0.5
	5-8	1	1	2	2	2	ns	0.6
	9-12	1	1	1	1	1	ns	0.4
	13-16+	0	0	1	0	0	*	0.2
Position 3+	1-4	1	0	1	0	0	ns	0.4
	5-8	1	0	1	0	0	ns	0.3
	9-12	0	0	1	0	1	**	0.3
	13-16+	0	0	1	0	0	**	0.4
Experiment 3								
Nodes		18	19	20	22	23	**	0.9
Vegetative bolls		2	3	3	4	4	*	1.4
Vegetative branches		2	2	2	2	1	*	0.4
Bolls - Position 1	1-4	2	3	3	3	3	ns	0.4
	5-8	3	3	3	3	4	**	0.4
	9-12	0	1	2	2	3	**	0.4
	13-16+	0	0	0	1	1	**	0.2
Position 2	1-4	2	2	2	2	2	ns	0.5
	5-8	0	1	1	2	1	**	0.4
	9-12	0	0	0	1	1	**	0.2
	13-16+	0	0	0	0	0	*	0.1
Position 3+	1-4	0	0	0	1	0	*	0.3
	5-8	0	0	0	0	0	*	0.2
	9-12	0	0	0	0	0	*	0.1
	13-16+	0	0	0	0	0	n/a	n/a

Separation of plant height and the number of nodes across irrigation treatments was observed in both Experiment 2 and Experiment 3 (Figure 5.8). Water stress inhibited plant growth through both decreased plant height and node production. Adequate and excessive water supply resulted in increased plant height and number of nodes.

Cutout is the physiological point when a plant ceases to produce nodes and the competition for assimilates exceeds supply, resulting in the cessation of both vegetative growth and the production of reproductive sites that influence cotton lint yield (Hearn and Constable, 1984). Cutout occurred earlier in the drier irrigation treatments. In Experiment 2, cutout occurred in the Treatment 1 at 99 DAS, followed by 104, 107, 116 and 120 DAS in Treatments 2, 3, 4 and 5. Cutout in Experiment 3 followed the same trend with water application as Experiment 2; however, it occurred earlier and over a shorter window of time in Experiment 3. Cutout occurred in Treatment 1 at 94 DAS, followed by 95, 97, 99 and 100 DAS in Treatments 2, 3, 4 and 5. As cotton is an indeterminate crop, fruit loss due to biotic and abiotic stress (such as water stress) may not result in lint yield losses as compensation can occur, although delays in crop maturity may be observed as the plant needs to continue vegetative growth to produce new fruiting sites. This is significant as, once cutout occurs, compensation can usually not occur and yield reductions due to a given stress permanently affect crop lint yield.

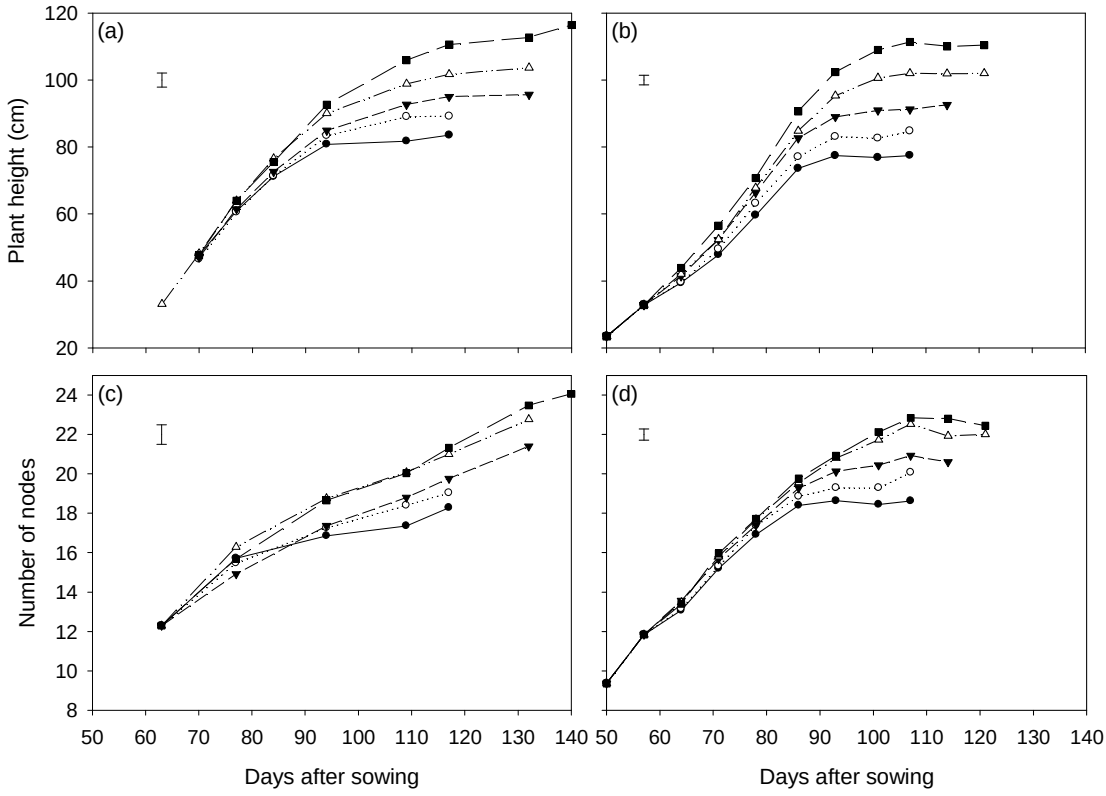


Figure 5.8. Plant height for (a) Experiment 2 and, (b) Experiment 3 and number of nodes for (c) Experiment 2 and, (d) Experiment 3 in Treatment 1 (—●—), Treatment 2 (· · · · ○ · · · ·), Treatment 3 (- —▼— -), Treatment 4 (· · —△— · ·) and, Treatment 5 (· —■— -). Vertical bar represents l.s.d. Dotted lines are included to assist comparison between treatments.

5.3.4 Above ground biomass accumulation and partitioning

Differences in biomass accumulation and numbers of fruit were observed in both Experiment 2 (Figure 5.9) and Experiment 3 (Figure 5.10). In Experiment 2, broad treatment differences in total dry matter were not evident until the end of the season (173 DAS) (Figure 5.11a). Total dry matter in Treatment 5 increased by 55% in the 35 d following the 138 DAS biomass harvest, compared with rises of ~ 22% in Treatments 3 and 4. During this period, total dry matter accumulation stabilised in Treatments 1 and 2, and was predominantly due to leaf senescence and plant maturation. Increases in the treatments 3, 4 and 5 were due to boll filling, and the production of new vegetative

structures (stem and leaves), especially in Treatment 5 where an increase in stem dry matter of 55% and leaf dry matter of 15% was observed (see Appendix 2). This sustained increase in vegetative growth observed in Treatments 5 suggests these treatments had access to an excessive water supply, leading to the formation of rank vegetative growth.

Total dry matter accumulation in Experiment 3 followed the same trends as Experiment 2. The highest dry matter production was observed in Treatment 5 and reductions in dry matter were observed with a corresponding increase in water stress (Figure 5.11b). However, contrary to the growth patterns of Experiment 2, the treatments receiving more irrigation did not produce an excessive amount of rank growth at the end of the season (Figure 5.7b). Peak leaf and stem dry matter accumulation occurred earlier in Experiment 2 than Experiment 3, suggesting an earlier reduction in vegetative growth across all treatments (see Appendix 2). This pattern of vegetative biomass accumulation (leaf and stem) suggests that when comparing Experiment 2 and Experiment 3, the crop grown in Experiment 2 was less stressed and grew over a longer season (Table 5.1), which lead to the formation of rank growth in treatments with excess water supply.

Figure 5.9. Examples of variation in above ground biomass accumulation across treatments in the 2007/08 season during (a) peak water consumption and vegetative growth at 112 DAS; and (b) the pre-harvest period, post-defoliation at 206 DAS. Treatments are left to right: 1, 2, 3, 4 and 5. Measuring stick represents 1 m.

Figure 5.10. Examples of variation in above ground biomass accumulation across treatments in the 2008/09 season during (a) peak water consumption and vegetative growth at 132 DAS; and (b) the pre-harvest period, post-defoliation at 196 DAS. Treatments are left to right: 1, 2, 3, 4 and 5. Measuring stick represents 1 m.

Experiment 3 was a later crop where, in comparison to Experiment 2, cutout was delayed. All treatments in Experiment 3 produced late season re-growth, where excess water conditions (Figure 5.3), adequate ambient temperatures and an excess supply of carbohydrates to mature bolls, allowed the plants to continue to grow. As late season re-growth occurred in all treatments prior to a delayed harvest, altering the partitioning of the crop by favouring vegetative biomass accumulation, the late season re-growth was excluded from all treatments on the final biomass collection date (162 DAS). The late season re-growth was excluded from the final biomass collection date as this re-growth occurred after crop maturation, and in a commercial setting this re-growth would not have occurred as the crop would have been harvested.

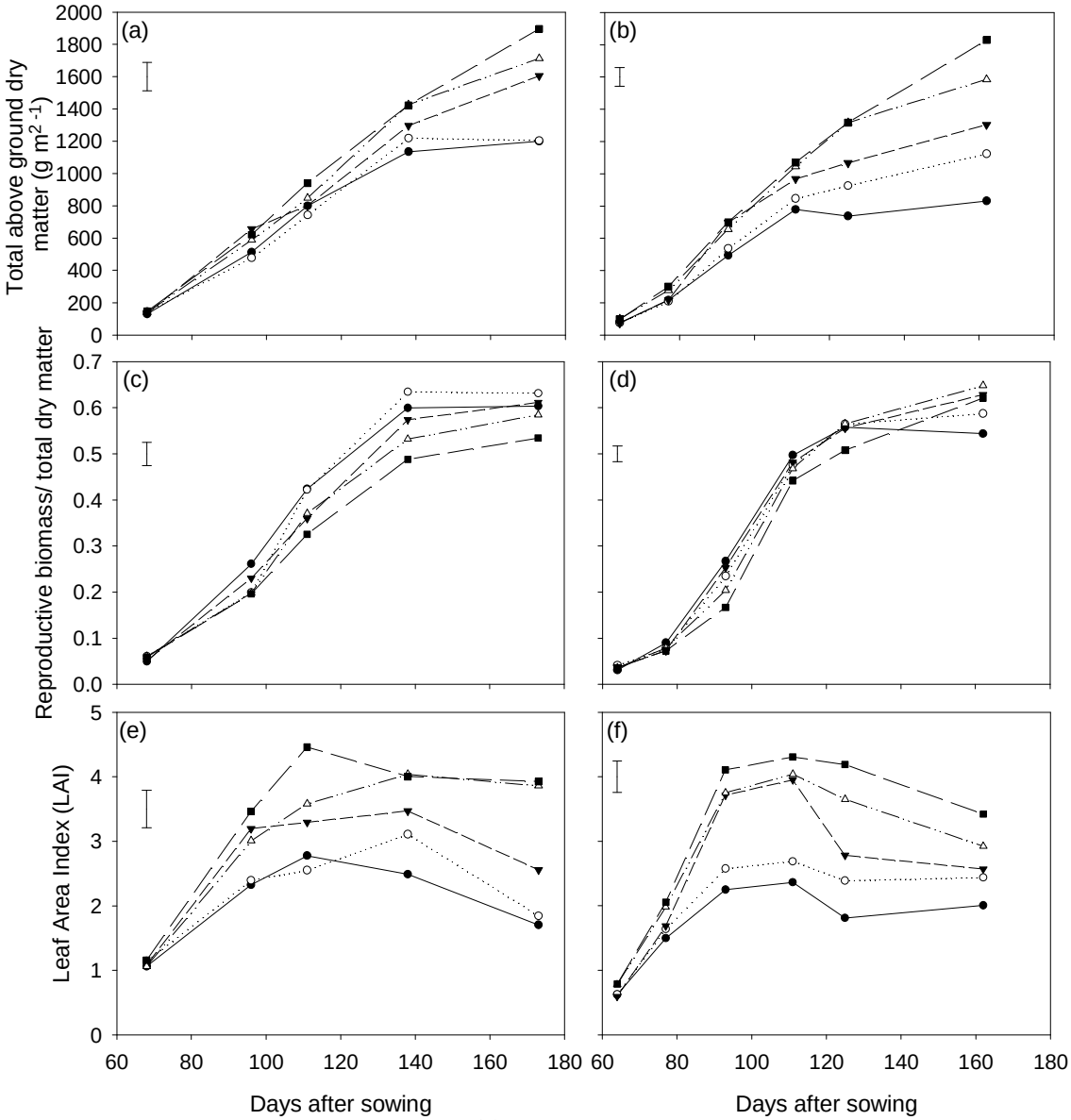


Figure 5.11. Total dry matter accumulation (g m^{2-1}) in (a) Experiment 2 and (b) Experiment 3; The ratio of reproductive to vegetative biomass in (c) Experiment 2 and (d) Experiment 3; and leaf area index (LAI) in (e) Experiment 2 and (f) Experiment 3 in all treatments; Treatment 1 (—●—),Treatment 2 (·····○·····),Treatment 3 (- —▼— -),Treatment 4 (···—△—···) and Treatment 5 (· —■- -). Vertical bar represents l.s.d. Dotted lines are included to assist comparison between treatments.

Differences in the ratio of vegetative to reproductive biomass were observed in Experiment 2 (P= 0.004) and Experiment 3 (P<0.001), after 90 DAS. In Experiment 2, drier treatments generally maintained a higher ratio of reproductive growth than the

wetter treatments (Figure 5.11c). This is expected, as it is generally considered that drought stress treatments mature earlier than treatments with more luxurious water conditions. However, at the final biomass harvest taken at ~ 65% open bolls (173 DAS), all treatments, except Treatment 5, showed a similar ratio of reproductive to vegetative biomass (60% reproductive dry matter). At this time, Treatment 5 displayed a lower ratio of vegetative to reproductive dry matter (55% reproductive dry matter), due to its excessive vegetative, rank growth pattern. This pattern of reproductive and vegetative biomass production parallel the lint yields in Experiment 2 (Figure 5.5a).

Like lint yields, the ratio of reproductive to vegetative growth was different in Experiment 3 when compared to Experiment 2. Initially (93 DAS), higher percentages of reproductive dry matter were observed in Treatments 1, 2 and 3 (drier treatments) than Treatments 4 and 5 (well-watered treatments) (Figure 5.11d). However, by 111 DAS all treatments except Treatment 5 (the slowest maturing, well-watered treatment) exhibited similar ratios of reproductive to vegetative dry matter (50% reproductive dry matter). At the final biomass harvest at 65% open bolls, the treatments that received more irrigation water (Treatments 3, 4 and 5) displayed higher percentages of reproductive dry matter (63% reproductive dry matter). At this time, incrementally lower percentages of reproductive dry matter were observed in the more water stressed treatments, with 59% and 54% reproductive growth in Treatments 2 and 1, respectively. In a similar fashion to Experiment 2, the ratio of the reproductive to vegetative dry matter in Experiment 3 followed the same trends as lint yield (Figure 5.5b).

The LAI is an important factor in crop development as it reflects leaf expansion rates, and can be related to plant growth and crop vigour. In addition, it is especially important to discuss LAI in the context of canopy sensors, such as the IRTs used in this study. This is because measurement errors, such as the effects of background surface soil temperatures within the IRT field of view, can be introduced at low LAIs before canopy closure. Peak LAI in Experiment 2 occurred between 111 and 138 DAS, where the driest (Treatment 1) and wettest (Treatment 5) treatments tended to peak earlier (Figure 5.11c). Peak LAI occurred in Experiment 3 earlier in the season with peaks in LAI observed at 93 DAS, which were sustained until 111 DAS (Figure 5.11d). As a result, the rate of LAI increase in Experiment 3 was much faster than observed in Experiment 2.

Throughout the season, biomass accumulation and water relations in Experiment 2 and Experiment 3 exhibited a linear function. Total biomass accumulation increased with an increase in water application (Figure 5.12). The regressions of total dry matter-water relations across Experiment 2 and Experiment 3 were not significantly different ($P<0.001$) and were combined. The regression model accounted for 91% of the variance, with an estimated standard error of biomass accumulation of 151 g m^{-2}.

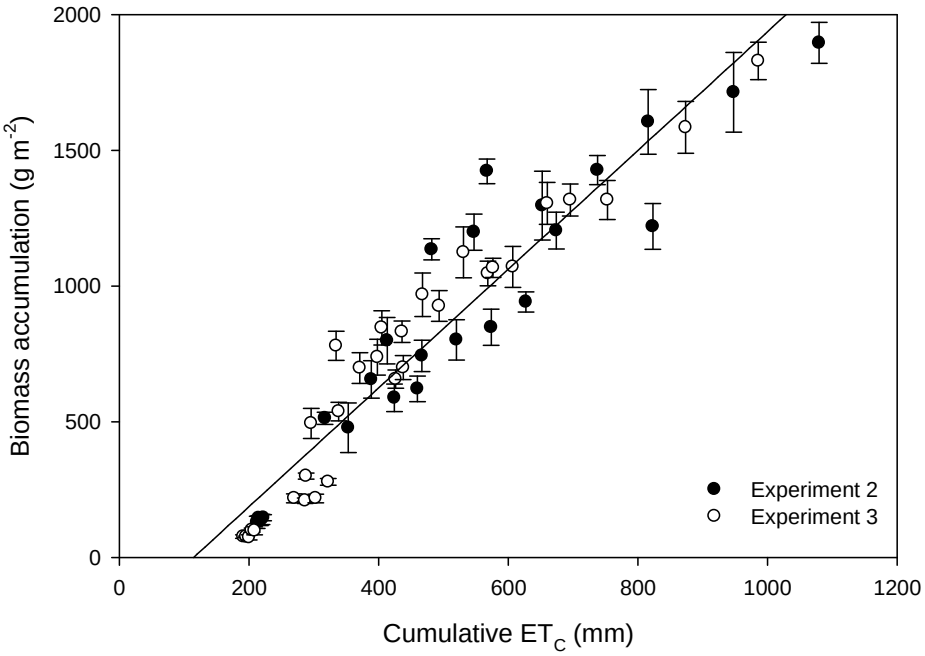


Figure 5.12. Regression of above ground biomass and water requirement throughout the season from squaring to maturity in Experiment 2 and Experiment 3 ($y = 2.1875x - 250.6$; R^2=0.91). Vertical bars represent standard error.

5.3.5 Canopy temperatures (T_c)

Average T_c in Experiment 2 and Experiment 3 reflected the trend where higher T_c for longer durations correlated with increased water stress (Figure 5.15 and Figure 5.16). Irrigation treatments that received less irrigation water consistently resulted in elevated canopy temperature and longer durations of canopy temperatures above 28 °C, compared with treatments which received higher water supply (Table 5.4). Like Wanjura *et al.* (1992), treatment differences were only observed when irradiance levels were > 300 W m^{-2} (Table 5.4). Therefore, average T_c from this point refers to T_c measured when irradiance levels > 300 W m^{-2}. The T_c in all treatments in Experiment 2 was lower than those observed in Experiment 3. This trend is supported by the measured soil water status (where Experiment 3 is characterised by consistently drier soils; see Figure 5.4),

evaporative demand (where a higher cumulative crop water demand was observed in Experiment 3) and the consistently lower rain and irrigation application in Experiment 3 compared to Experiment 2 (Table 5.1).

Table 5.4. Average canopy temperature (T_c), average T_c when short-wave irradiance (R_g) < 300 W m^{-2} and > 300 W m^{-2}, canopy temperature depression (CTD) when R_g > 300 W m^{-2} and ambient air temperature > 28 °C, and duration of time that canopy temperatures exceed 28 °C (%) between 993 and 1971 cumulative degrees days in Experiment 2 and 983 and 1981 cumulative degree days in Experiment 3. The same superscript letter within a column represents values that are not statistically different at the *P*=0.05 level.

Experiment 2					
Treat	Average T_c (°C)	Average T_c (°C) (R_g < 300 W m^{-2})	Average T_c (°C) (R_g > 300 W m^{-2})	CTD (R_g > 300 W m^{-2}, T_a > 28 °C)	Time T_c > 28 °C (%)
1	23.1 ^{a}	20.5 ^{a}	27.8 ^{a}	-1.1 ^{ab}	21.1 ^{a}
2	22.5 ^{b}	20.5 ^{a}	26.5 ^{b}	-2.4 ^{c}	16.0 ^{b}
3	22.1 ^{b}	20.4 ^{a}	25.6 ^{c}	-3.4 ^{d}	11.4 ^{c}
4	22.0 ^{bc}	20.4 ^{a}	25.4 ^{c}	-3.8 ^{e}	9.5 ^{c}
5	21.9 ^{c}	20.3 ^{a}	25.2 ^{c}	-4.3 ^{f}	8.2 ^{c}
Experiment 3					
Treat	Average T_c (°C)	Average T_c (°C) (R_g < 300 W m^{-2})	Average T_c (°C) (R_g > 300 W m^{-2})	CTD (R_g > 300 W m^{-2}, T_a > 28 °C)	Time T_c > 28 °C (%)
1	25.6 ^{a}	22.3 ^{b}	31.4 ^{d}	-0.6 ^{a}	34.3 ^{d}
2	25.5 ^{a}	22.3 ^{b}	31.1 ^{d}	-0.6 ^{a}	34.4 ^{d}
3	24.9 ^{b}	22.2 ^{b}	29.6 ^{e}	-1.9 ^{bc}	30.4 ^{de}
4	24.5 ^{c}	21.9 ^{b}	29.0 ^{ef}	-2.9 ^{cd}	27.6 ^{e}
5	24.2 ^{d}	21.9 ^{b}	28.3 ^{g}	-3.2 ^{d}	24.8 ^{f}

Canopy temperature depression (CTD) shows the effect of transpirational cooling on canopy temperatures. Average CTD in Experiment 2 and Experiment 3 shown in Table 5.4, where treatments with increasing soil water became more negative, indicating a greater capacity for canopy cooling by transpiration. The CTD was calculated for periods when short-wave irradiance (R_g) > 300 W m^{-2} and T_a > 28 °C. These environmental conditions were first proposed by Wanjura *et al*. (1992), and are intended to show that

differences in canopy temperature, due to limitations in soil water availability, can be attributed to transpirational cooling differences when environmental conditions (solar energy input and T_a) are sufficient to raise $T_c > 28$ °C.

Average seasonal T_c and the per cent ET_C water applied exhibited a curvilinear relationship where average T_c decreased as water application increased (Figure 5.13). The average T_c and per cent ET_C applied data could not be combined into one regression model this model was significantly improved when Experiment 2 and Experiment 3 were allowed to have different intercepts (P<0.001). However, no improvement to the regression was achieved when the two experiments were given different slopes (P=0.869). The regression model accounted for 99 per cent of the variance, with an estimated standard error of average T_c of 0.2 °C.

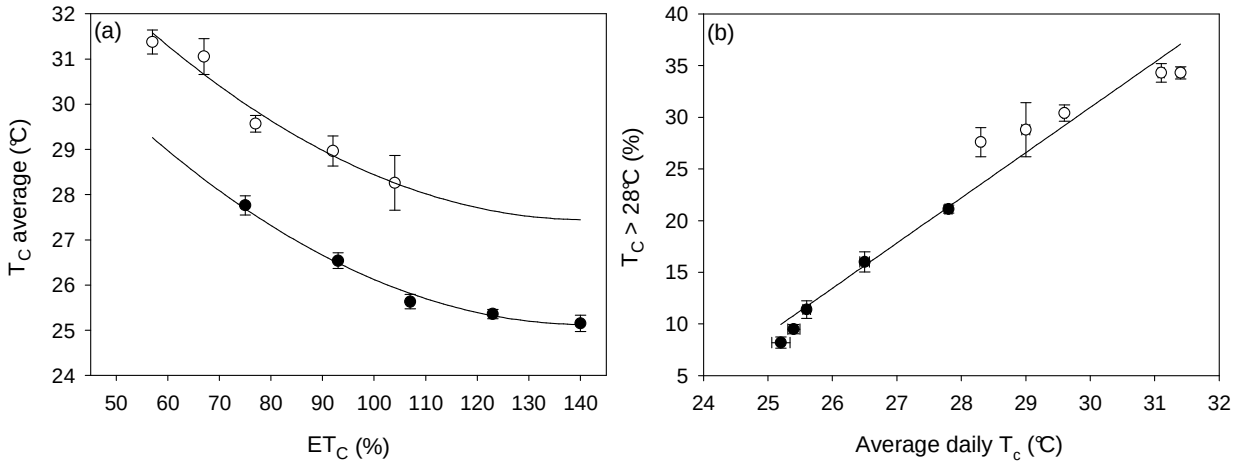


Figure 5.13. (a) Average seasonal T_c and seasonal ET_C (%) applied regression in Experiment 2 (●) (y = $0.00058x^2$ -0.1641x + 36.73) and Experiment 3 (○) (y = $0.00058x^2$ -0.1641x + 39.05). Vertical bars represent standard error of canopy temperatures. (b) Average canopy temperature and time canopy temperature exceeds 28 °C (%) regression in Experiment 2 (●) and Experiment 3 (○) (y = 4.374x - 100.28; R^2 = 0.96).

The amount of time that T_c > 28 °C followed the same pattern as T_c, where increased soil water deficits resulted in an increase in time period (Table 5.4). Average daily T_c was positively related to the amount of time T_c > 28 °C (P<0.001) (Figure 5.13b). Average T_c were related to final cotton lint yield (P<0.001) (Figure 5.14), where lint yields peaked at average T_c 26.4ºC. The range in T_c that produced lint yields similar to the peak of 3196 kg (lint) ha^{-1} was 24.8 to 28.1 ºC. The T_c outside of this temperature range experienced lint yield penalties. This relationship is pivotal in the strength of the BIOTIC irrigation system that schedules irrigations based on the concept of an optimal canopy temperature of a crop.

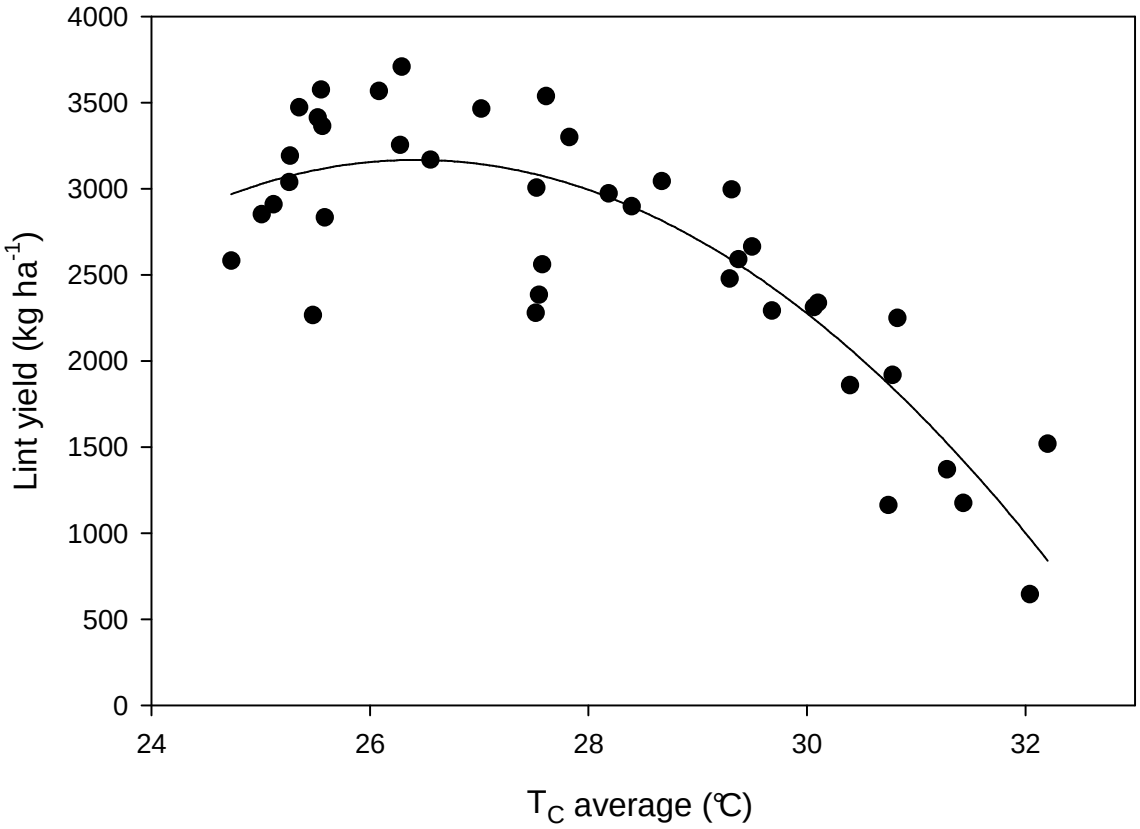


Figure 5.14. Average daily canopy temperature and lint yield regression (y = -69.6x^2 + 3680x -45448, R^2 = 0.75) (P<0.001).

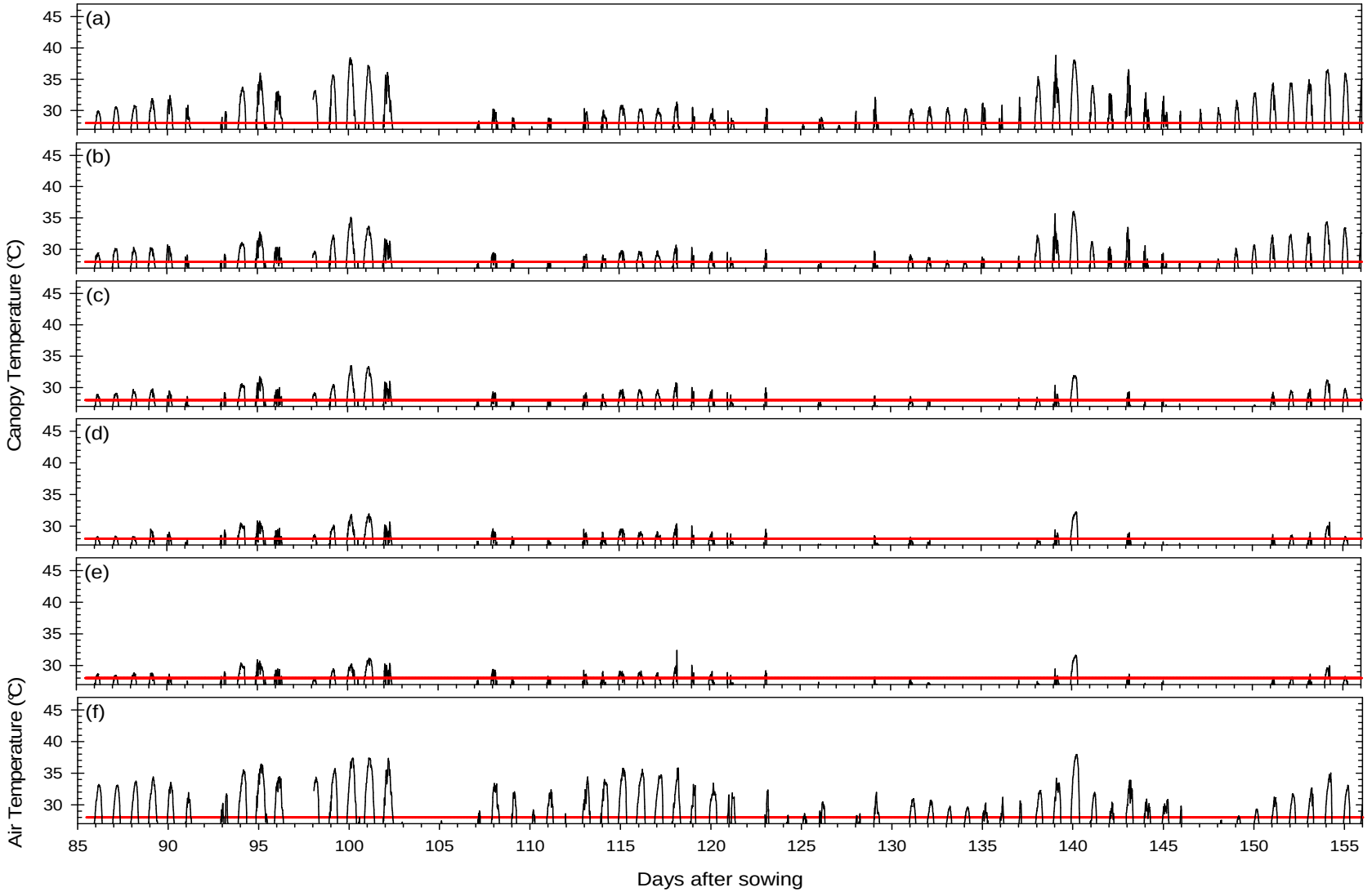


Figure 5.15. Average canopy temperatures exceeding 27 °C in Experiment 2 experienced in (a) Treatment 1, (b) Treatment 2, (c) Treatment 3, (d) Treatment 4, (e) Treatment 5 irrigation treatments, and (f) air temperature. The red line at 28 °C represents the optimal canopy temperature for cotton, and only canopy temperature in excess of 27 °C are shown.

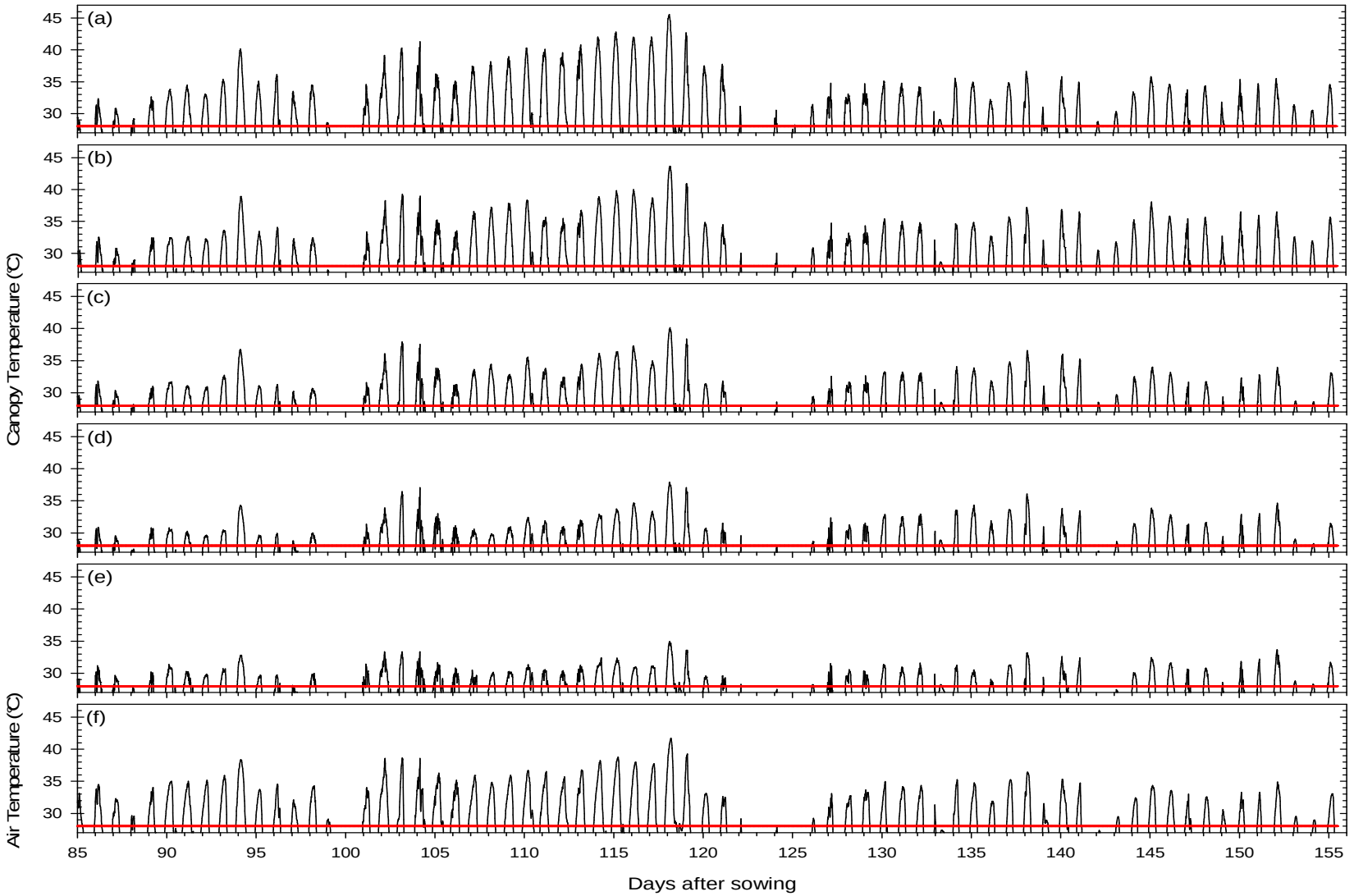


Figure 5.16. Average canopy temperatures exceeding 27 °C in Experiment 3 experienced in (a) Treatment 1, (b) Treatment 2, (c) Treatment 3, (d) Treatment 4, (e) Treatment 5 irrigation treatments, and (f) air temperature. The red line at 28 °C represents the optimal canopy temperature for cotton, and only canopy temperature in excess of 27 °C are shown.

5.4 Discussion

The growing season at ACRI during Experiment 2 (2007/08) was close to ideal for cotton production. The crop was only exposed to 13 high temperature stress days (> 36ºC), compared with a long term average of 44 d at the start of the season (BOM, 2009). Although the season was characterised by lower than average T_a, the number of low temperature stress days was low (13) compared with the regional average of 30 d (Bange and Milroy, 2004). An increase in season length (17 d), aided by an earlier planting date, compensated for the below-average temperatures ensuring sufficient degree-day accumulation for crop maturity. Insect pressure throughout Experiment 2 was low, with only one event where green vegetable bugs (*Nezara viridula*) and aphids (*Aphis sp.* and *Myzus persicae*) were above the threshold (Farrell, 2008), resulting in a single spray for these sucking pests. This resulted in lint yields of 3400 kg ha^{-1} (15 bales ha^{-1}), 1.9 times more than the average Australian cotton yield (1800 kg ha^{-1}) (CRDC, 2009).

Experiment 3 (2008/09) had a higher degree of stress imposed in comparison to Experiment 2, with higher average T_a, VPD, and evaporative demand (Table 5.1). Seasonal T_a remained above average with 43 high temperature stress days that more accurately reflected the regional average of 44 d (BOM, 2009) than Experiment 2. Hot and dry weather conditions were experienced in late January and early February, with 18 consecutive days > 36 °C, where temperatures in the last five of these days were > 40 °C. Insect pressure was low to moderate during Experiment 3. Green vegetable bugs, spider mites (*Tetranychus sp.*) and whitefly (*Trialeurodes vaporiorum* and *Bemisia tabaci*) were above threshold levels from late February 2009 (Farrell, 2008), resulting in a

diafenthiuron spray for these pests. Although green vegetable bugs were controlled, spider mite and whitefly pressure remained above threshold levels from late February for the remainder of the season. This insect pressure is significant, as it can reduce photosynthates, increasing competition for assimilates between maturing bolls and contaminate lint with honey dew (Farrell, 2008). Despite this insect pressure, lint yield reductions as a result of insect pressure were not expected as this pressure was experienced late in the season, however some lint quality differences may have occurred (data not shown). The combined effect of higher ambient temperatures, higher average evaporative demand, vapour pressure deficit, wind speed and irradiance, increased insect pressure and reduced in-crop rainfall in Experiment 3, resulted in a higher stress potential in Experiment 3 than in Experiment 2. Subsequently, peak lint yields in Experiment 3 were 2840 kg lint ha^{-1} (12.5 bales ha^{-1}). Despite this increased stress potential, lint yields also remained 1.4 times above the average Australian cotton yield in 2008/09 (1980 kg ha^{-1}) (ABS, 2009). The increased stress potential experienced in Experiment 3 as compared to Experiment 2 was not only manifested in crop yields. Crop growth patterns, biomass accumulation and T_c were also influenced by the higher stress potential in Experiment 3. As a result when compared to Experiment 2, Experiment 3 was characterised by smaller, lower yielding cotton crops with higher average T_c.

Cotton growth and lint yield in Experiment 2 and Experiment 3 were influenced markedly by water supply. Yield-water relations exhibited a second order polynomial function where yield rose to a peak at 822 mm of applied water (108% ET_C). This curvilinear function of cotton yield-water supply relations was also observed by

Tennakoon and Milroy (2003). They showed that lint yields of Australian cotton (grown predominantly on grey cracking clays of Northern New South Wales and Southern Queensland) increased to an ET_C of ~ 700 mm, and beyond this additional water consumption did not increase lint yield. Peak cotton yields at ~ 700 mm ET have been observed in numerous studies conducted in various production settings including California (Grimes *et al.*, 1969b; DeTar, 2008), Texas (Wanjura *et al.*, 2002) and Spain (Orgaz *et al.*, 1992). This yield-water response where peak lint yield at 108% ET_C, were evident in both Experiment 2 and Experiment 3 (Figure 5.6b). Similar lint yields were observed over the range of 97 to 118% applied ET_C. This range is relatively narrow, representing 158 mm of water in Experiment 2, and 172 mm of water in Experiment 3. This relatively narrow range highlights the complexity of the response of cotton to both sub and supra-optimal water conditions. Although the optimum water application remained the same over the two experiments, yield-water supply relations were different (Figure 5.6). The difference between the two experiments can be attributed to the influence of the different seasons and associated changes in stress potential, where higher ambient air temperatures, vapour pressure deficits (VPD) and irradiance were experienced in Experiment 3 (Table 5.1). This response is important as it outlines the need to monitor weather conditions and their associated influences on the stress potential and water stress physiology of a crop. Furthermore, the integration of this data with real-time plant based stress detection tools such as BIOTIC may provide a decision support tool for irrigation scheduling.

Vegetative growth in the cotton plant continues until three-quarters of plant available soil water is used (Hearn, 1994). Therefore, when other factors, such as decreasing photoperiod and differential day-night temperatures (Hearn, 1994), are held constant, a plant with access to more soil water usually has a longer growing season. This ensures the production of a larger plant with more biomass. Parallel with previous research (Grimes *et al.*, 1969a; Grimes and El-Zik, 1990), biomass production in Experiment 2 and Experiment 3 was linearly correlated to water supply, and appears to have followed a single season-independent, water dependent trend (Figure 5.12), in contrast to lint yield (Figure 5.6a). Although an increase in water supply increases biomass production, it is generally accepted that an excessive supply in water will eventually lead to reduced biomass production. Although this was not observed in Experiments 2 and 3, more excessive water applications > 1000 mm may have resulted in a reduction of biomass accumulation due to excessive water supply and associated waterlogging and disease susceptibility.

In addition to the production of more biomass, a plant with access to more soil water will produce more main stem nodes, resulting in more fruiting positions and thus a greater lint yield potential (DeTar, 2008). This growth pattern was observed in Experiment 3 and Treatments 1, 2 and 3 of Experiment 2 (Figure 5.7). However, Treatments 4 and 5 of Experiment 2 did not follow this trend as these treatments produced larger plants that yielded less lint than some of the treatments with smaller plants (Figure 5.7). Therefore, correlations between above ground biomass and lint yield could not be made. This is because cotton has an indeterminate growth pattern and thus has no clearly-defined

seasonal cycle to complete, hence the water relations of the cotton plant are complex, and can have a large effect on lint yield (Hearn, 1979).

The production of rank vegetative growth in Treatments 4 and 5 of Experiment 2 was the predominant cause of lint yield reductions in these well-watered treatments. This is because although a larger plant has a greater lint yield potential, if a plant has access to additional soil water conditions the ratio between vegetative and fruiting characteristics can become unbalanced (Grimes *et al.*, 1969a; Mutsaers, 1984) and maturity can be delayed (Wanjura *et al.*, 1992). This unbalanced growth pattern is an evolutionary adaptive response to water regime, where delays in the setting of fruit while rank vegetative growth continues are observed under luxurious water conditions. This results in a larger plant with a larger source of carbohydrates for use in boll production when vegetative growth ceases (after three-quarters of soil water has been used), increasing reproductive flexibility in the face of unpredictable water supply (Hearn, 1994). Rank growth is most pronounced in cotton when adequate soil water conditions occur in association with excessive rain, cloudy weather, early insect damage and dense plant stands (Gibb *et al.*, 2004). This results in lint yield reductions caused by heavy boll shedding, predominantly in the lower crop strata, and excessive vegetative growth (Hearn, 1975). This explains why the yield-water relations of cotton follow a polynomial trend, where excessive water application in Experiment 2 resulted in reduced lint yields due to rank vegetative growth. As a result, Treatments 4 and 5 grew larger plants with more main stem nodes and biomass, whilst maturing less monopodial (vegetative) branch bolls, as well as less sympodial (fruiting) branch bolls than the highest yielding treatment

(Treatment 3). This is significant as fruiting branches near the bottom of the plant have the greatest survival rates and largest bolls, and therefore the greatest contribution to lint yield (Constable, 1991). Although peak yields were calculated to be at ~ 108% ET_C, calculated yields similar to the peak were observed between 97 and 118% ET_C.

It is important to note that rank vegetative growth was only observed in Experiment 2 in Treatments 4 and 5. This may be due to the higher degree of imposed stress (due to higher ambient temperatures and evaporative demand), the lower number of cloudy days and lower gross amounts of water applied in Experiment 3 (Gibb *et al.*, 2004), or simply because only a 4% excess in ET_C was observed in Treatment 5. The treatments that produced rank vegetative growth were not exposed to waterlogging. This is evident because of the nature of the drip system and the fact that plant growth was not suppressed, therefore fruit shedding probably occurred due to self shading (Bange *et al.*, 2004). Hence lint yield reductions in Treatments 4 and 5 of Experiment 2 were not due to soil hypoxia; rather it was the alteration in the balance between vegetative and fruiting characteristics due to excessive soil water.

All treatments in Experiment 3 produced late season re-growth, whilst this did not occur in any treatments of Experiment 2. Late season re-growth is another adaptive growth habit of cotton, stemming from the plant's indeterminate growth pattern, and allows for the potential for further fruit production. Late season re-growth is generally undesirable in production systems and management practices such as growth regulators, early defoliation and precise water management, are put in place to avoid late season re-

growth. Notable exceptions to the undesirable nature of this adaptive growth habit are dryland production systems, where cultivars used are bred to grow during periods of available water resources, and tropical northern Australian production systems where the bulk of crop yield is achieved on the upper portion of the crop. As late season re-growth is undesirable in most irrigated commercial cotton crops, and has no effect on final lint yield, late season re-growth was excluded from biomass harvests in Experiment 3.

Plant node production and height are in general good indicators of water stress experienced by a cotton crop. Until the plant's carrying capacity is reached, crop lint yield potential increases with plant height, and hence the number of fruiting sites increases (Hearn and Da Roza, 1985). In both Experiment 2 and Experiment 3 there was separation of heights and nodes between treatments, with well-watered treatments exhibiting more sustained growth, resulting in plants with longer inter node lengths and increased node numbers. The number of nodes and inter-node length of a cotton cultivar is largely driven by temperature, where a new node is produced every 40 degree-days (Hearn, 1969) (three to four days at 28/20 °C), until water stress or other limiting conditions develop. Again, care must be taken when interpreting plant node production and plant height as rank vegetative growth can skew the appearance of lint yield potential, as in the case of Treatments 4 and 5 in Experiment 2. Furthermore, differences in plant height in Experiment 2 and Experiment 3 occurred as a result of the timing of cutout. Cutout occurs when the demand for assimilates by fruiting structures exceeds the supply of photosynthates, resulting in the slowing and eventual cessation of production of fruiting sites. Assimilate supply is limited by the amount and interception of solar

radiation, plant growth (as it ultimately lowers intercepted irradiance, especially by leaves nearest to the heaviest boll load, due to self shading of lower leaves in an enclosed canopy) and any plant stress (such as insect damage, water supply and disease). Cutout in Experiment 2 and Experiment 3 occurred much earlier in drier treatments than in the wetter treatments, resulting in smaller plants in drier treatments. This pattern is a common occurrence in water stressed cotton (Bielorai *et al.*, 1983; DeTar, 2008; Gerard and Cowley, 1969). Increased soil water deficits in Experiment 2 and Experiment 3 resulted in slower growth, smaller plants, fewer nodes and fruiting branches and a lower leaf area index. Therefore, while plant height and number of nodes are not always accurate measures of potential cotton yield, they can be used to gauge the water stress experienced by a particular crop.

As soil water availability declines, transpirational cooling of the leaf is reduced and T_c rise (Mahan *et al.*, 2005). Therefore, T_c can potentially be used to infer transpiration rates, and provide the basis for determining plant water stress. The average T_c of Experiment 2 and Experiment 3 reflected this trend, where T_c increased with increasing water stress. It is important to note that treatment differences in T_c were not observed at irradiance levels < 300 W m^{-2} (Table 5.4). Furthermore, differences in T_c -T_a were observed at irradiance levels > 300 W m^{-2} and T_a > 28ºC (Table 5.4). The fact that differences in CTD became apparent only after these environmental conditions were reached, indicated that these differences in T_c were due to varying rates of transpirational cooling when solar input is sufficient to raise T_c > 28ºC. These divergent transpiration rates were driven by differences in soil water conditions.

The relationship between measured T_c and per cent ET_C applied varied between Experiment 2 and Experiment 3. This is because R_g, T_a, humidity, wind speed and the position of the leaf surface in relation to the incident solar irradiance can modify T_l, adding to the effect of water stress on T_c (Fuchs, 1990). Previous research using the BIOTIC protocol for irrigation scheduling by Wanjura *et al.* (2006) concluded that season variation in environmental conditions resulted in differences in daily T_c over a range of irrigation treatments and seasons. It is important to note that the slope of the line of the regressions for T_c-water relations in Experiment 2 and Experiment 3 is similar. Hence the relative response of T_c to changes in water stress is similar across different seasons. Again, this response is significant as the seasonal variation in canopy temperature-water relations is due to differences in environmental stressors, and the merger of this data by the BIOTIC irrigation scheduling system may provide a higher degree of sensitivity to water stress detection across a range of seasonal pressures.

Despite a varying response in T_c-ET_C relations across seasons, the relationship between T_c and the duration of time T_c > 28 °C (optimal temperature) across the two experiments was similar across seasons (Figure 5.13b). Although this similarity in the relationship is self-evident, it is important as the BIOTIC protocol must perform in the same manner across all seasons, regardless of evaporative demand and environmental conditions. In Experiment 2 and Experiments 3, for each degree rise in average T_c, the amount of time T_c > 28 °C increase by 4.4% (Figure 5.13b). Canopy temperature-yield relations were also similar across Experiment 2 and Experiment 3, where peak lint yields were recorded at average daytime canopy temperatures of 26.4 °C. It is important to note that although

this value is below the stress threshold of 28 °C, the range of average T_c that produce similar lint yields as the peak was 24.8 °C to 28.1 °C. This suggests that when average daytime T_c > 28 °C, lint yield penalties ensue.

It is important not to confuse average T_c with the temperature stress threshold. The stress threshold is an estimate of the thermal optimum of metabolism of the plant, representing the approximate midpoint of the studied crop's TKW. Burke *et al.* (1988) determined that the TKW for cotton is 23.5 to 32 °C and that although cotton foliage can only be expected to be within its TKW 30% of the season, biomass accumulation principally occurred during this period. This was observed through a linear relationship between the times that foliage temperature was within the TKW and plant biomass production. Therefore, through the maintenance of T_c within the TKW by supplying irrigation water for transpirational cooling at the T_c stress threshold, peak plant productivity should be achieved.

Burke and Oliver (1993) showed that leaf enzymes operate most efficiently in a narrow temperature range called the TKW. This led to the concept of optimal T_c, which have been determined through the temperature dependence of metabolic indicators (Mahan *et al.*, 2005). These optimal temperatures were originally defined in terms of the thermal dependence of the apparent K_m of a given plant enzyme (Burke *et al.*, 1988; Mahan, 2000; Mahan *et al.*, 1990). Burke (1990) also developed an alternative method for determining optimal temperatures that was based on the recovery of dark adapted photosystem II variable fluorescence (PS II) rates following illumination. Optimal

temperatures calculated from both methods are identical (Mahan *et al.*, 2000), with an optimal temperature of 28 °C identified for upland cotton (Wanjura *et al.*, 2006). This optimal temperature was supported by Wanjura *et al.* (1992) and Upchurch *et al.* (1996) approach for scheduling irrigation based on T_c and a stress time (ST) index that accumulates the amount of daily time a crop exceeds its specified optimal or threshold T_c.

The relative duration of time in which treatments experienced supra-optimal canopy temperatures (28 °C) in Experiment 2 and Experiment 3 followed the same trend as average T_c, where drought stressed treatments experienced not only higher average temperatures but longer periods of supra-optimal T_c. Similar results were observed by Wanjura *et al.* (1988), where the per cent of time dryland cotton canopies were above 28 °C was significantly higher than for irrigated cotton canopies and Wanjura *et al.* (1990), where reductions in water application resulted in a corresponding increase in average daily T_c with subsequent reductions in lint yield.

5.5 Conclusion

Experiments were conducted over two seasons using the ET_C approach to irrigation scheduling in order to achieve differences in plant water status. The water relations of cotton were observed in deficit, adequate and excessive water treatments, resulting in differences in lint yield, plant architecture, growth, biomass accumulation and T_c. The observed stress potential was higher in Experiment 3 than Experiment 2 due to a combination of higher T_a, VPD, irradiance and average evaporative demand. This increased stress potential resulted in differences in lint yield-water relations and canopy

temperature-water relations across the two experiments. However, the slope of both the yield-water and canopy-temperature-water regressions was the same in both Experiment 2 and Experiment 3. Therefore, the assumption that the variation in yield-water relations and canopy temperature-water relations across the experiments was the result of the differing stress potentials across the two seasons can be made. This is because the relative difference in yield-water and canopy-temperature-water relations was constant across experiments. This relationship adds weight to the assumption that the BIOTIC protocol can consistently detect water stress across a range of environmental conditions and seasons.

The T_c data from my experiment suggest that the BIOTIC irrigation scheduling protocol can consistently detect water stress, producing peak lint yields across different seasons, despite variations in seasonal pressures resulting in differences in evaporative demand. My experiments also confirm that when average daytime $T_c > 28$ °C, lint yield reductions occur. This observation is important in the context of the BIOTIC irrigation scheduling system, which uses a threshold T_c for stress detection and irrigation scheduling. Therefore, irrigation scheduling based on T_c offers the potential for precise control of crop growth and development, across varying seasonal pressures. Therefore, when combined with environmental factors affecting T_c and crop development (such as T_a and VPD) the use of T_c may provide valuable insights into plant water stress for the purpose of irrigation scheduling. This is significant as scheduling drip irrigation with the BIOTIC irrigation system is practical. This is noteworthy as historically problems have been encountered scheduling irrigation in drip systems. Thus, the potential utility of BIOTIC

for water stress detection and irrigation scheduling is significant, and must be further explored. However, it must be determined whether the BIOTIC system has the capacity to accurately detect water stress when the plant is physiologically water stressed; whether BIOTIC is sensitive enough to external environmental pressures that the plant is exposed to and which environmental parameters have the most significant effect on BIOTIC; and whether BIOTIC can optimise water use and effectively use.

6. SOIL WATER DEFICITS AND THEIR INFLUENCE ON CANOPY TEMPERATURES IN DEFICIT FURROW IRRIGATED COTTON

6.1 Introduction

Furrow irrigation is an irrigation application technique particularly operationally suited to broadacre row crops where water is applied and distributed over the soil surface by gravity. It is conducted by creating parallel channels along the field length in the direction of predominant slope and water is applied to the top end of each furrow and flows down the field. Furrow irrigation is the dominant method of irrigation delivery in the Australian cotton industry (Tennakoon and Milroy, 2003), accounting for more than 90% of all irrigated cotton (Hodgson *et al.*, 1990).

As furrow irrigation is essentially a method of controlled inundation, for uniformity of applied irrigation water the technique involves a balance between field slope, field length and the rate of irrigation application. Due to the nature of the system, roots are waterlogged after each irrigation (Hodgson *et al.*, 1990), and either an excess amount of water will be supplied to the upper end of the field or insufficient amounts at the lower end of the field. A high rate of application and a long run time can result in excessive runoff, whilst low rates of application result in slow water advance, cause poor water distribution and deep drainage losses. Soil type, heterogeneity and associated infiltration rates across the field will also affect the efficiency of furrow irrigation (Hansen *et al.*, 1980).

Despite the inherent limitation of poor application efficiency of furrow irrigation, the predominant water losses from a well managed system are through evaporative and drainage losses from supply and tail water irrigation channels (Purcell, 2006). Furrow irrigation, although restricted, is a very reliable and flexible system that can be managed to achieve reasonable WUE while requiring little pumping of water as the system is gravity fed. Furthermore, such a system encourages deeper rooting of the crop in order to use water from the whole profile.

Canopy temperatures, in the form of CWSI, have been shown to closely parallel a plot of extractable soil water to 1.1 m when plotted as a function of time in furrow irrigated wheat (Jackson *et al.*, 1981). Jackson *et al.* (1981) found that CWSI followed nearly parallel paths with soil water throughout numerous wetting and drying cycles, except during the post-irrigation recovery period. They concluded that this is evidence for the close coupling of soil water and T_c, supporting the use of T_c as a method of evaluating plant water stress. However, Jackson *et al.* (1981) and in his review the following year (Jackson, 1982) notes that a unique relationship does not exist between T_c and soil water. This was shown by the fact that CWSI did not drop to its lowest value immediately after irrigation. Instead CWSI required five to six days to reach a minimum stress value, showing that the crop required some time to recover from the imposed water stress. Jackson (1982) concluded that this may be because leaves need to re-hydrate and roots in previously dry soil need to produce new root hairs. He also noted that the length of recovery time depends on the degree of previous stress, plant species and age. Similar recovery periods have also been documented in cotton (Ehrler, 1973) and sorghum (Idso

and Ehrler, 1976). Jackson *et al.* (1981) further noted that variation in the response of CWSI to extractable soil water may be dependent on the fact that PAWC was not assessed, rather a fixed depth of soil (1.1 m) was assessed, which may over- or under-estimate the soil water available to roots. Furthermore, CWSI is also dependent on the evaporative demand experienced by the plant, and if the evaporative demand exceeds the ability of the roots to take up water, then the CWSI should increase without a corresponding decrease in extractable soil water.

Furrow irrigation is often scheduled on the basis of a fixed plant available soil water deficit. Once this deficit is reached, the soil is refilled to near saturation, then drains to field capacity, thus furrow irrigation is characterised by a series of wetting and drying cycles throughout the season. This cyclical scheduling is characterised by the slow depletion of available soil water through ET until irrigation, where the soil water is rapidly returned to saturation and field capacity. As a result, plants are exposed to moderate dehydration on both a daily basis (diurnal changes in environmental load experienced by the crop) and throughout irrigation and rainfall cycles during the season (as plant available soil water deficits become increasingly severe between soil water refill points), which can lead to plant adaptation to water stress. The concept of adaptation to water deficits is relatively old (Maximov, 1929), and it has been widely recognised that plants can become hardened to water stress, and thus are more able to survive subsequent drought with less injury than plants not previously stressed (Levitt, 1972). There is some indirect as well as direct evidence (Brown *et al.*, 1976; Cutler and Rains, 1977; McCree,

1974) to suggest that plants grown under occasional stress show a lessened sensitivity of several physiological processes to subsequent water deficits.

This study was conducted to determine the degree of stress imposed, and the effect of various soil water deficit irrigation regimes on the growth and development, lint yield and T_c of cotton grown on a grey Vertosol (Isbell, 1996) at Narrabri, NSW Australia. This data will outline the effect of deficit furrow irrigation and its cyclical nature of water stress on cotton T_c. This is important as BIOTIC has not been used in furrow irrigation systems, which generally have larger irrigation deficits, potential water stress and adaptation periods, than either drip and sprinkler systems. This information will determine the potential efficacy of the BIOTIC irrigation scheduling system in furrow irrigation.

6.2 Materials and methods

Experiment 4 was conducted at the Australian Cotton Research Institute (ACRI), Narrabri during the 2008/09 season. Four deficit furrow irrigation treatments based on plant available soil water deficits (mm) from field capacity, calculated from NAM readings were imposed. Deficit furrow irrigation is characterised by refilling the soil water profile when a predetermined water deficit is reached. The deficits used in this study were a frequently irrigated (~ 30 mm to 40 mm soil water deficit), control (~ 40 mm to 50 mm soil water deficit- that represents a conservative soil water deficit target in commercial furrow irrigated cotton production) and two extended deficit irrigation treatments: a moderately extended (~ 65 mm to 75 mm soil water deficit) and fully

extended (~ 100 mm to 110 mm soil water deficit) treatment. This resulted in eleven irrigations in the frequently irrigated plots, nine in the control plots, four in the moderately extended plots and only two irrigations in the extended irrigation plots (Table 6.1). Rainfall throughout the growing season totalled 327 mm.

Table 6.1. Irrigation dates for each deficit irrigation treatment and corresponding number of days after sowing and cumulative degree days.

Treatment	Irrigation date	Days after sowing	Cumulative degree days
Frequent	9th December 2008	55	550
(~ 35 mm)	22nd December 2008	68	708
	2nd January 2009	79	866
	9th January 2009	86	976
	15th January 2009	92	1068
	23rd January 2009	100	1189
	30th January 2009	107	1309
	5th February 2009	113	1414
	11th February 2009	119	1526
	27th February 2009	135	1721
	13th March 2009	149	1957
Control	12th December 2008	58	597
(~ 45 mm)	24th December 2008	70	739
	7th January 2009	84	944
	15th January 2009	92	1068
	25th January 2009	102	1225
	2nd February 2009	110	1361
	10th February 2009	118	1512
	3rd March 2009	139	1777
	16th March 2009	152	1993
Moderate	11th January 2009	88	1001
(~ 70 mm)	28th January 2009	105	1276
	8th February 2009	116	1471
	6th March 2009	142	1808
Extended	16th January 2009	93	1087
(~ 105 mm)	6th February 2009	114	1434

Weather conditions, soil water, crop growth and development, lint yield and T_c using IRTs (SmartCrop^{TM}, Lubbock, Texas) were monitored throughout the experiments. Details on all measurements taken in Experiment 4 are described in Chapter 3.

6.3 Results

6.3.1 Weather

The weather conditions experienced in Experiment 4 were close to the 82 year long-term seasonal average (Table 6.2). Rainfall throughout the growing season of Experiment 4 totalled 327 mm (64 mm below the seasonal average), with the majority of the rainfall occurring in November, December and February and dry conditions in January (Figure 6.1a). These dry conditions were associated with hot weather, where late January and early February saw 18 consecutive days > 36 °C, culminating in the last five of these days > 40 °C. As a result, monthly average temperatures were above long term averages from January through to March (Figure 6.1b), however the number of seasonal high temperature stress days recorded (43 d) was close to the long term seasonal average (44 d). The number of low temperature stress days and average daily solar irradiance in Experiment 4 was the same as the long term seasonal average, while average 9 am relative humidity similar to the long term seasonal average (Table 6.2).

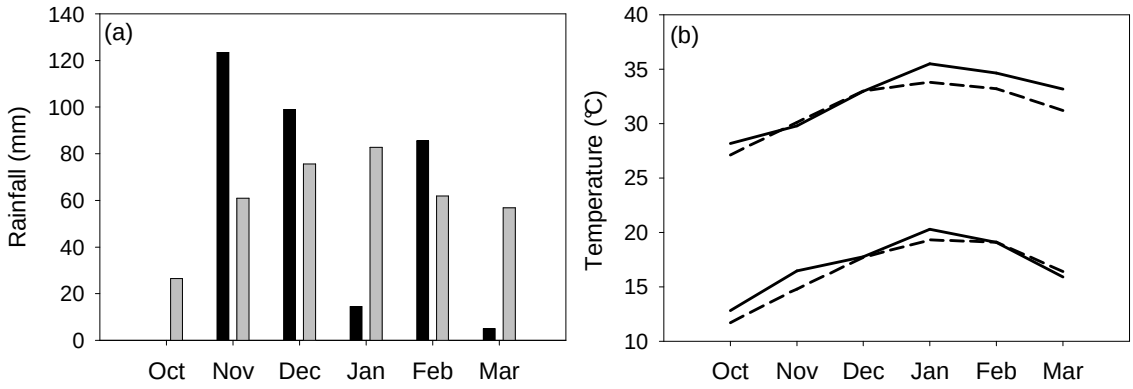


Figure 6.1. (a) Monthly rainfall (mm) in Experiment 4 (▬) and long term seasonal averages (▭). Average maximum and minimum monthly temperatures (°C) in Experiment 4 (———) and long term averages (– – – –).

Table 6.2. Rainfall, temperature and evaporative demand and other environmental factors that affect stress potential in Experiment 4 and corresponding long term seasonal average (BOM, 2009).

	Experiment 4	**Long term seasonal average**
Rainfall		
Total rainfall (mm)	327	391
Days with rain	25	26
Days with rain > 10 mm	11	11
Ambient temperature		
Average maximum temperature (°C)	32.2	32.4
Average minimum temperature (°C)	16.8	16.6
High temperature stress days (> 36 °C)	43	44
Low temperature stress days (< 11 °C)	10	10
Irradiance		
Average daily (MJ m^{2-1})	25.0	24.9
Wind speed		
Average 9 am (m s^{-1})	4.1	4.9
Relative humidity		
9 am average RH (%)	60	57
Evaporative demand		
ET_C to 60% open bolls (mm)	721	700*

* Data from Tennakoon and Milroy (2003)

6.3.2 Soil water and irrigation

Treatments were furrow irrigated when the predetermined soil water deficit was reached. This was calculated with measured NAM soil water content to 1.2 m, using the methodology described by Tennakoon and Hulugalle (2006). The measurement frequency was about weekly, where frequency was increased as the predetermined soil water deficit approached. The NAM was used to measure volumetric soil water in the profile before and after each irrigation or rain event. The amount of water applied was calculated by the difference between the measured soil water content just before irrigation, and the soil water content measured the day after an irrigation event. As a result, a significant proportion of treatment differences were due to the extent of soil drying to the refill point. This resulted in treatment differences in the duration between soil water profiles at field capacity as well as the potential stress period. In addition, treatment differences were observed in the net amount of irrigation water stored in the soil profile ($P<0.001$), with three different treatments formed. The frequently irrigated treatment and the control treatment received the largest and statistically similar amounts of total irrigation water, ~ 397 mm. This was achieved in 11 irrigation events between 55 and 149 DAS in the frequently irrigated treatment and nine irrigations between 58 and 152 DAS in the control. The moderately extended treatment received 288 mm net of irrigation water between 88 and 142 DAS in four irrigation events. The fully extended treatment received the least total irrigation water in only two irrigations on 93 and 114 DAS, totalling 213 mm. The soil water deficits throughout the growing season are shown in Figure 6.2.

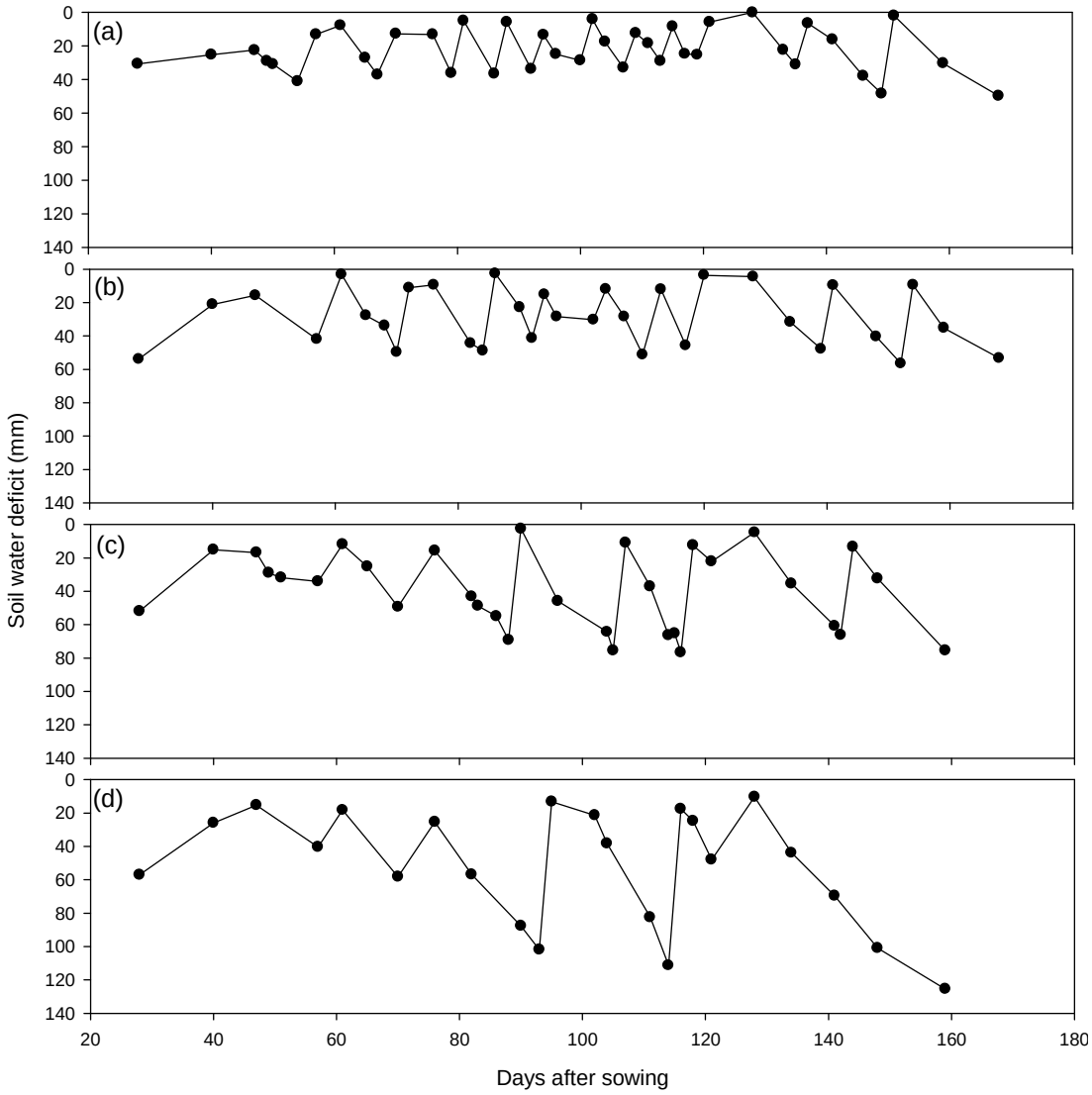


Figure 6.2. Soil water deficits, calculated from the soil's drained upper limit, measured with a NAM in the (a) frequently irrigated, (b) control, (c) moderately extended, and (d) fully extended deficit treatments throughout the growing season. Lines are included to assist comparison between treatments.

6.3.3 Crop development

Variation in lint yield was characterised into three statistically significant groups in Experiment 4 (P<0.001) (Figure 6.3a). The highest yielding treatments were the frequently irrigated and control treatments at ~ 2700 kg ha^{-1}, followed by the moderately extended treatment yielding 2450 kg ha^{-1} and the fully extended treatment producing

2000 kg ha^{-1}. Yield-water relations exhibited a polynomial function, where lint yield rose to a peak of 2728 kg ha^{-1} at 730 mm applied water, where applied water is the sum of rain and infiltrated irrigation water (P<0.001) (Figure 6.3b). Water application in excess of 730 mm resulted in a decrease in lint yield. The regression model accounted for 65% of the variance, with an estimated yield standard error of 184 kg ha^{-1}. The calculated range of applied water producing yield similar to the peak was 655 mm to 802 mm. This range was calculated by substituting the peak yield ± the standard error of the yield into the fitted regression model.

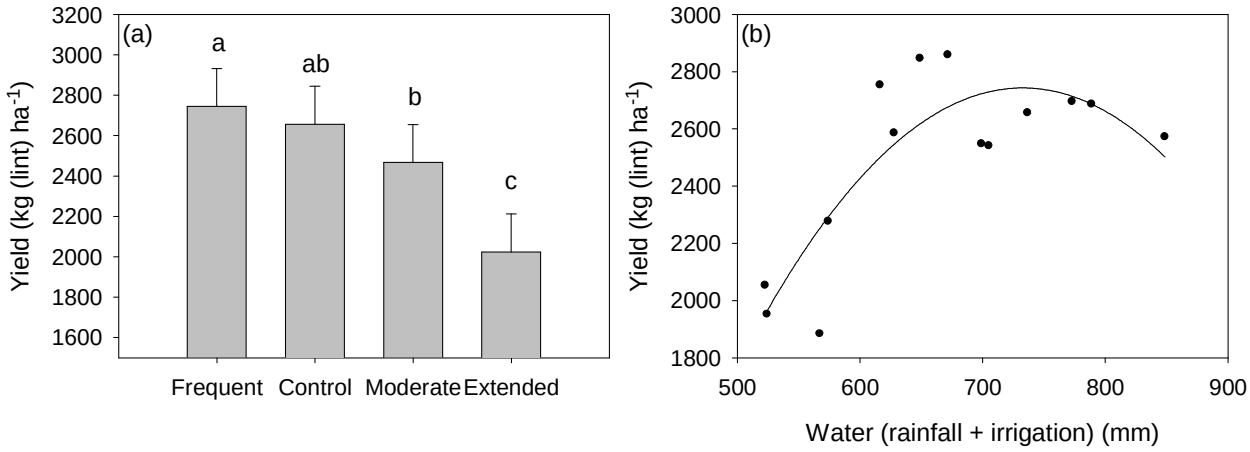


Figure 6.3. (a) Machine picked lint yield (kg ha^{-1}) for each treatment in Experiment 4, vertical bars represent l.s.d.; (b) Yield-water relations in Experiment 4, y= -0.017x^2 + 24.77x -6295, R^2= 0.65 (P<0.001).

Differences in plant height were observed (P<0.001) with the formation of three statistically separate groups at the end of the season (Figure 6.4a). Plant heights of 91 cm were the highest in the frequently irrigated plots followed by the control and moderately extended treatments with an observed plant height of 80 cm. The fully extended treatment recorded the lowest plant heights of 73 cm. The number of nodes was also influenced by

irrigation deficit (P<0.001), with the formation of two statistically significant groups: the frequent and control plots with 23 nodes formed, and the two extended plots producing 21 nodes (Figure 6.4b). Cutout, the cessation of reproductive and vegetative growth to ensure the maturation of developing bolls, occurred earliest in the extended irrigation treatments. This took place in the fully extended treatment 96 DAS, the moderately extended treatment 107 DAS, the control 112 DAS and the frequently irrigated treatment 117 DAS.

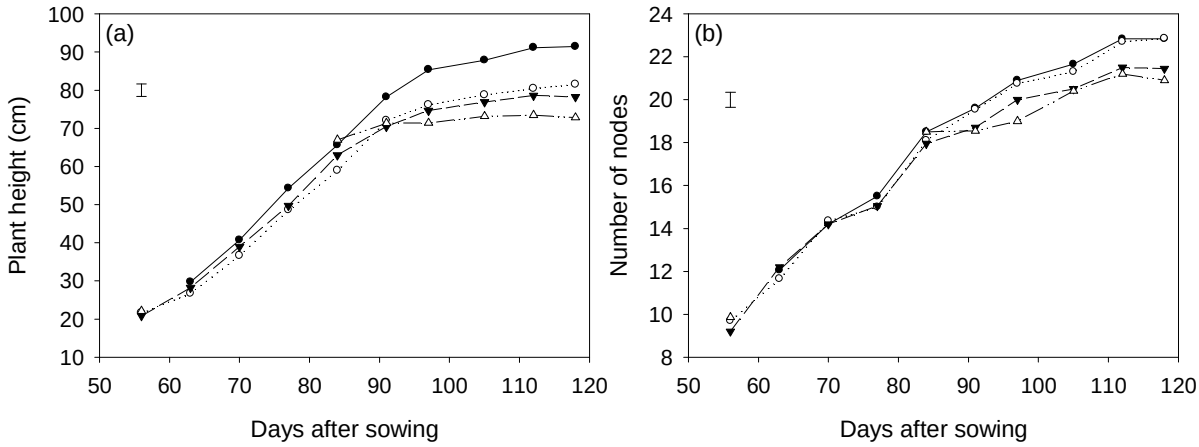


Figure 6.4. Plant height (a) and number of nodes (b) produced throughout the growing season in the frequently irrigated (——●——), control (·····○·····), moderately extended (- —▼— -) and fully extended (···—△—···) irrigation treatments of Experiment 4. Vertical bar represents l.s.d. Dotted lines are included to assist comparison between treatments.

6.3.4 Above ground biomass accumulation and partitioning

Treatment differences in above ground biomass accumulation were most pronounced in vegetative plant structures, which resulted in differences in total dry matter (P=0.009) (Figure 6.5 and Figure 6.6a). By the peak vegetative growth phase of crop development (118 DAS), the frequently irrigated treatment had produced a higher total dry matter than all other treatments. It maintained this higher total dry matter throughout cutout, but by

the end of the season, during boll development, total dry matter in the control and moderately extended irrigation treatments had matched the frequently irrigated treatment. This was partially due to the fact that the frequently irrigated plots were constantly moist and thus were affected by Verticillium wilt (*Verticillium dahliae*). Verticillium wilt is a soil borne fungal pathogen that proliferates in cool wet soil conditions affecting the vascular system of plants. This results in reduced water availability, regardless of soil water conditions, and can result in leaf and fruit shedding, wilting and stunted growth as well as other symptoms similar to water stress conditions. The potential effects of Verticillium wilt are significant, especially when considering the similarities between Verticillium wilt infection and water stress. The control, moderately and fully extended treatments total dry matter remained similar throughout the season until the final biomass harvest at 167 DAS where the fully extended treatment had a lower total dry matter of 1130 g m^{-2} compared to ~ 1420 g m^{-2} in all other treatments (Figure 6.6a).

Treatment differences in the ratio of vegetative to reproductive biomass were observed in Experiment 4 (P= 0.016) (Figure 6.6b). Treatment differences were not observed until after 76 or 92 DAS, when all treatments displayed 6% and 22% reproductive biomass, respectively. By 118 DAS the extended irrigation treatments had a higher ratio of reproductive dry matter (0.53) than the frequently irrigated and control treatments (0.41). This higher ratio was maintained by the extended irrigation treatments (0.62) compared with the more frequently watered irrigation treatments (0.56); however, no differences were observed at the final biomass harvest where all treatments displayed 60% reproductive dry matter.

The reproductive and vegetative dry matter ratios reflected the increased rates of maturity in the extended irrigation treatments. At the biomass harvest on 118 DAS, the moderately and fully extended treatments had reached cutout 12 and 22 d before harvest, and the control and frequently irrigated treatments has only just reached cutout. Therefore, although the squares and young bolls measured at 118 DAS may not contribute to final lint yield of the frequently irrigated plots, the frequently watered treatments maintained fruiting site production for longer, and hence, produced a higher lint yield potential. Differences in average boll size may have had an effect on lint yield as open boll size at 65% open bolls was different across treatments ($P<0.001$). At this point the frequently watered treatment had a larger average boll size of 6.7 g compared with the control with an average boll size of 6.3 g. The control and the moderately extended treatment had a similar average boll size, whilst the fully extended treatment exhibited the lowest average boll size of 5.8 g. As differences were not observed in boll numbers (data not shown) and biomass (Figure 6.6), and yet differences in lint yield at maturity were recorded, the size of the bolls may have had a large effect on final lint yield.

Treatment differences in LAI were observed during Experiment 4 ($P<0.001$), following 118 DAS (Figure 6.6c). At this point, the frequently irrigated plots had the greatest LAI, followed by the control and the two extended irrigation plots with similar LAIs. Peak LAI occurred at ~ 118 DAS and following this point, the frequently irrigated and control plots exhibited reductions in LAI. This was partially due to plant maturation, as well as the effects of Verticillium wilt in the wetter plots. At the final biomass harvest at 60% open bolls (167 DAS), LAI was the same in most plots, with the exception of the fully

extended plots, which had a lower LAI. It is important to consider LAI as leaf expansion is the most sensitive physiological effect of water stress, and in the context of the monitoring of T_c is important for the reduction of background soil effects.

Figure 6.5. Examples of variation in biomass accumulation across treatments during (a) peak water consumption and vegetative growth at 112 DAS; and (b) the pre-harvest period, post-defoliation at 196 DAS. Treatments are left to right: Fully extended, moderately extended, control and frequently irrigated irrigation treatments. Measuring stick represents 1 m.

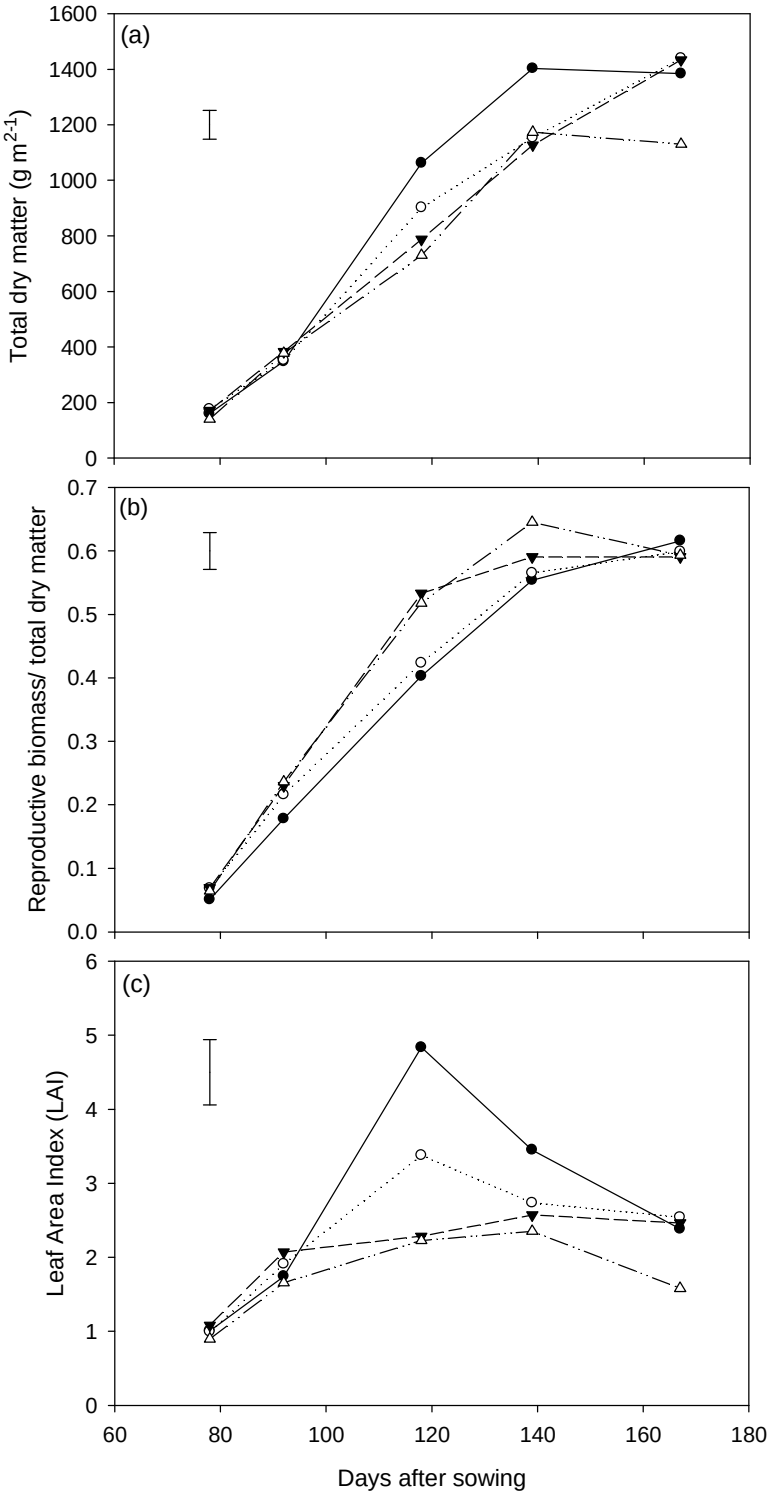


Figure 6.6. Total dry matter accumulation ($g.m^{-2}$); the ratio of reproductive to vegetative biomass; and leaf area index (LAI) in Experiment 4 in all treatments; frequently (—●—), control (·····○·····), moderately extended (- —▼— -), and fully extended (···—△—···) irrigation treatments. Vertical bar represents l.s.d. at *P*=0.05. Dotted lines are included to assist comparison between treatments.

6.3.5 Canopy temperatures

The four deficit irrigation treatments exhibited different average T_c (P<0.001). These T_c consistently followed the trend where irrigation treatments with larger soil water deficit, and hence longer durations of moisture stress, resulted in higher average T_c (Table 6.3). Like Wanjura *et al.* (1992), treatment differences were not observed when R_g < 300 W m^{-2} (Table 6.3), average T_c from this point forward refer to T_c when R_g > 300 W m^{-2}. Under these environmental conditions, treatment differences that correspond to irrigation treatments were observed (Table 6.3).

Table 6.3. Average canopy temperature (T_c), average T_c when R_g < 300 W m^{-2} and > 300 W m^{-2}, and duration of time that T_c > 28 °C (%) between 972 (82 DAS) and 2024 (155 DAS) cumulative degrees days in Experiment 4. The same superscript letter within a measurement represents values that are not statistically different at the P=0.05 level.

Treatment	Average T_c (°C)	Average T_c (°C) (R_g < 300 W m^{-2})	Average T_c (°C) (R_g > 300 W m^{-2})	Time T_c > 28 °C (%)
Frequent	23.8 [a]	21.3 [a]	29.1 [a]	24.1 [a]
Control	24.1 [b]	21.7 [a]	29.1 [a]	25.5 [a]
Moderately extended	24.3 [c]	21.4 [a]	29.6 [b]	25.2 [a]
Fully extended	24.5 [d]	21.8 [a]	30.4 [c]	28.8 [b]

Average T_c (between 82 and 155 DAS) and water application exhibited an exponential decay function (R^2=0.83) (Figure 6.7a). This relationship saw a rapid reduction in average T_c with increased water application, up to 685 mm applied water. Beyond 685 mm applied water, average T_c was less responsive to an increase in total water application (Figure 6.7a). Average T_c was also correlated to final lint yield (Figure 6.7b), where the highest yield was observed at average canopy temperatures of 28.5 °C.

Although second order polynomial was fitted to the data, peaks in lint yield and corresponding average T_c were not observed, suggesting that these results may be range limited. This is because significant lint yield reductions were not observed with excess total water application. Despite this range limitation, the fitted regressions calculate peak lint yields at average daylight T_c of 28.6 °C (over a range of 28 to 29 °C).

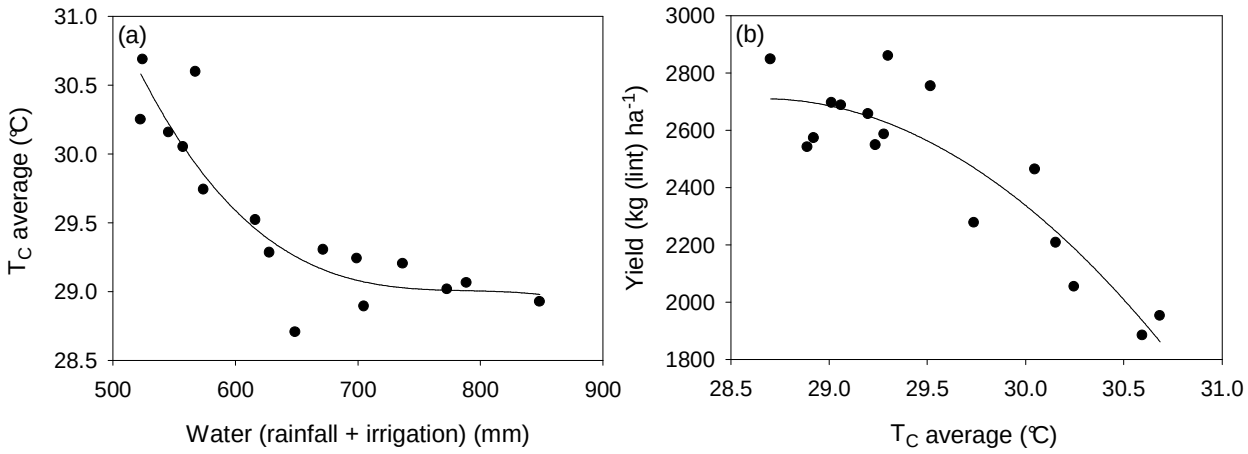


Figure 6.7. (a) Average canopy temperature (°C) vs. water application (mm) (rainfall + infiltrated irrigation water) regression (P<0.0001) with a mathematically calculated base temperature of 28.9 °C, y= 28.87 + 518.72 ($e^{(-0.109x)}$), R^2= 0.83; (b) Average daily canopy temperature (°C) and yield regression (kg ha^{-1}), y= -206.0x^2 + 11802.9x -166391.7, R^2= 0.82 (P<0.0001).

A comparison between T_c measured in Experiment 3 and Experiment 4 is shown in Table 6.4. Experiment 3 and 4 were irrigated on different time scales. Experiment 3 was conducted on a surface drip irrigation system where irrigation was applied in small amounts daily or every second day, depending on the evaporative demand experienced by the crop, where irrigation amounts varied between 2 mm and 14 mm. Experiment 4 was conducted using a deficit furrow irrigation system where water was applied to fill the soil

profile between two and eleven times throughout the growing season. The soil water deficits achieved ranged from 35 mm to 105 mm PAWC.

Lint yield, water applied and T_c showed consistent trends across both experiments, where similar T_c and lint yields were observed at similar total applications of water (irrigation and rainfall) (Figure 6.8). Despite differences in the frequency of water applied, average T_c and lint yield exhibited a strong (R^2=0.97) second order polynomial function across both experiments (P<0.0001), where peak lint yields were measured at average T_c of 28.0 °C. This result suggests that T_c is a dynamic predictor of water stress, and can be used consistently over vastly different intervals between irrigation applications.

Table 6.4. Comparison of average T_c (°C), lint yield (kg (lint) ha^{-1}) and ET_C (%) observed in Experiment 3 (surface drip irrigation) and Experiment 4 (deficit furrow irrigation).

Irrigation delivery	Treatment	Average T_c (°C)	Yield (kg (lint) ha^{-1})	ET_C (%)
Drip	1	31.4 ^{a}	985 ^{a}	57
Drip	2	31.0 ^{ab}	1746 ^{b}	67
Furrow	Fully extended	30.4 ^{bc}	2024 ^{b}	62
Furrow	Moderately extended	29.6 ^{cd}	2468 ^{c}	73
Drip	3	29.4 ^{de}	2413 ^{c}	77
Furrow	Control	29.1 ^{de}	2657 ^{cd}	90
Furrow	Frequent	29.1 ^{de}	2745 ^{cde}	86
Drip	4	28.4 ^{de}	2789 ^{de}	92
Drip	5	27.7 ^{f}	2882 ^{e}	104

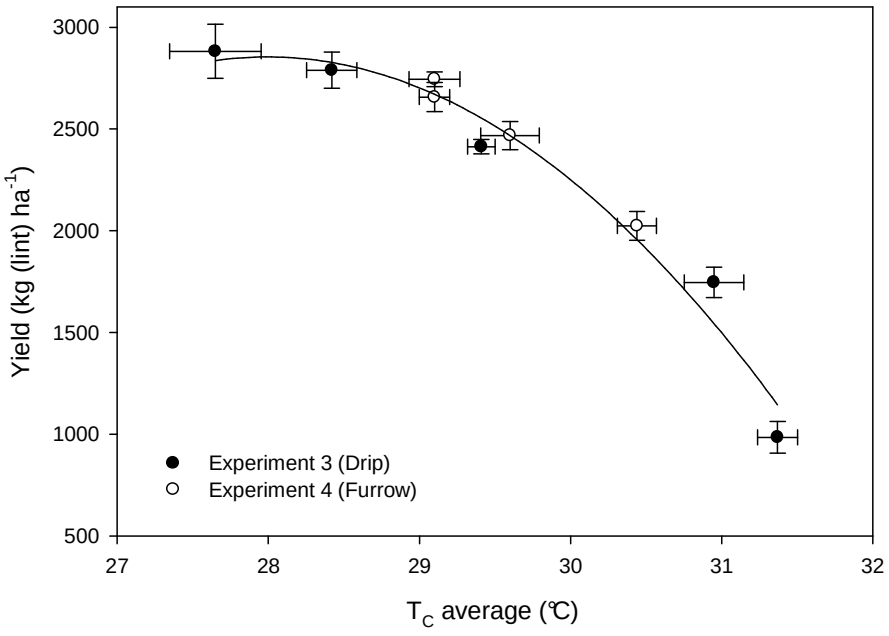


Figure 6.8. Average T_c vs. lint yield regression in Experiment 3 (surface drip irrigation) (●) and Experiment 4 (○) (deficit furrow irrigation) over the same measurement days (5th Jan 2009 to 18th March 2009) showing peak yields at 28 °C, $y = -150.1x^2 + 8405.2x - 114797$, $R^2 = 0.97$ ($P<0.0001$).

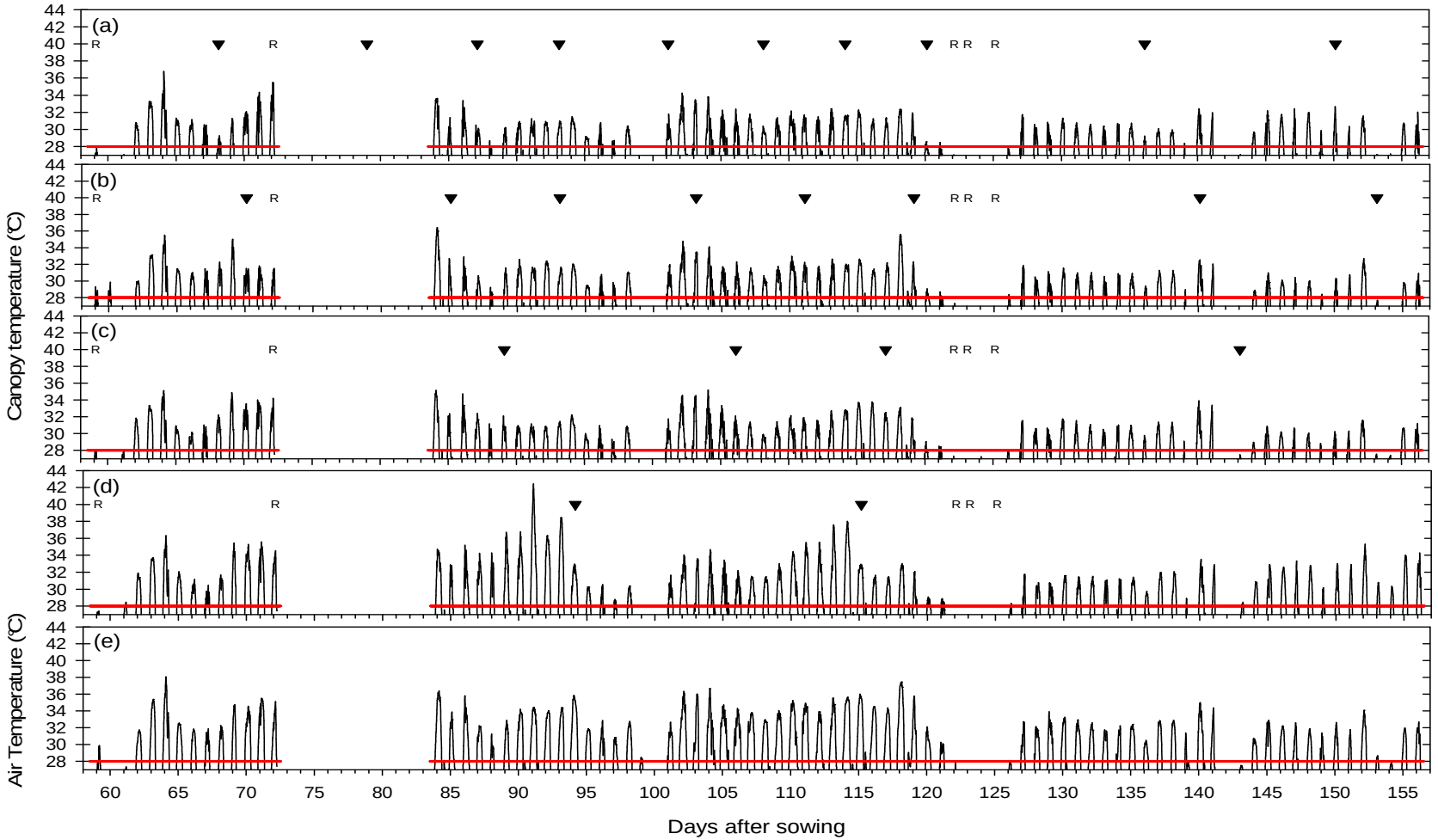


Figure 6.9. Average canopy temperatures above 27ºC in Experiment 4 measured in the (a) frequent, (b) control, (c) moderately extended, (d) fully extended irrigation treatments and (e) air temperature between 58 and 156 DAS. R= days with rainfall above 15 mm; ▼= irrigation events; and the red line at 28ºC represents the optimal canopy temperature for cotton. Missing data between 73 and 83 DAS was due to base station failure following a lightning strike.

6.4 Discussion

The growing conditions during in Experiment 4 were very similar to long term averages at ACRI (Myall Vale), Narrabri (Table 6.2), with the number of high and low temperature stress days, and a season length of 171 d being very representative of an average year (Table 6.2). Insect pressure throughout Experiment 4 was moderate (five pesticide applications), particularly towards the end of the season as whitefly (*Trialeurodes vaporiorum* and *Bemisia tabaci*) were consistently above threshold levels from late February 2009; however, average lint yields were high suggesting little impact on final lint yield.

Cotton growth and lint yield in Experiment 4 were affected by water supply. Peak lint yields occurred in the plots with a larger total volume of net irrigation water applied and more frequent replenishments of soil water. The control and frequently irrigated treatments yielded the most with 2700 kg ha^{-1} from ~ 397 mm of net irrigation water, followed by the moderately extended, producing 2450 kg ha^{-1} from 288 mm net irrigation water. The lowest yielding treatment was the largest deficit treatment, the fully extended irrigation producing 2000 kg ha^{-1} from 213 mm net irrigation application. Despite this variation, all lint yields were high and above the average Australian cotton yield in 2008/09 (1980 kg ha^{-1}) (ABARE, 2009). Yield-water relations exhibited a second order polynomial function, where yield rose to a peak at 729 mm ± 74 mm applied water (104% ± 13% ET_C to crop maturity). This curvilinear response was also observed in Experiments 2 and 3 (Chapter 5), as well as in numerous other studies in various locations that have shown that peak cotton lint yield occurs at approximately 700 mm

ET_C (Tennakoon and Milroy, 2003; DeTar, 2008; Grimes *et al.*, 1969b; Wanjura and Upchurch, 2002; Orgaz *et al.*, 1992). Similar peak yields and corresponding ET_C were observed in Experiment 2 and 3. The range of ET_C producing peak lint yields was 97% to 118% in Experiments 2 and 3, and is 91% to 111% in Experiment 4. This range is relatively narrow, representing 144 mm water, highlighting the responsiveness of cotton to both sub- and supra-optimal water application.

As observed in numerous other studies (Grimes *et al.*, 1969a; Grimes and El-Zik, 1990; DeTar, 2008; Hearn, 1994), the effect of extending the soil water deficit in Experiment 4 also affected plant growth patterns, where exposure to larger soil water deficits resulted in smaller plants that matured earlier (Figure 6.4, Figure 6.5 and Figure 6.6). By 118 DAS, treatment differences were observed in the ratio of reproductive to total dry matter, where the extended irrigation treatment had a higher ratio of reproductive dry matter than the control and frequently irrigated treatments. This higher ratio was maintained in the extended irrigation treatment in comparison to the frequently irrigated treatments, until the final biomass harvest where all treatments displayed 60% reproductive dry matter. This confirms that the frequently irrigated treatments were not as stressed as the extended irrigation plots, as the extended irrigation treatment had matured and stopped producing new reproductive growth earlier in the season. Although no difference in the ratio of reproductive dry matter was observed at crop maturity, treatment differences in final lint yields occurred. It is however important to note that although differences in the ratio of reproductive to total dry matter were not different at the final biomass harvest, this does not take into account the fact that the more frequently irrigated treatments had altered

growth patterns to the extended irrigation treatments. The frequently irrigated plants were characterised by bigger plants with larger and more numerous bolls than the extended irrigation treatments (Figure 6.5).

The value of T_c measurements in agriculture has been established since the early 1980s (Idso, 1982; Jackson, 1982). The importance of T_c measurements is that under well-watered conditions, T_c can be significantly lower than T_a. The converse of this is also true and patterns of the T_c -T_a occur as a result of transpiration rates and the effect these rates have on the evaporative cooling of a leaf. Therefore, when soil water availability declines, transpirational cooling of a leaf is reduced and T_c rise. Average T_c in Experiment 4 followed this trend, where treatments with more frequent and an increased total applied water, yielded lower average T_c. Like in Experiments 2 and 3, differences in T_c were not observed at R_g < 300 W m^{-2} (Table 6.3). Again, this suggests that differences in T_c are only observed when radiation levels, and therefore T_c (which are driven by radiation levels), are sufficient to potentially warm T_c above T_a.

The relationship between T_c and ET_C applied (%) exhibited an exponential decay response (P<0.0001), where a rapid reduction in average T_c was observed with increasing water application, up to 685 mm (Figure 6.7a). Interestingly, average daylight T_c were not significantly reduced < 29.2 °C when total water applied > 685 mm. This result is similar to those reported in Chapter 5, where water application in Experiments 2 and 3 beyond 105% ET_C did not influence canopy temperatures. Furthermore, this result is

aligned with Tennakoon and Milroy's (2003) finding that average lint yields of Australian grown cotton peak at an average of 700 mm ET_C.

Although peaks in canopy temperature-yield relations were outside the range of data collected, the fitted regressions calculate peak lint yields at average daylight T_c of 28.6 °C. The average T_c that produces peak lint yield ranged from 28.0 to 29.2 °C. This range was outside and warmer than that produced from the surface drip irrigation data from Experiment 2 and Experiment 3, which produced peak lint yield over the 24.8 to 28.1 °C range. It is important to note that these ranges in average T_c were not altered when T_c from only Experiment 3 were considered for comparison with Experiment 4 (data not shown). The significance of this is that Experiment 3 and 4 were exposed to the same environmental conditions, and differences in T_c patterns between Experiment 3 and 4 are therefore due to irrigation delivery method and irrigation treatment. This suggests that furrow irrigated cotton may experience greater levels of water stress than surface drip irrigated systems, thus exhibiting higher average T_c. This may be a result of the nature of furrow irrigation, where large amounts of water, usually between 50 mm and 100 mm (depending on the soil water deficit and water holding capacity), are applied in a single irrigation event at intervals up to two to three weeks apart. In comparison, drip irrigation is characterised by smaller volumes of water applied, with more frequency. Therefore, furrow irrigated systems will result in a higher level of water stress, even though crop water use may not be substantially different.

The response of average T_c and yield was similar in Experiment 3 and 4 (P<0.001). This suggests that the data from Experiment 4 may be range limited, and the peak lint yield in Experiment 4 observed at a warmer T_c (28.6 °C ± 0.6 °C) than Experiment 3 may be skewed towards warmer T_c. As yield reductions (due to oversupply of water) were not observed in Experiment 4, it is difficult to determine whether peak lint yields under furrow irrigated conditions were associated with higher average T_c. However, previous research has shown that the response of T_c to the interval between irrigation events do not necessarily change, provided gross water applications are similar. Wanjura *et al.* (1990) studied the effect of irrigation regimes on T_c. Two of their irrigation treatments were based on hydrological data, where soil water was filled to field capacity at different intervals. The first of their treatments involved replacing the soil water extracted from the root zone on a weekly basis as measured by a NAM. The second of Wanjura *et al.* (1990) treatments was characterised by refilling the root zone soil water after the first square fruiting stage on a two week basis; however, irrigation was extended by one day for every 7 mm rainfall, and retracted by a day when maximum T_a > 40 °C. Although polyethylene drip-line emitter hose (rate of 2.0 mm hr^{-1}) was used to apply the irrigation water, the second of these irrigation treatments was designed to replicate Australian furrow irrigation scheduling for cotton production. These irrigation treatments were compared with irrigation treatments based on physiological criteria- where irrigation was initiated for fifteen minutes when the previous fifteen minute T_c average exceeded either 28, 30 or 32 °C (Wanjura *et al.*, 1990). Warmer average seasonal T_c of 25.3 °C (when radiation > 200 W m^{-2}) were observed in the two week "Australian" treatment, while the weekly soil water replacement (with a smaller soil water defect before irrigation) yielded lower

average T_c of 24.1 °C. The average T_c observed in the 28, 30 and 32 °C treatments were 26.6, 26.8 and 27.8 °C, respectively. The 28 °C treatment received 700 mm total water, compared with 750 mm in the "Australian" treatment. As a result of this similar water application, similar average T_c and lint yields were observed. Therefore, we can conclude that although average T_c will increase when the interval between irrigation events is increased, similar lint yields and T_c can be achieved between large soil water deficits based on two week soil water replenishment and presumably smaller water deficits where irrigation is based on fifteen minute average T_c, especially when the total water applied is similar. It is, however, important to note Wanjura *et al.* (1990) study was only conducted over one season, and did not measure rooting characteristics which may be able to shed some light into the plant's response to the soil environment.

Experiment 3 was conducted on a surface drip irrigation system where irrigation was applied in small amounts daily or every second day, whilst Experiment 4 was conducted using a deficit furrow irrigation system where water was applied to fill the soil profile between two and eleven times throughout the growing season. Despite vast differences in the frequency of water applied, average T_c and lint yield exhibited a strong (R^2=0.97) second order polynomial function across both experiments (P<0.0001), where peak lint yields were observed at average T_c of 28.0 °C (Figure 6.8). This shows that cotton will produce a higher lint yield when average T_c are maintained as close to 28 °C as possible. Lint yields, T_c and water applied in both experiments followed the same trend, where a decrease in water application resulted in a decrease in yield and a corresponding increase in T_c (Table 6.4). The similar response of T_c and lint yield in Experiment 3 and 4 suggests

that T_c are dynamic predictors of water stress, and can be used consistently over vastly different intervals between irrigation applications. Furthermore, this also suggests that field grown cotton T_c, grown in environments similar to commercial production, do not undergo significant adaptation to water stress. This is because treatments that received similar amounts of total water, displayed similar average T_c and lint yields; even though the interval between water application and gross amount of water applied each application was vastly different.

This similar response also highlights the inherent limitations of furrow irrigation. Although the T_c-yield response was similar in both surface drip and furrow irrigated cotton, differences in crop performance were observed. The lowest average T_c in a furrow irrigated system were observed to be ~ 29 °C, with corresponding lint yields of 2745 kg (lint) ha^{-1}. In comparison, the highest yielding surface drip irrigated cotton exhibited average T_c of 28 °C, and yielded 5% more than the furrow irrigated treatment mentioned above. This shows that even with similar net water applications, small gains in lint yield can be achieved with surface drip irrigated systems. The differences in yield were not due to a lack of water availability in the furrow irrigated system as field observations of the frequently irrigated treatment were characterised by wet conditions, where the soil surface was exposed to significant drying events. Therefore, it would be difficult to supply more irrigation water than what was achieved, especially without inducing significant waterlogged conditions. Rather, the differences are due to the nature of the irrigation systems and the ability of drip irrigation to provide more targeted water application, providing precise amounts of water directly to the root zone at almost any

irrigation frequency. This is important as although current cotton cropping systems are efficient, in a future climate of reduced irrigation water availability, producers may be required to transform their irrigation systems to more water use efficient and higher yield producing systems, where even a small increase in yield is of value to the producer.

6.5 Conclusion

This study shows that an investment in maintaining soil water deficit at control level through furrow irrigation practices is rewarded by maintaining average T_c as close to 28 °C as possible, and hence producing peak lint yields. Although average T_c of furrow irrigated cotton appear to be warmer than average T_c of drip irrigated cotton, an inspection of T_c in both furrow and drip irrigated cotton show similar responses to water application in both lint yields and T_c, regardless of the net volume of applied water per irrigation event and interval between irrigation events. This suggests that that T_c are dynamic predictors of water stress, where the amount of the soil water deficit and potential plant adaptation to previous water stress in the wetting and drying cycles of a furrow irrigated crop, do not influence the average T_c patterns in response to soil water deficits. This suggests that T_c have potential utility for irrigation scheduling and water stress detection in both deficit furrow and surface drip irrigation systems. Therefore, the capacity of the BIOTIC irrigation scheduling system in these two divergent irrigation delivery systems must be further studied to determine whether the potential benefits of BIOTIC at least match or outweigh existing irrigation scheduling systems. However, due to their nature, drip irrigation systems have an increased ability to maintain average crop T_c at 28 °C, producing increased lint yield with similar net water application.

7. IMPLEMENTING THE THERMAL OPTIMUM AND STRESS TIME CONCEPT IN SURFACE DRIP AND FURROW IRRIGATED COTTON

7.1 Introduction

The majority of irrigation scheduling methods either monitor soil and/or plant water status or compute a soil water budget to schedule irrigations based on estimates of soil water depletion within the crop root zone (Fereres, 1999). However, viewing the plant as a natural integrator of its environment through T_c has also been used as in indicator of field crop water stress (Upchurch *et al.,* 1996). The knowledge of plant T_c is a valuable tool for irrigation scheduling as all plant species have an optimal *in vivo* temperature threshold for metabolism (Mahan *et al.,* 2000). This has ramifications as reduced transpiration, due to limited water conditions, can result in T_c elevated above the thermal optimum. Therefore, a reduction in evaporative cooling results in a corresponding rise in leaf and canopy temperature, and is thus used as a signal for irrigation scheduling. BIOTIC is an irrigation management tool based on optimal temperatures for plant metabolism and integrates the plant and environment through deriving stress levels from canopy temperature (Upchurch *et al.*, 1996). BIOTIC differs from previous efforts to use T_c to detect water stress in that it uses a species-specific optimal plant temperature as the basis for determining when a T_c is indicative of plant water deficit. Previous methods compared T_c to either air temperatures or a "non-stressed" temperature that was calculated. The BIOTIC method can be referred to as a "thermal optimum" approach as it compares T_c to an invariant optimal temperature while other methods use a variable temperature standard.

Upchurch *et al.* (1996) developed BIOTIC and its temperature-time threshold system. The specific amount of time that a T_c of a given crop exceeds its species-specific optimum temperature threshold determines the need for irrigation scheduling (Mahan *et al.*, 2000). The time that the T_c exceeds its optimum is referred to as the stress time (ST) index (Wanjura *et al.*, 1992). The main underlying principle of the BIOTIC irrigation system is that plant productivity is proportional to the amount of time that a plant's temperature is observed to be within its thermal kinetic window (TKW) (Burke *et al.*, 1988; Mahan *et al.*, 1987). Burke *et al.* (1988) found that although cotton foliage can only be expected to be within its TKW 30% of the season, biomass accumulation principally occurred during this period. This was observed through a linear relationship between the times that foliage temperature was within the TKW and when plant biomass accumulation occurred.

The BIOTIC uses IRTs and a three step threshold system (temperature, time and humidity) to determine if and when to irrigate (See Chapter 2). The species-specific temperature threshold is based on the optimal temperature for enzyme function (enzyme thermal stability) or the optimal temperature for stress recovery following dark adaptation (measured by variable fluorescence), and has been determined to be 28 °C for a current Australian cotton cultivar (Chapter 4). Therefore, stress time (ST) is defined as the cumulative sum of time that $T_c > 28$ °C (time $T_c > 28$ °C). The daily stress time-threshold (STT), which represents the period of time a fully irrigated crop T_c is theoretically likely to exceed the optimal temperature in a given environment, is based on environmental variables (temperature, relative humidity, wind speed and irradiance), and is specific to a

particular region. The STT differs from ST in that STT, under the BIOTIC protocol, is the recommended duration of time a T_c should exceed its thermal optimum before irrigation is scheduled, and ST is the duration of time a canopy exceeds its thermal optimum. Using an energy balance approach (see 2.5.4 of Chapter 2), a calculated STT for scheduling irrigation was determined to be 2.75 h ST per day (165 min > 28 °C) for ACRI (Myall Vale), Narrabri. This STT is a calculated reference rate for the initiation of thermal stress conditions responsive to additional water application. Average daily stress times were calculated using a temperature threshold of 28 °C, and irrigation signals were calculated after 2.75 hours ST was accumulated on a given day.

Even though an optimal temperature may be definable, physiological limits to supplying water for transpiration, especially under conditions of high evaporative demand (see Chapter 2), may lead to circumstances where the canopy cannot be sufficiently cooled to maintain optimal temperature. Hence, any time the T_c might be above the optimal temperature threshold, the stress time concept is considered. The stress time concept has been previously used and studied in drip irrigation systems (Wanjura *et al.*, 1995; Wanjura *et al.*, 2004; Wanjura *et al.*, 2006). These studies found a consistent relationship between the number of irrigation signals and the magnitude of temperature-time thresholds, where daily T_c was positively related to ST, but differed among seasons presumably due to environmental variability (Wanjura *et al.*, 2006). Wanjura *et al.* (1995) noted the sensitivity of the system to capturing rainfall, as the interval between irrigation signals significantly increased after rainfall events. While these studies showed that peak lint yields were correlated with specific average daily stress times, they reported that

similar lint yields could be produced by extending the stress time-threshold and reducing irrigation water application (Wanjura *et al.*, 1995). Wanjura *et al.* (2004; 2006) showed that cotton lint yield and water application was characterised by a negative linear relationship, where an average decline of 343 kg (lint) ha^{-1} was estimated for an hourly increase in average daily stress time > 5.5 h at Lubbock, Texas.

This chapter explores the relationship between stress time (the duration and extent of canopy temperatures exceeding 28 °C) and the growth and development of cotton. This will determine the optimal ST threshold, for use in a thermal optimal approach to irrigation scheduling, to adequately schedule irrigation in both precision irrigation systems such as drip irrigation, as well as large deficit irrigation systems that characterise the Australian cotton industry.

7.2 Materials and methods

The thermal optimum approach to irrigation scheduling system was analysed through data collected from two surface drip-irrigated cotton (*Gossypium hirsutum* L.) field experiments conducted during the 2007/08 (Experiment 2) and 2008/09 (Experiment 3) seasons, and one deficit furrow-irrigated field experiment conducted during the 2008/09 (Experiment 4) season, at the Australian Cotton Research Institute (ACRI) at Narrabri. It is important to note that the BIOTIC protocol was not used to schedule irrigations in this study. Thus, while the plant responses are not the result of the BIOTIC theory, it is believed that they provide insight into the suitability of the BIOTIC method in an Australian cotton production environment. The BIOTIC protocol performance is thus

inferred, as opposed to measured, in this study. Data was analysed between 85 and 155 days after sowing across all experiments. This was to ensure the same physiological growth stages were analysed and that the cumulative seasonal stress times were not affected by the duration of data collection. Detailed materials and methods of these experiments are described in Chapter 3.

The concept of ST is central to the thermal optimum approach for irrigation scheduling. Wanjura *et al.* (1992) and Upchurch *et al.* (1996) developed this concept, defining it as the daily amount of time that a crop's canopy temperature exceeds an optimum or threshold canopy temperature. Historically, a stress temperature threshold of 28 °C has been used for scheduling cotton irrigation using the thermal optimum concept. This threshold is calculated by estimating the thermal optimum of plant metabolism determined from the temperature dependence of a selected metabolic indicator (Mahan *et al.*, 2005). The significance of the optimum temperature values is discussed in Chapter 4 of this thesis, which concludes that the optimum canopy temperature of 28 °C should be used in Australian cotton cultivars.

The concept of a time threshold (calculated using a leaf energy balance approach) is central to irrigation scheduling using a thermal optimum. This approach calculates canopy temperatures of a well-watered, non-stressed plant at a specific site. The time threshold uses historic weather data collected over the crop growing season and site of interest to produce an arithmetic mean of the length of time per day that the *calculated* temperature of a well-watered crop canopy is in excess of the threshold temperature of

the crop of interest (Mahan *et al.*, 2005) (for more details see Chapter 2). Using this energy balance approach, a calculated irrigation signal STT of 2.75 h (165 min) was determined for ACRI (Myall Vale), Narrabri. Using this method an irrigation signal for cotton growing at ACRI (Myall Vale), Narrabri, would be calculated using a temperature threshold of 28 °C and a time threshold of 165 minutes.

The BIOTIC protocol for irrigation scheduling is based on the cumulative amount of time that a crop canopy exceeds both the temperature and time thresholds. Therefore, a signal to irrigate will occur when the crop canopy is above its site specific, calculated STT. Stress time is the cumulative amount of daily time canopy temperatures exceed 28 °C. Irrigation calls are on a daily basis and represent days when ST exceeds 2.75 hours. Stress times and irrigation calls were calculated using the above methodology for Experiments 2, 3 and 4. It is important to note that humidity was never a limiting factor for transpirational cooling, and thus is not further discussed. The BIOTIC irrigation scheduling protocol was used as a basis for establishing the merits of irrigation scheduling using the thermal optimum concept.

All "BIOTIC irrigation calls" in this analysis were derived from comparison of the crop canopy temperature to the temperature and time thresholds specified in the BIOTIC protocol. A key aspect of the BIOTIC protocol is that it creates a closed irrigation loop in which the T_c over an interval results in an irrigation that in turn determines the T_c over the next interval. It is thought that this repeating "temperature begets irrigation begets temperature" cycle serves to poise the plant on the edge of optimal metabolism. In this

study the loop is not fully present and thus the irrigation/T_c relationships can only be theoretically assessed with respect to the BIOTIC method. It is believed that the linkages will be sufficient to effectively gauge the suitability of the BIOTIC approach to the Australian system and perhaps more importantly to identify avenues for improvement in this approach.

7.3 Results

7.3.1 Evaluating the BIOTIC (average daily stress time) approach to irrigation scheduling

Seasonal stress time patterns were analysed and compared with corresponding soil water deficits and irrigation treatments. This analysis was conducted to determine the stress time-T_c, and stress time-yield relations of precision application and deficit furrow irrigated cotton in Narrabri. As in previous chapters, average canopy temperature refers to mean day-time canopy temperatures estimated for the period when R_g was > 300 W m^{-2}.

Average daily stress time was related to irrigation treatment and average T_c. Stress time followed the same trend as T_c, where stress time increased with corresponding increase in soil water deficit (Figure 7.1, Figure 7.2, Figure 7.3 and Figure 7.4). Stress times were analysed in all experiments over a standardised time period of 85 and 155 days after sowing (between flowering and crop maturity). This was due to a combination of both data availability and confidence in the canopy temperature data following crop canopy

closure (> 85% light interception), and enabled comparisons over similar crop physiological growth stages.

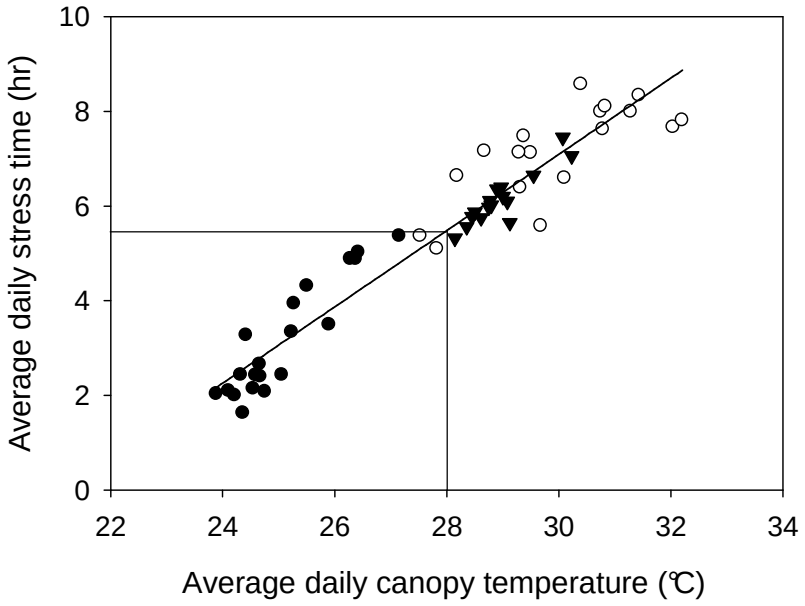


Figure 7.1. Association between average canopy temperature and average daily stress time in Experiment 2 (●), Experiment 3 (○) and Experiment 4 (▼) (y = 0.8056x -17.076; R^2 = 0.92) (P<0.001). When average daily canopy temperature is 28 °C, average daily stress time equals 5 h 24 min.

Average T_c and ST displayed a positive linear relationship (Figure 7.1), where average ST increased by ~ 0.8 hours for every one degree increase in average T_c (P<0.001). It is evident from the T_c and lint yield data that the plants experienced different degrees of water stress within and across years. The data in Figures 7.1 to 7.4 and Table 7.1 indicated that T_c of the irrigation treatments varied as well. This variation is parallel to the variation in water stress response observed in Experiments 2, 3 and 4 of Chapters 5 and 6.

Table 7.1. Average canopy temperature (T_c), duration of time that canopy temperatures exceeded 28 °C (%), average daily stress time (ST), BIOTIC irrigation calls and lint yield (kg ha^{-1}) between 85 and 155 DAS in Experiment 2, 3 and 4. The same superscript letter within a column represent values that are not statistically different at the *P*=0.05 level.

Experiment 2						
Treat	**ET_C (%)**	**Average T_c (°C) (R_g > 300 Wm^{-2})**	**Time T_c > 28 °C (%)**	**Average daily ST (hr)**	**BIOTIC irrigation calls**	**Lint yield (kg ha^{-1})**
1	75	27.8 ^{a}	21.1 ^{a}	5.0 ^{a}	47 ^{a}	2531 ^{ab}
2	93	26.5 ^{b}	16.0 ^{b}	3.8 ^{b}	36 ^{b}	3399 ^{c}
3	107	25.6 ^{c}	11.4 ^{c}	2.7 ^{c}	27 ^{c}	3507 ^{c}
4	123	25.4 ^{c}	9.5 ^{c}	2.2 ^{d}	22 ^{d}	2894 ^{b}
5	140	25.2 ^{c}	8.2 ^{c}	1.9 ^{e}	19 ^{d}	2865 ^{b}
Experiment 3						
Treat	**ET_C (%)**	**Average T_c (°C) (R_g > 300 Wm^{-2})**	**Time T_c > 28 °C (%)**	**Average daily ST (hr)**	**BIOTIC irrigation calls**	**Lint yield (kg ha^{-1})**
1	57	31.4 ^{d}	34.3 ^{d}	8.1 ^{f}	62 ^{ef}	1089 ^{d}
2	67	31.1 ^{d}	34.4 ^{d}	8.1 ^{g}	64 ^{f}	1887 ^{e}
3	77	29.6 ^{e}	30.4 ^{de}	7.2 ^{h}	59 ^{fg}	2518 ^{a}
4	92	29.0 ^{ef}	27.6 ^{e}	6.5 ^{i}	57 ^{gh}	2826 ^{ab}
5	104	28.3 ^{g}	24.8 ^{f}	5.9 ^{j}	55 ^{h}	3039 ^{b}

Treat	**ET_C (%)**	**Average T_c (°C) (R_g > 300 Wm^{-2})**	**Time T_c > 28 °C (%)**	**Average daily ST (hr)**	**BIOTIC irrigation calls**	**Lint yield (kg ha^{-1})**
Full.	62	30.4 ^{d}	28.8 ^{e}	6.9 ^{k}	62^{ef}	2024 ^{e}
Mod.	73	29.6 ^{e}	25.2 ^{f}	6.4 ^{i}	59^{fg}	2468 ^{a}
Cont.	90	29.1 ^{ef}	25.5 ^{f}	6.1 ^{i}	59^{fg}	2657 ^{ab}
Freq.	86	29.1 ^{ef}	24.1 ^{f}	5.8 ^{j}	57^{gh}	2745 ^{ab}

Although it is self evident that average T_c and ST will be correlated, it is important to show that the stress time, calculated by the thermal optimum concept, is consistent over different seasonal pressures. Although crop lint yield is related to crop T_c (see Figure 5.14 and Figure 6.8), more information can be derived from ST than T_c. Furthermore, the ST concept provides a more practical method of irrigation scheduling as irrigation signals represent an accumulation of stress. Therefore, they are not characterised by the need for

an instantaneous irrigation requirement every time T_c exceeds the threshold temperature, which can occur at potential rates of more than once a day, as a T_c threshold does.

Under surface drip irrigated conditions (Experiments 2 and 3), the control and well-watered treatments (Treatments 4 and 5) consistently produced lower stress times than the deficit irrigation treatments (Treatments 1, 2 and 3) (Table 7.1). Under furrow irrigated conditions (Experiment 4) the frequent and control irrigation treatments produced the highest lint yields, and lowest average T_c and daily ST. As soil water deficit increased (under moderately and fully extended irrigation treatments), so too did average daily stress time. Although water supply was adequate in the frequently and control irrigated treatments (85% to 90% calculated ET_C), stress times were relatively high (approximately 6 hours). This may be due to the increased stress experienced by the wetting and drying cycles inherent in furrow irrigation systems.

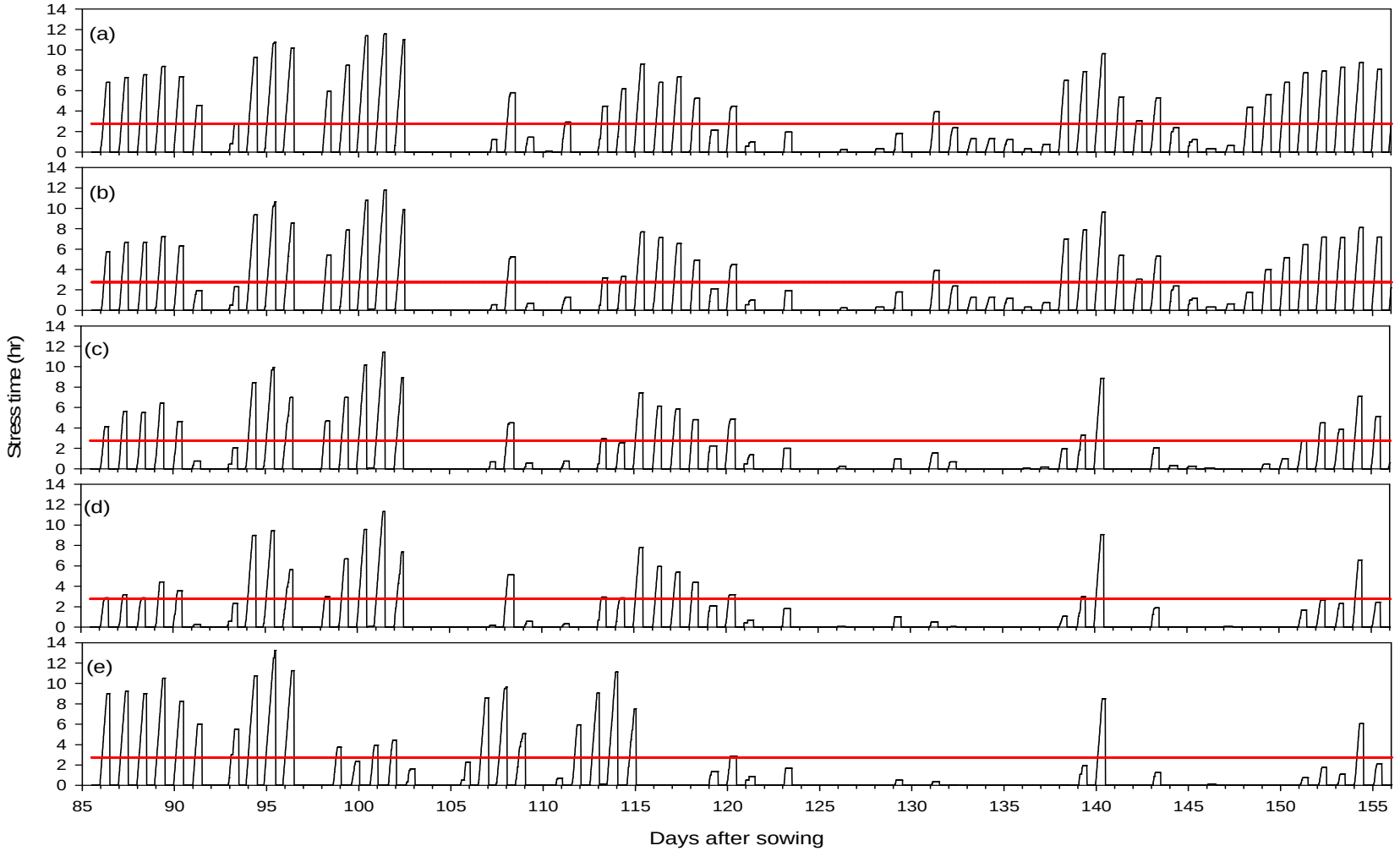


Figure 7.2. Average cumulative daily stress times in Experiment 2 experienced in (a) Treatment 1, (b) Treatment 2, (c) Treatment 3, (d) Treatment 4, (e) Treatment 5 irrigation treatments between 85 and 115 DAS. Peak daily values represent the daily sum of stress time. The red line at 2.75 h represents the calculated stress time-threshold for Narrabri.

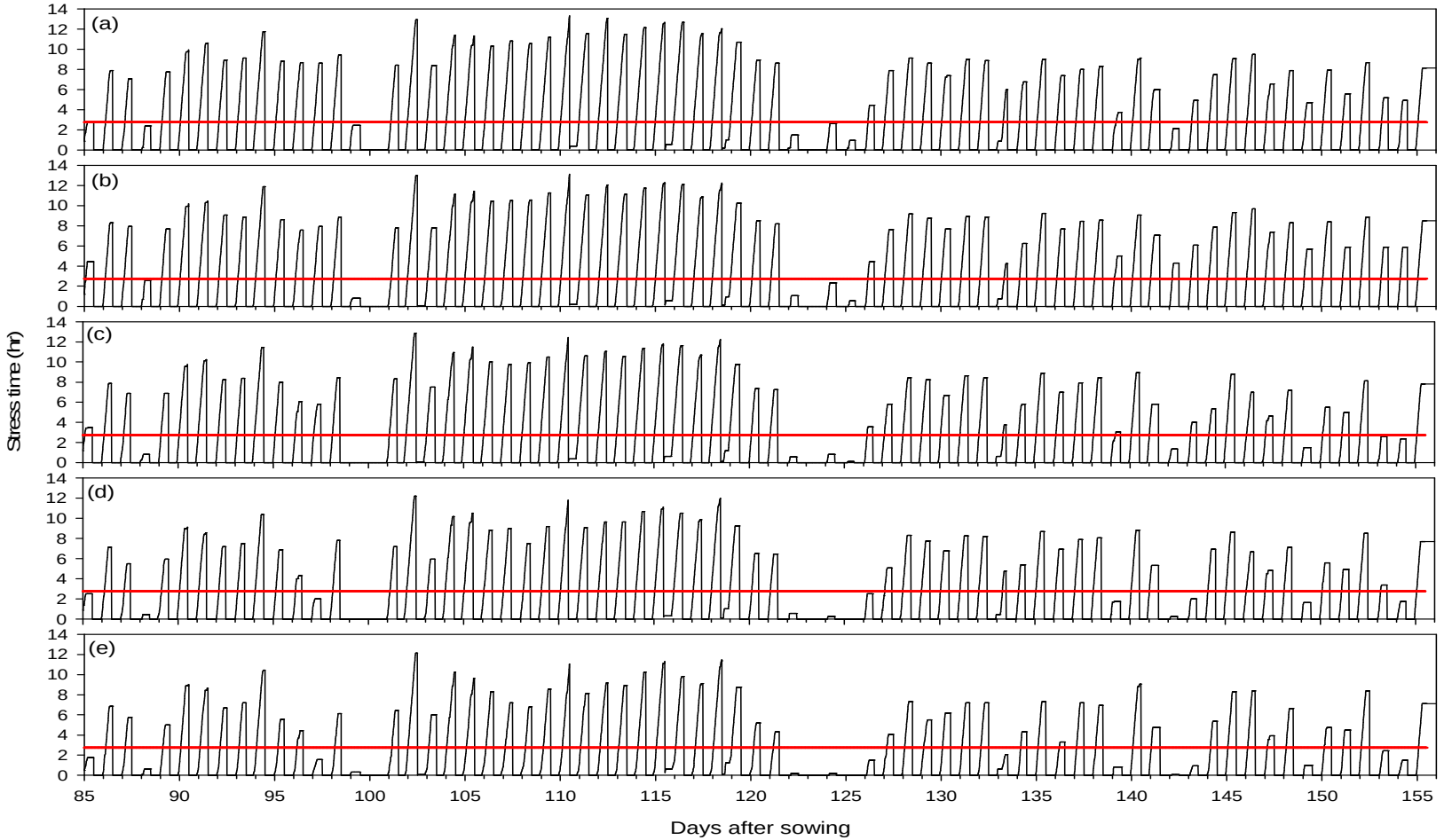


Figure 7.3. Average cumulative daily stress times in Experiment 3 experienced in (a) Treatment 1, (b) Treatment 2, (c) Treatment 3, (d) Treatment 4, (e) Treatment 5 irrigation treatments between 85 and 115 DAS. Peak daily values represent the daily sum of stress time. The red line at 2.75 h represents the calculated stress time-threshold for Narrabri.

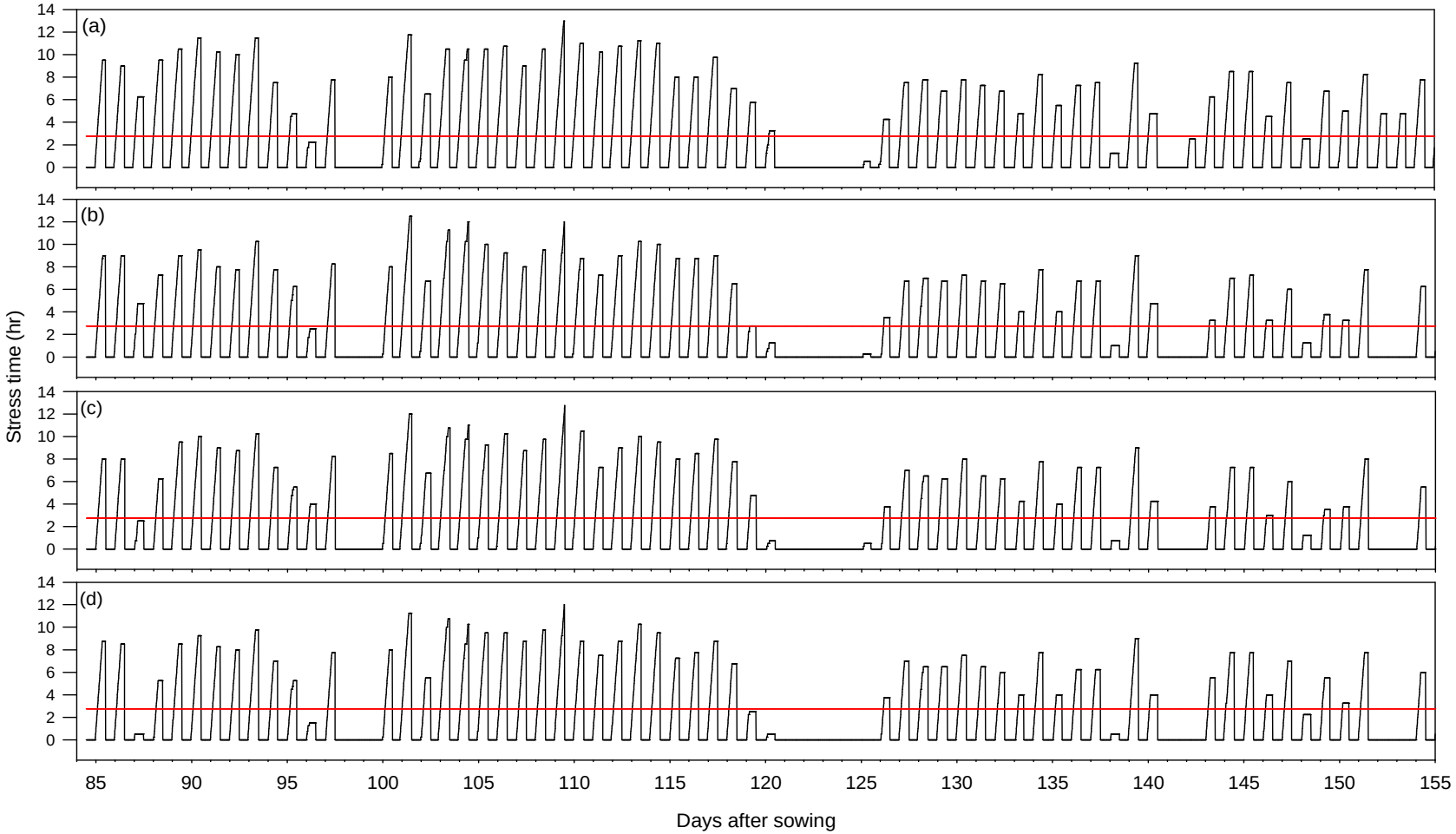


Figure 7.4. Average cumulative daily stress times in Experiment 4 experienced in (a) fully extended, (b) moderately extended, (c) control, and (d) frequently irrigated treatments between 85 and 115 DAS. Peak daily values represent the daily sum of stress time. The red line at 2.75 h represents the calculated stress time-threshold for Narrabri.

An increase in average daily stress time resulted in both an increase in BIOTIC irrigation calls and a decrease in lint yield (Table 7.1). A quadratic relationship was fitted to average daily stress time and final lint yield (R^2=0.65; P<0.001), where peak lint yields were observed between 1.8 h – 5.2 h stress time, with an average of 3.5 h (Figure 7.5a). The difference between the average daily stress time and the calculated STT was 0.75 h (3.5 h – 2.75 h). This suggests that in practice, peak lint yields might be achieved at a slightly higher STT than the calculated STT. Therefore, according to this fitted regression, an average daily stress time-threshold of 4.45 h (5.2 h – 0.75 h) should produce maximum lint yields at ACRI (Myall Vale), Narrabri.

Wanjura *et al.* (1995) proposed that, in lieu of the leaf energy balance for calculating the stress time-threshold, it is possible to estimate the correct time threshold based on measuring the average period of time on a daily basis that the T_c of a well-watered crop would exceed its optimal temperature threshold. Coincidentally, that the value of the time threshold derived from temperature data in Table 7.1 (with respect to the treatment with the highest yield) is 2.7 h ST in Treatment 3 of Experiment 2. This value is in agreement with the calculated STT of 2.75 h, based on weather data for a period preceding this study.

Another common form of plant response to stress is that of a threshold, showing a range of stresses for which no growth penalty is encountered, but with declining performance beyond some critical stress threshold. To test whether this form was a better description of cotton response to stress time, a broken linear equation where the initial linear

response is constrained to exhibit a slope of zero, was fitted to the stress time and yield data (Figure 7.5b). This response saw the threshold ST for yield reduction at 5.16 h ± 0.086 (95% CI of 3.55 to 6.00). Interestingly, the threshold value of ST resulting in lint yield reductions is similar to the calculated upper threshold of ST for maximum yield observed in the quadratic polynomial fit of the same data. A large degree of variation was accounted for in the broken linear response curve (R^2 = 0.6); however, the mean squared error was higher for this threshold regression (*MSE* = 163015) compared with the quadratic regression (*MSE* = 147615), which suggests that the quadratic relationship is a better statistical fit. The implications of this are explored in the discussion.

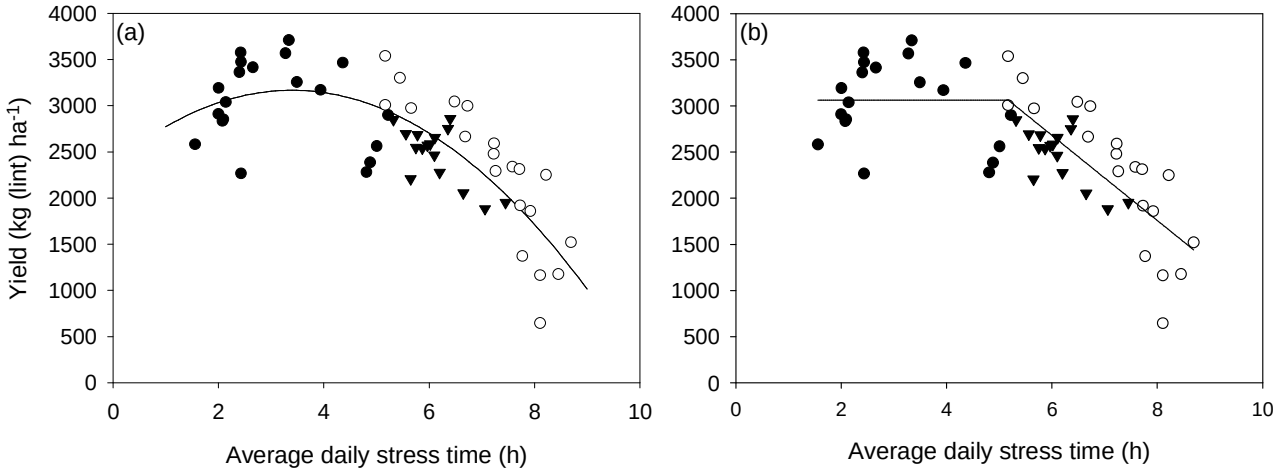


Figure 7.5. (a) Average daily stress time and yield quadratic polynomial regression in Experiment 2 (●), Experiment 3 (○) and Experiment 4 (▼) (y = -68.697x^2 + 467.15x + 2372.8, R^2 = 0.65) (P<0.001); (b) Average daily stress time and yield broken linear regression in Experiment 2 (●), Experiment 3 (○) and Experiment 4 (▼) (when x ≤ 5.16, y = 3061.8; when x > 5.16, y = -461x + 5447.3, R^2 = 0.6).

7.3.2 Evaluating a cumulative stress time index for use in deficit furrow irrigation systems

Under similar total water applications, cotton T_c under furrow irrigation can be warmer than those under drip irrigated conditions (see Chapter 6). The reason for this is the large fluctuations in soil water deficits between relatively infrequent irrigation events (compared with systems such as drip irrigation that can provide irrigation water at almost any frequency). Therefore, furrow irrigated cotton T_c can experience significant periods of time above the temperature threshold of 28 °C, thus experiencing extended durations of stress time before mitigation through irrigation can be applied. However, unlike drip irrigated systems, the nature of furrow irrigation systems limits the frequency and volume of irrigation application, and water cannot be applied as frequently as advised by thermal optimum irrigation scheduling protocols. The following analysis was conducted in order to evaluate and modify the thermal optimum concept of irrigation scheduling in deficit irrigation systems.

Due to the nature of furrow irrigation, and its differences to precision application systems, the frequent (potentially daily) BIOTIC irrigation calls observed in Experiment 4 (Table 7.2) are not physically possible to implement in a furrow irrigated system. In an attempt to adapt the thermal optimum concept to deficit furrow irrigation systems, an analysis of the accumulated stress time for each soil water deficit per scheduled furrow irrigation application was conducted (Table 7.2). This analysis assumed the same starting date as the first soil water based scheduled furrow irrigation. Using the average cumulative stress time between scheduled furrow irrigation events (which were

determined via soil water measured with a neutron moisture meter) the average cumulative stress time for the desired soil water deficit to occur was calculated.

Table 7.2. The number of BIOTIC irrigation calls and number of irrigation calls scheduled with a modified thermal optimum protocol between the first and last studied furrow irrigation events and the cumulative stress time per furrow irrigation event for each irrigation treatment.

	Frequently irrigated	Control irrigated	Moderately extended	Fully extended
Soil water deficit (mm) (av. water applied/irrigation)	35	45	70	105
Range of irrigation volumes applied (mm)	25 to 48	30 to 56	66 to 77	102 to 111
First irrigation event of studied period (DAS)	86	84	88	93
Last irrigation event of studied period (DAS)	149	153	142	114
BIOTIC irrigation calls during studied period (No.)	49	56	43	19
Days in study period with BIOTIC irrigation calls (%)	78	81	79	90
Furrow irrigation events (No.)	8	7	4	2
Irrigations scheduled with a modified thermal optimum protocol (No.)	8	7	4	3
Average stress time between furrow irrigations (h)	53	70	115	167

The fitted regression model (Figure 7.6) shows that the average cumulative stress time increases linearly with an increase in soil water deficit. This relationship occurs over a physiologically viable range of water deficits and is characterised by one ST hour representing an additional 0.61 mm soil water deficit. The measured soil water deficits, scheduled furrow irrigation events and predicted furrow irrigation events based on the thermal optimum concept (calculated from the cumulative stress time for each deficit irrigation treatment) are shown in Figure 7.7 and Table 7.2. In all irrigation treatments the number of calculated furrow irrigation events based on the thermal optimum concept is

the same as the scheduled furrow irrigation events, with the exception of the fully extended (105 mm) irrigation treatment. In this case an extra irrigation event was calculated with the modified thermal optimum protocol. However, this extra calculated irrigation event occurred after crop maturity, and would therefore be ignored in a commercial production setting. In all irrigation treatments the calculated irrigation event occurred within a few days of the scheduled furrow irrigation event, indicating the robustness of this altered protocol (Figure 7.8). This shows that the modified protocol can determine plant stress levels, and indirectly schedule furrow irrigation based on soil water deficits. This is advantageous as the thermal optimum protocol is easier to implement and less time consuming than existing soil water measurement techniques.

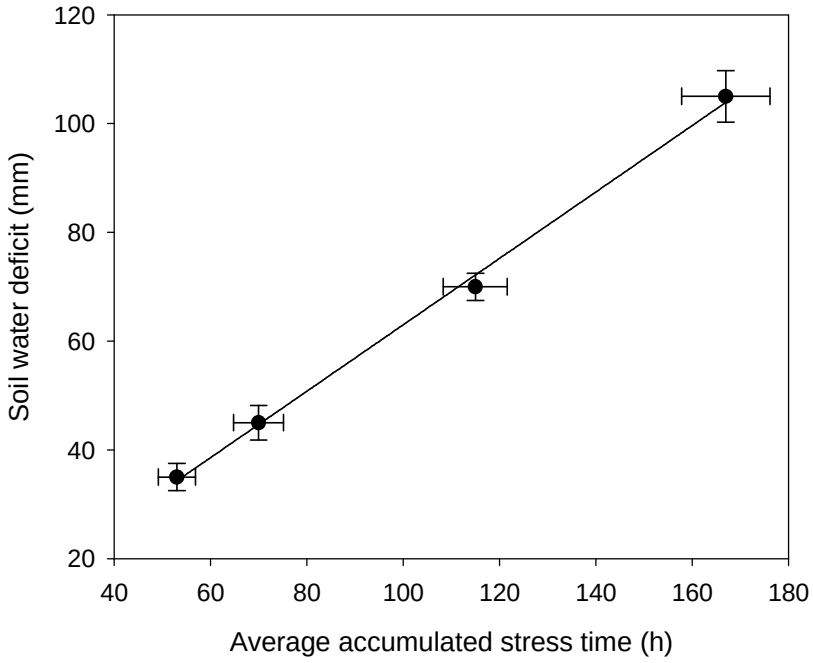


Figure 7.6. Regression model predicting the accumulated stress time between furrow irrigation events on a medium-heavy clay (Vertosol) at 'Myall Vale' Narrabri, at a given soil water deficit ($y = 0.6104x + 1.9482$, $R^2 = 0.99$) (P=0.0011). Bars represent standard error of mean.

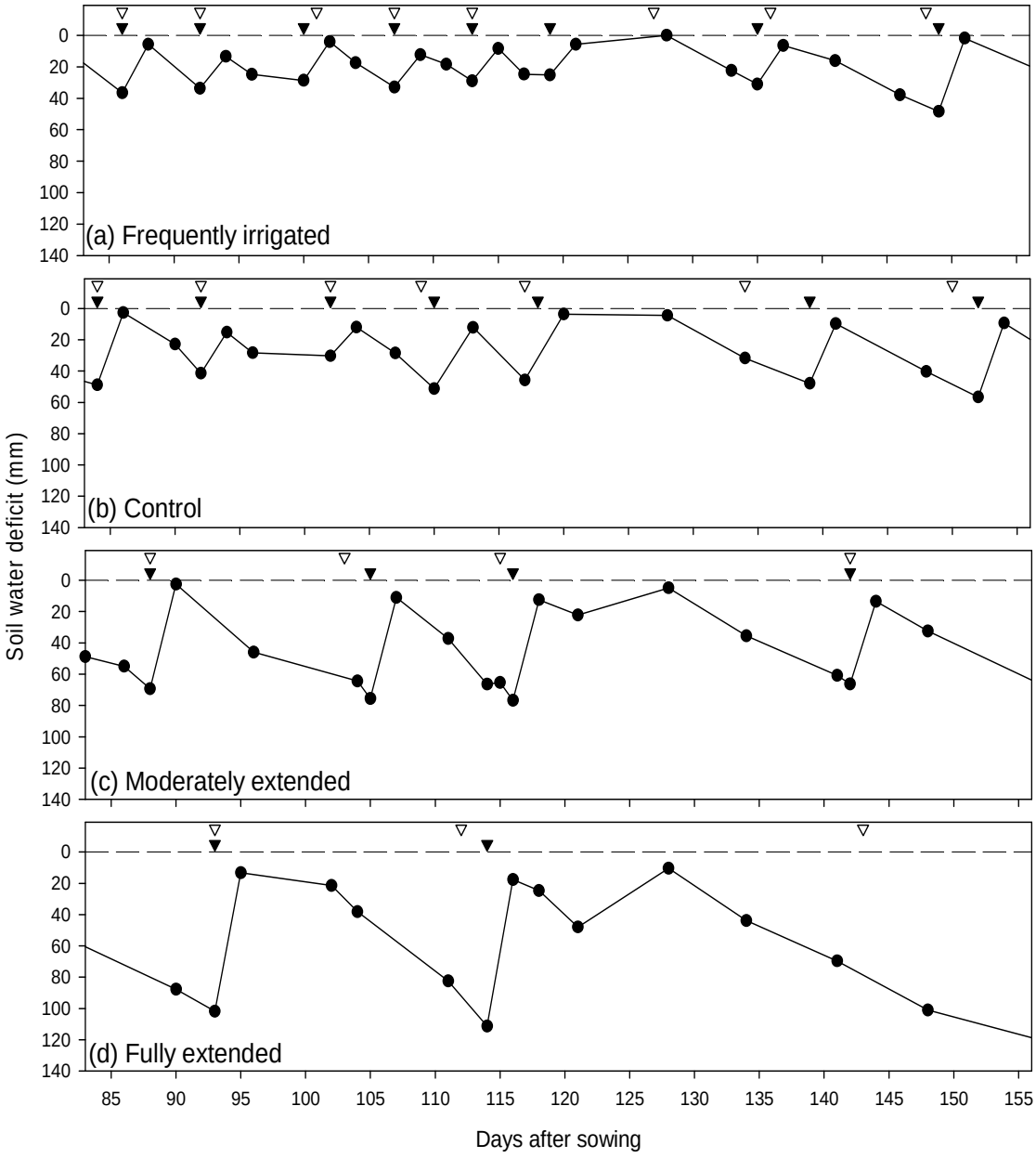


Figure 7.7. Soil water deficits in the (a) frequent, (b) control, (c) moderately extended, and (d) fully extended irrigation treatments with the scheduled irrigation events determined by a NAM (▼) and irrigation events calculated with a modified thermal optimum protocol (▽) using an accumulated stress time for each deficit as shown in Table 7.2.

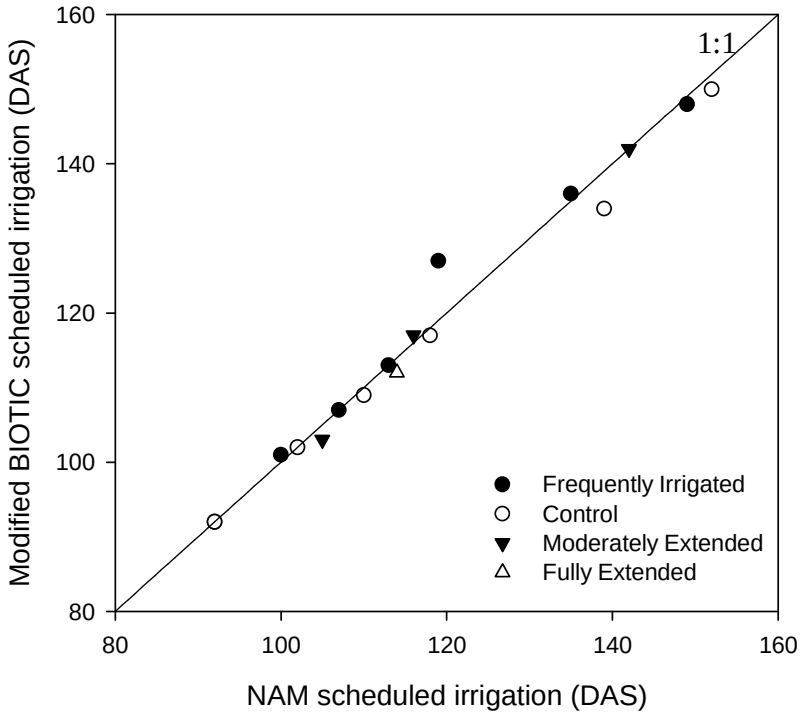


Figure 7.8. Irrigation events scheduled with neutron attenuation meter (NAM) soil water deficit measurements vs. predicted irrigation events with the modified thermal optimum protocol. The line represents a 1:1 line.

7.4 Discussion

Average daily stress times were higher in the 2008/2009 season (Experiment 3 and 4) than in the 2007/08 season (Experiment 2) (Table 7.1). This is aligned with the lower stress potential and higher total water application in the 2007/08 season compared with the 2008/09 season (see Chapter 5). The existing approach to irrigation scheduling using a thermal optimum, BIOTIC, was analysed under conditions observed at Narrabri, NSW. The relationship between stress time and lint yield was similar across Experiments 2, 3 and 4 (Figure 7.5). Wanjura *et al.* (2006) also found a common relationship between ST and yield over three seasons. Their relationship saw an average decline of 343 kg ha^{-1} for every 1 h increase in stress time (above a stress time of 5 h) for days with irrigation signals during the irrigation period. This value is comparable to the data from this thesis,

where yield reductions of 461 kg ha^{-1} for every 1 h increase in ST > 5.2 h. This relationship saw peak lint yields at an average daily ST of 3.5 ± 1.7 h, where yield reductions were observed at ST outside this range. A broken linear equation was also fitted to the data. Although the broken linear equation did not fit the data as well as the quadratic polynomial, the inflection point of yield reduction in this regression was observed at ~ 5.2 hours ST. This value is similar to the upper limit of yield reduction in the quadratic regression.

Using the stress time calculator described by Mahan *et al.* (2005), the calculated stress time-threshold for Narrabri is 2.75 h. This value is at the lower end of the range of ST that resulted in a peak yield. This is because the BIOTIC protocol is designed to meet full irrigation requirement. Furthermore, the STT calculations are based on a combination of theoretical calculations and historical weather data, and thus are subject to error and interpretation. The extent to which more accurate STT values can be obtained has been largely unexplored from an experimental perspective. Average daily stress time values, even in well-watered plots producing lint yields that approached expected peak yields, were often larger than this threshold stress time of 2.75 h (Table 7.1). As peak yields on the quadratic polynomial data fit between 1.8 and 5.2 h ST, and yield reductions were observed at 5.2 h ST on the broken linear equation fit, the calculated stress time of 2.75 h may be conservative in its estimate. Hence, the daily stress time-threshold for ACRI (Myall Vale), Narrabri may be extended to as much as 5.2 h. Although the ST threshold could theoretically be extended to as long as 5.2 h, the potential risk of yield reduction at a longer ST threshold is higher. A new and more water efficient stress time-threshold for

use in the existing BIOTIC protocol, is proposed by calculating the difference between the average daily stress time at peak yield (3.5 h ST) and the calculated stress time-threshold (2.75 h ST). As average daily stress time exceeded the time threshold by 0.75 h (3.5 h – 2.75 h), a theoretical stress time-threshold of 4.45 h is proposed (5.2 -0.75). This proposed threshold utilises the buffer observed between the empirically calculated and the experimentally calculated ST thresholds. Extending the stress threshold from 2.75 to 4.45 h will result in less frequent irrigation applications, ensuring water application is more targeted, providing increased avenues for the full utilisation of in-crop rainfall. This approach may also result in reduced irrigation water application, enabling the production of both peak yields with optimal water use, whilst minimising the risk of yield reductions due to management constraints.

This existing thermal optimum approach to irrigation scheduling, BIOTIC, is limited in that it is designed for precision, low volume irrigation application systems. Therefore in its original form, BIOTIC has not been implemented in large deficit and furrow irrigation systems. A regression model was fitted to calculate the cumulative stress time calculated by the thermal optimum approach before a given soil water deficit is reached by a cotton crop grown on a medium-heavy clay (grey Vertosol) at Narrabri (Figure 7.6). This was determined to be an average of 0.61 mm soil water depletion per stress time hour, and can be used as a guide for the desired soil water deficit to be scheduled by the thermal optimum approach to irrigation scheduling. This method appears to be robust as it consistently calculates irrigation events in a similar time frame as those determined from soil water measurements from a neutron moisture meter (Figure 7.7). Furthermore, this

stress time accumulation method takes into account the potential for different degrees of stress experienced by a crop. For example, the daily water demand of a crop can be as high as 10 mm to 14 mm, and as this regression integrates an accumulated stress time period, it presumably takes into account daily differences in stress potential. This cumulative stress time approach to irrigation scheduling with a thermal optimum is advantageous as it can be easily implemented in the existing thermal optimum protocols, is simple and less time consuming than existing soil water measurement techniques.

Furrow irrigation data from this experiment was collected from only one field season, and further data analysis over a range of growing seasons needs to be conducted. Furthermore, as the soil water deficit increased the data set for the cumulative average stress time correspondingly decreased. This is because the number of irrigation cycles was reduced in a large soil water deficit treatment. Therefore, to increase the confidence of these average cumulative stress times at higher water deficits, these conditions should be further investigated in field experiments replicated over numerous growing seasons. No irrigation scheduling was determined directly by the stress time or cumulative stress time approach to irrigation scheduling in drip or furrow irrigated systems; hence, further research should be conducted in this area. Once these limitations are addressed, the stress time and cumulative stress thresholds proposed in this thesis should be adequate for scheduling of irrigation at Narrabri, NSW.

The protocol for irrigating with the daily stress time approach and cumulative stress time approach was calculated with field based observations. These observations may be site-

specific, and their use may be limited in environments that differ to that of Narrabri. Therefore, when using either of these approaches to irrigation scheduling with a thermal optimum outside of the Narrabri environment, caution should be exercised when scheduling with these parameters. The use of STT estimation outlined by Mahan *et al.* (2005) is still valuable in determining a theoretical guide before multiple seasons of data can be used to accurately calculate the threshold for the site in question. Finally, both the daily stress time approach and cumulative stress time approach assume a metabolic equivalence of all T_c in excess of the putative optimum. Therefore, a thermal optimum approach that does not assume such temperature equivalence would presumably be advantageous.

The previous analysis (see 7.3.1) indicated that the T_c as processed according to a BIOTIC protocol reflected much of the variability in plant performance in terms of yield and irrigation. The calculated time threshold of 2.75 h was similar to the amount of time over optimal temperature that was measured in optimally irrigated treatments (based on lint yield). However the data suggest that yield might be optimised across a wider range of time thresholds indicating the possibility that another form of accumulated stress might be useful.

The BIOTIC protocol was developed to provide irrigation scheduling in settings where the goal was to apply full irrigation with a short irrigation interval. Initial development used surface drip with an irrigation interval of 15 min. The protocol has been validated using irrigation intervals of up to 5 d using lateral move irrigation systems (Mahan *et al.*,

2005; Wanjura *et al.*, 2006). With increasing use of deficit irrigation there is an ongoing need for irrigation scheduling schemes that are designed for conditions where irrigation amounts may be less than optimal and irrigation intervals will be more on the level of days than hours.

While the developers of BIOTIC investigated the response of crops to non-optimal temperature and time thresholds, these efforts were directed toward defining optimality, not deficit irrigation. Modifications of the BIOTIC protocol could involve non-optimal temperature thresholds or modified time thresholds. Either approach is valid. In this study the modification of the time thresholds has been investigated.

A potentially important limitation in the ST concept as a means of accumulating and quantifying time at temperatures above the temperature threshold lies in the fact that temperatures above the temperature threshold are accumulated without regard to the extent of the temperature elevation. The concept of an intrinsic thermal optimum for plant metabolism implies that temperatures above the thermal optimum are most probably not equal in terms of their metabolic impact on the plant. The BIOTIC protocol is based on the goal of avoiding excess temperatures, through irrigation, so that both the water status and metabolic activity of the plant will be optimised. Under conditions where there is a significant (hours to days) delay between the observation of elevated temperatures and the application of irrigation, the assumption that elevated temperatures are the equivalent becomes tenuous. This assumption is apparently sufficiently accurate to provide acceptable irrigation management under many conditions but may not be universally

applicable. In an effort to limit metabolic effects on plants when water cannot be managed in such a way as to prevent excessive temperatures, a more mechanistic approach to the accumulation and interpretation of ST might result in an improved ability to manage irrigation with T_c measurements.

A stress time accumulator that takes into account both the amount of time above the temperature threshold and the extent to which the threshold is exceeded might improve the mechanistic basis of the method and improve the ability to manage deficit irrigation using canopy temperature. A theoretical analysis of stress time accumulation was constructed (Figure 7.9). With respect to the T_c over the course of a day, there are three general possibilities for ST and yield:

(1) Average daily canopy temperature is less than the optimal temperature, stress time accumulation is minimal, resulting in theoretical yield production of less than the optimum (Option 1);

(2) Average daily canopy temperature is equal to the optimal temperature, stress time accumulation is moderate, resulting in optimal yield production (Option 2);

(3) Average daily canopy temperature is greater than the optimal temperature, resulting in a high level of ST accumulation, resulting in theoretical yield production of less than the optimum (Option 3).

By definition, given these conditions, there will be a finite and optimal ST accumulation when average daily canopy temperature is equal to the optimum canopy temperature for the crop. Hence the yield vs. stress time response will result in a maximum.

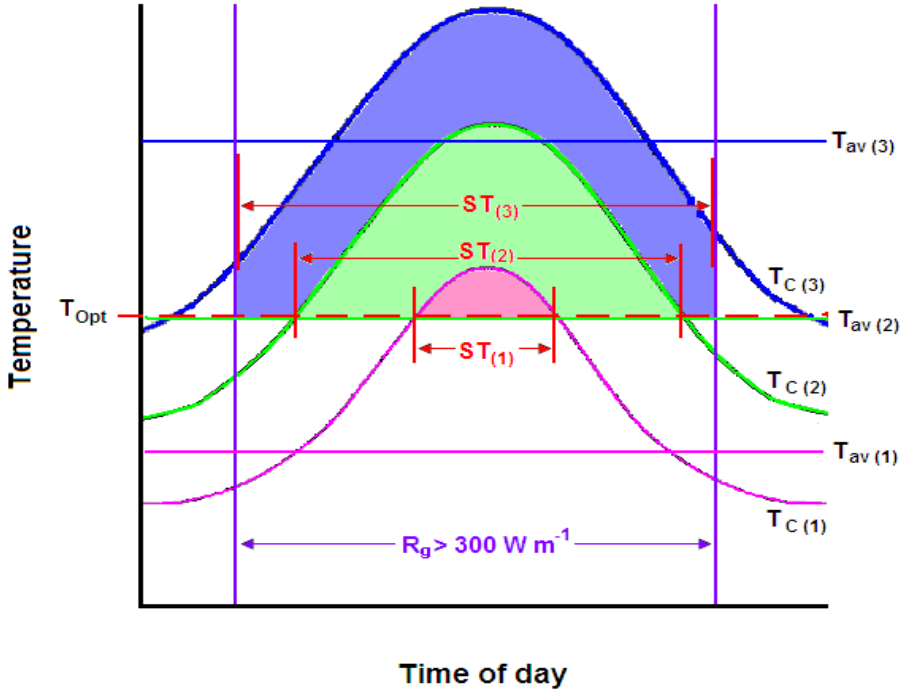


Figure 7.9. Sketch showing three possible outcomes for stress time accumulation. Option 1 is represented by the pink thermal trace, Option 2 by the green thermal trace, and option three by the blue thermal trace. Cumulative stress time accumulation is represented by the shaded areas between the optimal temperature and the daily thermal trace, when a net irradiance is greater than 300 W m^{-1}. R_g= short-wave irradiance, T_c = Canopy temperature, T_{av} = Average canopy temperature when R_g > 300 W m^{-1}, ST = Stress time, T_{Opt} = Optimal temperature.

By definition, stress time is the area under the temperature curve and above the optimal temperature when R_g exceeds the lower limit of 300 W m^{-1}. The thermal environment and water use are driven by solar irradiance. Whilst significant amounts of energy are intercepted by the crop canopy over a given season, only a fraction is used by photosynthesis and the rest, including heat energy has to be dissipated to keep plant T_c within a range that is conducive to biological processes. A potential limitation of the ST approach is that it treats all T_c in excess of the temperature threshold as equivalent. This stress time equivalence limits the utility of the BIOTIC approach as a tool for deficit irrigation scheduling. A more accurate description should be able to account for the

degree of stress imposed. Therefore, a new parameter, the sum of daily stress time accumulation is proposed. This is essentially the sum of the thermal stress experience, in terms of temperature and time over the growing season, and accounts for differences in the magnitude of the thermal stresses experienced by the plant. The purpose of this approach is not only to capture periods of thermal variation, but also attempt to capture some of the effect of thermal variation on metabolism. The original BIOTIC approach, outlined by Mahan *et al.* (2005), was to prevent non-optimal temperatures through water application. This new approach attempts to weight the metabolic impact of elevated temperatures against the water savings that can be realised.

The sum of stress time accumulation is calculated using Equation 14, and has units of degree-days, similar to other responses to thermal experience such as germination and shoot elongation (Oryokot *et al.*, 1997).

Equation 14. Cumulative sum of stress time approach to stress detection between the study period of 85 to 155 DAS

$$Cum.\ Sum\ ST_i = \sum_{i=85}^{115} \frac{(T_{C,i} - 28)}{96}$$

Where T_c is the average canopy temperature (°C) for a 15 minute period as measured by BIOTIC IRTs, and T_{Opt} is the optimal temperature of the crop, which for cotton is 28 °C as outlined in Chapter 4. The difference between the actual T_c and the optimal temperature is multiplied by 15 and divided by the product of 60 and 24 in order to convert the units to cumulative sum of stress time 'degree-days'. This is a function of the

15 minute temperature sampling interval used in the experiments and would have to be modified to suit other sampling frequencies.

The integration of the thermal experience over the life of the crop has a basis in the robust stability of the optimal temperature across various time scales, from fluorescence traces on an instantaneous timescale, through to photosynthesis measurements, and finally yield measurements which integrate stress on a seasonal time scale (see Chapter 4). This shows that the plant performance reflects an accumulation of short-term responses to instantaneous thermal experience.

The sum of cumulative stress time in Experiments 2, 3 and 4 was calculated using the above methodology (Figure 7.10). This response was fitted with a linear equation with a negative slope, where lint yield decreased as the sum of cumulative stress time increased. Using this regression, a theoretical maximum yield of ~ 3400 kg (lint) ha^{-1} could be obtained if the crop experienced zero degree-days cumulative stress time. This value could represent a maximum achievable lint yield under regular environmental conditions where some stress is inevitable. Although this value is 900 kg (lint) ha^{-1} short of the maximum sustainable cotton yield proposed by Constable and Bange (2006), they conclude that no stress, perfect sunshine and peak values for boll growth rates must occur for a maximum yield of 4300 kg (lint) ha^{-1} to be achieved. The fit of this regression was improved (with an R^2 of 0.7) compared with the fitted regressions of Figure 7.5b and Figure 7.5a. Therefore, this new measure may provide a clearer picture on the T_c response to water stress.

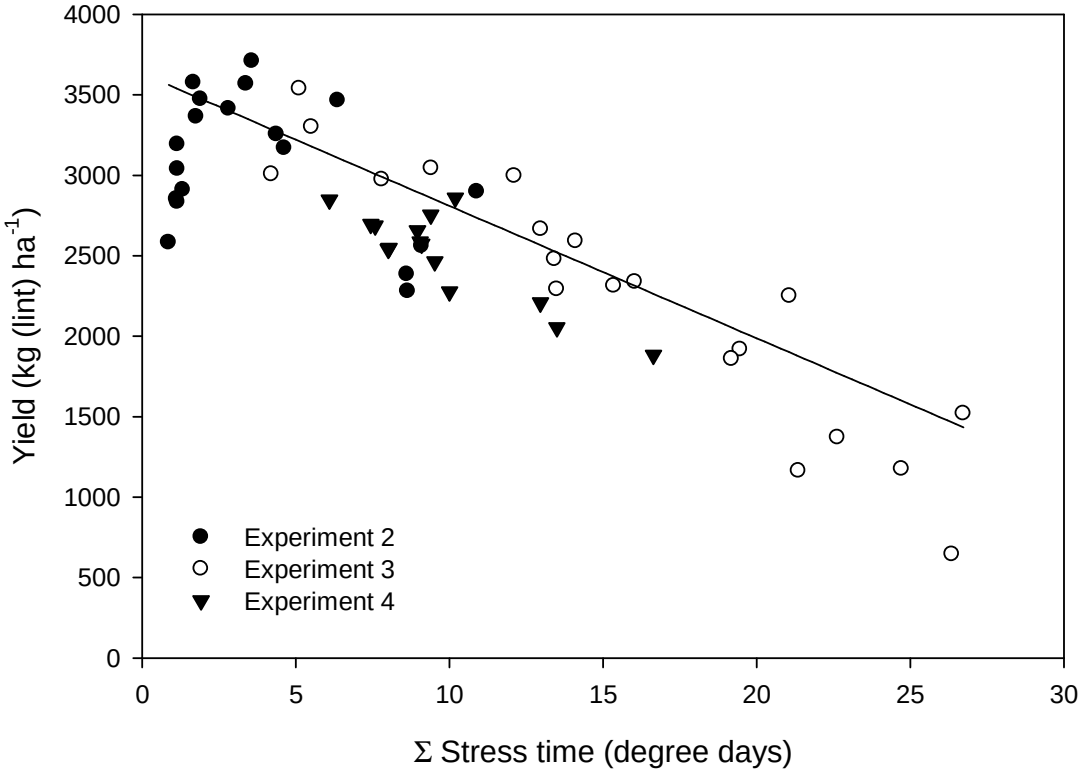


Figure 7.10. Sum of stress time and yield regression in Experiment 2 (●), Experiment 3 (○) and Experiment 4 (▼) (y = -82.2x + 3431.6, R^2 = 0.75) (P<0.001) calculated based on an optimal temperature of 28 °**C**. The R^2 value is significantly improved from 0.6 in Figure 7.5b and 0.65 in Figure 7.5a.

This response did not account for sum of cumulative stress time when average daily T_c is less than the optimal temperature threshold. Therefore, the increased scatter in the data at sum of ST between zero and one degree-days may be the effect of crops with a reasonable proportion of sub-optimal thermal experience, and hence, the reduced lint yield. However, this may also be the result of poor agronomic management observed in Experiment 2 where treatments with higher water applications resulted in rank growth and reduced lint yields (see Chapter 5). Future work should consider how to incorporate into the sum of cumulative stress time approach when average daily canopy temperatures

are less than the optimal temperature. This can potentially further improve the explanation of yield differences at low sum of ST.

Since plant water deficits develop over timescales of days to weeks, and some developmental and adaptive responses also occur over similar timescales, it is generally regarded that the most appropriate measures of stress for agronomic purposes are integrated over time and space (Jones, 2007). Examples of successful integrated measurements in plant physiology include growing and germination degree-day requirements (Oryokot *et al.*, 1997; Jones, 2007). As the sum of cumulative stress time approach to stress detection is an integrated approach to stress detection, it may be considered superior to existing measures of stress time accumulation. This is because this determination of stress time includes both the duration and degree of stress imposed. Therefore, despite the modifications and improvements made to the original ST threshold approach (outlined in sections 7.3.1 and 7.3.2 of this chapter), a sum of cumulative stress time approach to irrigation scheduling may be a more accurate indicator of water stress.

Unlike the average daily stress time and cumulative stress time approach to irrigation scheduling, this proposed method to irrigation scheduling using the thermal optimum approach does not assume an equivalence of canopy temperatures in excess of the temperature threshold. However, in its current form, an adequate threshold value for the sum of cumulative stress time needs to be determined for its use in a thermal optimal approach to irrigation scheduling. At present a sum of cumulative stress time of zero should produce maximum lint yields. However, this value is problematic as a value of

sum of cumulative stress time of zero would schedule irrigation events at very high frequencies, resulting in problems with the practical implementation of this threshold. This of course highlights the essence of effective irrigation management that occurs on the edge between theory and practice. Improved understanding of plant water relations inevitably lead to new paradigms in management. Unfortunately for these ideas to have impact in the field, they must be modified to accommodate the realities of the irrigation system in which they will be implemented. Therefore, this proposed protocol needs field validation, where different sums of cumulative stress time values are tested for lint yield response and WUE. It was not the intention of this thesis to evaluate, with field based experimentation, the proposed modifications to the thermal optimum protocol. This would be a potential focus for further research.

Further limitations of the thermal optimum approach to irrigation scheduling need to be addressed. These include the ability of the system to accurately measure T_c before canopy closure and the effect of background T_s, the effect of lower than optimal ambient temperatures on the T_c and hence stress detection, determining whether flowering, the most susceptible physiological growth phase to water stress (Grimes *et al.*, 1970), requires a different ST threshold to the more water stress tolerant growth phases, and a method to predict the first irrigation of the season using a thermal optimal approach. These limitations, and others, have been recognised and will be further discussed in the General Discussion (Chapter 8).

7.5 Conclusion

This chapter addressed some of the issues faced by current thermal optimum approaches to irrigation scheduling. It provided either modifications to existing practices, and proposed new protocols, for use in thermal optimum irrigation scheduling protocols. Although none of these protocols have been validated under field conditions, they are supported by empirical field data. This chapter is the beginning of research opportunities in fine-tuning a system of irrigation scheduling using a thermal optimum protocol, and further work is required in this field.

Using the average daily stress time approach to water stress detection, significant lint yield reductions were observed when average daily ST > 5.2 h. Although the STT could theoretically be extended to as much as this value, it is suggested that average daily ST should not exceed 4.45 h. This new threshold should produce similar yields to that of the calculated estimate of 2.75 h, and result in higher water use efficiencies, as similar yields can potentially be achieved with a reduction in the number of irrigation events. This proposed threshold system could be effectively used in the existing thermal optimum irrigation scheduling protocol, BIOTIC, but needs to be validated under field conditions over a number of growing seasons.

A new thermal optimum irrigation scheduling protocol was developed for use in large deficit and furrow irrigation systems. A cumulative stress time approach, spanning over a number of days, which provides an estimate of a given soil water deficit, is proposed to adapt the thermal optimum approach to such irrigation systems. This adaptation to the

thermal optimum concept calculates a 0.61 mm reduction in soil water for every one hour accumulation of ST. This proposed threshold system should be further validated with multiple seasons of data collection, and by using this protocol to schedule irrigation. Further research may also investigate the use of this protocol in commercial situations such as when to apply a strategic irrigation event when the volume of available water is limited to one irrigation event, and when the first irrigation event of the season should occur.

Finally an integrated approach to stress detection was proposed. This approach is the sum of cumulative stress time and should improve the accuracy of a stress time-threshold. This sum of cumulative stress time incorporates both a duration and degree of stress time accumulation. This approach showed an 82 kg (lint) ha^{-1} decrease in lint yield with every degree-day increase in sum of cumulative stress time. This is a novel theoretical approach to determining a stress time-threshold, and has not yet been validated under field based situations. Therefore, future work should aim to incorporate this approach to stress detection in thermal optimal protocols. Future work should also investigate how to incorporate sum of cumulative stress time for days when average daily canopy temperatures are below the thermal optimum threshold.

The thermal optimum concept and scheduling irrigation based on stress time accumulation has been shown to be a robust irrigation scheduling method, ensuring effective stress detection for irrigation scheduling in both precision application and deficit irrigation systems. Now that temperature and stress time-thresholds have been

analysed in Australian production systems using an Australian cultivar, the modified thermal optimum protocols can be validated in both drip and furrow irrigation systems. With some modification to the existing protocol, it is conceivable that this system could be used to schedule deficit irrigation using the thermal optimum approach proposed in this thesis.

8. GENERAL DISCISSION

Water is one of the most limiting factors to Australian cotton production (Roth, 1993). This dependence has been highlighted by recent trends in the area of cotton plantings in Australia, which has been severely reduced due to the combination of drought and decreased water allocations. Water stress adversely affects numerous physiological and biochemical pathways, ultimately resulting in reduced plant growth, performance and lint yield (Hearn, 1994; Hearn and Constable, 1984). The Australian cotton industry has historically been characterised as an intensive production system, based on high inputs of irrigation water, fertiliser and intensive integrated pest management (Fitt, 1994). However, in the current climate of increasing demand between end users of water, irrigation scheduling for efficient water use has become a central issue to ensure the sustainability of the Australian irrigated cotton industry. Currently, cotton farmers use a combination of soil water deficit measurements from capacitance and neutron probes, evapotranspiration calculations, or simply experience and subjective field observations of crop symptoms to make irrigation decisions (Roth, 1993). Due to limitations in irrigation scheduling systems such as cost, complexity and inability of the system to adequately and easily detect water stress, and calculate when irrigation is necessary, many of the proposed irrigation scheduling techniques are not used by farmers for commercial crop management. This study aims to assess the utility of a potential simplified method of irrigation scheduling, based on crop T_c.

Although plant based measurements of water stress correlate the soil and atmospheric load contributing to plant water deficit; it is not common to schedule irrigations using plant based measurements (Mahan *et al.*, 2000). Plant based stress detection tools use the plant to directly determine stress levels, not indirect measurements of the plant's growing environment such as soil water and atmospheric load. Therefore, these plant based measurements are theoretically advantageous (Jones, 2004b; Jones, 2008). The advent of increasingly affordable and reliable IRTs and imagery has stimulated plant based stress detection, through the monitoring of crop canopy temperatures (Jackson *et al.*, 1981; Jones, 2004a). It is well established that water stressed plants exhibit higher T_c due to reduced evaporative cooling (Jackson *et al.*, 1981; Idso, 1982; Mahan *et al.*, 2005; Jones, 2004a). The Biologically Identified Optimal Temperature Interactive Console (BIOTIC) protocol uses the relationship between T_c and plant water status to schedule irrigation based on a temperature-time-humidity threshold system. This protocol works by scheduling irrigations when the crop's T_c exceeds an optimal temperature threshold for a pre-determined period of time, and when relative humidity is not limiting evaporative cooling (Mahan *et al.*, 2005). The optimum temperature is derived from the thermal dependence of metabolic indicators and the time threshold represents the average daily period of time that a well-watered crop's T_c can exceed its optimum temperature (Mahan *et al.*, 2005). This study is the first step in adapting the BIOTIC protocol to Australian cotton production systems for use in both precision application and deficit furrow irrigation systems. This chapter discusses the primary goal of this thesis, assessing the utility and proposed modifications required to schedule irrigation in Australian cotton production systems using the BIOTIC protocol.

The hypothesis that T_c provides sufficient information for irrigation scheduling was investigated in surface drip and furrow irrigated cotton. Drip irrigation experiments were conducted over two seasons using the ET_C approach to irrigation scheduling to achieve differences in plant water status. The water relations of cotton were observed in deficit, adequate and excessive water treatments, resulting in differences in lint yield, plant architecture, growth, biomass accumulation and T_c. Differences in seasonal stress potential imposed on the experiments resulted in differences in both yield-water relations and canopy temperature-water relations across the two experiments. However, the relative difference in lint yield-water relations was constant across both experiments, where peak yields occurred at 822 mm water (108% ET_C). Canopy temperature consistently detected water stress over a range of environmental conditions and seasons in the drip irrigation experiments. Similar peaks in T_c-yield relations across growing seasons were observed, despite variations in seasonal pressures resulting in differences in evaporative demand. Significant yield benefits were observed when average T_c was maintained close to 28 °C. This observation is important in the context of the BIOTIC irrigation scheduling system, which uses a threshold T_c for stress detection and irrigation scheduling.

Similar experiments conducted in furrow irrigated cotton showed that average T_c of furrow irrigated cotton were warmer than those of drip irrigated cotton. However, further inspection of T_c in both furrow and drip irrigated cotton showed similar responses to water application with regards to lint yield-T_c relations, regardless of the net volume of applied water per irrigation event and interval between irrigation events. This suggests

that that T_c is a dynamic predictor of water stress. The size of the soil water deficit and potential plant adaptation to previous water stress in the wetting and drying cycles of a furrow irrigated crop do not influence the average canopy temperature patterns in response to soil water deficits. Therefore, T_c have potential use in irrigation scheduling and water stress detection in both deficit furrow and surface drip irrigation systems, with precise detection of crop water stress across varying seasonal pressures. However, further analysis of the temperature-time threshold system was conducted to determine whether modifications to this protocol are required for the production of peak yield and WUE.

The optimum temperature range for cotton metabolism has been extensively studied, with evolutionary, physiological, enzymatic and lint yield responses all indicating an optimal plant temperature of ~ 28 °C. Enzymatically, the minimum observed K_m of a studied enzyme has been used to determine optimal temperatures for plant metabolism and enzyme function. Mahan *et al.* (1987) and Burke *et al.* (1988) observed the minimum K_m of cotton glyoxylate reductase at 27.5 °C, between a range of 23.5 °C to 32 °C. As the thermal optimum of plant metabolism is an important concept in the BIOTIC protocol and research on the optimal temperature of cotton has previously been conducted predominantly in the USA, the accuracy of this threshold in an Australian cultivar was verified. Using chlorophyll fluorescence recovery rates and photosynthetic and stomatal rates at discrete leaf temperatures, the optimal plant temperature of the commercial Australian cotton cultivar Sicot 70BRF also was determined to be ~ 28 °C (27 °C to 31 °C). This optimal plant temperature of 28 °C was supported by the observation that lint yield benefits occur when average canopy temperatures are maintained as close to 28 °C

as possible (Chapters 5 and 6). Furthermore, the thermal optima of Sicot 70BRF is similar to that of cotton cultivars studied by Burke (1990), Burke *et al.* (1988), Upchurch *et al.* (1996) and Mahan (2000), which use both similar physiological methods and divergent enzymatic and plant performance indicators to determine a thermal optimum of cotton at ~ 28 °C ± 3 °C.

The effect of stress time on the growth and development of cotton was investigated to determine the optimal BIOTIC stress time threshold. The determination of the stress time threshold is imperative for irrigation scheduling using the BIOTIC protocol in both precision irrigation systems such as drip irrigation, as well as large deficit irrigation systems that characterise the Australian cotton industry. The response of average daily stress time and BIOTIC irrigation calls to irrigation treatment and canopy temperature was monitored in field based surface drip and furrow irrigated conditions over two seasons. Average T_c-stress time relations and stress time-lint yield relations were similar across all experiments. For an increase in stress time of one hour, average daily T_c rose by 0.81 °C, which ultimately resulted in a 414 kg ha^{-1} lint yield reduction (when average daily ST > 4 h).

An increase in average daily T_c was associated with irrigation treatments receiving less frequent and/or less total water. This resulted in a larger daily stress time accumulation period, which was correlated with decreased lint yield where peak yields were observed at 3.5 ± 1.7 ST h (1.7 -5.2). This highlights the sensitivity of cotton to both sub- and supra-optimal water supply. As average daily ST exceeded the calculated stress time

threshold of 2.75 h by 0.75 h, a new stress time threshold of 4.45 h (5.2 -0.75) was proposed for drip irrigation systems. This new threshold should result in higher water use efficiencies, as similar yields can potentially be achieved with a reduction in the number of irrigation events. This proposed threshold system needs to be validated in field conditions for numerous growing seasons.

The BIOTIC protocol was not designed for use in deficit and furrow irrigation systems and modifications to the protocol were necessary for use in scheduling large volume irrigations on a broader time scale. A cumulative stress time approach, spanning over numerous days, is proposed to adapt the BIOTIC protocol to such irrigation systems. This adaption to the BIOTIC protocol calculates a 0.61 mm reduction in soil water for every one hour accumulation of stress time. This proposed threshold system is advantageous as it is easier to implement and less time consuming than existing soil water measurement techniques. However, it should be further validated with multiple seasons of data collection, and by using this protocol to schedule irrigation.

Finally, an integrated approach to stress detection is proposed. This approach is the sum of cumulative stress time and should theoretically improve the accuracy of a stress time-threshold. This sum of cumulative stress time incorporates both a duration and degree of stress time accumulation. The approach showed an 82 kg (lint) ha^{-1} decrease in lint yield with every degree-day increase in sum of cumulative stress time. However, this is a theoretical approach to determining a stress time-threshold, and therefore has not been applied in field-based situations. Therefore, future work should aim to incorporate this

approach to stress detection in thermal optimal protocols. Future work should also investigate how to incorporate sum of cumulative stress time for days when average daily T_c < thermal optimum threshold.

8.1 Suggested future work

This study evaluated the temperature-time threshold system of irrigation scheduling in Australian environmental conditions and under precision application and large deficit furrow irrigation. However, there are several opportunities for further research as a result of this study, as summarised below:

(i) Evaluate the efficacy of the BIOTIC protocol to schedule irrigation in precision application systems. Research should also be extended into a variety of environments, soil types and cultivars.

(ii) Further investigate the cumulative stress time threshold proposed in this study, over more growing seasons and in a variety of soil types to validate this cumulative stress time approach to furrow irrigation scheduling. Once this achieved, schedule furrow irrigation with the modified BIOTIC protocol. It needs to be acknowledged that in its present state, this method assumes that one particular growth phase is not more susceptible to water stress than another. However, the effects of water stress on cotton yield are most pronounced during flowering (Grimes *et al.*, 1970). Therefore, it must be investigated whether the current ST threshold has been artificially lowered to

ensure yield reductions are not observed, or is too high based on the average of the data from flowering to crop maturity. This future investigation may necessitate the requirement for two or more separate ST thresholds, which are used during the different physiological growth stages, ensuring more efficient water use.

(iii) Once the BIOTIC protocol has been used to schedule irrigation in Australia, modifications to the protocol can be made to adapt the system to a variety of commercial situations such as to:

- Determine the cumulative stress time threshold to schedule a single supplementary irrigation for skip-row or dryland systems with access to only enough water for a single irrigation.
- Determine the cumulative stress time experienced by a crop before the first irrigation is necessary. This approach may be difficult as there are problems associated with viewing the background soil before canopy closure has occurred. Therefore, the boundary conditions for accurate canopy temperature due to incomplete canopy closure need to more rigorously defined.

(iv) Investigate when T_c, and hence stress times, may not be reliable indicators of water stressed conditions. In situations where ambient air temperatures are below the optimal temperature threshold it is unlikely that canopy temperatures will exceed this threshold, regardless of plant available moisture.

This may be critical during the beginning and end of the growing season when there is an increasing probability that significant plant available soil water deficits will occur when ambient temperatures fall below the optimal temperature threshold. If these conditions occur, plant water stress may not be detected. This is because there is insufficient incident energy to raise the canopy temperature above the optimal temperature threshold.

(v) Investigate the utility of the BIOTIC protocol for use in an irrigation scheduling system that is characterised by dynamic deficits. In such systems, current plant stress (determined via T_c), previous plant stress (determined via cumulative stress time) and forecasted plant stress (estimated from seasonal weather forecasts) could be used to schedule irrigation events, making the most of in-crop rainfall and only supplying supplementary irrigation water when the plant is sufficiently moisture stressed.

(vi) Addressing the limitations to the functionality of IRTs such as spectral reflectance, the effect of the angle of the sun and viewing background soil within the field of view of the thermometer should also be investigated. This will aid in adapting the system to these limitations, potentially improving the quality of data collected.

(vii) Further investigation of the applicability of the sum of cumulative stress time approach to water stress detection is required before it can be implemented on

commercial farms, outside of experimental field conditions. An adequate threshold value for the sum of cumulative stress time needs to be determined for its use in a thermal optimal approach to irrigation scheduling. A sum of cumulative stress time of zero should theoretically produce maximum yields. However, this value is problematic as a value of sum of cumulative stress time of zero would schedule irrigation events at very high frequencies, resulting in problems with the practical implementation of this threshold. This proposed protocol needs field validation, where different sums of cumulative stress time values are tested for yield response and WUE. Furthermore, the potential influence of lower than optimal canopy temperatures on this approach needs to be investigated and quantified.

8.2 Conclusion

The utility and proposed modifications required to schedule irrigation in Australian cotton production systems using the BIOTIC protocol were assessed in this thesis. Plant performance, T_c-yield and T_c-water responses to soil water deficits in precision drip application irrigation systems (Chapter 5) and deficit furrow irrigation systems (Chapter 6) were assessed. The issue of plant adaptation, in terms of T_c, in furrow irrigated systems was also investigated (Chapter 6). The data from these experiments displayed the potential use of T_c and the BIOTIC protocol for water stress detection and irrigation scheduling in Australian drip and furrow irrigated cotton. However, the BIOTIC protocol had not been extensively studied outside the USA, and was not designed for use in deficit and furrow irrigation systems that scheduling large volume irrigations on a broader time

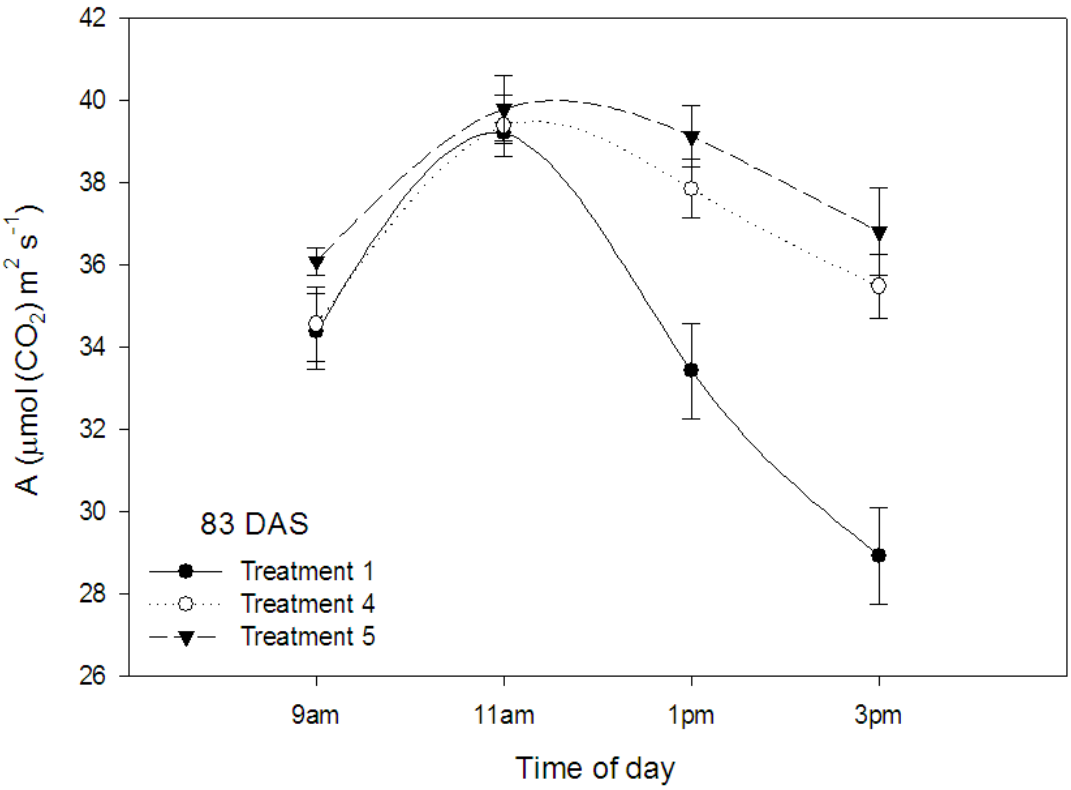
scale. Therefore, the use and potential modifications required to schedule irrigation in Australian cotton production systems using the BIOTIC protocol were also addressed in this thesis. Particular reference was made to the temperature threshold (Chapter 4), the time threshold (Chapter 7), and the modifications to the BIOTIC protocol that were required to schedule irrigation in Australian precision and deficit irrigation systems.

The thermal optimal approach to irrigation scheduling, based on stress temperature thresholds and stress time accumulation, has been shown to be robust, universally ensuring effective stress detection for irrigation scheduling in both precision application and deficit irrigation systems. This study shows that an investment in maintaining average T_c as close to 28 °C as possible is rewarded with peak plant performance and yield. Due to their nature, drip irrigation systems have an increased ability to maintain average crop T_c at 28 °C, producing a lint yield advantage with similar net water application. Scheduling drip irrigation with the proposed thermal optimal protocol is simple and effective. This is noteworthy as historically problems have been encountered scheduling irrigation in drip systems.

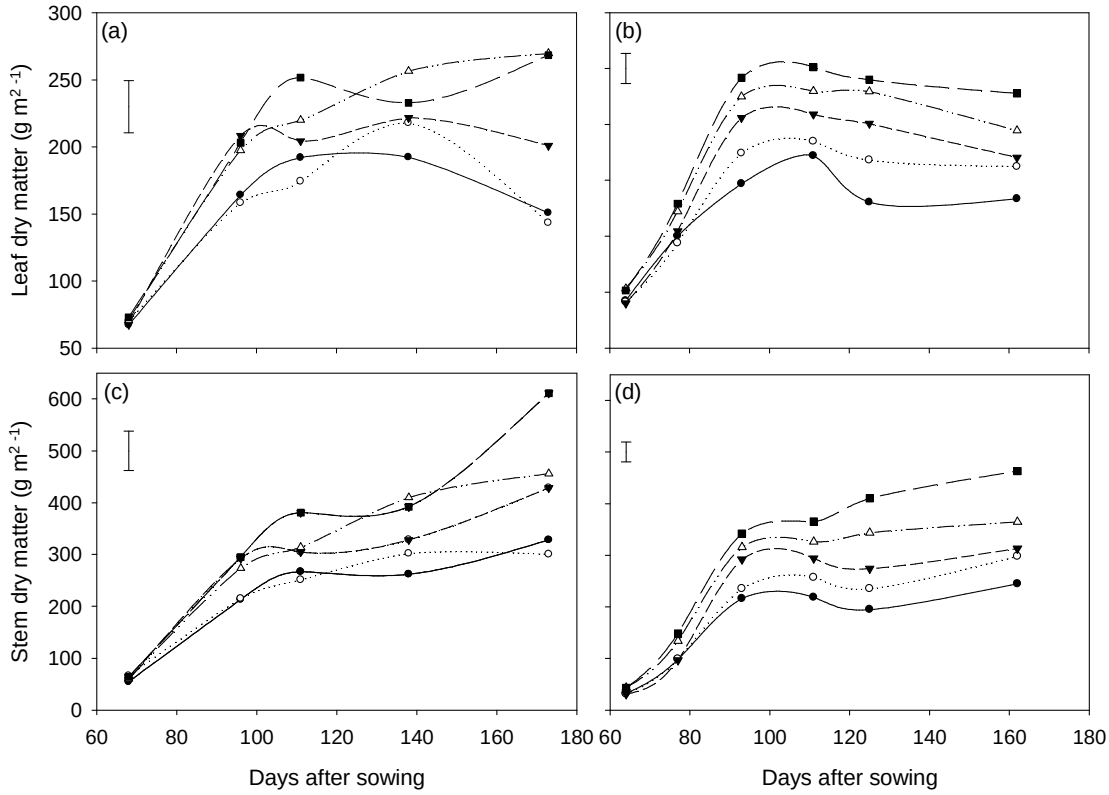
The temperature-time thresholds used to produce peak yield and WUE at Narrabri are a temperature threshold of 28 °C and a stress time threshold of 4.45 h in drip irrigation, and 0.61 mm plant available soil water deficit per stress time hour in furrow irrigation. This modified protocol is a significant advancement to the adaptation of thermal optimal irrigation protocols to Australian precision and deficit furrow irrigated cotton production systems. Judging from the success of previous research conducted on the BIOTIC

protocol in the USA, we may be able to infer that the proposed modifications to the system will adequately schedule irrigation in Australian cotton production systems. However, now that temperature and stress time thresholds have been analysed in an Australian cotton cultivar and in Australian production systems, the amended BIOTIC protocol should be further validated with field based thermal optimum irrigation scheduling. Furthermore, it must be determined whether the benefits of the proposed thermal optimum irrigation scheduling system match or outweigh existing irrigation scheduling systems.

9. APPENDICES



Appendix 1. An example diurnal curve of photosynthetic rate (A), with peak photosynthetic rates observed at the 11am measurement period (10:30am to 11:30am). This curve was measured on 83 DAS in Experiment 3.



Appendix 2. Leaf dry matter accumulation (g.m$^{2-1}$) in (a) Experiment 2 and (b) Experiment 3; and stem dry matter accumulation (g.m$^{2-1}$) in (c) Experiment 2 and (d) Experiment 3 in all treatments; Treatment 1 (—●—), Treatment 2 (·····○·····), Treatment 3 (- —▼— -), Treatment 4 (···—△—···) and Treatment 5 (· —■- -). Vertical bar represents l.s.d.

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