

**TEMPERATURE-TIME THRESHOLDS FOR IRRIGATION
SCHEDULING IN PRECISION APPLICATION AND
DEFICIT FURROW IRRIGATED COTTON**

By

Warren Charles Conaty

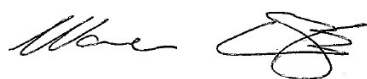
B.Sc.Agr. (Hons)
The University of Sydney

A thesis submitted for the degree of Doctor of Philosophy
Faculty of Agriculture, Food and Natural Resources
The University of Sydney
Australia

October, 2010

DECLARATION OF ORIGINALITY

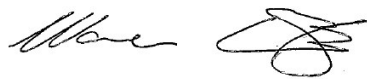
This thesis contains no material which has been accepted for the award of any other degree or diploma at this or any other University and to the best of my knowledge, contains no copy paraphrase of material previously published or written by any other person except where due reference is made in the text of this thesis

A handwritten signature in black ink, appearing to read 'Warren C. Conaty', followed by a stylized flourish or second signature.

Warren C. Conaty

AUTHORITY OF ACCESS

This thesis may be made available for loan and limited copying in accordance with the *Copyright Act 1968*.

A handwritten signature in black ink, appearing to read 'Warren C. Conaty', followed by a stylized flourish or second signature.

Warren C. Conaty

ABSTRACT

Water is one of the most limiting factors to Australian cotton production. Improved irrigation scheduling for efficient water use is central to the sustainability of the Australian irrigated cotton industry. Producers must aim to optimise crop water use through timely irrigation scheduling and efficient utilisation of in-crop rainfall. Presently, 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 has been investigated.

Water stressed plants exhibit elevated canopy temperatures. This is a consequence of the closing of stomata, in response to soil moisture 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 defines 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 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 experimentation, the optimal temperature of an Australian cultivar was identified to be approximately 28°C. This was consistent with values obtained from US cotton cultivars, and average day-time canopy temperatures which were achieved in the field at close to optimal water applications.

The TKW theory has been used as the basis for the BIOTIC (Biologically Identified Optimal Temperature Interactive Console) protocol. This protocol was developed by researchers at the United States Department of Agriculture, 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 canopy temperature exceeds an optimal temperature threshold (TT) 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 irrigation scheduling, with particular emphasis on its use in precision application and large soil moisture deficit irrigation systems of the Australian cotton industry. The thermal optimal approach has been 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 canopy temperatures of 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 moisture deficits (mm) from field capacity calculated from neutron moisture meter data.

The hypothesis that canopy temperatures provide sufficient information for irrigation scheduling was investigated in the surface drip and furrow irrigated cotton. Irrigation treatments resulted in differences in yield, plant architecture, growth, biomass accumulation and canopy temperatures. Canopy temperatures were correlated with crop yield and the volume of water applied to the crop. Peak yields occurred at average day-time ($R_n > 300 \text{ W m}^{-2}$) T_C of $26.4 \pm 1.7^\circ\text{C}$ and total water of 108% predicted ET_C under surface drip conditions, and at T_C of $28.6 \pm 0.6^\circ\text{C}$ and water supplies of 99% predicted ET_C in furrow irrigated conditions. Acclimation of canopy temperatures 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 yields occurred at canopy temperatures 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 yield is proportional to the thermal optimum, the physiological limitations of a plant can mean that a well-watered plant's canopy temperature 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 canopy temperature can exceed its optimum temperature. The ST concept was tested and adapted to Australian field based drip and furrow irrigation systems. Peak yields and water use efficiency in drip-irrigated cotton occurred at 4.45 hours ST, considerably higher than the empirically calculated threshold of 2.75 hours. A thermal optimum protocol was developed to schedule furrow irrigation events through a cumulative ST approach, where one ST hour represents 0.61mm 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 stress time, is theoretically advantageous as it takes into account both the degree and duration of time canopy temperatures 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 well correlated with peak yields, and canopy temperatures were responsive to irrigation. Therefore, the use of temperature-time thresholds in a thermal optimal irrigation scheduling system has potential utility in the irrigated Australian cotton industry. The thresholds that were determined in this study were developed through monitoring cotton crops with infra red thermometers; however irrigations were not scheduled with a thermal optimum protocol in this study. With further field validation, these irrigation protocols could potentially 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.

TABLE OF CONTENTS

DECLARATION OF ORIGINALITY	I
AUTHORITY OF ACCESS	I
ABSTRACT	II
TABLE OF CONTENTS	VI
LIST OF TABLES.....	IX
LIST OF FIGURES.....	X
LIST OF EQUATIONS	XIV
LIST OF APPENDICES.....	XIV
ABBREVIATIONS.....	XV
PUBLICATIONS BY THE CANDIDATE RELAVANT TO THE THESIS	XVII
ACKNOWLEDGEMENTS	XVIII
1. GENERAL INTRODUCTION	1
1.1 BACKGROUND	1
1.2 BIOLOGICALLY IDENTIFIED OPTIMAL TEMPERATURE INTERACTIVE CONSOLE (BIOTIC) ...	5
1.3 OBJECTIVES	7
2. LITERATURE REVIEW.....	9
2.1 INTRODUCTION	9
2.2 IRRIGATION AND IRRIGATION SCHEDULING	12
2.2.1 IRRIGATION DELIVERY	12
2.2.2 IRRIGATION SCHEDULING	18
2.3 WATER AND TEMPERATURE RELATIONS OF COTTON.....	20
2.3.1 WATER STRESS	22
2.3.2 TEMPERATURE STRESS	39
2.4 WATER STRESS DETECTION AND IRRIGATION SCHEDULING FROM LEAF AND CANOPY TEMPERATURE MEASUREMENTS	49
2.4.1 CANOPY TEMPERATURE DEPRESSION (CTD)	51
2.4.2 THE CROP WATER STRESS INDEX (CWSI)	53
2.5 BIOLOGICALLY IDENTIFIED OPTIMAL TEMPERATURE INTERACTIVE CONSOLE (BIOTIC) ..	55
2.5.1 THE DEVELOPMENT OF BIOTIC.....	56
2.5.2 HOW DOES BIOTIC WORK?	58
2.5.3 TEMPERATURE THRESHOLD: BIOCHEMICALLY BASED OPTIMAL PLANT THERMAL ENVIRONMENTS.....	60
2.5.4 TIME THRESHOLD: THE AMOUNT OF TIME A WELL-WATERED CROP CAN EXCEED OPTIMAL PLANT TEMPERATURE.....	67
2.5.5 LIMITING RELATIVE HUMIDITY THRESHOLD.....	70
2.5.6 ADVANTAGES AND LIMITATIONS OF BIOTIC	71
2.6 CONCLUSION.....	72
3. GENERAL MATERIALS AND METHODS.....	75
3.1 SITE AND CLIMATE DESCRIPTIONS.....	75
3.2 CULTIVAR	76
3.3 EXPERIMENTS	76
3.3.1 THERMAL OPTIMA FOR AUSTRALIAN COTTON CULTIVARS MATERIALS AND METHODS (EXPERIMENT 1).....	77
3.3.2 SURFACE DRIP IRRIGATION MATERIALS AND METHODS (EXPERIMENTS 2 AND 3).....	80

3.3.3	DEFICIT FURROW IRRIGATION MATERIALS AND METHODS (EXPERIMENT 4)	92
3.4	DATA ANALYSIS	99
4.	SOIL MOISTURE DEFICITS AND THEIR INFLUENCE ON CANOPY TEMPERATURES IN SURFACE DRIP IRRIGATED COTTON	100
4.1	INTRODUCTION	100
4.2	MATERIALS AND METHODS	104
4.3	RESULTS	105
4.3.1	CLIMATE	105
4.3.2	SOIL MOISTURE AND IRRIGATION	108
4.3.3	CROP DEVELOPMENT	112
4.3.4	BIOMASS ACCUMULATION AND PARTITIONING	121
4.3.5	CANOPY TEMPERATURES	126
4.4	DISCUSSION	132
4.5	CONCLUSION	143
5.	SOIL MOISTURE DEFICITS AND THEIR INFLUENCE ON CANOPY TEMPERATURE IN FURROW IRRIGATED COTTON	145
5.1	INTRODUCTION	145
5.2	MATERIALS AND METHODS	148
5.3	RESULTS	150
5.3.1	CLIMATE	150
5.3.2	SOIL MOISTURE AND IRRIGATION	152
5.3.3	CROP DEVELOPMENT	153
5.3.4	BIOMASS ACCUMULATION AND PARTITIONING	155
5.3.5	CANOPY TEMPERATURES	160
5.4	DISCUSSION	165
5.5	CONCLUSION	172
6.	THERMAL OPTIMA FOR AN AUSTRALIAN COTTON CULTIVAR	174
6.1	INTRODUCTION	174
6.2	MATERIALS AND METHODS	181
6.2.1	TEMPERATURE DEPENDENCE OF THE REAPPEARANCE OF VARIABLE CHLOROPHYLL FLUORESCENCE FOLLOWING ILLUMINATION	181
6.2.2	OPTIMAL TEMPERATURE FOR GAS EXCHANGE IN FIELD GROWN COTTON	183
6.2.3	SENSITIVITY ANALYSIS OF BIOTIC IRRIGATION CALLS TO TEMPERATURE THRESHOLDS	185
6.3	RESULTS	188
6.3.1	TEMPERATURE DEPENDENCE OF THE REAPPEARANCE OF VARIABLE CHLOROPHYLL FLUORESCENCE FOLLOWING ILLUMINATION	188
6.3.2	OPTIMAL TEMPERATURE FOR GAS EXCHANGE IN FIELD GROWN COTTON	190
6.3.3	SENSITIVITY ANALYSIS OF BIOTIC IRRIGATION CALLS TO TEMPERATURE THRESHOLDS	192
6.4	DISCUSSION	195
6.5	CONCLUSION	206
7.	IMPLEMENTING THE THERMAL OPTIMUM AND STRESS TIME CONCEPT IN SURFACE DRIP AND FURROW IRRIGATED COTTON	208
7.1	INTRODUCTION	208
7.2	MATERIALS AND METHODS	211
7.3	RESULTS	214
7.3.1	EVALUATING THE BIOTIC (AVERAGE DAILY STRESS TIME) APPROACH TO IRRIGATION SCHEDULING	214
7.3.2	EVALUATING A CUMULATIVE STRESS TIME INDEX FOR USE IN DEFICIT FURROW IRRIGATION SYSTEMS	223
7.4	DISCUSSION	227
7.5	CONCLUSION	240

8.	GENERAL DISCISSION	243
8.1	SUGGESTED FUTURE WORK	249
8.2	CONCLUSION	253
9.	APPENDICES	255
10.	REFERENCE LIST	257

LIST OF TABLES

Table 3.1. Location, irrigation delivery method and growing season of field experiments conducted in this study.	77
Table 3.2. Agronomic management including fertiliser, herbicide, pesticide and defoliant application in Experiment 2.	84
Table 3.3. Agronomic management including fertiliser, herbicide, pesticide and defoliant application in Experiment 3.	85
Table 3.4. Deficit irrigation treatments and deficit range.	93
Table 3.5. Irrigation dates for each deficit irrigation treatment and corresponding number of days after sowing and cumulative degree days.	95
Table 3.6. Agronomic management including fertiliser, herbicide, pesticide and defoliant application in Experiment 4.	96
Table 4.1. 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.	107
Table 4.2. Irrigation treatment, rainfall, and the actual percent of ET_C applied to each treatment in Experiment 2 and Experiment 3.	109
Table 4.3. 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.	117
Table 4.4. Average canopy temperature (T_C), average canopy temperature when net radiation $< 300 \text{ W m}^{-2}$ and $> 300 \text{ W m}^{-2}$, canopy temperature depression (CTD) when net radiation $> 300 \text{ W m}^{-2}$ and ambient air temperature $> 28^\circ\text{C}$, 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.	127
Table 5.1. Irrigation dates for each deficit irrigation treatment and corresponding number of days after sowing and cumulative degree days.	149
Table 5.2. Rainfall, temperature and evaporative demand and other environmental factors that affect stress potential in Experiment 4 and corresponding long term seasonal average (BOM 2009).	151
Table 5.3. Average canopy temperature (T_C), average canopy temperature when net radiation $< 300 \text{ W m}^{-2}$ and $> 300 \text{ W m}^{-2}$, and duration of time that canopy temperatures exceed 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.	160
Table 5.4. Comparison of average canopy temperatures ($^\circ\text{C}$), yield (kg (lint) ha^{-1}) and ET_C (%) observed in Experiment 3 (surface drip irrigation) and Experiment 4 (deficit furrow irrigation).	162
Table 6.1. Sensitivity analysis of the BIOTIC irrigation scheduling system to temperature thresholds and the average canopy temperature during stress time (ST) accumulation ($T_C > 28^\circ\text{C}$) 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.	193
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.	217
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.	225

LIST OF FIGURES

Figure 1.1. The seasonal pattern of daily cotton water use (Source: NSW department of Agriculture)2	
Figure 1.2. The major cotton growing regions of Australia (Source: Lovett <i>et al.</i> (2003)).....3	
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 measured CTD and corresponding VPD and the maximum water stressed baseline, and the difference between the non-water stressed baseline and the maximum water stress base line, i.e. $CWSI = a/b$54	
Figure 3.1. Regional map of experimental site showing the location of “Myall Vale”.75	
Figure 3.2. The experimental plan showing the layout of the drip irrigation system82	
Figure 3.3. Lay out 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.83	
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.87	
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.....90	
Figure 3.6. The experimental plan showing the layout of one treatment block including the location of neutron moisture meter probe tubes, infra-red thermometers, and the area machine picked for yield analysis. The bottom 25m and top 10m of the field are discounted from measurements due to water-logging from the backing up of water in the tail drain and compaction from previous rotorbuck formations at the head ditch.94	
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.....97	
Figure 4.1. (a) Monthly rainfall (mm) in Experiment 2 (■) and Experiment 3 (□) and the long term average monthly rainfall (—). Average maximum and minimum monthly temperatures (°C) in Experiment 2 (—●—), Experiment 3 (—○—); and long term averages (—).....106	
Figure 4.2. 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.106	
Figure 4.3. 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_C110	
Figure 4.4. Soil moisture (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 moisture in comparison to Experiment 3, and the soils of Experiment 3 were consistently drier over the entire season.111	
Figure 4.5. Machine picked lint yield ($kg\ ha^{-1}$) for Experiment 2 (a) and Experiment 3. Vertical bars represent l.s.d.115	
Figure 4.6. (a) Yield-water relations regression in Experiment 2 ($y = -0.0143x^2 + 23.5x - 6179$) and Experiment 3 ($y = -0.0143x^2 + 23.5x - 6797$). Numbers beside each data point is 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 ($y = -0.7239x^2 + 156.4x - 5485$). Vertical bars represent standard error of mean.116	
Figure 4.7. 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.....116	

Figure 4.8. 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.	119
Figure 4.9. Examples of variation in 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 5. Measuring stick represents 100cm.	120
Figure 4.10. Examples of variation in 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 5. Measuring stick represents 100cm.	120
Figure 4.11. Total dry matter accumulation (g.m^{-2}) 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.	123
Figure 4.12. Regression of biomass accumulation 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.	125
Figure 4.13. (a) Average canopy temperature and per cent 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 (○) ($y = 4.374x - 100.28$; $R^2 = 0.96$).	128
Figure 4.14. Average daily canopy temperature and yield regression ($y = -69.6x^2 + 3680x - 45448$, $R^2 = 0.75$) ($P<0.001$).	129
Figure 4.15. 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.	130
Figure 4.16. 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.	131
Figure 5.1. (a) Monthly rainfall (mm) in Experiment 4 (■) and long term seasonal averages (□). Average maximum and minimum monthly temperatures ($^\circ\text{C}$) in Experiment 4 (—) and long term averages (---).	151
Figure 5.2. Soil moisture deficits, calculated from the soil's drained upper limit, measured with a neutron moisture meter in the (a) frequently irrigated, (b) control, (c) moderately extended, and (d) fully extended deficit treatments throughout the growing season.	153
Figure 5.3. (a) Machine picked yield (kg ha^{-1}) for each treatment in Experiment 4, vertical bars represent l.s.d.; (b) Yield-water relations in Experiment 4, $y = -0.017x^2 + 24.77x - 6295$, $R^2 = 0.64$ ($P<0.001$).	154
Figure 5.4. Plant height (a) and number of nodes (b) produced through out the growing season in the frequently irrigated (—●—), control (····○····), moderately extended (—▼—) and fully extended (····△····) irrigation treatments of Experiment 4. Vertical bar represents l.s.d.	155
Figure 5.5. 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 1m.	158
Figure 5.6. 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 $P=0.05$	159

- Figure 5.7. (a) Average canopy temperature ($^{\circ}\text{C}$) vs. water application (mm) (rainfall + infiltrated irrigation water) regression ($P<0.0001$) with a mathematically predicted base temperature of 28.9°C , $y = 28.87 + 518.72 (e^{(-0.109x)})$, $R^2 = 0.83$; (b) Average daily canopy temperature ($^{\circ}\text{C}$) and yield regression (kg ha^{-1}), $y = -206.0x^2 + 11802.9x - 166391.7$, $R^2 = 0.82$ ($P<0.0001$).....161
- Figure 5.8. Average canopy temperature vs. 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 , $y = -150.1x^2 + 8405.2x - 114797$, $R^2 = 0.97$ ($P<0.0001$).....162
- Figure 5.9. Average canopy temperatures above 27°C 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 15mm; ▼= irrigation events; and the red line at 28°C represents the optimal canopy temperature for cotton. Missing data between 73 and 83 DAS was due to base station failure following a lightning strike.....164
- Figure 6.1. Sequence of a typical fluorescence trace. A measuring light is switched on (↑MB) and the zero fluorescence level is measured (F_0). 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'_0) to be estimated. Source: (Maxwell and Johnson 2000).....179
- Figure 6.2. 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_0 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_0 and the rate to maximum F_v/F_0 . The maximum normalised F_v/F_0 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_0 measurements.....188
- Figure 6.3. Fluorescence optimal temperature assay of the Australian cotton cultivar Sicot 70BRF showing the normalised F_v/F_0 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_0 and the rate to maximum F_v/F_0 . The maximum normalised F_v/F_0 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_0 measurements.190
- Figure 6.4. (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.....191
- Figure 6.5. Calculated ET_c vs. average canopy temperature during the stress time (ST) period at temperature thresholds (TT) of 26°C (●), 28°C (○), and 30°C (▼). Note the reduced response of canopy temperature to an increase in ET_c above 100% ET_c application.195
- Figure 7.1. Average canopy temperature and average daily stress time regression 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 5.406 hr.216
- 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 hr represents the calculated stress time-threshold for Narrabri.218
- 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 hr represents the calculated stress time-threshold for Narrabri.219
- 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 hr represents the calculated stress time-threshold for Narrabri.220

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 $x \leq 5.16$, $y = 3061.8$; when $x > 5.16$, $y = -461x + 5447.3$, $R^2 = 0.6$).....	222
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 moisture deficit ($y = 0.6104x + 1.9482$, $R^2 = 0.99$) ($P = 0.0011$). Bars represent standard error of mean....	224
Figure 7.7. Soil moisture deficits in the (a) frequent, (b) control, (c) moderately extended, and (d) fully extended irrigation treatments with the scheduled irrigation events determined by a neutron moisture meter (▼) and irrigation events predicted with a modified thermal optimum protocol (▽) using an accumulated stress time for each deficit as shown in Table 3.....	226
Figure 7.8. Irrigation events scheduled with neutron moisture meter (NMM) soil moisture deficit measurements vs. predicted irrigation events with the modified thermal optimum protocol. The regression represents a 1:1 line.	227
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 radiation is greater than 300 W m^{-1} . R_s = Net radiation, T_c = Canopy temperature, T_{av} = Average canopy temperature when net radiation levels are above 300 W m^{-1} , ST = Stress time, T_{Opt} = Optimal temperature.	234
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.	237

LIST OF EQUATIONS

Equation 1: Canopy temperature depression	52
Equation 2: Crop Water Stress Index	53
Equation 3: Crop Water Stress Index	55
Equation 4: Net radiation	68
Equation 5: Canopy-air temperature differential	69
Equation 6: The apparent psychrometric constant	69
Equation 7: Crop Water Stress Index	69
Equation 8: Canopy to aerodynamic resistance.....	70
Equation 9: FAO56 Evapotranspiration equation	80
Equation 10: Locally calibrated crop co-efficient.....	81
Equation 11: Cotton degree-day equation.....	92
Equation 12: The quadratic equation.....	185
Equation 13. Cumulative sum of stress time approach to stress detection between the study period of 85 to 155 DAS	235

LIST OF 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.	255
Appendix 2. Leaf dry matter accumulation ($\text{g.m}^{-2}\text{d}^{-1}$) in (a) Experiment 2 and (b) Experiment 3; and stem dry matter accumulation ($\text{g.m}^{-2}\text{d}^{-1}$) 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.	256

ABBREVIATIONS

A	Photosynthetic rate ($\mu\text{mol (CO}_2\text{) m}^2 \text{ s}^{-1}$)
ABA	Absciscic 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	<i>Bacillus thuringiensis</i>
CO ₂	Carbon dioxide
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 _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	Stomatal conductance rate ($\text{mol (H}_2\text{O) m}^2 \text{ s}^{-1}$)
H ₂ O	Water
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
lsd	Least significant difference
N	Nitrogen
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 0-14
PSII	Photosystem II
QLD	Queensland
RCBD	Randomised Complete Block Design
RDI	Regulated Deficit Irrigation
R_n	Net Radiation
Rubisco	Ribulose-1,5- biphosphate carboxylase-oxygenase
ST	Stress time (hours)
STT	Stress time threshold for irrigation scheduling (hours)
T_a	Air temperature ($^{\circ}C$)
T_c	Canopy Temperature ($^{\circ}C$)
T_l	Leaf temperature ($^{\circ}C$)
T_n	Normative plant temperature ($^{\circ}C$)
TDM	Total Dry Matter
TKW	Thermal Kinetic Window
TT	Temperature Threshold
USDA	United States Department of Agriculture
VPD	Vapour Pressure Deficit (kPa)
WUE	Water Use Efficiency ($kg\ (lint)\ mm^{-1}\ ha^{-1}$)
Ψ_l	Leaf water potential

PUBLICATIONS BY THE CANDIDATE RELAVANT 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

Conaty, W.C., Mahan, J.R, Neilsen, J.E., Sutton, B.G. and Tan, D.K.Y. (2009) Water stress detection using infra red canopy temperatures for irrigation scheduling. In '*Proceedings of the Interdrought III, The 3rd international conference on integrated approaches to sustain and improve plant production under drought stress*'. Shanghai, China, 11 – 16 October 2009

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 and Jane Caton 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 over 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 flattened 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 (approximately 90%), which was first developed by the Mayan civilisation in Mexico.

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 approximately 180 days 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

radiation 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 yields, with peak yields occurring at approximately 700mm evapotranspiration (Tennakoon and Milroy 2003) (Figure 1.1).

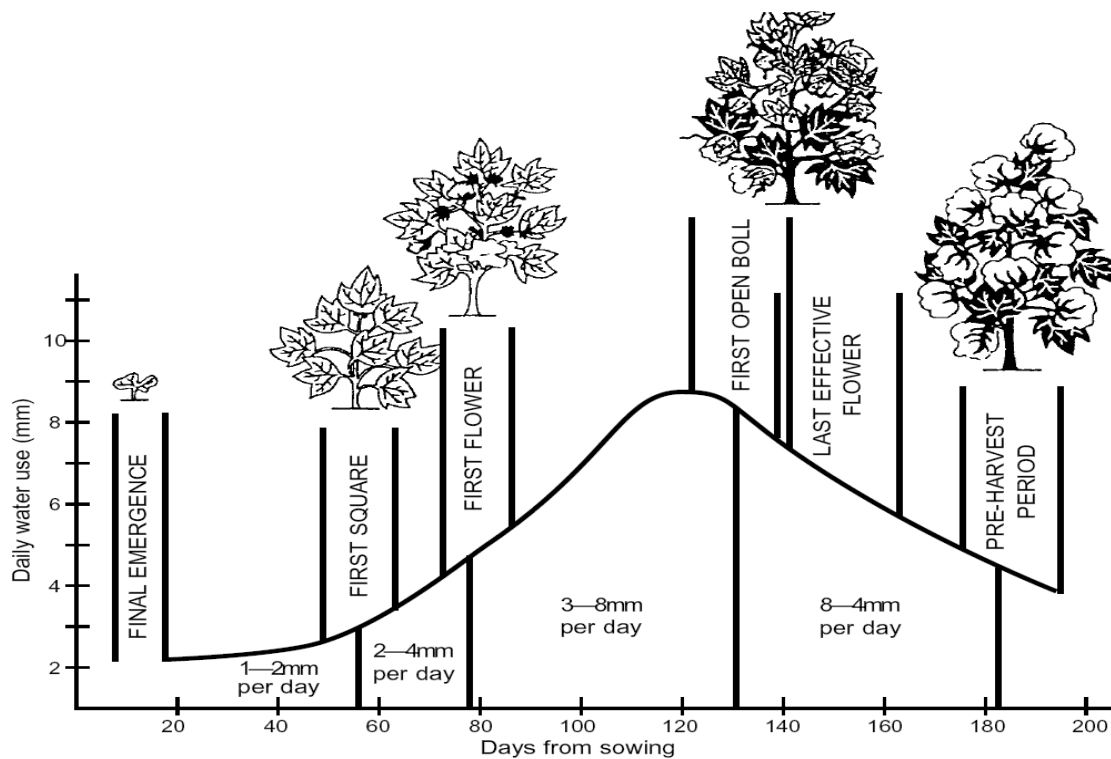


Figure 1.1. The seasonal pattern of daily cotton water use (Source: NSW department of Agriculture)

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 dependant on world cotton prices, only producing approximately 3% of the world cotton crop, but in non-drought years represents the third largest cotton exporter and generates in excess of \$1 billion in revenue (Writeability 2006). Cotton production in Australia steadily increased to a maximum area of 562,000 hectares 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 has been severely affected by one of the worst recorded droughts in history. Production area fell to as low as 63,000 hectares in the 2007/08 season, but has since more than doubled to 164,000 in the 2008/09 season and continues to rise in the 2009/10 season with an estimated planting area of 195,000 hectares (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.

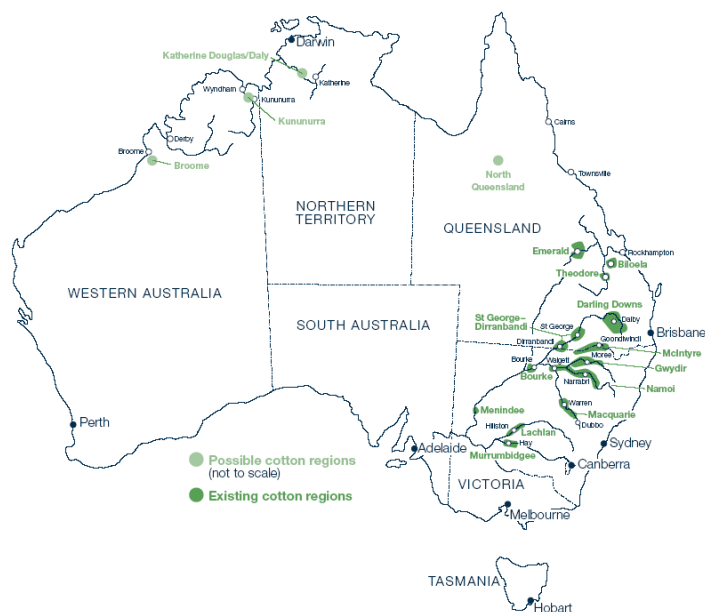


Figure 1.2. The major cotton growing regions of Australia (Source: Lovett *et al.* (2003))

In the past decade the Australian industry has achieved a 126% increase in 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 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 quality and yields can be attributed to improvements in crop management systems, variety breeding and the cotton industry's willingness to adopt new technologies such as transgenic cotton cultivars. Furthermore, the majority of the crop is grown under irrigation, with around 85% of the crop irrigated. Although a high proportion of the crop is irrigated, cotton growers have achieved significantly higher 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).

Upland cotton is a tropical, indeterminate, perennial, xerophytic shrub. When discussing the water relations of cotton, cultivated as an irrigated, broad acre, annual crop, it is essential to recognise these growth habits and origins. Cotton production is affected significantly by water supply, and the relationship between water application and physiological response and cotton yield has been studied extensively (Constable and Hearn 1981; Cull *et al.* 1981; DeTar 2008; Grimes and El-Zik 1990; Hearn 1994; Pettigrew 2004a; b), with publications documenting 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 yield, whilst over-watering can lead to rank growth and fruit shedding. The challenge for irrigation scheduling is to find the optimum application regime, which responds accurately to conditions over a range of seasonal pressures.

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 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 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 canopy temperature. The BIOTIC protocol also utilises the theory that all 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 canopy temperature 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 (Mahan 2000; Peeler and Naylor 1988; Terri and Peet 1978) 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 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 canopy temperatures may exceed the optimum, regardless of soil moisture. 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 canopy temperature 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 used or studied outside the United States of America or in large deficit irrigation systems, such as deficit 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) Determine weather canopy temperatures can adequately capture plant stress.

This was achieved through:

- (a) Experiments conducted under surface drip (Chapter 4) and deficit furrow (Chapter 5) in order to evaluate the effect of soil water on plant growth and canopy temperature;

- (b) Investigation of the ability of canopy temperatures to capture plant moisture stress in comparison to soil and atmospheric environmental conditions (Chapter 4 and 5).
 - (c) Determine the potential effect of plant adaptation of canopy temperatures to the wetting and drying cycles of furrow irrigation (Chapter 5).
- (ii) Define the thermal optima for one Australian cotton cultivar, in order to compare this cultivar with those grown and studied in the United States (Chapter 6).
- (iii) Determine if the thermal optimal approach to irrigation scheduling system can be effectively used for irrigation scheduling in precision application and large deficit furrow irrigation systems. Particular reference will be made to the temperature threshold (Chapter 6), the stress time threshold (Chapter 7), and any modifications to the BIOTIC protocol that may be required to schedule irrigation in Australian precision 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 and can aggravate pest and disease problems. Water stress adversely affects the production of flower buds, reduces boll set, and can reduce yield by reducing boll size (Hearn 1979). Temperature and 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 based moisture 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 canopy temperatures, 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). 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 water stress index known as the crop water stress index (CWSI). CWSI 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 (Alderfasi and Nielsen 2001; Baker *et al.* 2007; Balota *et al.* 2008; Cohen *et al.* 2005; Gonzalez-Dugo *et al.* 2006; Guilioni *et al.* 2008; Jones 1999; Leinonen *et al.* 2006; Mahan *et al.* 2005; Qiu *et al.* 2009; Wanjura *et al.* 2006; Widmoser 2010).

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 canopy temperature as an indicator of crop water stress. The specific amount of time that a canopy temperature of a given crop exceeds its species-specific optimum temperature threshold determines the need for irrigation scheduling (Mahan *et al.* 2000). The daily amount of time that a crop's canopy temperature exceeds this threshold value directly produces the 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 moisture and thermal stress, as well as some of the contemporary irrigation scheduling and delivery methods used by the Australian cotton industry. This review will also outline the historic use and physiological basis of using canopy temperatures 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 90-95% 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 water use efficiency; 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 water use efficiency. 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 is receiving 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 utilise 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 *et al.* 2009; Grabham and Williams 2005). 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 (approximately 0.1ML/ha) 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 broad acre 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 irrigation water use efficiency (WUE) by minimizing evaporative loss 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 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 utilised 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 yields and net profits, as well as WUE, have been improved using drip irrigation (Ayars *et al.* 1998; Collins 2004; Hodgson *et al.* 1990; Radin *et al.* 1992; Smith *et al.* 1991).

(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 moisture 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 (Collins 2004; Lyle and Brodovsky 1981).

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 water use efficiency. 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 three categories, soil based moisture measurements such as neutron moisture meters 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) and plant based scheduling from on-the-ground (Jones 2004b) or remotely sensed data (Bastiaanssen and Bos 1999). 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 Lyster 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). PRD is an irrigation strategy that aims to maintain plant water status and create favourable physiological response due to biochemical signalling (Bravdo 2005). It utilises 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 alkalinisation of sap pH. These biochemical signals result in a decrease in vegetative growth and stomatal conductance, which leads to improved crop water use efficiency (WUE) (Bravdo 2005). 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). 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 moisture gradients (White and Raine 2009).

2.3 Water and temperature relations of cotton

Water and temperature relations 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 2-3 days. Squares are produced on lateral fruiting branches every 5-7 days. Node and square initiation continue as long as conditions are favourable, thus their number increases exponentially throughout the season. The demand for carbohydrates and nitrogen, 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 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 moisture and during periods of high radiation 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 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 yield are still obtained in the face of reduced photosynthesis and growth due to water deficit (Moreshet *et al.* 1979).

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 have a strong negative

correlation with crop yield, with 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 originate 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 moisture 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 which 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 moisture 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 yield traits

(i) Seedling and root growth

Water is imbibed by the seed due to a steep gradient of water potential between the seed exterior and the low matric 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 ($>18^{\circ}\text{C}$) and moisture 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 dependant, with emergence occurring in 5 days at soil water potentials of -0.03 MPa, 7 days 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 3m, depending on the soil type, soil bulk density and soil water content (Hearn and Constable 1984). The rate of root growth is usually $8\text{-}90\text{mm day}^{-1}$ (Hearn and Constable 1984), however under favourable conditions this can be increased to $100\text{-}150\text{mm day}^{-1}$ (Bielorai *et al.* 1983). At optimum temperatures and osmotic potentials of -0.08, -0.66 and -1.24 MPa, maximum root elongation averaged 3.3 , 1.8 and 0.8mm hour^{-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 moisture 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 nitrogen from developing bolls (Bielorai *et al.* 1983). The depletion of water in the upper 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 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 water deficits is vegetative, where a reduction in leaf expansion, inhibition of growth rate and reductions in height, leaf area index 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 below 0.8 MPa (Bielorai *et al.* 1983). The growth of stems decreases with time following an irrigation event, however 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 leaf water potential decreases from -1.0 MPa to -2.4 MPa and is dependant 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 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 moisture, and a corresponding positive relationship between the number of squares and plant height (Bruce and Römken 1965). The development of the flower is dependant on vegetative growth, where new flowering sites are formed through the formation of additional main-stem and branch nodes, which is primarily thermal dependant. 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 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 moisture stress and results in a higher cotton seed yield and higher lint quality (Bielorai *et al.* 1983). Water deficits during floral initiation considerably reduce yield, however, during peak flowering the effect is less pronounced. This is because soil moisture stress at a particular date is associated with a reduction in the number of flowers 20 to 30 days later (Shimshi and Marani 1971). Thus 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 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 moisture (Bielorai *et al.* 1983). Using soil moisture as a surrogate for plant moisture status, Bruce and Römken (1965) found that the rate of initiation of squares was associated with a soil moisture 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 moisture 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 leaf water status between -1.0MPa and -2.4MPa where young bolls were most sensitive to water stress, but those that were 14 days or older were retained even after exposure to severe water deficits (McMichael *et al.* 1972). However, boll growth is not affected until leaf water potential reaches -2.7 to -2.8MPa (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 moisture tends to slow maturity (Hearn 1979; 1994; Marani and Amirav 1971a; b). This occurs as a result of the inherent plant water relations fixed within commercial cotton varieties derived from its wild xerophytic ancestors. As a result, when two thirds of the soil water had been utilised, 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).

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 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 production. Cotton maintained at leaf water potentials of -1.5 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 so have some minor water stress on the crop as minimal stress (> 1.5 MPa) 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 (leaf water potential of -2.0 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. 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 (< -2.5 MPa) prevents square production and greatly reduces boll production.

(c) Physiological traits

(i) Leaf water potential

Leaf water potential (ψ_l) 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 moisture availability, which in turn influences the water potential of aerial plant parts. Therefore, measurement of leaf water potential may be indicative of soil and canopy water conditions, particularly when taken during the pre-dawn period when soil moisture 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 radiation is reduced and ψ_l becomes a product of soil moisture availability, environmental

conditions driving evaporative demand (air temperature, wind speed and humidity) and the subsequent leaf stomatal aperture (Loveys *et al.* 2005). Leaf water potential is not a direct measurement of water stress physiology. Therefore, using ψ_l as a means of detecting physiological stress is limited, as ψ_l does not directly quantify physiological stress. There is doubt as to the physiological significance of ψ_l (Hearn 1994; Passioura 1988), 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 leaf water potential. 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 leaf water potential data 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 moisture conditions.

(ii) Gas exchange

Gas exchange measurements have been used to quantify and detect water stress. Generally, transpiration rates proceeded at a maximum according to environmental demand until approximately 0.3- 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 (Ray *et al.* 2002; Ritchie 1981; Sinclair 2005; Sinclair and Ludlow 1986) decline until the remainder of transpirable water is utilised or soil moisture is replenished. A linear decline in photosynthesis has been observed in cotton at leaf water potentials below -2.0 MPa (Ackerson *et al.* 1977; Hearn and Constable 1984; Karami *et al.* 1980; Sung and Krieg 1979). 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 dependant on stomatal conductance than measured leaf water status (relative water content or leaf water potential). 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 CO₂ 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 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 (Hearn 1979; Jordan 1986; Ritchie 1981). However, it is generally accepted that gas exchange rates are an adequate indicator of the degree of moisture 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 dependant 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 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; Gimenez *et al.* 1992; Krieg and Hutmacher 1986; von Caemmerer and Farquhar 1981). Krieg (1986) cites six papers where stomatal closure in cotton induced by 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 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; Shangguan *et al.* 1999; Wise *et al.* 1990) where non-stomatal effects are generally considered more prevalent in long-term or increasingly extreme water deficits or hot arid environmental conditions (Flexas and Medrano 2002; Hearn 1994; Pankovic *et al.* 1999).

The potential non-stomatal limitations to photosynthesis include inhibition of CO₂ 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 has been 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 can be 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- 0.4 of transpirable soil water content). After this point transpiration rate is decreased linearly (Ray *et al.* 2002; Sadras and Milroy 1996; Weisz *et al.* 1994). This is because as the soil progressively dries, the corresponding reduction of soil 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 moisture 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 moisture 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 radiation 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 moisture 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), 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 cells 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 leaf water potential, 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_1 0.2 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_1 , however osmotic adjustment does not always confer maintenance of photosynthesis under at low Ψ_1 (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 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_1 .

(ii) *Stomatal and gas exchange response*

Stomatal closure provides a mechanism for the reduction of water loss. The response of stomata to Ψ_1 is well established and has been extensively studied (Turner 1986). Osmotic adjustment of cotton leaves in response to 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 water potentials (Ψ_1 -2.8MPa) lower than those required to close stomata of well-watered plants (Ψ_1 -1.8 MPa). Brown *et al.* (1976) observed similar results in growth chamber grown cotton.

Stomatal resistance on the upper surface of cotton leaves is greater than that of the lower surface, partly because of the higher stomatal density for the lower epidermis (McMichael and Hesketh 1982). However, the stomata located on the upper surface of the leaf have a greater sensitivity to lowering of Ψ_1 , and have a reduced response to water stress conditioning (Grimes and El-Zik 1990). Brown *et al.* (1976) found the osmotic potential of lower guard cells to be 0.7 MPa lower than those of the upper 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 radiation effects, of older leaves before younger leaves. Low nitrogen status has also been reported to change osmoregulation, where stomatal closure was observed at higher Ψ_1 under low nitrogen conditions and plants that deplete their nitrogen supply throughout the season lose their ability to osmoregulate (Grimes and El-Zik 1990). This suggests a physiological response to increase WUE under nitrogen and water limited conditions. The Ψ_1 that result in stomatal closure is dynamic, being different at contrasting leaf positions in the canopy, upper and lower leaf surfaces, and water and nitrogen stress histories.

As water stress develops, photosynthesis is reduced from its maximum rate of 40 to 45 $\mu\text{mol (CO}_2\text{) m}^2 \text{ s}^{-1}$. For non-osmotically adjusted plants, a reduction in Ψ_1 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_1 , but diffusive resistance may remain low over the range of declining Ψ_1 (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 temperatures are routinely observed in many cotton-producing regions. These sub-optimal temperatures place limitations on cotton production due to associated morphological, yield, physiological and biochemical temperature constraints. Low temperatures are 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 reduced cropping seasons. High temperatures are 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 yield traits

(i) Seedling and root growth

The base temperature (lower limit) for germination is 12°C and for seedling growth it is approximately 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 are induced, with maximum protection levels reached at 37.7°C to 40°C. However, at higher temperatures, the protection gained from acquired thermotolerance rapidly declines.

The optimal range of day/ night temperatures for root development in cotton is 30/22-35/27°C (Reddy *et al.* 1997a; Singh *et al.* 2007). Higher temperatures 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 very 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). Neilsen (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 temperature (Singh *et al.* 2007). Reddy *et al.* (1992c) reported the optimal temperature for leaf area development as 26°C, and that 20 days after emergence the leaf area of plants grown at 28°C was six times greater than those grown at 21°C. Temperature also plays a major role in main stem elongation, leaf area expansion, and biomass accumulation (Singh *et al.* 2007), with optimal day/ night temperatures 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 days after emergence (Reddy *et al.* 1992a). Although growth rates were highly affected by temperatures 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 temperatures increased from 20/12°C to 40/34°C. However, the optimal temperatures 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 aboreum*) as 21-27°C, where cool nights are needed for best growth rates. However, plants are also able to withstand temperatures as high as 43-46°C, provided adequate moisture 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, approximately 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 dependant on temperatures (Reddy *et al.* 1992b; Singh *et al.* 2007). High temperature 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 metre was reduced three weeks after a day where temperature exceeded 42°C (Singh *et al.* 2007). High temperatures approximately 17 days before flowering can lead to decreased pollen viability and fertilisation (Oosterhuis 1999). Similarly, Meyer (1969) observed that daily maximum temperature 15 to 16 days before anthesis affected pollen sterility more than any other aspect of the external environment. At temperatures 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 temperatures exceeded 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.* (Burke 2001; 2004) reported optimal pollen germination and pollen tube elongation in cotton at 28°C, where both are reduced as temperatures 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 which often exhibit temperatures in excess of 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 temperatures exceed 30°C (Reddy *et al.* 1992b), whilst at day temperatures above 40°C all squares and flowers were shed in a range of upland cotton cultivars (Reddy *et al.* 1991b). Similarly, an increase in day temperature from 28°C to 32°C resulted in increased abortion of bolls less than 10 days old after anthesis in chronological order (Zeihner *et al.* 1995). If this increased day temperature was coupled with increased night temperatures, further increases in boll abortion were observed. Reddy *et al.* (1995a; 1997b; Reddy *et al.* 2004) found that pima cotton was generally more susceptible to high temperatures than upland cotton, where some pima cotton varieties failed to produce

fruiting branches and reproductive sites when average temperatures 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 temperatures are important for fruit set and boll development. In an experiment with constant temperature of 29.4°C plants did not produce fertile pollen, whilst plants grown at a constant 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 temperature 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 temperatures accelerate crop growth, thus reducing the developmental time for bolls, resulting in smaller bolls, lower quality and reduced yield. At high temperatures, crop development rates proceed at a much faster rate. The time

required to produce squares, flowers and mature bolls is reduced by an average of 1.6, 3.1 and 6.9 degree days respectively, per 1°C increase in 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 temperatures above this optimum resulted in boll abortion. Only approximately 50% of the squares and bolls produced at 33°C were retained, whilst none were retained at 36°C.

(v) *Yield and fibre quality*

Temperature effects on yield are somewhat complex as yield is the summation of the crop's response to changes in temperature 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 temperature is below the optimum for net photosynthesis, a small increase in temperature can stimulate crop growth. However the converse is also true where a small increase in temperature above the optima can dramatically reduce yield (Singh *et al.* 2007). Oosterhuis (1999) showed a gradual decline in boll development from 32°C, where increased temperatures 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 yields. As cotton lint is predominantly carbohydrate, a reduction in carbohydrates for the plant inevitably results in reduced fibre production and lower yields.

The evidence suggests that there is an optimal temperature for cotton growth, and plant growth and 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 temperature 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 temperature range between 20 and 35°C, with peak photosynthetic rates at 30°C. An increase in temperatures above range is detrimental to carbon assimilation as high temperatures reduce photosynthetic respiration through the stimulation of photorespiration and damage to photosynthetic apparatus (Sailsbury and Ross 1992). Prolonged exposure to high temperatures (>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 below 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 ribulose 1,5-biphosphate carboxylase-oxygenase (Rubisco) accompanies the reduction in carbon assimilation (Kim and Portis 2005).

The photosynthetic rate of cotton was found to peak at 28°C, the temperature optima determined by Reddy *et al.* (1995b). Heat stress decreases the maximum quantum yield of photochemistry of PSII and inhibits CO₂-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 temperatures increase the rate of photorespiration, reducing carbon assimilation in cotton. When leaf temperature

was rapidly (30sec) 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 dependant, 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 approximately 50% net photosynthesis. Heat stress can have a profound effect on photosynthesis and photorespiration rates. Leaf stomatal conductance increased to temperatures of 21/ 23°C and following this temperature had no effect on stomatal conductance. Transpiration rates also increase with temperature, 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 stomatal conductance 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 temperature in the 23 to 36°C range, whilst stomatal conductance increased linearly within this range. Similarly, photosynthetic rates between 24 and 36°C remained constant in a moderately heat-tolerant line of pima cotton (Pima S-6), however an associated increase in stomatal conductance was observed (Radin *et al.* 1994). Although this increase in stomatal conductance 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

conductance increased with air temperature, 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. HSPs are intracellular, cytoplasmic proteins and are one method of plant response to heat stress. Heat shock proteins 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 temperature range for the induction of HSPs was 38 - 41°C in laboratory grown cotton. Therefore, heat shock response is of little significance in agricultural settings as it is initiated at such high temperatures.

Water and heat stress often occur in unison, and are often accompanied by high solar radiation 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 canopy temperatures. The significance of monitoring plant canopy temperatures is that through the opening and closing of stomata (in response to soil moisture deficits) canopy temperatures are altered. The closure of stomata results in a decrease in transpiration and consequently 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 plant and environmental factors (Fuchs 1990).

Numerous studies have correlated canopy temperatures with soil moisture, environmental conditions and plant physiological responses. Jackson *et al.* (1981) showed that durum wheat (*Triticum durum* Desf.) canopy temperatures (in the form of the CWSI) closely paralleled the extractable soil water to 1.1 metres in a variety of flood irrigation regimes. The relationships between leaf and plant water potential with respect to canopy temperatures have also been outlined (Cohen *et al.* 2004; Howell *et al.* 1984; Idso *et al.* 1981b; c). These relationships are especially evident when plant water potentials or canopy temperatures are normalised with air vapour pressure deficit (VPD) (Cohen *et al.*

2004; Idso *et al.* 1981b; c). 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 leaf water potential (ψ_l) by calculating CWSI shows that the use of canopy temperatures for stress detection can be adapted to various meteorological conditions (Cohen *et al.* 2004), and that canopy temperatures 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 highly correlated with CWSI in rice (*Oryza sativa* L.), and concluded that the CWSI represents a significant 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 stomatal conductance, but also noted that potential non-stomatal effects

were not measured. However, the strong relationship between photosynthesis and stomatal conductance with leaf temperatures observed by Ledi *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 relatively small window of leaf temperatures (30 to 38°C).

More recently, Hirayama *et al.* (2006) showed that rice cultivars with lower leaf temperatures can maintain high transpiration and photosynthetic rates, resulting in higher 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 canopy temperatures. They concluded that canopy temperature depression (CTD), the difference in leaf and air temperatures, especially when used in combination with VPD, is a much better predictor of the degree of drought stress, in terms of gas exchange, than canopy temperature alone. This body of research suggests that there is potential utility in canopy temperatures as an indicator of physiological water stress, which needs to be further explored for the use of canopy temperatures in irrigation scheduling systems.

2.4.1 Canopy temperature depression (CTD)

The value of canopy temperature measurements in agriculture has been established since the early 1980s (Idso 1982; Jackson 1982). The importance of leaf temperature measurements is that under well-watered conditions leaf temperatures can be

significantly lower than ambient air temperatures. The converse of this is also true and patterns of the differential between canopy and air temperature occur as a result of transpiration rates and the effect these rates have on the evaporative cooling of a leaf. Therefore, when soil moisture availability declines, transpirational cooling of a leaf is reduced and canopy temperatures rise (Mahan *et al.* 2005).

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

Equation 1: Canopy temperature depression

$$CTD = T_c - T_a$$

Where T_c is canopy temperature and T_a is air temperature ($^{\circ}\text{C}$). CTD is negative when the canopy temperature is cooler than the air and has been used in numerous applications. CTD was first studied with 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. The application of CTD has been used in plant response to environmental stress (Baker *et al.* 2007; Ehrler *et al.* 1978; Howell *et al.* 1984; Idso 1982; Jackson *et al.* 1981), irrigation scheduling (Evelt *et al.* 1996; Hatfield 1983; Wanjura *et al.* 1995), and to evaluate cultivar water use (Hatfield *et al.* 1987b; Pinter *et al.* 1990), heat tolerance (Amani *et al.* 1996; Reynolds *et al.* 1994) and, drought tolerance (Blum *et al.* 1989; Hirayama *et al.*

2006; Rashid *et al.* 1999). 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 stomatal conductance was significantly improved. CTD has been 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 yield, must be determined for individual environments as, for example, its use is restricted when yield is limited by the amount of stored soil moisture (Balota *et al.* 2007).

2.4.2 The Crop Water Stress Index (CWSI)

Following the findings of Ehrlir (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). CWSI 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 canopy and air temperature vs. air VPD under non-limiting soil water conditions. The crop water stress index can be represented as:

Equation 2: Crop Water Stress Index

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

Where T_c and T_a are the canopy and air temperature ($^{\circ}\text{C}$), D_1 is the maximum water stressed baseline and D_2 is the non-water stressed baseline. CWSI can be represented graphically, as shown in Figure 2.1, where CWSI is the ratio of a to b.

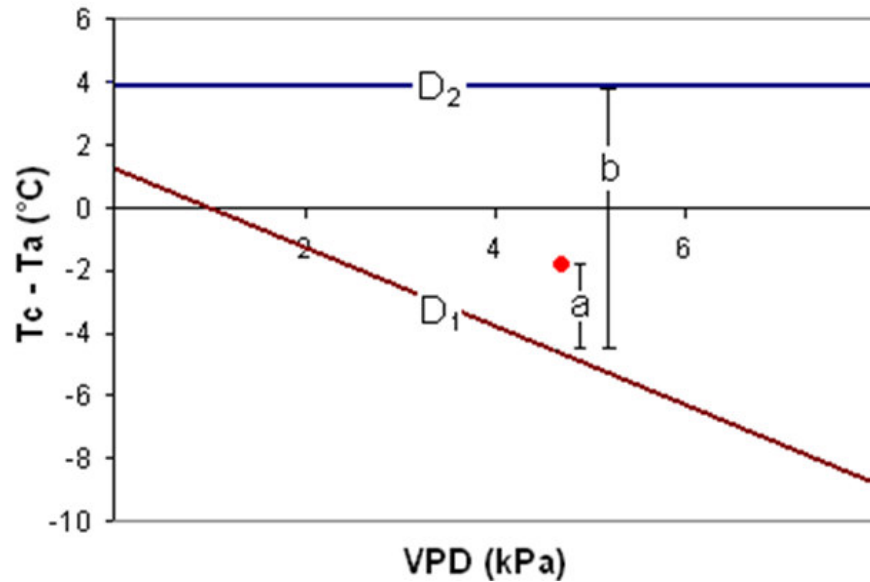


Figure 2.1. A graphical representation of the crop water stress index (CWSI) which can be calculated as the ratio of the difference between a measured CTD and corresponding VPD and the maximum water stressed baseline, and the difference between the non-water stressed baseline and the maximum water stress base line, i.e. $\text{CWSI} = a/b$.

Jackson *et al.* (1981) presents the theory behind the energy balance that separates net radiation 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 below air temperature and the CWSI is 0. As the transpiration decreases, the leaf temperature rises and can reach to 4 to 6 degrees above air temperature 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, E_p is the potential latent heat flux to the air, γ is psychrometric coefficient, which depends on surface temperature and atmospheric pressure ($\text{Pa } ^\circ\text{C}^{-1}$), 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 ($\text{Pa } ^\circ\text{C}^{-1}$).

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

2.5 Biologically Identified Optimal Temperature Interactive Console (BIOTIC)

Most current irrigation scheduling techniques involve the measurement of soil moisture, atmospheric parameters, and other plant measurements such as canopy temperature, stomatal aperture, leaf colour and leaf water potential. 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 moisture requirement. BIOTIC utilises direct plant measurements for irrigation scheduling, through the use of infra red thermometers to measure plant canopy temperatures. The knowledge of plant canopy temperatures 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 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 integration of the environment derived from then plant's canopy temperature (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 (Idso 1982; Jackson *et al.* 1981). As a result, thermal stress, through the measurement of canopy temperature, 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 canopy temperature remains within its TKW was found to correlate with above ground biomass (Burke *et al.* 1988). Therefore, plants exhibit homeothermic 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 which would allow for transpirational cooling to the normative plant temperature (Mahan and Upchurch 1988). Following this, automated irrigation scheduling using continuous canopy temperature measurements was studied by Wanjura *et al.* (1988; 1990; 1992). In these studies cotton was irrigated when the average canopy temperature over a 15 minute time period exceeded a predetermined temperature threshold of either 26, 28, 30 or 32°C. The hypothesis behind these experiments was that by attempting to maximise the amount of time canopy temperatures are within the TKW, yield should be maximised. Lint yield was determined to be consistently highest for the 28°C threshold temperature, and decreased for higher or lower temperature thresholds. A 28°C threshold temperature provided maximum yield where water and season length were not limiting. These experiments compared canopy temperature 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 canopy temperature provided the departure from previous irrigation scheduling methods using canopy temperatures (Mahan *et al.* 2005).

The initial studies by Wanjura *et al.* (1988; 1990; 1992) used a fifteen minute 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 3-7 days (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?

BIOTIC was developed in 1996 as an irrigation scheduling tool (Mahan *et al.* 2005). It manages crop irrigation using their canopy temperature measurements by use of a specific time threshold (Upchurch *et al.* 1996). BIOTIC continually measures the canopy temperature of the target crop with an infrared thermometer. After each measurement, the canopy temperature is compared with a predetermined threshold of water stress canopy temperature, where if the crop's canopy temperature is above this value it is thermally stressed. This temperature threshold is based on the observation of the thermal

dependence of plant metabolic activity (Peeler and Naylor 1988; Teeri and Peet 1978). If the measured canopy temperature is less than or equal to the threshold temperature, irrigation is not initiated and canopy temperature measurements continue. However, if both the canopy temperature is greater than 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 compared to the time threshold, a predetermined constant defined as the species-specific mean length of time per day that a well-watered non-stressed plant will naturally exceed its canopy temperature threshold in the target geographical area (Upchurch *et al.* 1996). As long as the accumulated time is less than the time threshold, irrigation is either unnecessary or inefficient to achieve transpirational cooling, and the process is again repeated with measurements of canopy temperature, humidity and accumulated time. However, once the accumulated time exceeds the time threshold, an irrigation signal is generated, and once irrigation is supplied to the crop transpirational cooling is induced. Once a signal to irrigated is initiated the BIOTIC protocol advises sufficient application of water to meet the predicted evaporative demand until the next possible irrigation event. If the applied water is not fully utilised by the crop before the next possible irrigation, it is delayed until the water is consumed and canopy temperatures are elevated.

The quantity of applied water (combined 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 moisture 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. The largest quantity of water was applied in the weekly soil water balance method at 1380mm. The approximate two week irrigation cycle and the 28°C were similar at 750mm and 700mm respectively followed by 30°C (460mm) and 32°C (360mm) which were also similar. The dryland system used the smallest amount of water at 180mm. The statistical ranking of lint yields was highest in the 28°C (1431 kg ha⁻¹) and approximate two week irrigation cycle (1430 kg ha⁻¹), followed by the soil water balance method (1147 kg ha⁻¹) and 30°C (1073 kg ha⁻¹), and the 32°C (902 kg ha⁻¹) and the dry-land system (353 kg ha⁻¹). Therefore, the irrigation management of cotton with threshold canopy temperatures based on enzyme thermal stability produced yields equal to, if not greater than those obtained from tradition irrigation scheduling techniques (Wanjura *et al.* 1990). However, specific threshold canopy temperatures that induce comparative levels of water stress may depend on climatic factors.

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 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 – 32°C (Burke *et al.* 1988) and high temperatures (>36°C) will adversely affect the growth and

development potential, and ultimately 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 temperature threshold 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 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). 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 Michaelis-Menten constant (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 thermal kinetic window (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 $\pm 200\%$ of the observed minimum value (Mahan *et al.* 1987). The relevance of 200% was based on earlier work which suggested that enzymes could function optimally within $\pm 200\%$ of the minimum K_m value (Somero and Low 1976; Teeri 1980; Teeri and Peet 1978). The temperature dependence of enzyme function has been used to explain the ecological niche and limitations of organisms to thermal environments (Burke 1994; 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 canopy temperature. 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 approximately 3% of the absorbed light. When photosynthesis is at its peak and all photochemical reaction centres are operating fluorescence yield is much lower (approximately 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.

Kasutsky *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 (Burke 1990; Maxwell and Johnson 2000; Peeler and Naylor 1988). 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_0 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 variable fluorescence (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; Burke and Oliver 1993; Ferguson and Burke 1991).

(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 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 canopy temperature can exceed the temperature threshold, in the absence of a water deficit. In the BIOTIC protocol, irrigation is considered appropriate when the canopy temperature exceeds the temperature threshold for a period of time in excess of the time threshold. Wanjura *et al.* (1995) describes three methods for calculating time thresholds: empirical analysis of historical crop canopy temperatures grown under well-watered conditions, empirical field testing of multiple time thresholds that optimise crop yield, and an energy

balance approach which 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 canopy temperatures is the simplest method of determining the time threshold. This method averages the daily amount of time that the canopy temperature exceeds the temperature threshold, 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 predicts canopy temperatures 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 threshold temperature (Mahan *et al.* 2005; Wanjura *et al.* 1995). The energy balance of a crop canopy is described by Monteith (1973) as:

Equation 4: Net radiation

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

Where R_n is net radiation, G is the heat flux below the canopy, H is the sensible heat flux from the canopy and E is the latent heat flux to the air. By substituting the 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 ($^{\circ}\text{C}$), r_a is the aerodynamic resistance (s m^{-1}), R_n is the net radiation (W m^{-2}), 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 ($\text{Pa }^{\circ}\text{C}^{-1}$), $e_A^* - e_A$ is the vapour pressure deficit of the air (kPa), and γ^* is the apparent psychrometric constant ($\text{Pa }^{\circ}\text{C}^{-1}$) in a well-watered crop. In a well-watered crop transpiring at its potential rate the apparent psychrometric constant 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 apparent psychrometric constant. 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: Canopy to aerodynamic resistance

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

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 canopy temperatures are determined (Mahan *et al.* 2005). The analysis is further filtered by excluding times when air temperature is below the temperature threshold, the net radiation 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 canopy temperature to the biologically calculated temperature threshold, and transpirational cooling to temperatures below the temperature threshold is possible.

2.5.5 Limiting relative humidity threshold

High humidity can limit transpirational cooling, to the point where canopy temperatures exceed temperature thresholds, regardless of water availability. Under these conditions canopy temperatures are not reliable indicators of water stress, and canopy temperature will not respond to irrigation. The BIOTIC method continuously corrects plant stress through comparisons of canopy temperature 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). 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). BIOTIC is best suited to controlling crop water stress levels in regions with low rainfall and low probability of uncontrolled water application (Wanjura *et al.* 1992). At present, only one temperature threshold 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 carefully measured in order to ensure repeatable and accurate depiction of crop canopy temperatures. Measured variations in canopy temperatures 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).

2.6 Conclusion

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 utilised as a plant based irrigation scheduling tool, enabling producers to better manage irrigation application for increased water use efficiency, yield or peace of mind.

Although the BIOTIC irrigation scheduling system has evolved over numerous years and is supported by much research, its utilisation, 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 yet 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 moisture 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 utilises a plant threshold temperature in order to maintain plant canopy temperature at or below the thermal optimum.

In addition to the response of the BIOTIC irrigation scheduling system to the temperature threshold 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 moisture 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”. ACRI is located on the Wee Waa Road approximately 30km west of Narrabri, NSW (149°35'E, 30°12'S) (Figure 3.1). ACRI 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 (maximum 35.3°C, minimum 19.4°C) and mild winters (maximum 17.0°C, minimum 3.4°C). The region experiences summer-dominant rainfall patterns, with an annual average of 642mm (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.

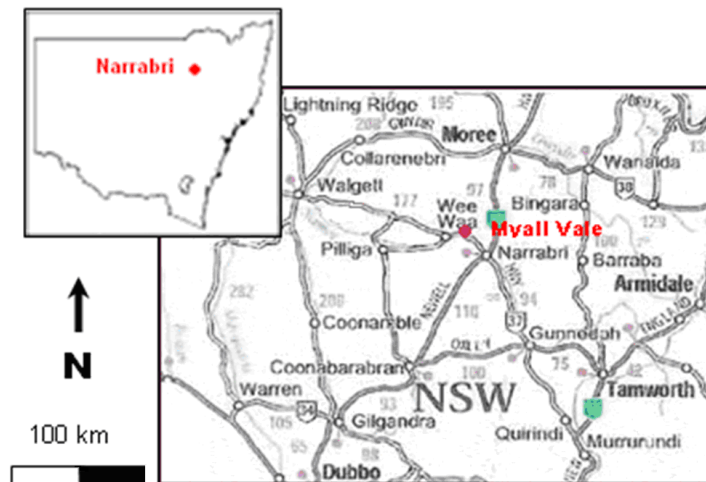


Figure 3.1. Regional map of experimental site showing the location of “Myall Vale”.

3.2 Cultivar

All experiments used the CSIRO-developed cultivar Sicot 70BRF. This cultivar is a full season variety with compact growth habit suited to Australian production systems (CSD 2008). It performs well in all Australian production regions, maintaining high yield potentials, good disease resistance and good fibre quality. It is the current Australian industry standard variety, 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 variety (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 deficit furrow irrigation experiment.

Table 3.1. Location, irrigation delivery method and growing season of field experiments conducted in this study.

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

3.3.1 Thermal optima for Australian cotton cultivars materials and methods

(Experiment 1)

Chlorophyll fluorescence recovery rates

The Australian cotton cultivar (*Gossypium hirsutum* L.) Sicot 70BRF (CSIRO, Australia) was used in this study. Sicot 70BRF was selected to represent a standard commercial Australian variety as in it's first year of full release (2008/09) an excess of 70% of the total area of cotton production in Australia was sown in this variety (Cotton Seed Distributors, *Pers. Comm.*). 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 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 3mm filter paper on top of a wet sponge in a glass dish and covered with CO₂ permeable plastic film (GladwrapTM),

to avoid desiccation. Leaf discs were illuminated at 25°C under a high pressure sodium lamp, emitting a light intensity of $650 \mu\text{mol } \mu\text{m}^2 \text{ s}^{-1}$. An illumination period of one minute was used, however this period was adjusted if the normalised F_v/F_o ratio taken immediately after the illumination period was greater than 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 ten second excitation period of light intensity of $22 \mu\text{mol } \mu\text{m}^2 \text{ s}^{-1}$, 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 with the Brancker SF-30 (Richard Brannkner Research, Ottawa, Canada). 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 (F_v/F_o), and were normalised in order to observe trends in dark adapted fluorescence recovery. Data was 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 plant temperature for the recovery of PSII fluorescence is 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 (Burke 1990).

Gas exchange at discrete leaf temperatures

Leaf photosynthetic rate and stomatal conductance 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 moisture 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, carbon dioxide 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 - 70%, carbon dioxide maintained at 360 $\mu\text{mol}(\text{CO}_2)\text{mol}^{-1}\text{air}$, photosynthetically active radiation (PAR) set to 1800 - 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and air temperatures ranging from 23 to 42°C. Equations used in the instrument for calculating photosynthetic rate or net

carbon assimilation (A, in $\mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$) and stomatal conductance (g, in $\text{mol (H}_2\text{O) m}^{-2} \text{ s}^{-1}$) are given in the Li-COR Biosciences manual (Li-COR 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 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 irrigation rates were calculated according to Allen *et al.* (1998) where the daily water requirement (crop evapotranspiration) = ET_o*K_C. ET_o was calculated using on site weather station data and the Penman-Monteith equation (Allen *et al.* 1998):

Equation 9: FAO56 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, G is the soil heat flux, (e_s - e_a) represents the vapour pressure deficit of the air, ρ_a is the mean air density at constant pressure, c_p is the specific heat of the air, Δ represents the slope of the saturation vapor pressure temperature relationship, γ is the psychrometric constant, and r_s and r_a are the (bulk) surface and aerodynamic resistances.

A locally calibrated and tested crop coefficient was calculated for the experiments using Equation 10 and light interception data (Yeates, *Pers. Comm.*), where K_C = Crop coefficient and LI = Light interception (0 -1).

Equation 10: Locally calibrated crop co-efficient

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

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 13m long plots in Experiment 2, and 10m 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.

The rate of water application in the surface drip irrigation system was determined by measuring the water collected in containers in 30-minute periods. A container was placed at two randomly allocated drip emitters in each plot. The irrigation rate was determined to be a uniform 2.4mm hr^{-1} , at an operating pressure of 103 kPa (15 psi). The cotton crop was surface drip-irrigated approximately every two to three days, depending on daily ET_0 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.

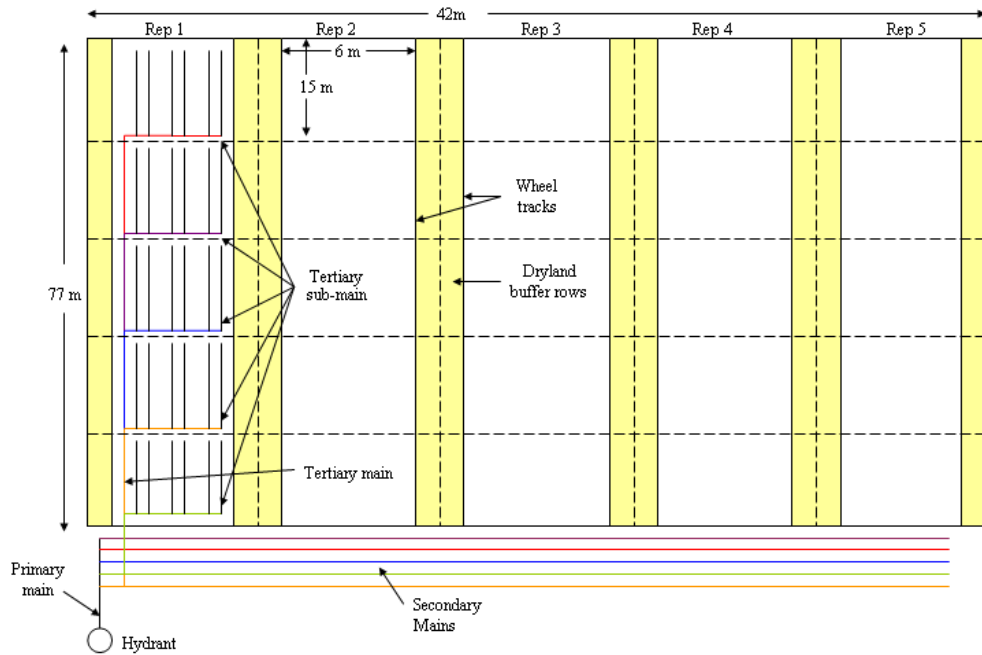


Figure 3.2. The experimental plan showing the layout of the drip irrigation system



Figure 3.3. Lay out 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 September 28th and was planted one week later on October 5th 2007. Emergence occurred six days after sowing. 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 60mm 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
<i>Fertiliser history</i>		
Anhydrous ammonia	14 th Sep 2007	160 kg N ha ⁻¹
<i>Herbicide application</i>		
Fluometuron (Cotoran SC)	5 th Oct 2007	5.0 L ha ⁻¹
Glyphosate (Round up) (Spot spray)	6 th Oct 2007	0.8 L ha ⁻¹
Glyphosate (Roundup Ready Herbicide)	16 th Oct 2007	1.5 kg ha ⁻¹
Glyphosate (Round up) (Spot spray)	6 th Dec 2007	0.8 L ha ⁻¹
<i>Pesticide management</i>		
Indoxacarb (Steward) + Petroleum oil (D-C-Tron canopy oil)	29 th Jan 2008	0.850 L ha ⁻¹ 2.0 L ha ⁻¹
<i>Defoliant application</i>		
Thidiazuron (Dropp Liquid) + Ethephon (Prep 720) + Petroleum oil (D-C-Tron canopy oil)	9 th Apr 2008	0.2 L ha ⁻¹ 2.0 L ha ⁻¹ 2.0 L ha ⁻¹
Thidiazuron (Dropp Liquid) + Petroleum oil (D-C-Tron canopy oil)	21 st Apr 2008	0.2 L ha ⁻¹ 2.0 L ha ⁻¹
Thidiazuron (Dropp Liquid) + Petroleum oil (D-C-Tron canopy oil)	22 nd Apr 2008	0.2 L ha ⁻¹ 2.0 L ha ⁻¹

Experiment 3 (2007/08 growing season)

Experiment 3 was planted on October 14th 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 approximately 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
<i>Fertiliser history</i>		
Ammonia (NH ₃) via nitrogen fixation- Purple vetch (<i>Vicia sativa ssp. nigra</i>)	May - Sep 2008	60 kg N ha ⁻¹
Urea (Fertigation)	3 rd Jan 2009	25 kg N ha ⁻¹
Urea (Fertigation)	8 th Jan 2009	25 kg N ha ⁻¹
Urea (Fertigation)	12 th Jan 2009	25 kg N ha ⁻¹
Urea (Fertigation)	16 th Jan 2009	25 kg N ha ⁻¹
<i>Herbicide application</i>		
Pendimethalin (Stomp*Xtra)	30 th Sep 2008	3.0 L ha ⁻¹
Fluometuron (Cotoran SC)	14 th Oct 2008	5.0 L ha ⁻¹
Glyphosate (Round up) (Spot spray)	20 th Oct 2008	0.8 L ha ⁻¹
Glyphosate (Round up) (Spot spray)	24 th Nov 2008	0.8 L ha ⁻¹
<i>Pesticide management</i>		
Diafenthiuron (Pegasus 500EC)	24 th Feb 2009	0.800 L ha ⁻¹
<i>Defoliant application</i>		
Thidiazuron (Dropp Liquid) + Ethephon (Prep 720) + Petroleum oil (D-C-Tron canopy oil)	3 rd Apr 2009	0.2 L ha ⁻¹ 2.0 L ha ⁻¹ 2.0 L ha ⁻¹
Thidiazuron (Dropp Liquid) + Ethephon (Prep 720) + Petroleum oil (D-C-Tron canopy oil)	7 th Apr 2009	0.2 L ha ⁻¹ 2.0 L ha ⁻¹ 2.0 L ha ⁻¹

(c) *Data collection*

Biologically Identified Optimal Temperature Interactive Console (BIOTIC)

Wireless, battery-operated “SmartCropTM” infrared thermometers (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 infrared thermometer (IRT) (Zytemp, HsinChu, Tiwan 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 (approximately 80 days).

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 10cm 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 air temperature and relative humidity were also logged (Smartfield Inc., Lubbock, Tx, USA) every 15 minutes, 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 moisture

Soil moisture to 100cm in depth at 10cm intervals was calculated every 2-3 days from four replicates in all treatments from the experiment using the Gopher® Soil Moisture Profiling System capacitance probe. 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 moisture content of the soil. Therefore, the measured dielectric constant increases as the water content of the soil increases.

The soil moisture to 120cm in 15cm intervals was also measured on a weekly basis using the CPN Corporation Hydroprobe®, model 503DR, neutron moisture meter (NMM) in the control (Treatment 4) plots only. This was conducted in order to provide a reference for the Gopher® probe measurements.

Water Use Efficiency

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

Light interception

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 fortnightly 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 light interception was used in the calculation of crop water requirements.

Biomass accumulation

The accumulation of 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 accumulation 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 square metre 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 was 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 leaf area index (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.

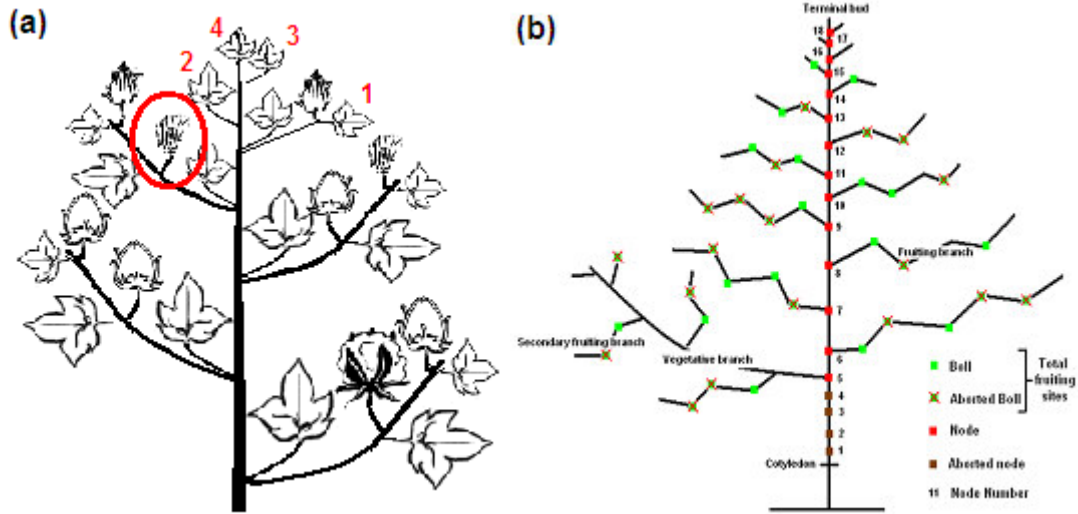


Figure 3.5. (a) Diagram showing a plant that has reached cut out. Cut out has occurred when the number of nodes above a first position one-day-old flower (in the red circle) is four; (b) Schematic diagram of a cotton plant showing the number of nodes and fruiting sites.

Plant mapping and yield

Plant mapping was carried out during the pre-harvest period, 179 days after sowing in Experiment 2 and 162 DAS in Experiment 3. One randomly allocated square metre of each plot with a uniform plant stand ($> 8 \text{ plants m}^{-2}$) 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 percent 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 (per cent lint of seed cotton) and fibre quality was then calculated from a

sub sample of the picked yield. Fibre quality (fibre length, strength, uniformity and micronaire) was measured on a high volume instrument (HVI).

Weather conditions

Weather conditions at 15 minute, 60 minute and 24 hour intervals were monitored directly adjacent to the crop with a customised weather station (Campbell Scientific, Logan, UT). The weather station measured average, maximum and minimum air temperature ($^{\circ}\text{C}$) 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, total and average radiation (KW m^{-2}) with the CS305-ETM solar radiation sensor, and total rainfall (mm) with the TE525-ET tipping bucket rain gauge, as well as calculated ET_0 (mm hr^{-1}) and vapour pressure deficits (kPa).

Rainfall (mm) was also manually measured with a rain gauge 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 crop requirement (ET_C) and 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 moisture to field capacity, the starting soil moisture following the initial furrow irrigation. The effects of deep drainage and runoff were ignored as these parameters were not measured.

Degree day accumulation was calculated with the CottASSIST day degree calculator (CSIRO 2008). The day degree calculator uses the formula:

Equation 11: Cotton degree-day equation

$$DD = \frac{(T_{\max} - 12) + (T_{\min} - 12)}{2}$$

Where DD is the degree day accumulation, $T_{\max}$ is the maximum daily temperature, and $T_{\min}$ is the minimum average temperature. The significance of 12 is that 12°C is considered the base temperature for cotton growth and development, and thus temperatures below 12°C do not contribute to degree day accumulation. High and low temperature stress days are those days where ambient temperatures exceed 36°C, or fall below 11°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 moisture deficits (mm) calculated from neutron moisture meter (Table 3.4). These four irrigation treatments included a control or theoretical optimum (40-50mm deficit), a frequently irrigated (30-40mm deficit) and two extended deficit irrigation treatments: a moderately extended (65-75mm deficit) and fully extended (105-110mm deficit) treatment.

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 164m 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 one metre. 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 more moist 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 yield was calculated from four 13m strips up the field in this same row (Figure 3.6).

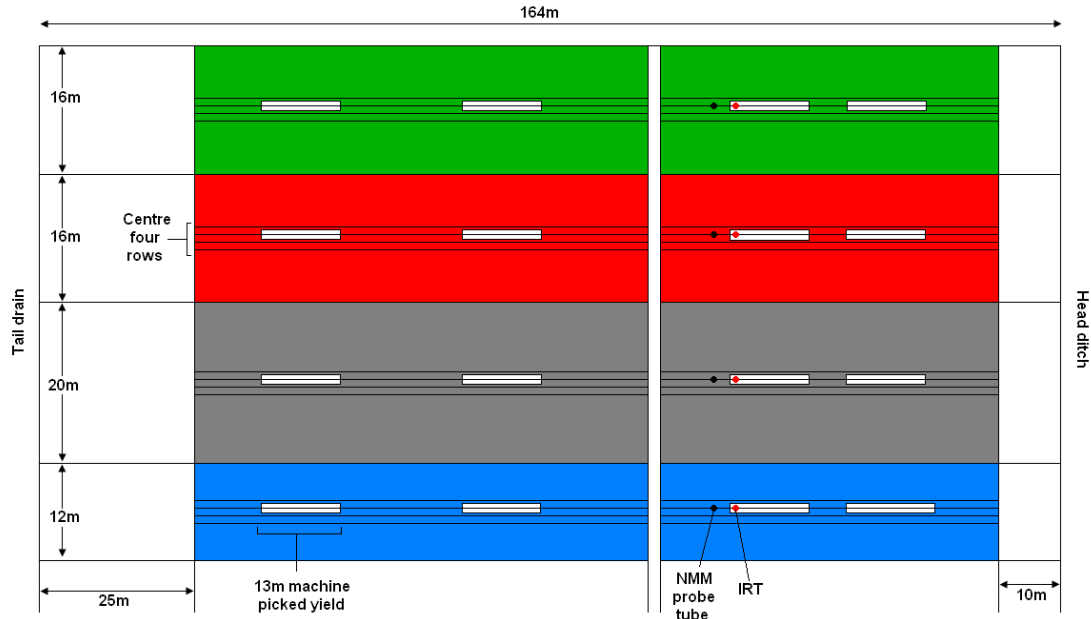


Figure 3.6. The experimental plan showing the layout of one treatment block including the location of neutron moisture meter probe tubes, infra-red thermometers, and the area machine picked for yield analysis. The bottom 25m and top 10m of the field are discounted from measurements due to water-logging 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 327mm.

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

(b) Crop management

The experimental site was pre-irrigated on October 2nd and was planted two weeks later on October 15th (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
<i>Fertiliser history</i>		
Anhydrous ammonia	12 th Sep 2008	200 kg N ha ⁻¹
Superphosphate	28 th Sep 2008	100 kg ha ⁻¹
<i>Herbicide application</i>		
Pendimethalin (Stomp*Xtra)	28 th Sep 2008	2.2 L ha ⁻¹
Fluometuron (Cotoran SC)	15 th Oct 2008	5.0 L ha ⁻¹
Glyphosate (Roundup Ready Herbicide)	26 th Nov 2008	1.5 kg ha ⁻¹
<i>Pesticide management</i>		
Fipronil (Regent)	14 th Nov 2008	0.125 L ha ⁻¹
Indoxacarb (Steward) + salt	27 th Jan 2009	0.850 L ha ⁻¹ , 1kg ha ⁻¹
Diafenthiuron (Pegasus 500EC)	18 th Feb 2009	0.800 L ha ⁻¹
Pyriproxyfen (Admiral) +	28 th 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 th Mar 2009	0.800 L ha ⁻¹
<i>Defoliant application</i>		
Thidiazuron (Dropp Liquid) +	3 rd Apr 2009	0.2 L ha ⁻¹
Ethephon (Prep 720) +		2.0 L ha ⁻¹
Petroleum oil (D-C-Tron canopy oil)		2.0 L ha ⁻¹
Thidiazuron (Dropp Liquid) +	9 th Apr 2009	0.2 L ha ⁻¹
Ethephon (Prep 720) +		2.0 L ha ⁻¹
Petroleum 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). 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.

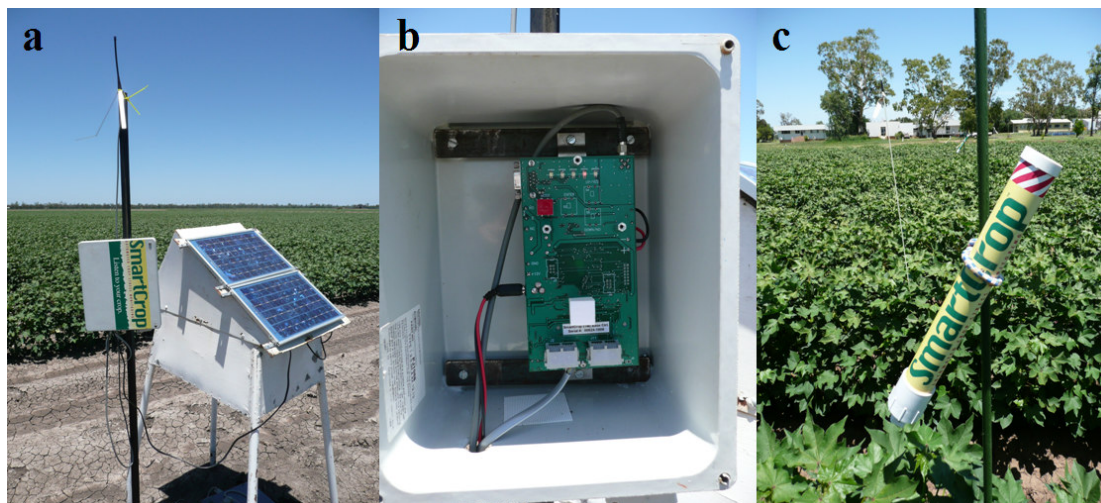


Figure 3.7. The installed BIOTIC equipment. a) receiver aerial, base station (in weather proof box) and solar panels (power source) located at the centre of the experimental field; b) The base station and data logger mounted inside the weather proof box; c) BIOTIC sensors installed in field experiment.

Soil moisture

The soil moisture to 120cm at 10cm intervals in the top 60cm of soil and at 20cm intervals below 60cm was measured using the CPN Corporation Hydroprobe®, model 503DR, neutron moisture meter. Using a calibration developed for the same field (Yeates, *Pers. Comm.*) for the NMM probe, the soil water was monitored throughout the season between 28 and 168 DAS. Irrigation was managed through soil moisture monitoring with the NMM. Irrigation was initiated when soil moisture content reached the desired soil water deficit range (Table 3.4). Soil moisture was measured again 48 hours prior to an irrigation event, and again during the dry down cycle.

Biomass accumulation

The accumulation of 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.

Yield

Mechanically picked seed cotton weight data was recorded from four 13 metre sections of the measurement row of cotton. It is important to note that the bottom 25 metres and the top ten metres of the field, as well as the area surrounding the neutron probe and the access path were excluded from yield and other measurements. The bottom of the field was excluded from measurements due to waterlogging from the backing up of water at the tail drain. The top of the field was excluded because this portion of the field receives the most irrigation water and is subject to compaction from the formation of previous season's rotorbucks. Rotorbucks are 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 yield. Fibre quality (fibre length, strength, uniformity and micronaire) were measured on a high volume instrument (HVI).

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.

4. SOIL MOISTURE DEFICITS AND THEIR INFLUENCE ON CANOPY TEMPERATURES IN SURFACE DRIP IRRIGATED COTTON

4.1 Introduction

Cotton production is affected significantly by water supply, and the relationship between water application, plant physiological response and cotton 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 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 stomatal conductance, leaf water potential, 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 moisture conditions (Hearn 1994). Hence,

it is important to note the divergence between an optimal agronomic and evolutionary water application. Evolutionarily, water supply has 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 moisture has been utilised vegetative growth abruptly ceases, and remaining water is used to mature fruit. This response to soil moisture, 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, radiation, ambient temperature, humidity, wind speed and the position of the leaf surface in relation to the incident solar radiation 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 (Gates 1964; Tanner 1963; Wiegand and Namken 1966). The difference between leaf and air temperatures ($T_c - T_a$) or canopy temperature differential (CTD) was first

studied with 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 yield and water requirements. They assumed that environmental factors such as VPD, radiation and wind would manifest in canopy temperatures, however this does not always hold true (Jackson *et al.* 1981). This is because canopy temperatures can be profoundly influenced by VPD, radiation 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 canopy temperatures is the stress time (ST) index developed by Wanjura *et al.* (1992). The stress time index accumulates the amount of daily time a canopy temperature exceeds its species-specific optimum temperature. Using infra-red thermometry 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. BIOTIC utilises infra-red thermometers 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 radiation), 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.

4.2 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 irrigation rates were calculated according to (Allen *et al.* 1998) where the daily water requirement = $ET_o * K_C$. A locally calibrated crop coefficient was calculated from the experiments using light interception (LI), where $K_C = 1.2719(LI - 0.0779)$. Weather conditions, soil moisture, crop growth and

development, yield and canopy temperatures were monitored throughout the experiments. Detailed materials and methods of these experiments can be found in Chapter 3.

4.3 Results

4.3.1 Climate

The experimental site has a long term average rainfall of 657mm per annum, and 391mm for the cotton growing season (October to March) (BOM 2009). Rainfall throughout Experiment 2 totalled 361mm and 353mm in Experiment 3. Although both seasons received similar amounts of rainfall, the distribution and intensity of rainfall events varied. Experiment 2 tended to be characterised by more numerous, smaller rainfall events, whilst Experiment 3 saw fewer rainfall events, but with a greater intensity (Table 4.1 and Figure 4.1a). 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 4.1a). According to the daily water requirement calculations (crop evapo-transpiration) in the control plots, only 66mm and 137mm of the total rainfall in Experiment 2 and Experiment 3 was effective in the respective years (Figure 4.2).

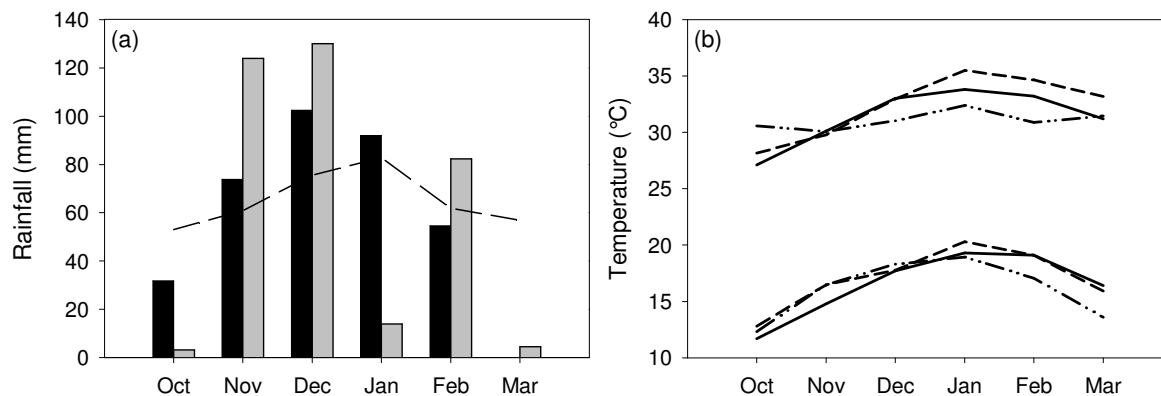


Figure 4.1. (a) Monthly rainfall (mm) in Experiment 2 (■) and Experiment 3 (▒) and the long term average monthly rainfall (— —). Average maximum and minimum monthly temperatures (°C) in Experiment 2(— · — · — ·), Experiment 3 (— — — —); and long term averages (———).

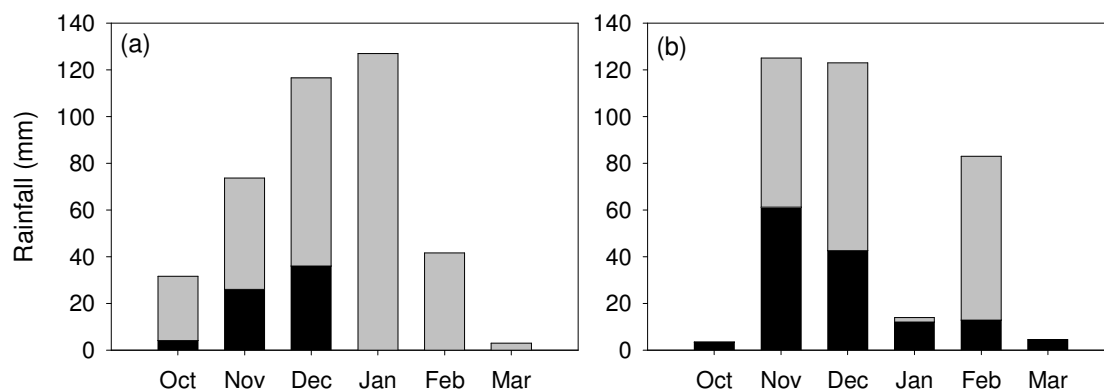


Figure 4.2. Effective (■) and ineffective (▒) rainfall (in relation to the target amount of total water) in the control plots (Treatment 4) in Experiment 2 (a) and Experiment 3 (b). Values were calculated from locally adapted FAO 56 crop evapotranspiration equations.

Table 4.1. 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 > 15mm (%)	13	37
Temperature		
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
Radiation		
Average daily (MJ m ⁻²)	23.6	25.0
Wind speed		
Average daily (m sec ⁻¹)	4.1	4.3
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 – 1 st Square	5.4	5.3
1 st Square – 1 st Flower	4.9	5.9
1 st 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 (Bange and Milroy 2004; Hodges *et al.* 1993).

Temperatures in Experiment 3 were consistently higher than those experienced in Experiment 2 (Figure 4.1b). Not only were average temperatures higher in Experiment 3, but a larger number of high temperatures stress days were experienced (Table 4.1). Higher ambient temperatures in Experiment 3 resulted in faster thermal time accumulation. Thus, the crop experienced a shorter season length of 145 days to 60% open bolls and 161 days to defoliation in Experiment 3, compared to 160 days and 178

days 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 evapo-transpiration from the development of the first square through to maturity (Table 4.1). Interestingly, during the crop establishment phase from planting to first square, water demand (ET_O) was lower in Experiment 3. Average daily radiation, wind speed and vapour pressure deficit, three environmental factors affecting the energy balance of a leaf and hence canopy temperatures, were also on average slightly higher in Experiment 3 compared with Experiment 2 (Table 4.1). The combination of higher temperatures, average net radiation, average wind speed and average evaporative demand resulted in an increased stress potential in Experiment 3 compared to Experiment 2.

4.3.2 Soil moisture and irrigation

Every effort was made to utilise rainfall in the irrigation treatments however, untimely rainfall altered the deficit levels of all treatments (Figure 4.3 and Table 4.2). 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 4.2). Despite the effect of rainfall, 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 4.3), 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 combined irrigation and rainfall. This resulted in more pronounced water stress and soil moisture deficits in Experiment 3 compared with Experiment 2 (Figure 4.3).

Table 4.2. Irrigation treatment, rainfall, and the actual percent of ET_C applied to each treatment in Experiment 2 and Experiment 3.

Treatment:	Experiment 2 (ET_C= 755mm)	Experiment 3 (ET_C= 820mm)
1 - Irrigation applied (mm)	187	25
- Stored soil moisture 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 moisture 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 moisture 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 moisture 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 moisture used (mm)	-30	30
- Total water (rain, irrigation & stored) (mm)	1056	853
- Desired ET_C	125	125
- Actual ET_C	140	104

Experiment 3 saw earlier soil moisture deficits, with Treatments 1, 2, 3 and 4 reaching a soil moisture 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 moisture 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 moisture 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 which were exposed to soil moisture deficits (Figure 4.3).

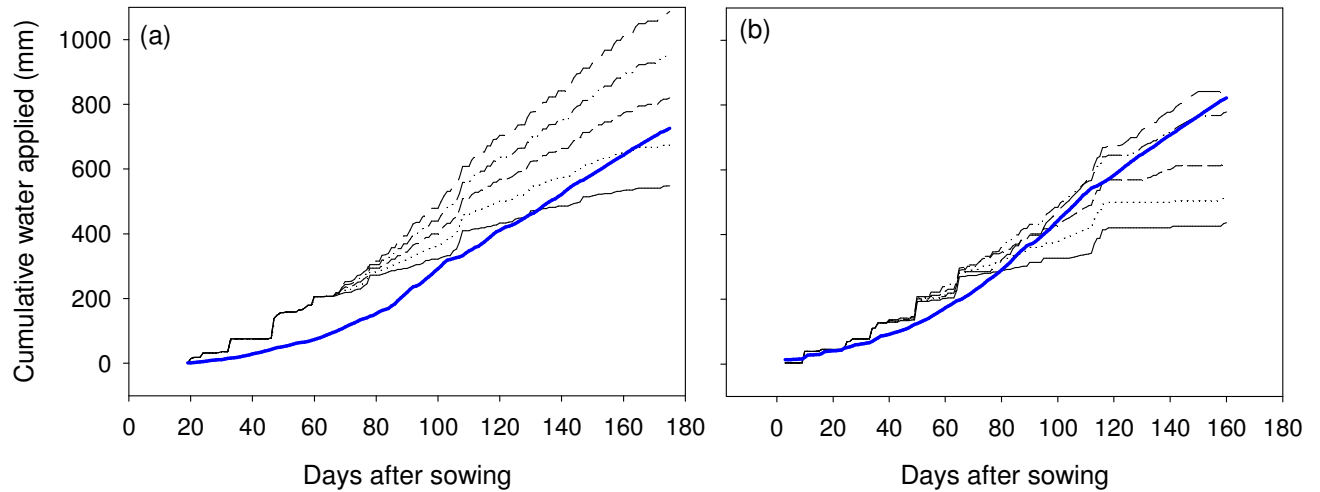


Figure 4.3. Cumulative water applied (rainfall + irrigation) (excluding initial furrow irrigation in both experiments) across all irrigation treatments in (a) Experiment 2 and (b) Experiment 3; — Treatment 1, Treatment 2, ---- Treatment 3, - · - · - Treatment 4, — — — Treatment 5 and ——— cumulative 100% ET_c.

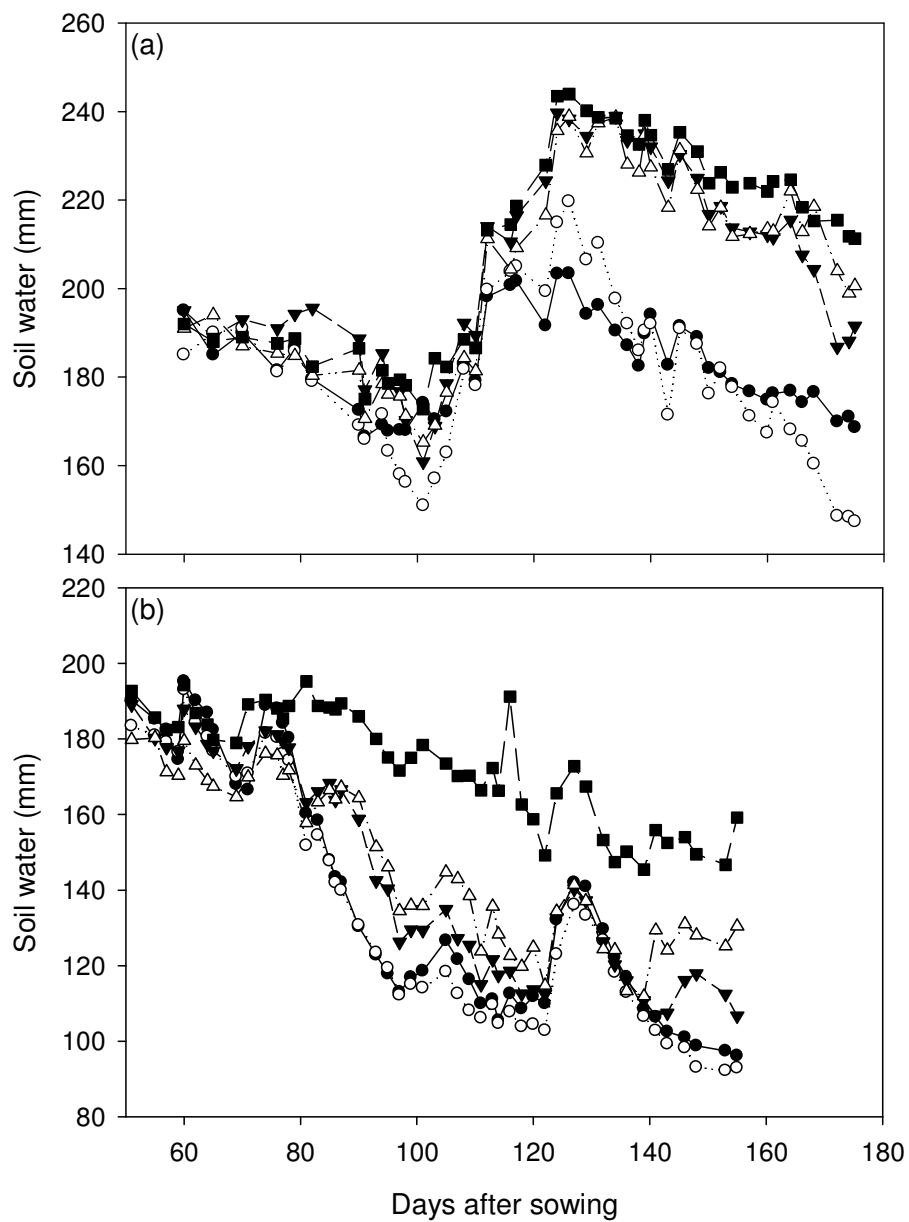


Figure 4.4. Soil moisture (mm) throughout the season in (a) Experiment 2 and (b) Experiment 3; Treatment 1 (—●—), Treatment 2 (····○···), Treatment 3 (---▼---), Treatment 4 (-·-△-·-) and Treatment 5 (- -■- -). Note that Experiment 2 used little stored moisture in comparison to Experiment 3, and the soils of Experiment 3 were consistently drier over the entire season.

Soil moisture curves measured using a GopherTM capacitance probe and calibrated with corresponding soil moisture measurements using a neutron moisture meter over the growing season are shown in Figure 4.4. Soil moisture curves in Experiment 2 are characterised by minor soil moisture depletion to 100 DAS, a significant increase in soil moisture between approximately 100 and 120 DAS, followed by minor soil moisture depletions for the remainder of the season (Figure 4.4a). This increase is due to high amounts of rainfall, and corresponds to the large amounts of rainfall resulting in excessive water application (Figure 4.2a). This ineffective rainfall (rainfall following irrigation application) resulted in minimal net soil moisture depletion over the growing season. Soil moisture depletions of 21 and 18mm occurred in Treatments 1 and 2, whilst net gains of soil moisture of 16, 22 and 30mm were recorded in Treatments 3, 4 and 5. The pattern of soil moisture depletion over Experiment 3 was different to that of Experiment 2. Although similar starting soil moistures of approximately 190mm were observed, Experiment 3 was characterised by sustained soil moisture depletion over the entire season, with the exception of a significant rainfall event around 125 DAS (Figure 4.4b). Regardless of this rainfall event, net soil moisture depletions of 89, 85, 73, 49 and 30mm were recorded across the season in Treatments 1, 2, 3, 4 and 5.

4.3.3 Crop development

In Experiment 2, treatment variation in crop yield was manifest in two statistically significant groups ($P < 0.001$) (Figure 4.5a). 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 4.2), 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 4.5b). 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 4.5b, Figure 4.6b and Table 4.2). 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 K_c 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 4.3 and Figure 4.7a). 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 15th 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 4.7a). 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 4.7b and Table 4.3). 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 822mm of applied water, and then fell as water application increased (Figure 4.6a). 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 4.6b). 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 $\pm$ 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 .

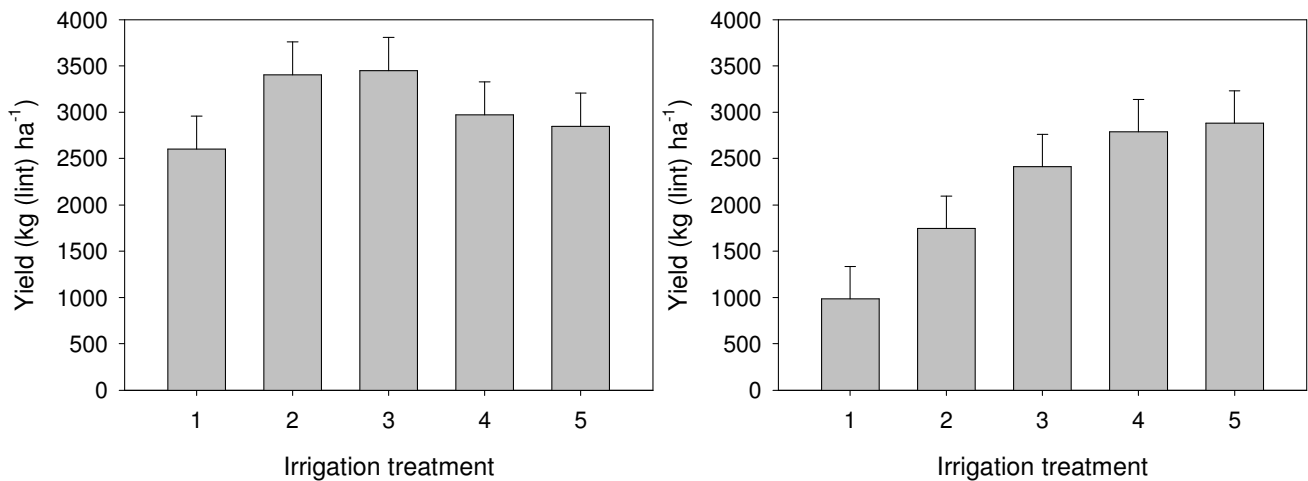


Figure 4.5. Machine picked lint yield (kg ha⁻¹) for Experiment 2 (a) and Experiment 3. Vertical bars represent l.s.d.

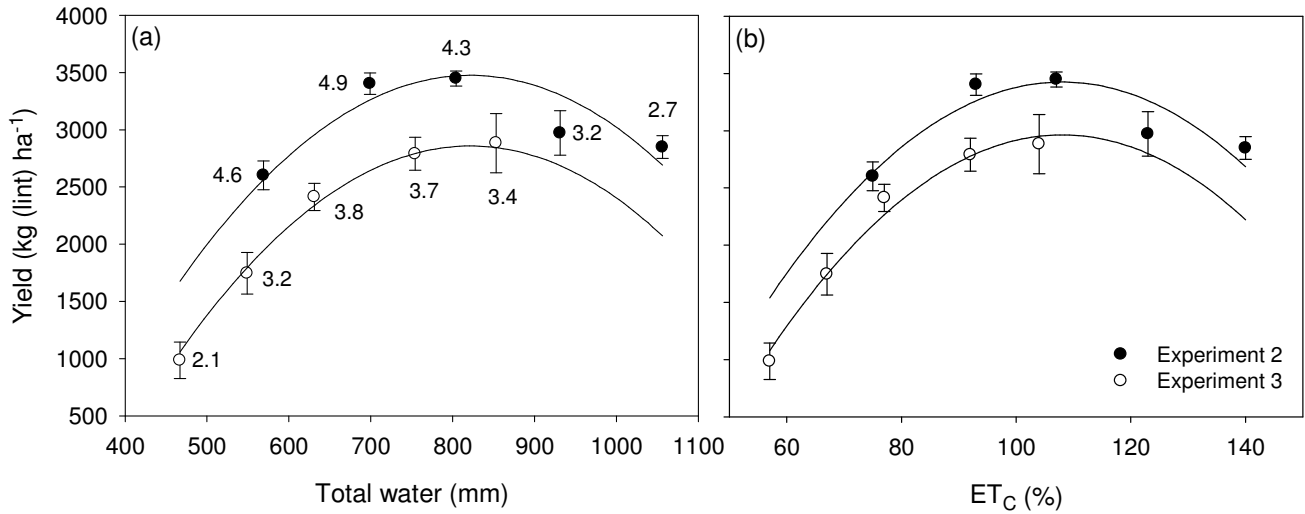


Figure 4.6. (a) Yield-water relations regression in Experiment 2 ($y = -0.0143x^2 + 23.5x - 6179$) and Experiment 3 ($y = -0.0143x^2 + 23.5x - 6797$). Numbers beside each data point is the water use efficiency (WUE) in kg mm⁻¹ ha⁻¹ for each treatment. Total water applied includes rainfall, surface drip irrigation and furrow irrigation events. (b) Yield-ET_C relations regression in Experiment 2 ($y = -0.7239x^2 + 156.4x - 5023$) and Experiment 3 ($y = -0.7239x^2 + 156.4x - 5485$). Vertical bars represent standard error of mean.

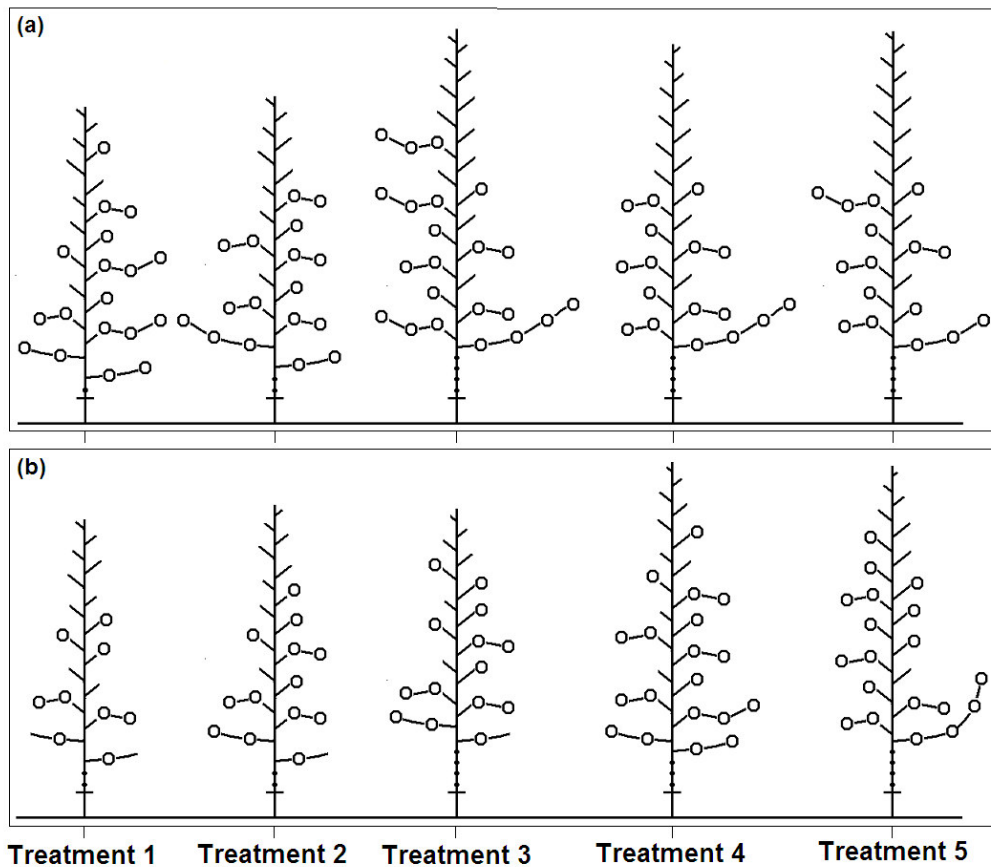


Figure 4.7. Schematic diagram of plant architecture showing the average number of nodes, bolls and boll position for all treatments in (a) Experiment 2 and, (b) Experiment 3.

Table 4.3. 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	1-4	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	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 4.8). 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 crop 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 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 yield.

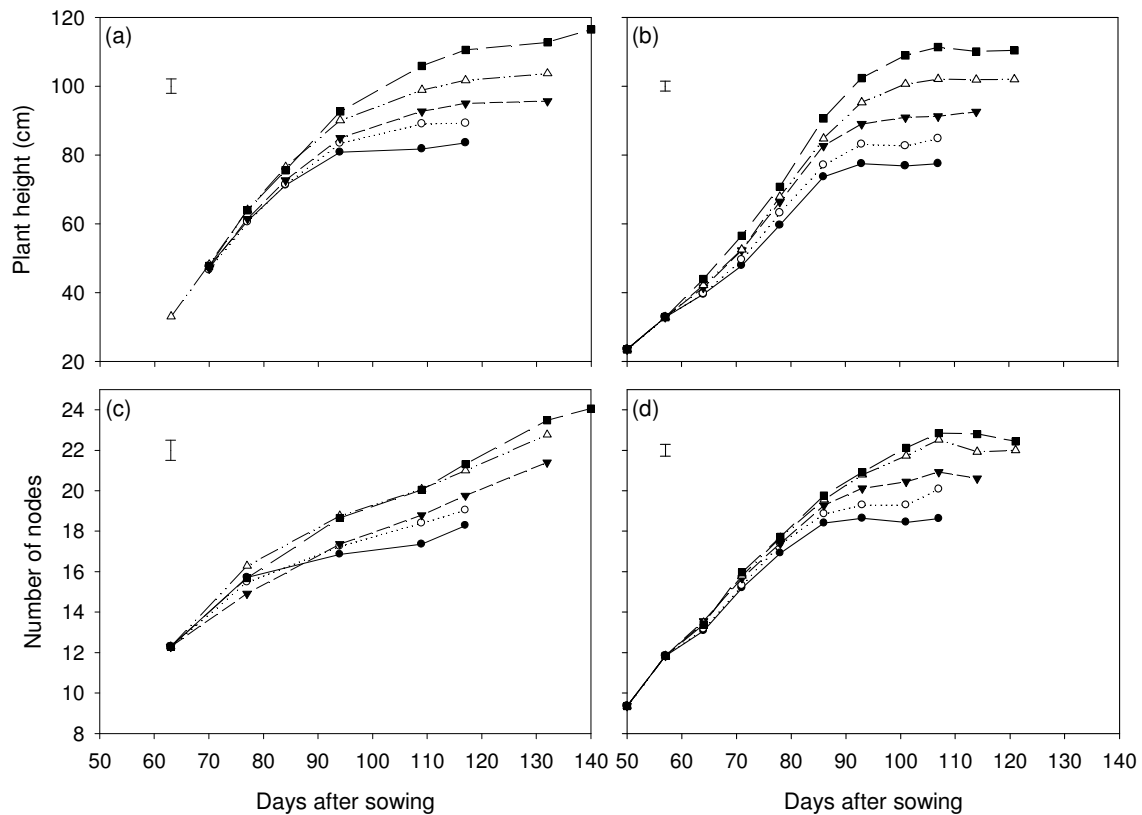


Figure 4.8. Plant height for (a) Experiment 2 and, (b) Experiment 3 and number of nodes for (c) Experiment 2 and, (d) Experiment 3 in Treatment 1 (—●—), Treatment 2 (····○····), Treatment 3 (—▼—), Treatment 4 (—△—) and, Treatment 5 (—■—). Vertical bar represents l.s.d.



Figure 4.9. Examples of variation in 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 5. Measuring stick represents 100cm.



Figure 4.10. Examples of variation in 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 5. Measuring stick represents 100cm.

4.3.4 Biomass accumulation and partitioning

Differences in biomass accumulation and numbers of fruit were observed in both Experiment 2 (Figure 4.9) and Experiment 3 (Figure 4.10). In Experiment 2, broad treatment differences in total dry matter were not evident until the end of the season (173 DAS) (Figure 4.11a). Total dry matter in Treatment 5 increased by 55% in the 35 days following the 138 DAS biomass harvest, compared with rises of approximately 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 moisture stress (Figure 4.11b). 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 4.7b). 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 4.1), which lead to the formation of rank growth in treatments with excess water supply.

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 4.3), adequate ambient temperatures and an excess supply of carbohydrates to mature bolls, allows the plant 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.

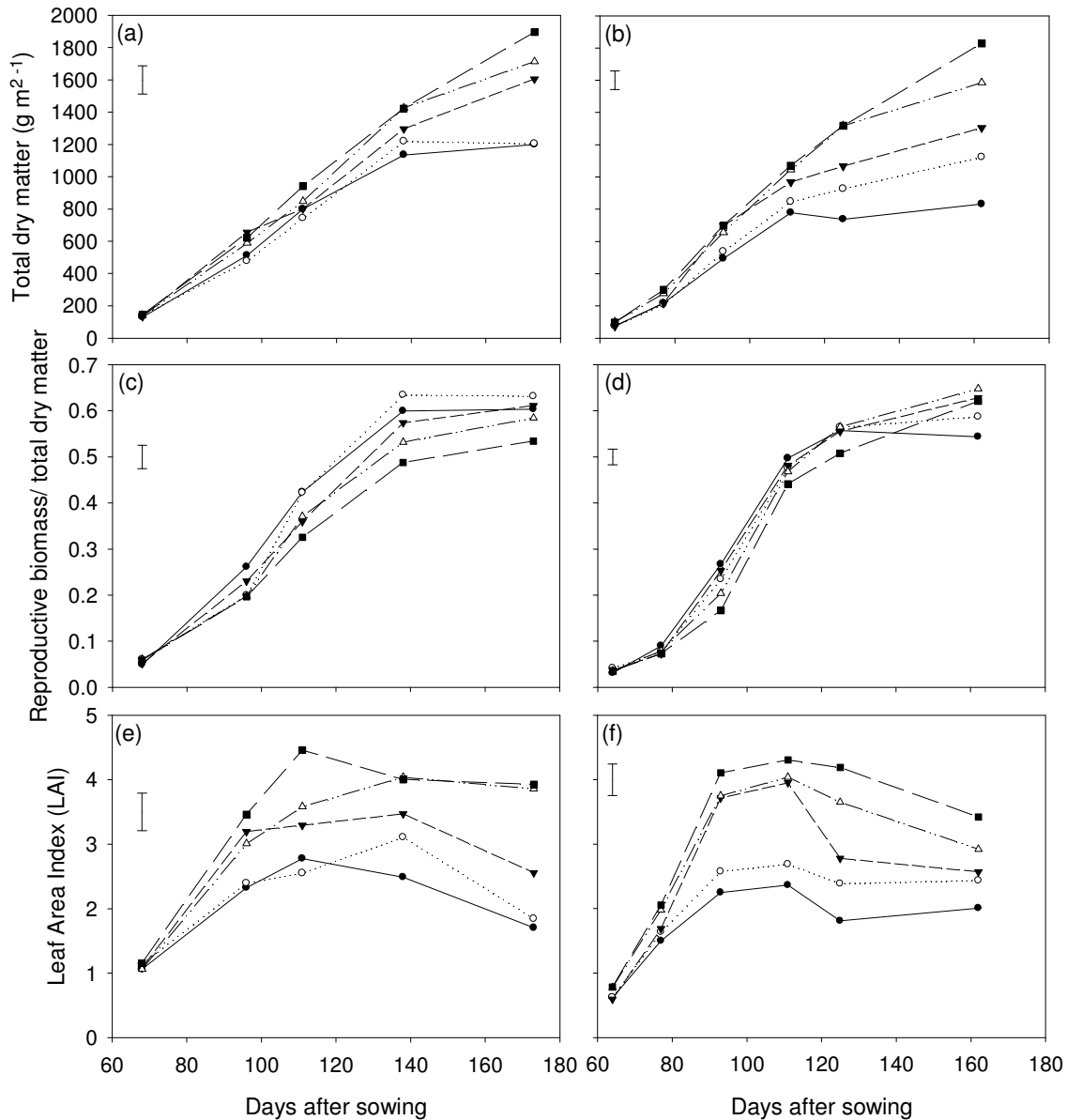


Figure 4.11. Total dry matter accumulation (g.m^{-2}) in (a) Experiment 2 and (b) Experiment 3; The ratio of reproductive to vegetative biomass in (c) Experiment 2 and (d) Experiment 3; and leaf area index (LAI) in (e) Experiment 2 and (f) Experiment 3 in all treatments; Treatment 1 (—●—), Treatment 2 (····○····), Treatment 3 (—▼—), Treatment 4 (—△—) and Treatment 5 (—■—). Vertical bar represents L.S.D.

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 4.11c). 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 approximately 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 4.5a).

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 4.11d). 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 which 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 4.5b).

Leaf area index (LAI) is an important factor in crop development as it strongly 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 infra-red thermometers used in this study. This is because measurement errors, such as the effects of background surface soil temperatures within the infra red thermometer's field of view, can be introduced at low LAIs before canopy closure. Peak LAI in Experiment 2 occurred at 138 DAS in all treatments with the exception of the driest (Treatment 1) and wettest (Treatment 5) treatments, which peaked earlier at 111 DAS (Figure 4.11c). 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 4.11d). As a result, the rate of LAI increase in Experiment 3 was much faster than observed in Experiment 2.

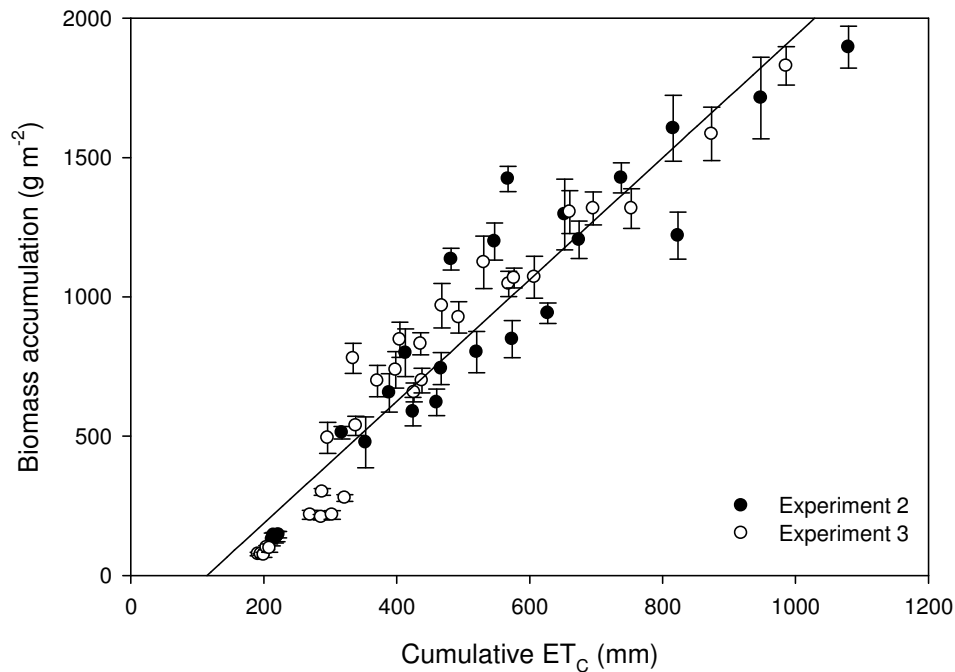


Figure 4.12. Regression of biomass accumulation and water requirement throughout the season from squaring to maturity in Experiment 2 and Experiment 3 ($y = 2.1875x - 250.6$; $R^2=0.91$). Vertical bars represent standard error.

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 4.12). 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 per cent of the variance, with an estimated standard error of biomass accumulation of 151 g m^{-2} .

4.3.5 Canopy temperatures

Average canopy temperatures in Experiment 2 and Experiment 3 reflected the trend where higher canopy temperatures for longer durations correlated with increased water stress (Figure 4.15 and Figure 4.16). Irrigation treatments which 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 4.4). Like Wanjura *et al.* (1992), treatment differences were only observed when radiation levels were above 300 W m^{-2} (Table 4.4). Therefore, average canopy temperatures from this point refer to canopy temperatures measured when radiation levels exceed 300 W m^{-2} . Canopy temperatures in all treatments in Experiment 2 were lower than those observed in Experiment 3. This trend is supported by observed soil moisture status (where Experiment 3 is characterised by consistently drier soils- see Figure 4.4), evaporative demand (where a higher cumulative crop water demand was observed in Experiment 3) and the consistently lower gross water (rainfall and irrigation) application in Experiment 3 compared to Experiment 2 (Table 4.1).

Table 4.4. Average canopy temperature (T_c), average canopy temperature when net radiation $< 300 \text{ W m}^{-2}$ and $> 300 \text{ W m}^{-2}$, canopy temperature depression (CTD) when net radiation $> 300 \text{ W m}^{-2}$ and ambient air temperature $> 28^\circ\text{C}$, 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 ($^\circ\text{C}$)	Average T_c ($^\circ\text{C}$) ($R_n < 300 \text{ W m}^{-2}$)	Average T_c ($^\circ\text{C}$) ($R_n > 300 \text{ W m}^{-2}$)	CTD ($R_n > 300 \text{ W m}^{-2}$, $> 28^\circ\text{C}$ $T_a > 28^\circ\text{C}$)	Time T_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 ($^\circ\text{C}$)	Average T_c ($^\circ\text{C}$) ($R_n < 300 \text{ W m}^{-2}$)	Average T_c ($^\circ\text{C}$) ($R_n > 300 \text{ W m}^{-2}$)	CTD ($R_n > 300 \text{ W m}^{-2}$, $> 28^\circ\text{C}$ $T_a > 28^\circ\text{C}$)	Time T_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), the difference between canopy temperature and ambient air temperature ($\text{CTD} = T_c - T_a$), shows the effect of transpirational cooling on canopy temperatures. Average CTD in Experiment 2 and Experiment 3 shown in Table 4.4, where treatments with increasing soil moisture became more negative, indicating a greater capacity for canopy cooling by transpiration. Canopy temperature depression was calculated for periods when net radiation (R_n) exceeded 300 W m^{-2} and air temperature was greater than 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 moisture availability, can be attributed to transpirational cooling

differences when environmental conditions (solar energy input and ambient temperature) are sufficient to raise canopy temperatures above 28°C.

Seasonal average canopy temperature and percent ET_C applied exhibited a curvilinear relationship where average canopy temperature decreased as water application increased (Figure 4.13). The average canopy temperature and per cent ET_C applied data could not be combined as the regression 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 98.9 per cent of the variance, with an estimated standard error of average canopy temperatures of 0.236°C.

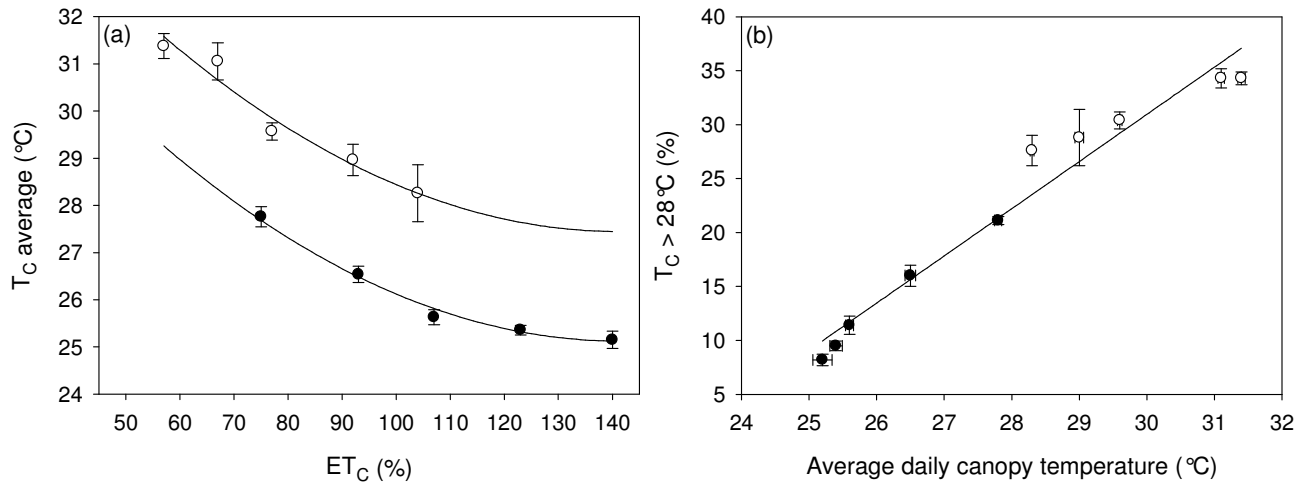


Figure 4.13. (a) Average canopy temperature and per cent ET_C applied regression in Experiment 2 (●) ($y = 0.00058x^2 - 0.1641x + 36.73$) and Experiment 3 (○) ($y = 0.00058x^2 - 0.1641x + 39.05$). Vertical bars represent standard error of canopy temperatures. (b) Average canopy temperature and time canopy 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 canopy temperatures exceeded 28 °C followed the same pattern as canopy temperature, where increased soil moisture deficits resulted in an increase in time period (Table 4.4). Average daily canopy temperature was positively related to the amount of time canopy temperatures exceeded 28 °C ($P<0.001$) (Figure 4.13b). Average canopy temperatures were related to final crop yield ($P<0.001$) (Figure 4.14), where yields peaked at average canopy temperatures of 26.4°C. The range in canopy temperatures which produced yields similar to the peak of 3196 kg (lint) ha⁻¹ was 24.8 to 28.1 °C. Canopy temperatures outside of this temperature range experienced 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.

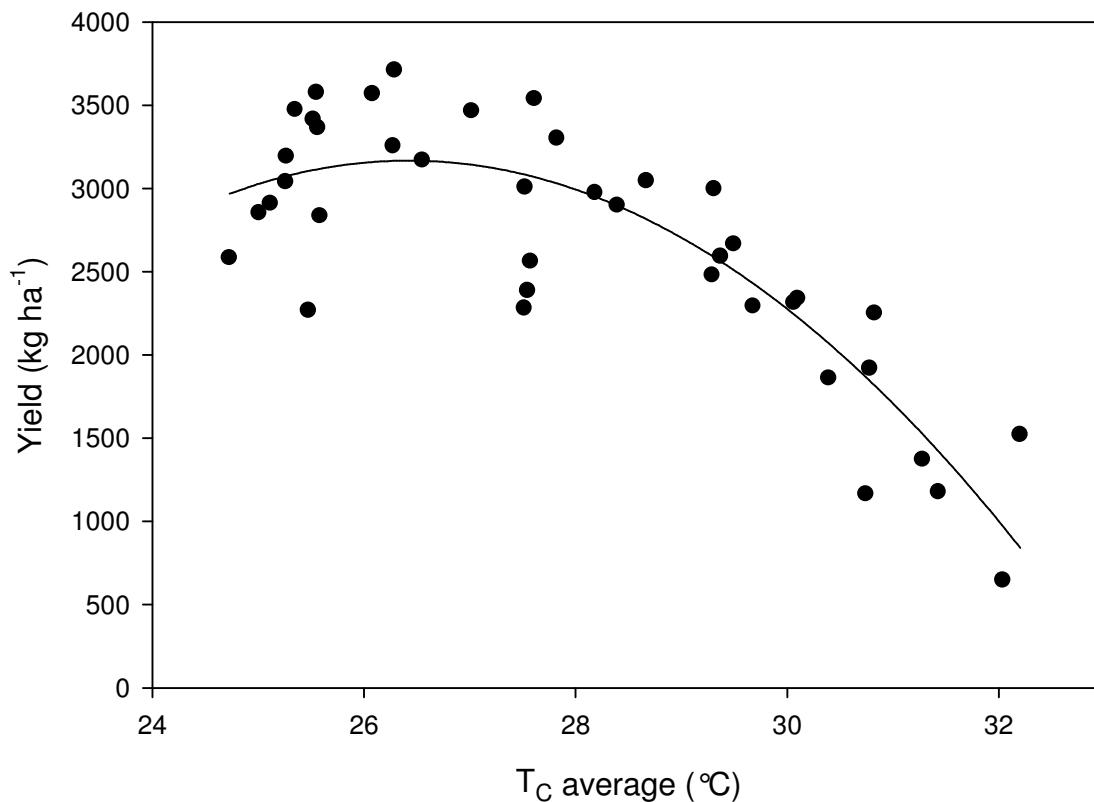
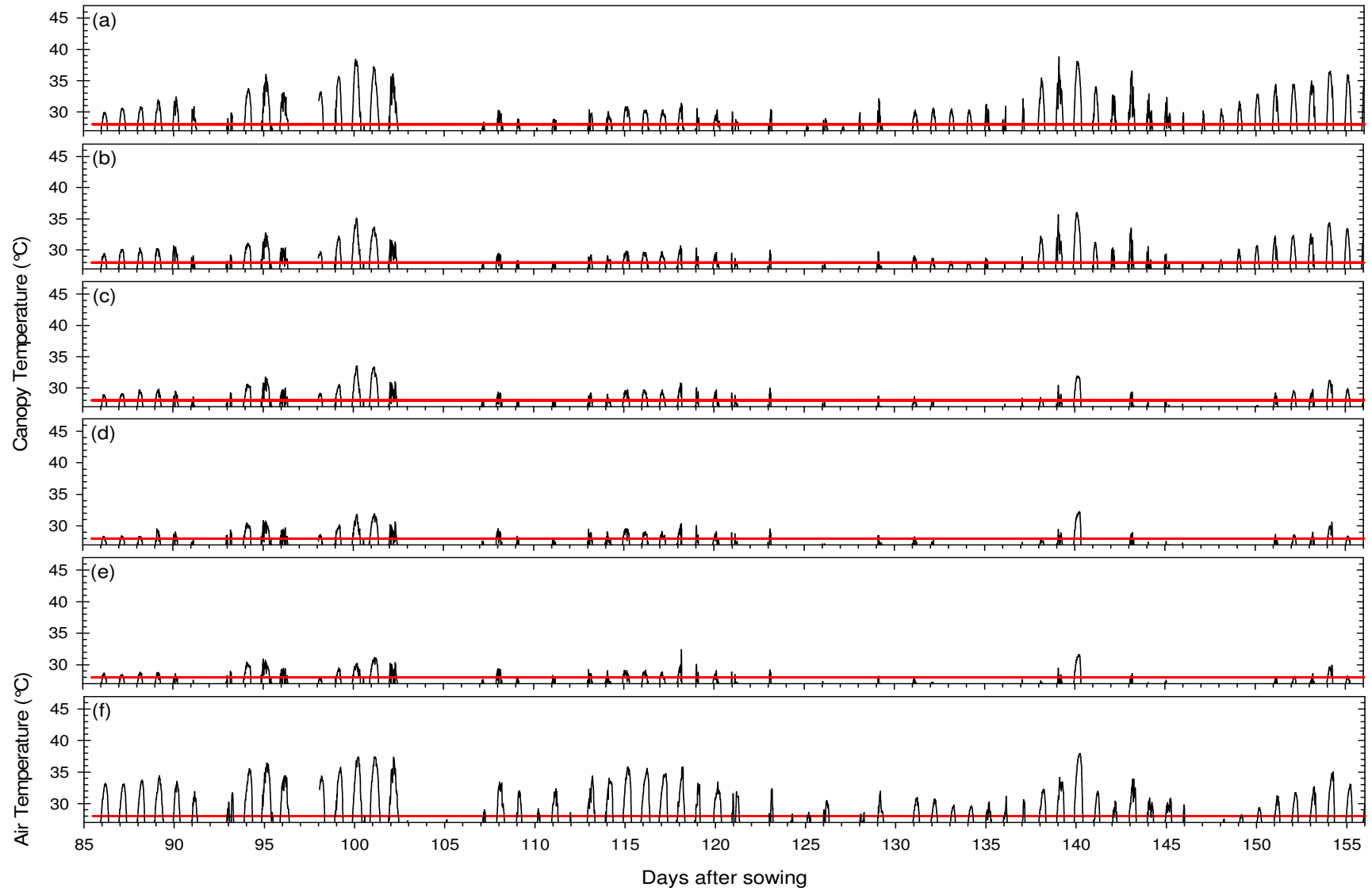
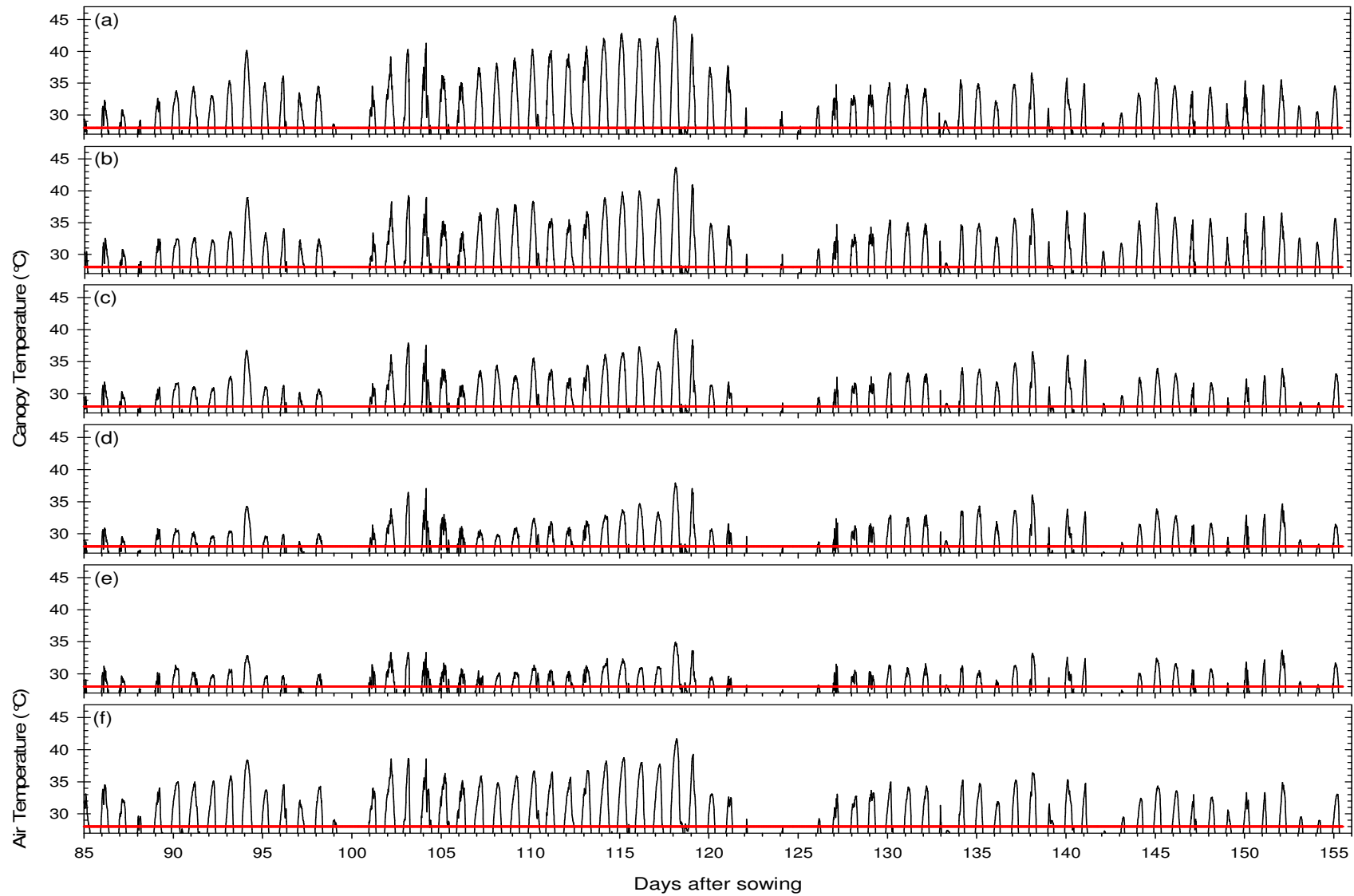


Figure 4.14. Average daily canopy temperature and yield regression ($y = -69.6x^2 + 3680x - 45448$, $R^2 = 0.75$) ($P<0.001$).



2 **Figure 4.15.** Average canopy temperatures exceeding 27°C in Experiment 2 experienced in (a) Treatment 1, (b) Treatment 2, (c) Treatment 3, (d) Treatment 4,
 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.



2 **Figure 4.16.** Average canopy temperatures exceeding 27°C in Experiment 3 experienced in (a) Treatment 1, (b) Treatment 2, (c) Treatment 3, (d) Treatment 4,
 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.

4.4 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 ($>36^{\circ}\text{C}$), compared with a long term average of 44 days at the start of the season (BOM 2009). Although the season was characterised by lower than average temperatures, the number of low temperature stress days was low (13) compared with the regional average of 30 days (Bange and Milroy 2004). An increase in season length (17 days), 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 very 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 yields of 3405kg lint ha^{-1} (15 bales ha^{-1}), significantly above 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 temperatures, VPD, and evaporative demand (Table 4.1). Seasonal temperatures remained above average with 43 high temperature stress days which more accurately reflected the regional average of 44 days (BOM 2009) than Experiment 2. Hot and dry weather conditions were experienced in late January and early February, with 18 consecutive days above 36°C , where temperatures in the last five of these days were above 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, significant 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 temperatures, higher average evaporative demand, vapour pressure deficit, wind speed and radiation, 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 treatment yields in Experiment 3 were reduced to 2840 kg lint ha⁻¹ (12.5 bales ha⁻¹). Despite this increased stress potential, yields also remained 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 manifest in crop yields. Crop growth patterns, biomass accumulation and canopy temperatures 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 crops with higher average canopy temperatures.

Cotton growth and yield in Experiment 2 and Experiment 3 was influenced markedly by water supply. Yield-water relations exhibited a second order polynomial function where

yield rose to a peak at 822mm 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 yields of Australian cotton (grown predominantly on grey cracking clays of Northern New South Wales and Southern Queensland) increased to an ET_C of approximately 700mm, and beyond this additional water consumption did not increase yield. Peak cotton yields at approximately 700mm ET have been observed in numerous studies conducted in various production settings including California (DeTar 2008; Grimes *et al.* 1969b), Texas (Wanjura *et al.* 2002) and Spain (Orgaz *et al.* 1992). This yield-water response where peak yield are observed at 108% ET_C, was evident in both Experiment 2 and Experiment 3 (Figure 4.6b). Similar yields were observed over the range of 97 to 118% applied ET_C. This range is relatively narrow, representing 158mm of water in Experiment 2, and 172mm 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 4.6). 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 radiation were experienced in Experiment 3 (Table 4.1). This response is important as it outlines the need for the monitoring of 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 an invaluable decision support tool for irrigation scheduling.

Vegetative growth in the cotton plant continues until three-quarters of plant available soil moisture is utilised (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 moisture 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 4.12), in contrast to lint yield (Figure 4.6a). 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 statistically observed in Experiments 2 and 3, some tailing off of biomass accumulation may be evident at water applications in excess of 1000mm (Figure 4.12).

In addition to the production of more biomass, a plant with access to more soil moisture will produce more main stem nodes, resulting in more fruiting positions and thus a greater yield potential (DeTar 2008). This growth pattern was observed in Experiment 3 and Treatments 1, 2 and 3 of Experiment 2 (Figure 4.7). However, Treatments 4 and 5 of Experiment 2 did not follow this trend as these treatments produced larger plants that yielded less than some of the treatments with smaller plants (Figure 4.7). Therefore, correlations between biomass and 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 yield (Hearn 1979).

The production of rank vegetative growth in Treatments 4 and 5 of Experiment 2 was the predominant cause of yield reductions in these well-watered treatments. This is because although a larger plant has a greater yield potential, if a plant has access to excess soil moisture 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 moisture has been utilised), 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 rainfall, cloudy weather, early insect damage and dense plant stands (Gibb *et al.* 2004). This results in 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 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 yield (Constable 1991). Although peak yields were calculated to be at approximately 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 which 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 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 moisture.

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 grown 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 yield, late season re-growth was excluded from biomass harvests in Experiment 3.

Plant node production and height are good general indicators of moisture stress experienced by a cotton crop. Until the plant's carrying capacity is reached, crop 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 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 yield potential, as in the case of Treatments 4 and 5 in Experiment 2. Furthermore, significant 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 of solar radiation and solar radiation

interception, plant growth (as it ultimately lowers intercepted radiation, especially by leaves closest 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 canopy temperatures rise (Mahan *et al.* 2005). Therefore, canopy temperatures can potentially be used to infer transpiration rates, and provide the basis for determining plant water stress. The average canopy temperatures of Experiment 2 and Experiment 3 reflected this trend, where canopy temperatures increased with increasing moisture stress. It is important to note that treatment differences in canopy temperature were not observed at radiation levels less than 300 W m^{-2} (Table 4.4). Furthermore, differences in canopy and air temperature were observed at net radiation levels above 300 W m^{-2} and ambient temperatures greater than 28°C (Table 4.4). The fact that differences in CTD became apparent only after these environmental conditions were reached, indicates that these differences in canopy temperature were due to varying rates of transpirational cooling

when solar input is sufficient to raise canopy temperatures above 28°C. These divergent transpiration rates were driven by differences in soil moisture conditions.

The relationship between observed canopy temperatures and per cent ET_C applied varied between Experiment 2 and Experiment 3. This is because radiation, ambient temperature, humidity, wind speed and the position of the leaf surface in relation to the incident solar radiation can modify leaf temperature, adding to the effect of water stress on canopy temperature (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 canopy temperatures over a range of irrigation treatments and seasons. It is important to note that the slope of the line of the regressions for canopy temperature-water relations in Experiment 2 and Experiment 3 is similar. Hence the relative response of canopy temperature 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 over a range of seasonal pressures.

Despite a varying response in canopy temperature - ET_C relations across seasons, the relationship between canopy temperature and the duration of time canopy temperatures exceeding 28°C (optimal temperature) across the two experiments was similar across seasons (Figure 4.13b). 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 canopy temperature, the amount of time canopy temperature exceeded 28°C increase by 4.4% (Figure 4.13b). Canopy temperature- yield relations were also similar across Experiment 2 and Experiment 3, where peak 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 canopy temperatures that produce similar yields as the peak is 24.8 – 28.1°C. This suggests that when average daytime canopy temperatures exceed 28°C, yield penalties ensue.

It is important not to confuse average canopy temperature with the temperature stress threshold. The stress threshold is an estimate of the thermal optimum of metabolism of the plant, representing the approximate mid point of the studied crop's thermal kinetic window (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 canopy temperatures within the TKW by supplying irrigation water for transpirational cooling at the canopy temperature 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 canopy

temperatures, 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 which 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 Wanjura *et al.*'s (1992) and Upchurch *et al.*'s (1996) approach for scheduling irrigation based on canopy temperatures and a stress time (ST) index that accumulates the amount of daily time a crop exceeds its specified optimal or threshold canopy temperature.

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 canopy temperatures, where drought stressed treatments experienced not only higher average temperatures but longer periods of supra-optimal canopy temperatures. 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 canopy temperatures with subsequent reductions in lint yield.

4.5 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 yield, plant architecture, growth, biomass accumulation and canopy temperatures. The observed stress potential was higher in Experiment 3 than Experiment 2 due to a combination of higher ambient temperatures, VPD, radiation and average evaporative demand. This increased stress potential resulted in differences in 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 over a range of environmental conditions and seasons.

The canopy temperature data from my experiment suggest that the BIOTIC irrigation scheduling protocol can consistently detect water stress, producing peak yields across different seasons, despite variations in seasonal pressures resulting in differences in evaporative demand. My experiments also confirm that when average daytime canopy temperatures exceed 28°C , yield reductions occur. This observation is important in the

context of the BIOTIC irrigation scheduling system, which utilises a threshold canopy temperature for stress detection and irrigation scheduling. Therefore, irrigation scheduling based on canopy temperatures offers the potential for precise control of crop growth and development, across varying seasonal pressures.

Therefore, when combined with environmental factors affecting canopy temperatures and crop development (such as ambient temperature and VPD) the use of canopy temperatures 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 simple and effective. 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 affect on BIOTIC; and whether BIOTIC can optimise water use and effectively utilise and capture in crop rainfall.

5. SOIL MOISTURE DEFICITS AND THEIR INFLUENCE ON CANOPY TEMPERATURE IN FURROW IRRIGATED COTTON

5.1 Introduction

Furrow irrigation is an irrigation application technique particularly operationally suited to broad-acre 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 water use efficiency 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 utilise 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 1.1m 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 conclude that this is evidence for the close coupling of soil water and plant temperatures, supporting the use of plant temperatures 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 plant temperatures and soil moisture. This is 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 moisture stress. Jackson 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 notes 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 notes that variation in the response of CWSI to extractable soil moisture may be dependent on the fact that plant available water capacity (PAWC) was not assessed, rather a fixed depth of soil (1.1 metres) was assessed, which may over- or under-estimate the soil moisture 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 moisture 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 evapotranspiration 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 moisture 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 moisture deficit irrigation regimes on the growth and development, yield and canopy temperatures of cotton grown on a grey vertosol (Isbell 1996) at Narrabri, NSW Australia. This data will be used to outline the effect of deficit furrow irrigation and its cyclical nature of water stress on cotton canopy temperatures. 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 drip and sprinkler systems. This information will be used to determine the potential efficacy of the BIOTIC irrigation scheduling system in furrow irrigation.

5.2 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 moisture deficits (mm) from field capacity, calculated from neutron moisture meter readings were imposed. Deficit furrow irrigation is characterised by refilling the soil water profile when a desired soil moisture deficit is reached. The deficits used in this study were a frequently irrigated (approximately 30-40mm soil moisture deficit), control (approximately 40-50mm soil moisture deficit- which represents a conservative soil moisture deficit target in commercial furrow irrigated cotton production) and two extended deficit irrigation treatments: a moderately extended

(approximately 65-75mm soil moisture deficit) and fully extended (approximately 100-110mm soil moisture 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 5.1). Rainfall throughout the growing season totalled 327mm.

Table 5.1. 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 ($\approx$ 35mm)	9 th December 2008	55	550
	22 nd December 2008	68	708
	2 nd January 2009	79	866
	9 th January 2009	86	976
	15 th January 2009	92	1068
	23 rd January 2009	100	1189
	30 th January 2009	107	1309
	5 th February 2009	113	1414
	11 th February 2009	119	1526
	27 th February 2009	135	1721
	13 th March 2009	149	1957
Control ($\approx$ 45mm)	12 th December 2008	58	597
	24 th December 2008	70	739
	7 th January 2009	84	944
	15 th January 2009	92	1068
	25 th January 2009	102	1225
	2 nd February 2009	110	1361
	10 th February 2009	118	1512
	3 rd March 2009	139	1777
	16 th March 2009	152	1993
Moderate ($\approx$ 70mm)	11 th January 2009	88	1001
	28 th January 2009	105	1276
	8 th February 2009	116	1471
	6 th March 2009	142	1808
Extended ($\approx$ 105mm)	16 th January 2009	93	1087
	6 th February 2009	114	1434

Weather conditions, soil moisture, crop growth and development, yield and canopy temperatures using infra-red thermometers (SmartCropTM, Lubbock, Texas) were monitored throughout the experiments. Further details on all measurements taken in Experiment 4 are described in Chapter 3.

5.3 Results

5.3.1 Climate

The weather conditions experienced in Experiment 4 were consistently close to the 82 year long-term seasonal average (Table 5.2). Rainfall throughout the growing season of Experiment 4 totalled 327mm (64mm below the seasonal average), with the majority of the rainfall occurring in November, December and February and notable dry conditions in January (Figure 5.1a). These dry conditions were associated with hot weather, where late January and early February saw 18 consecutive days above 36°C, culminating in the last five of these days above 40°C. As a result, monthly average temperatures were above long term averages from January through to March (Figure 5.1b), however the number of seasonal high temperature stress days recorded (43 days) was close to the long term seasonal average (44 days). The number of low temperature stress days and average daily solar radiation in Experiment 4 was the same as the long term seasonal average, while average 9am relative humidity similar to the long term seasonal average (Table 5.2).

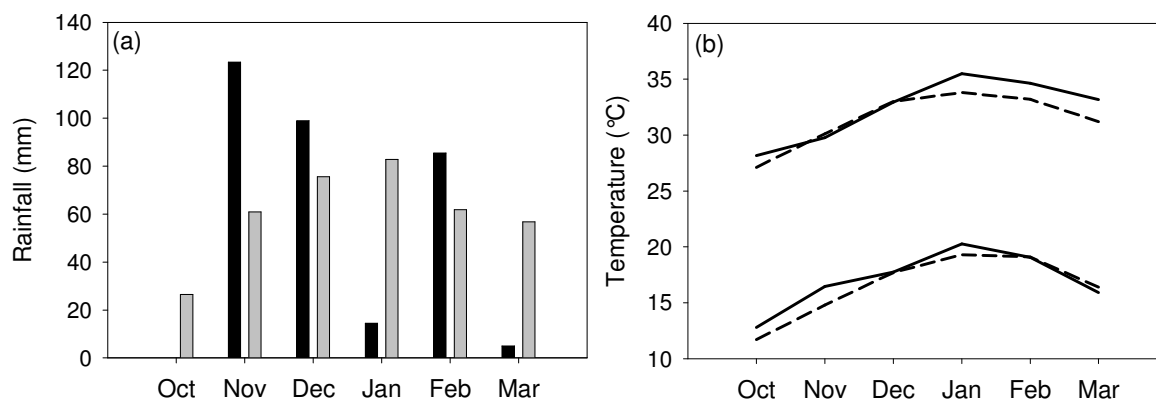


Figure 5.1. (a) Monthly rainfall (mm) in Experiment 4 (■) and long term seasonal averages (▒). Average maximum and minimum monthly temperatures (°C) in Experiment 4 (—) and long term averages (---).

Table 5.2. 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 > 10mm	11	11
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
Radiation		
Average daily (MJ m ⁻²)	25.0	24.9
Wind speed		
Average 9am (m sec ⁻¹)	4.1	4.9
Relative humidity		
9am average RH (%)	60	57
Evaporative demand		
ET _C to 60% open bolls (mm)	721	700*

* Data from Tennakoon and Milroy (2003)

5.3.2 Soil moisture and irrigation

Treatments were furrow irrigated when the desired soil moisture deficit was reached. 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 successfully 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 net irrigation water, approximately 397mm. 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 288mm net of irrigation water between 88 and 142 DAS in four irrigation events. The fully extended treatment received the least net irrigation water in only two irrigations on 93 and 114 DAS, totalling 213mm. The soil moisture deficits throughout the growing season are shown in Figure 5.2.

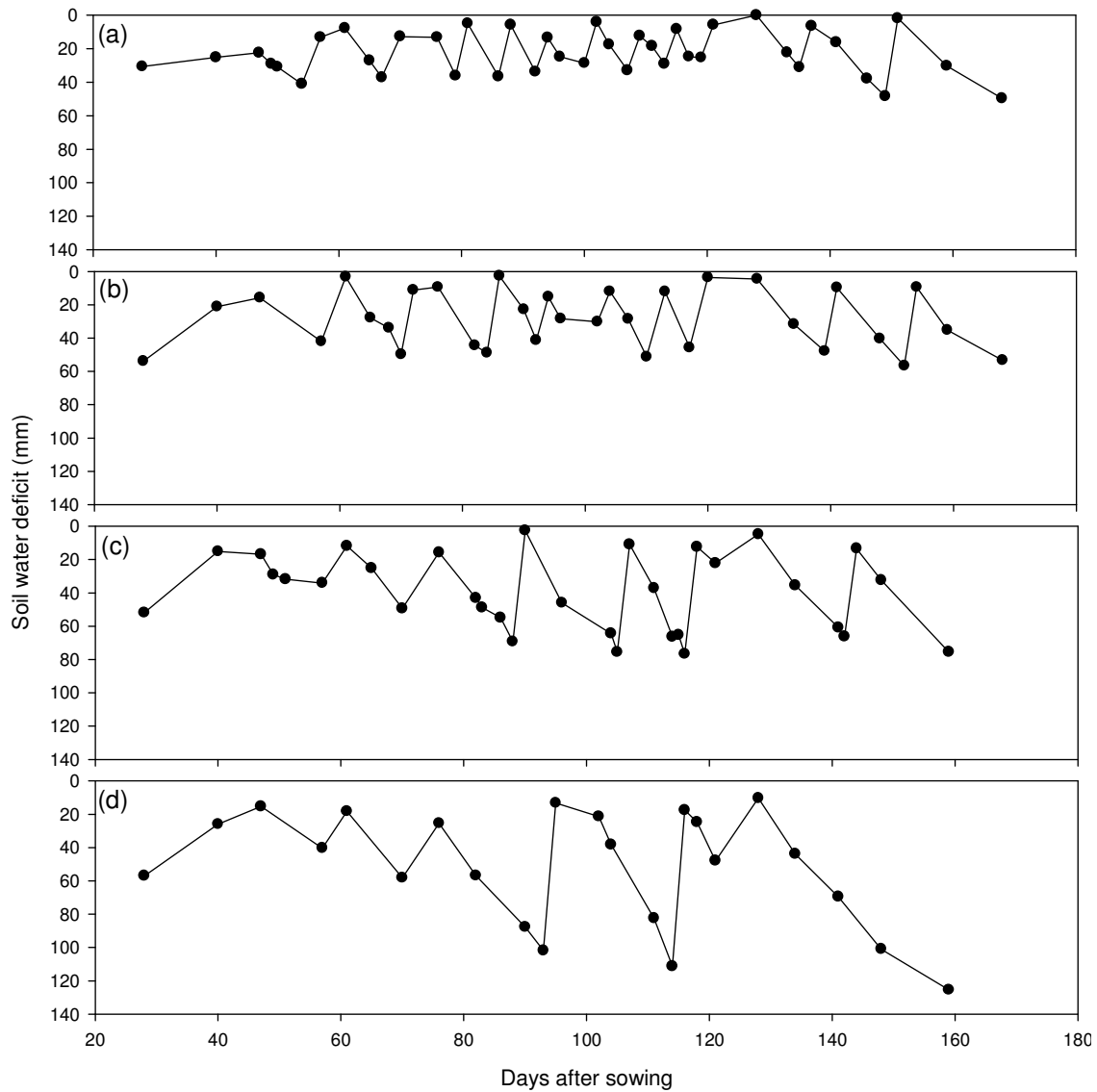


Figure 5.2. Soil moisture deficits, calculated from the soil's drained upper limit, measured with a neutron moisture meter in the (a) frequently irrigated, (b) control, (c) moderately extended, and (d) fully extended deficit treatments throughout the growing season.

5.3.3 Crop development

Variation in crop yield was characterised into three statistically significant groups in Experiment 4 ($P < 0.001$) (Figure 5.3a). The highest yielding treatments were the frequently irrigated and control treatments at approximately $2,700 \text{ kg ha}^{-1}$, followed by the moderately extended treatment yielding $2,450 \text{ kg ha}^{-1}$ and the fully extended

treatment producing 2,000 bales ha⁻¹. Yield-water relations exhibited a polynomial function, where yield rose to a peak of 2728 kg lint ha⁻¹ at 730mm applied water, where applied water is the sum of rainfall and infiltrated irrigation water ($P<0.001$) (Figure 5.3b). Water application in excess of 730mm resulted in a decrease in yield. The regression model accounted for 65 per cent 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 – 802mm. This range was calculated by substituting the peak yield $\pm$ the standard error of the yield into the fitted regression model.

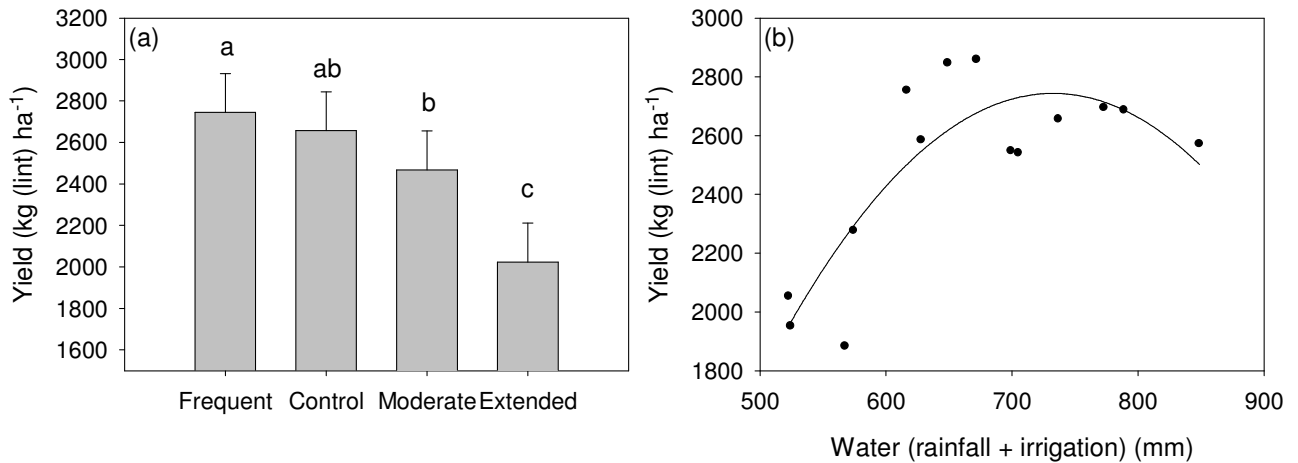


Figure 5.3. (a) Machine picked yield (kg ha⁻¹) for each treatment in Experiment 4, vertical bars represent l.s.d.; (b) Yield-water relations in Experiment 4, $y = -0.017x^2 + 24.77x - 6295$, $R^2 = 0.64$ ($P<0.001$).

Differences in plant height were observed ($P<0.001$) with the formation of three statistically separate groups at the end of the season (Figure 5.4a). Plant heights of 91cm were the highest in the frequently irrigated plots followed by the control and moderately extended treatments with an observed plant height of 80cm. The fully extended treatment recorded the lowest plant heights of 73cm. 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 5.4b). 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.

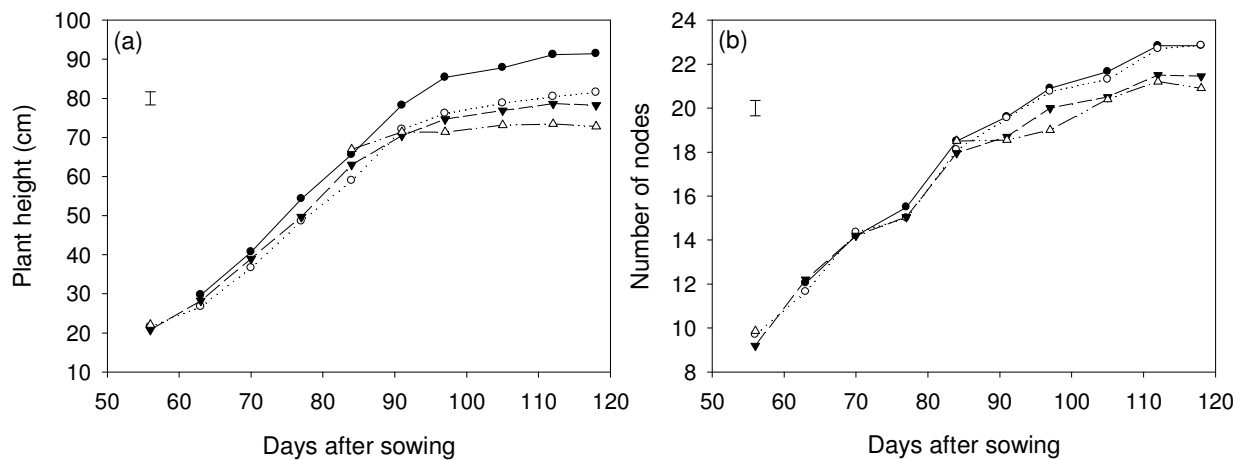


Figure 5.4. Plant height (a) and number of nodes (b) produced through out the growing season in the frequently irrigated (—●—), control (····○····), moderately extended (—▼—) and fully extended (····△····) irrigation treatments of Experiment 4. Vertical bar represents l.s.d.

5.3.4 Biomass accumulation and partitioning

Treatment differences in biomass accumulation were most pronounced in vegetative plant structures, which resulted in differences in total dry matter ($P=0.009$) (Figure 5.6a and Figure 5.5). 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 which proliferates in cool moist soil conditions affecting the vascular system of plants. This results in reduced water availability, regardless of soil moisture 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 approximately 1420 g m^{-2} in all other treatments (Figure 5.6a).

Treatment differences in the ratio of vegetative to reproductive biomass were observed in Experiment 4 ($P= 0.016$) (Figure 5.6b). Treatment differences were not observed until after 76 or 92 DAS, when all treatments displayed six per cent and 22 per cent 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 days before harvest, and the control and frequently irrigated treatments had 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 yield potential. Differences in average boll size may have had an effect on 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 5.6), and yet differences in yield at maturity were recorded, the size of the bolls may have had a large effect on final yield.

Treatment differences in leaf area index were observed during Experiment 4 ($P<0.001$), following 118 DAS (Figure 5.6c). At this point, the frequently irrigated plots had the greatest leaf area, followed by the control and the two extended irrigation plots with similar leaf area indices. 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 canopy temperatures is important for the reduction of background soil effects.



Figure 5.5. 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 treatments. Measuring stick represents 1m.

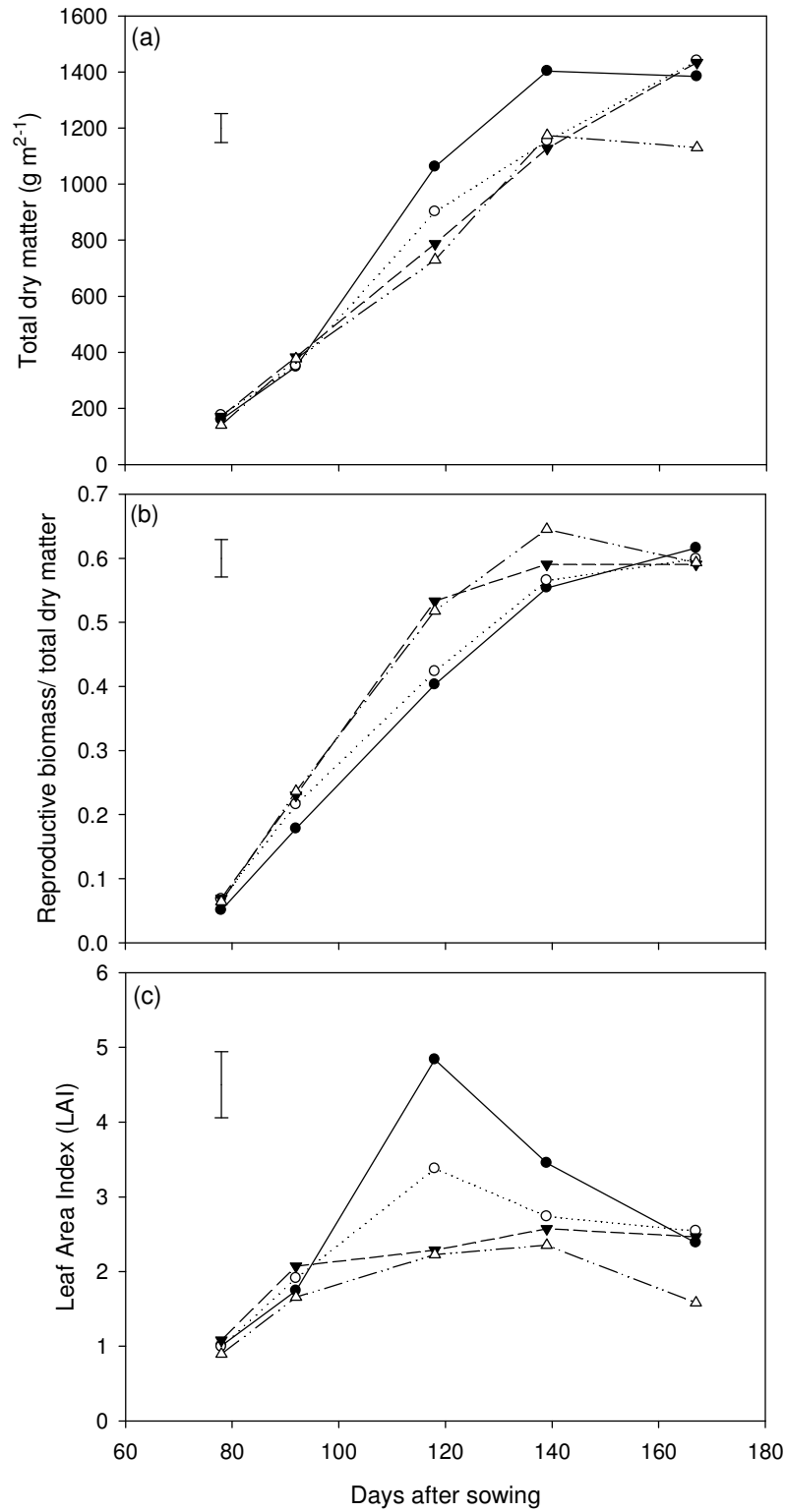


Figure 5.6. Total dry matter accumulation (g.m⁻²); The ratio of reproductive to vegetative biomass; and leaf area index (LAI) in Experiment 4 in all treatments; frequently (—●—), control (····○····), moderately extended (—▼—), and fully extended (—△—) irrigation treatments. Vertical bar represents l.s.d. at $P=0.05$.

5.3.5 Canopy temperatures

The four deficit irrigation treatments exhibited different average canopy temperatures ($P<0.001$). These canopy temperatures consistently followed the trend where irrigation treatments with larger soil moisture deficit, and hence longer durations of moisture stress, resulted in higher average canopy temperatures (Table 5.3). Like Wanjura *et al.* (1992), treatment differences were not observed when net radiation levels were less than 300 W m^{-2} (Table 5.3), average canopy temperatures from this point forward refer to canopy temperatures when net radiation levels were above 300 W m^{-2} . Under these environmental conditions, clear treatment differences that correspond to irrigation treatments can be observed (Table 5.3).

Table 5.3. Average canopy temperature (T_C), average canopy temperature when net radiation $< 300 \text{ W m}^{-2}$ and $> 300 \text{ W m}^{-2}$, and duration of time that canopy temperatures exceed 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 ($^\circ\text{C}$)	Average T_C ($^\circ\text{C}$)	Average T_C ($^\circ\text{C}$)	Time T_C $> 28^\circ\text{C}$ (%)
		($R_n < 300 \text{ W m}^{-2}$)	($R_n > 300 \text{ W m}^{-2}$)	
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 canopy temperature (between 82 and 155 DAS) and water application exhibited an exponential decay function ($R^2=0.83$) (Figure 5.7a). This relationship saw a rapid reduction in average canopy temperature with increased water application, up to 685mm

applied water. Beyond 685mm applied water, average canopy temperature was less responsive to an increase in total water application (Figure 5.7a). Average canopy temperatures were also correlated to final crop yield (Figure 5.7b), 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 yield and corresponding average canopy temperatures were not observed, suggesting that these results may be range limited. This is because significant yield reductions were not observed with excess total water application. Despite this range limitation, the fitted regressions predict peak yields at average daylight canopy temperatures of 28.6°C (over a range of 28.01 to 29.23°C).

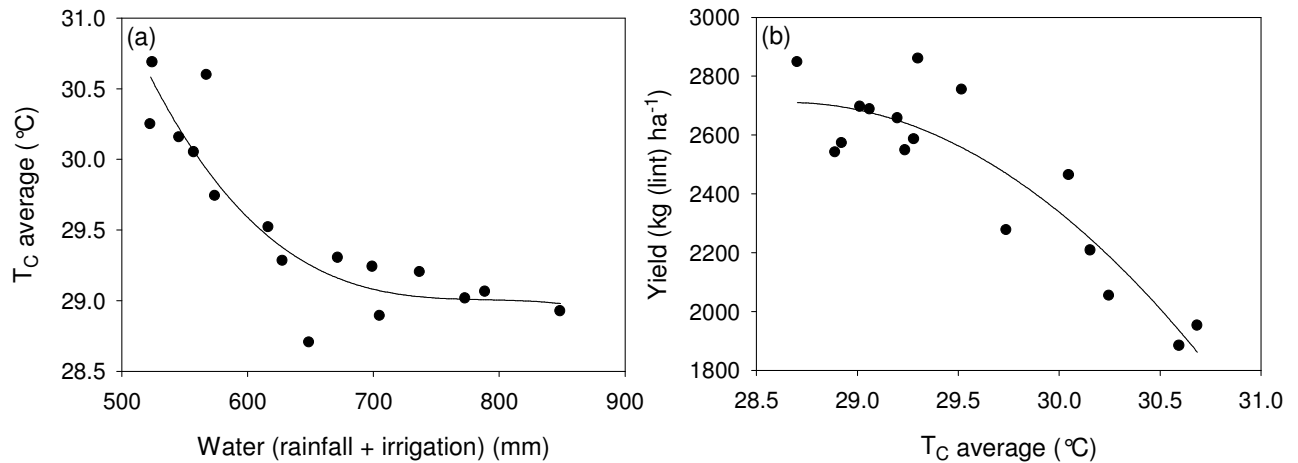


Figure 5.7. (a) Average canopy temperature (°C) vs. water application (mm) (rainfall + infiltrated irrigation water) regression ($P < 0.0001$) with a mathematically predicted base temperature of 28.9°C, $y = 28.87 + 518.72(e^{-0.109x})$, $R^2 = 0.83$; (b) Average daily canopy temperature (°C) and yield regression (kg ha⁻¹), $y = -206.0x^2 + 11802.9x - 166391.7$, $R^2 = 0.82$ ($P < 0.0001$).

Table 5.4. Comparison of average canopy temperatures (°C), 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

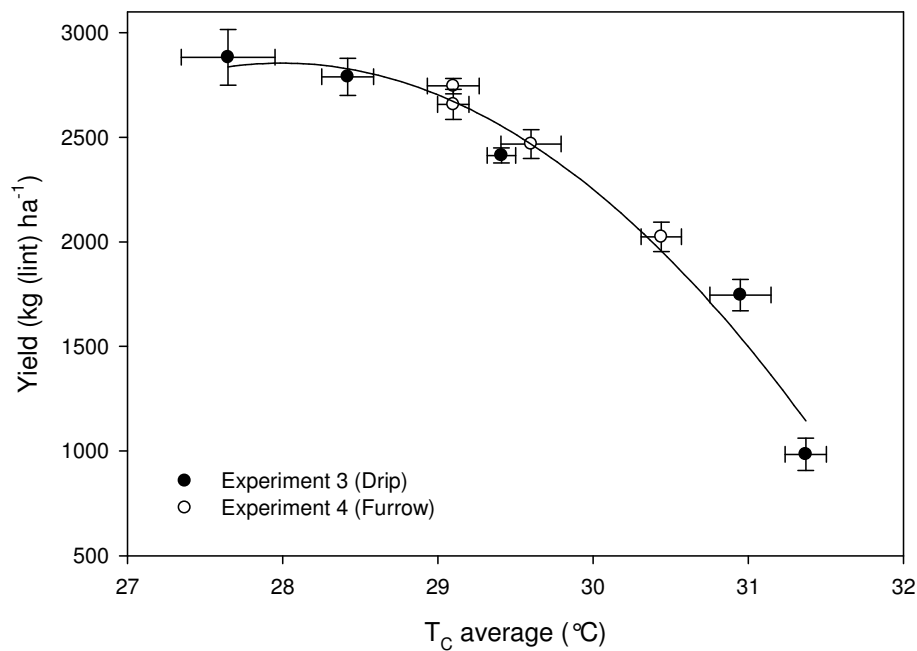
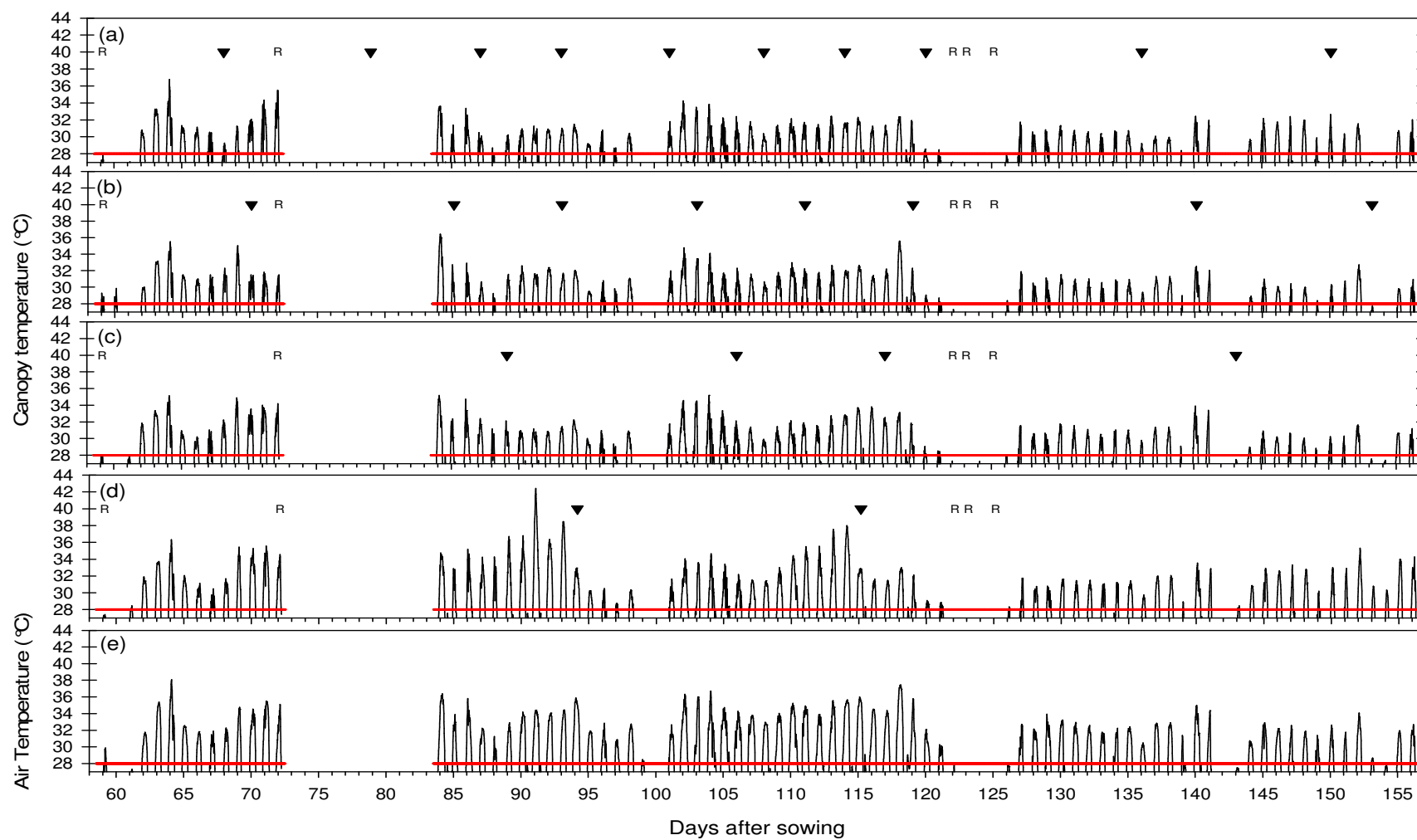


Figure 5.8. Average canopy temperature vs. yield regression in Experiment 3 (surface drip irrigation) (●) and Experiment 4 (○) (deficit furrow irrigation) over the same measurement days (5th Jan 2009 to 18th March 2009) showing peak yields at 28°C, $y = -150.1x^2 + 8405.2x - 114797$, $R^2 = 0.97$ ($P < 0.0001$).

A comparison between canopy temperatures observed in Experiment 3 and Experiment 4 is shown in Table 5.4. Experiment 3 and 4 were irrigated on vastly 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 and 14mm. 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 moisture deficits achieved ranged from 35mm to 105mm plant available water capacity.

Lint yield, water applied and canopy temperatures showed consistent trends across both experiments, where similar canopy temperatures and yields were observed at similar total applications of water (irrigation and rainfall) (Table 5.4). Despite vast differences in the frequency of water applied, average canopy temperature and lint yield exhibited a very strong ($R^2=0.97$) second order polynomial function across both experiments ($P<0.0001$), where peak yields were observed at average canopy temperatures of 28.0°C. This suggests that canopy temperatures are dynamic predictors of water stress, and can be used consistently over vastly different intervals between irrigation applications.



2 **Figure 5.9.** Average canopy temperatures above 27°C in Experiment 4 measured in the (a) frequent, (b) control, (c) moderately extended, (d) fully extended
4 irrigation treatments and (e) air temperature between 58 and 156 DAS. R= days with rainfall above 15mm; ▼= irrigation events; and the red line at 28°C
represents the optimal canopy temperature for cotton. Missing data between 73 and 83 DAS was due to base station failure following a lightning strike.

5.4 Discussion

The growing conditions experienced in Experiment 4 were very similar to long term averages at ACRI (Myall Vale), Narrabri (Table 5.2), with the number of high and low temperature stress days, and a season length of 171 days being very representative of an average year (Table 5.2). Insect pressure throughout Experiment 4 was moderate (five pesticide applications), particularly towards the end of the season as whitefly (*Trialeurodes vaporariorum* and *Bemisia tabaci*) were consistently above threshold levels from late February 2009, however average yields were high suggesting that this had little impact on final yield.

Cotton growth and yield in Experiment 4 were affected by water supply. Peak 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 2,700 kg ha⁻¹ from approximately 397mm of net irrigation water, followed by the moderately extended, producing 2,450 kg ha⁻¹ from 288mm net irrigation water. The lowest yielding treatment was the largest deficit treatment, the fully extended irrigation producing 2,000 kg ha⁻¹ from 213mm net irrigation application. Despite this variation, all yields were still 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 ±74mm applied water (104 ±13% ET_C to crop maturity). This curvilinear response was also observed in Experiments 2 and 3 (Chapter 4), as well as numerous other studies in various locations which have shown that peak cotton yield occurs at approximately 700mm ET_C (DeTar 2008; Grimes *et al.*

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

As observed in numerous other studies (DeTar 2008; Grimes *et al.* 1969a; Grimes and El-Zik 1990; 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 5.4, Figure 5.5 and Figure 5.6). 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 5.5).

The value of canopy temperature measurements in agriculture has been established since the early 1980s (Idso 1982; Jackson 1982). The importance of leaf temperature measurements is that under well-watered conditions, leaf temperatures can be significantly lower than ambient air temperatures. The converse of this is also true and patterns of the differential between canopy and air temperature occur as a result of transpiration rates and the effect these rates have on the evaporative cooling of a leaf. Therefore, when soil moisture availability declines, transpirational cooling of a leaf is reduced and canopy temperatures rise. Average canopy temperatures in Experiment 4 followed this trend, where treatments with more frequent and an increased total applied water, yielded lower average canopy temperatures. Like in Experiments 2 and 3, differences in canopy temperature were not observed at net radiation levels below 300 W m^{-2} (Table 5.3). Again, this suggests that differences in canopy temperature are only observed when net radiation levels, and therefore ambient canopy temperatures (which are driven by radiation levels), are sufficient to potentially warm canopy temperatures in excess of ambient air temperature.

The relationship between canopy temperature and ET_C applied (%) exhibited an exponential decay response ($P < 0.0001$), where a rapid reduction in average canopy temperature was observed with increasing water application, up to 685mm (Figure 5.7a).

Interestingly, average daylight canopy temperatures were not significantly reduced below 29.2°C when total water applied exceeded 685mm. This result is similar to those observed in Chapter 4, 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 yields of Australian grown cotton peak at an average of 700mm ET_C .

Although peaks in canopy temperature-yield relations were outside the range of data collected, the fitted regressions predict peak yields at average daylight canopy temperatures of 28.6°C. The average canopy temperatures which produces peak 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 yield over the 24.8 to 28.1°C range. It is important to note that these ranges in average canopy temperatures are not altered when canopy temperatures 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 canopy temperature 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 canopy temperatures. This may be a result of the nature of furrow irrigation, where large amounts of water, usually between 50 and 100mm (depending on the soil moisture 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 much smaller volumes of water applied, but on a much finer time scale (daily). Therefore, furrow irrigated systems are expected to be exposed to a higher level of water stress, even though crop water use may not be substantially different.

However, the combined Experiment 3 and 4 response of average canopy temperature and yield was similar in both experiments ($P < 0.001$). This suggests that the data from Experiment 4 may be range limited, and the peak yield in Experiment 4 observed at a warmer canopy temperature ($28.6 \pm 0.6^{\circ}\text{C}$) than Experiment 3 may be skewed towards warmer canopy temperatures. As yield reductions (due to over supply of water) were not observed in Experiment 4, it is difficult to determine whether peak yields under furrow irrigated conditions are associated with higher average canopy temperatures. However, previous research has shown that the response of canopy temperatures 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 canopy temperatures. 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 neutron moisture metre. The second of Wanjura *et al.*'s (1990) treatments was characterised by refilling the root zone soil water after the first square fruiting stage on a fortnightly basis, however irrigation was extended by one day for every 7mm rainfall, and retracted by a day when maximum air temperature exceeded 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 canopy temperature average exceeded either 28, 30 or 32°C (Wanjura *et al.* 1990). Warmer average seasonal canopy temperatures of 25.3°C (when net radiation exceeded 200 W m⁻²) were observed in the fortnightly “Australian” treatment, while the weekly soil water replacement (with a smaller soil moisture defect before irrigation) yielded lower average canopy temperatures of 24.1°C. The average canopy temperatures observed in the 28, 30 and 32°C treatments were 26.6, 26.8 and 27.8°C respectively. The 28°C treatment received 700mm total water, compared with 750mm in the “Australian” treatment. As a result of this similar water application, similar average canopy temperatures and yields were observed. Therefore, it can be concluded that although average canopy temperature will increase when the interval between irrigation events is increased, similar yields and canopy temperatures can be achieved between large soil moisture deficits based on fortnightly soil water replenishment and presumably smaller moisture deficits where irrigation is based on fifteen minute average canopy temperatures, especially when the total water applied is similar. It is, however, important to note Wanjura *et al.*’s (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 canopy temperature and lint yield exhibited a very strong ($R^2=0.97$) second order polynomial function across both experiments ($P<0.0001$), where peak yields were observed at average canopy temperatures of 28.0°C (Figure 5.8). This is significant as it shows that cotton will produce a higher lint yield when average canopy temperatures are maintained as close to 28°C as possible. Yields, canopy temperature 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 canopy temperature (Table 5.4). The similar response of canopy temperatures and yield in Experiment 3 and 4 suggests that canopy temperatures 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 canopy temperatures, grown in environments similar to commercial production, do not undergo significant adaptation to water stress. This is because treatments which received similar amounts of total water, displayed similar average canopy temperatures 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 canopy temperature-yield response was similar in both surface drip and furrow irrigated cotton, differences in crop performance were observed. The lowest average canopy temperatures in a furrow irrigated system were observed to be

approximately 29°C, with corresponding yields of 2745 kg (lint) ha⁻¹. In comparison, the highest yielding surface drip irrigated cotton exhibited average canopy temperatures 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 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 moist 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.

5.5 Conclusion

This study shows that an investment in maintaining soil water deficit at control level through furrow irrigation practices is rewarded by maintaining average canopy temperatures as close to 28°C as possible, and hence producing peak yields. Although average canopy temperatures of furrow irrigated cotton appear to be warmer than average canopy temperatures of drip irrigated cotton, an inspection of canopy temperatures in

both furrow and drip irrigated cotton show similar responses to water application in both lint yields and canopy temperatures, regardless of the net volume of applied water per irrigation event and interval between irrigation events. This suggests that canopy temperatures are dynamic predictors of water stress, where the size of the soil water deficit and potential plant adaptation to previous moisture 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. This suggests that canopy temperatures 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 canopy temperatures at 28°C, producing increased lint yield with similar net water application.

6. THERMAL OPTIMA FOR AN AUSTRALIAN COTTON CULTIVAR

6.1 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 varieties 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 air temperatures and plant temperatures can not be used interchangeably. Although air temperature 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 radiation, crop size, wind speed, the moisture content of the air and plant water status (Burke and Wanjura

2010). The value of measuring plant canopy temperatures for water stress detection has been recognised since the 1980s (Idso 1982; Jackson 1982; Jackson *et al.* 1981). The significance of monitoring plant canopy temperatures is that through the opening and closing of stomata (in response to soil moisture deficits) changes to the leaf energy balance occur and canopy temperatures 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 canopy temperatures as a thermal gradient to increase sensible heat loss is established. This has been used to indicate moisture stress in plants for use in irrigation scheduling. However, it is important to reiterate that ambient conditions can have a large influence on canopy temperatures, thus canopy temperatures are a combination of plant and environmental factors (Fuchs 1990).

The increase in availability of more affordable, portable and reliable infra-red thermometers 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 infra-red thermometers. Infra-red thermometers 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 proceeded at a maximum according to environmental demand until approximately 0.3-0.4 of the fraction of plant available water is remaining (Ray *et al.* 2002; Ritchie 1981). At this point plant growth (Hearn 1979) and gas exchange (Ray *et al.* 2002; Ritchie 1981; Sinclair 2005; Sinclair and Ludlow 1986) decline until the remainder of transpirable

water is utilised or soil moisture is replenished. As soil moisture availability can influence canopy temperatures, species-specific, stress threshold canopy temperatures 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 canopy temperature for cotton developed from the finding by Hatfield *et al.* (1987a) where canopy temperatures of well-watered cotton crops became cooler than air temperature at leaf temperatures above 27.5°C, whilst night canopy temperatures of field grown cotton tracked air temperatures. 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 thermal kinetic window (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 $\pm 200\%$ 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 $\pm 200\%$ of the minimum K_m value (Somero and Low 1976; Teeri 1980; Teeri and Peet 1978). 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 canopy temperature. 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 leaf temperatures grown under glasshouse conditions tracked air temperatures (to within 1°C) when ambient temperature 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 exceeded 30°C. They conclude that when energy input is insufficient to warm leaf temperature to the TKW, leaf temperatures track air temperatures. Burke and Upchurch (1989) support this theory, finding that transpiration is minimal at leaf temperatures below 24°C, the lower limit of cotton's TWK. Upchurch and Mahan (1988) also note that during daylight hours, incoming radiant energy must be dissipated by transpiration to avoid a rise in leaf temperature above the TKW. This is achieved through stomatal control, which has been shown to be responsive to leaf temperatures within the TKW (Burke and Upchurch 1989). This suggests that cotton has at least some capacity to maintain its canopy temperature at its preferred thermal range (TKW), and more specifically its optimum temperature for metabolism, through transpiration.

The preferred ambient temperature for high cotton yields is generally considered to be approximately 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 (Burke 1995; Mahan 2000; Mahan and Gitz 2007), 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 canopy temperatures exceeding a specific threshold temperature (Upchurch *et al.* 1996; Wanjura *et al.* 1990; 1992), and pollen germination rates (Burke *et al.* 2004). These methods all concur that the thermal optimum of cotton is approximately 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 6.1). 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.

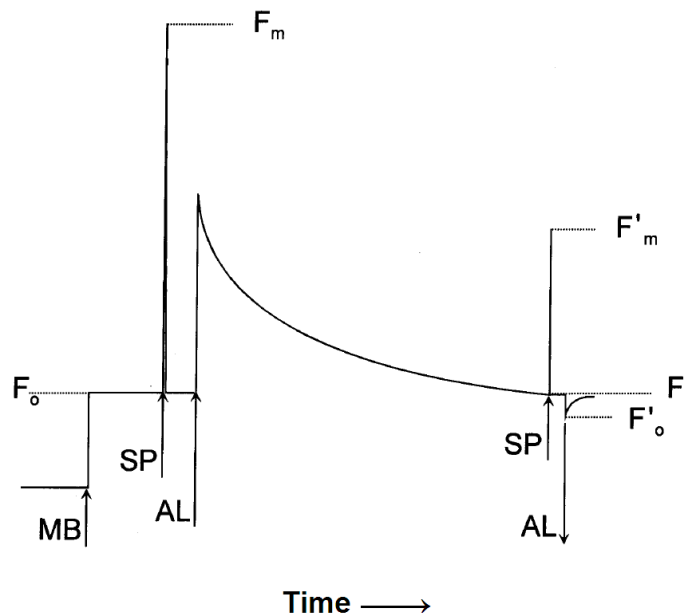


Figure 6.1. Sequence of a typical fluorescence trace. A measuring light is switched on ($\uparrow$ MB) and the zero fluorescence level is measured (F_o). Application of a saturating flash of light ($\uparrow$ SP) allows for the measurement of the maximum fluorescence level (F_m). A light to drive photosynthesis ($\uparrow$ AL) is then applied. After a period of time another saturating light flash ($\uparrow$ 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 ($\downarrow$ 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 predictions 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 (Ferguson and Burke 1991; Mahan *et al.* 1995).

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. Therefore, 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 the current industry standard commercial Australian cotton cultivar, 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.

6.2 Materials and methods

6.2.1 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 variety as in its first year of release (2008/09) more than 70% of the total area of cotton production in Australia was sown to this variety (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 to Australian cotton breeding programs.

Plants were grown under glasshouse conditions (fluorescent and incandescent lights with 16 hour photoperiod at $25^{\circ}\text{C} \pm 5^{\circ}\text{C}$) 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 3mm filter paper on top of a wet sponge in a glass dish and covered with CO₂ permeable plastic film (GladwrapTM), 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 $\mu\text{mol } \mu\text{m}^2 \text{ s}^{-1}$. 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 greater than 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 $\mu\text{mol } \mu\text{m}^2 \text{ s}^{-1}$, 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 Brannkner 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 - 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 was 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 plant temperature for the recovery of PSII fluorescence is 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.

6.2.2 Optimal temperature for gas exchange in field grown cotton

Leaf photosynthetic rate and conductance were measured using an infra-red gas analyser (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 (10:30am to 11:30am) (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 moisture 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 10:30am and 11:30am 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 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 carbon dioxide 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 50-70%, carbon dioxide maintained at 360 $\mu\text{mol (CO}_2\text{) mol}^{-1}$ air, photosynthetic active radiation (PAR) set to 1800- 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and air temperatures ranging from 23 to 42°C. Equations for calculating photosynthetic rate or net carbon assimilation (A, in $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$) and stomatal conductance (g, in $\text{mol (H}_2\text{O) m}^{-2} \text{s}^{-1}$) are given in the Li-COR Biosciences manual (Li-COR 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 12: 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 which resulted in similar A as the peak value was calculated by substituting the peak value of $A \pm$ 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 stomatal conductance and the range of leaf temperatures that produced similar stomatal conductance rates was calculated in the same fashion as photosynthetic rate calculations above.

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

6.3 Results

6.3.1 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 6.2. 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_0 maxima of 1.06 and 0.98 and rates to maximum of 0.21 and 0.20 respectively. F_v/F_0 maximums and rates to maximum declined on either side of this temperature range.

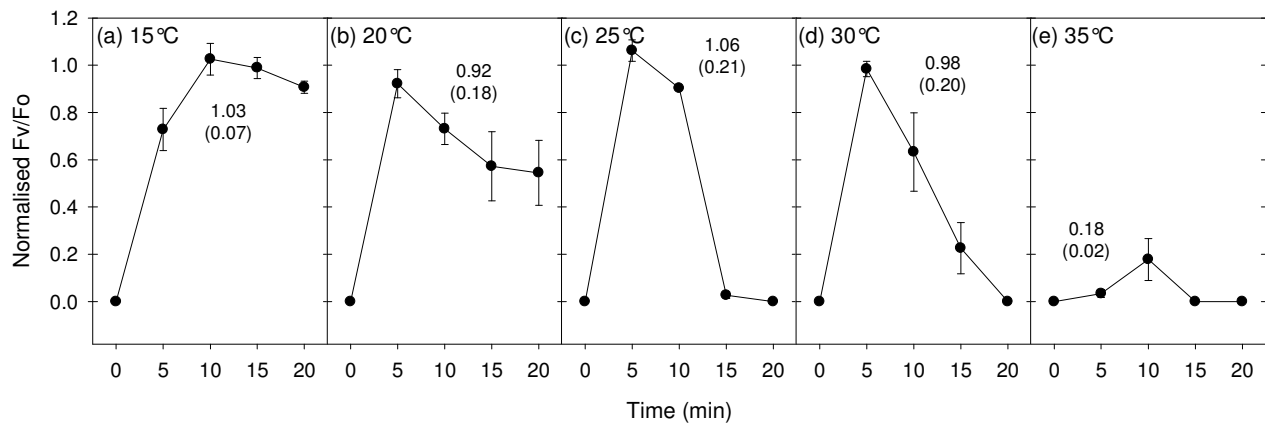


Figure 6.2. Temperature response curves of the recovery of the Australian cotton cultivar Sicot 70BRF's PSII F_v in the dark following illumination at 25°C. Graphs show the normalised F_v/F_0 over time at (a) 15°C, (b) 20°C, (c) 25°C, (d) 30°C and, (e) 35°C. The optimal temperature is determined by assessing both the maximum normalised F_v/F_0 and the rate to maximum F_v/F_0 . The maximum normalised F_v/F_0 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_0 measurements.

Measurements were then repeated over a smaller range of temperatures (24°C to 32°C) at two degree-Celsius intervals. The temperature response of PSII F_v recovery over this

refined range of temperatures at one minute intervals is shown in Figure 6.3. 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.

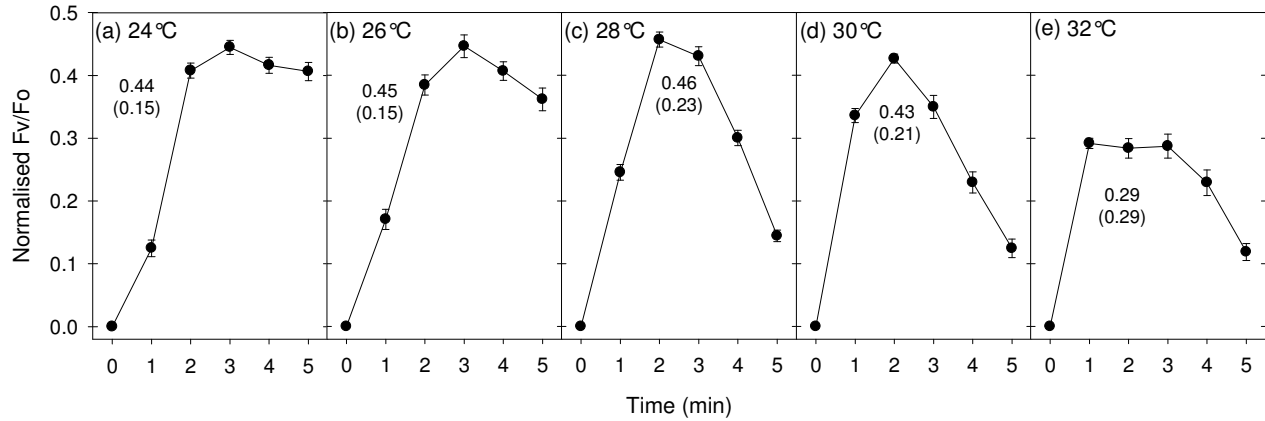


Figure 6.3. Fluorescence optimal temperature assay of the Australian cotton cultivar Sicot 70BRF showing the normalised F_v/F_o over time at (a) 24°C, (b) 26°C, (c) 28°C, (d) 30°C and, (e) 32°C. The optimal temperature is determined by assessing both the maximum normalised F_v/F_o and the rate to maximum 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.

6.3.2 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 photosynthetic rate and stomatal conductance 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 leaf temperature. This model saw peak carbon assimilation occurring at 29.3°C, with an observed standard error of 3.61 $\mu\text{mol (CO}_2\text{) m}^2 \text{ s}^{-1}$ (Figure 6.4a). Fifty per cent of the variation in stomatal conductance was accounted for in the regression with leaf temperatures (Figure 6.4b). This model saw a peak in stomatal conductance at 29.1°C, with an observed standard error of 0.124 $\text{mol (H}_2\text{O) m}^2 \text{ s}^{-1}$. Although the fit of these regressions was not particularly strong, obvious trends in gas exchange were observed with peak carbon assimilation and

stomatal conductance occurring at approximately 29°C. Using the standard error of observations generated from the regressions, ranges of leaf temperatures which represent statistically similar carbon assimilation and stomatal conductance were calculated. The range of leaf temperatures 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.

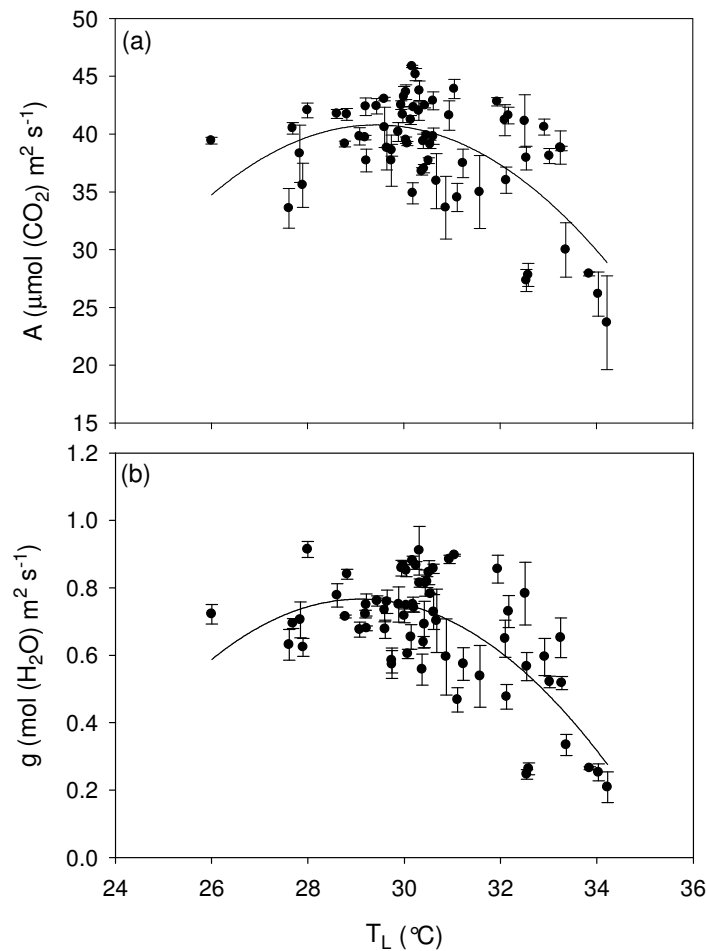


Figure 6.4. (a) Polynomial regression ($P<0.001$) of leaf net assimilation (A) peaking at 29.3°C ($y = -0.52x^2 + 30.50x - 407.83$, $R^2=0.41$); and (b) polynomial regression ($P<0.001$) of stomatal conductance (g) peaking at 29.1°C ($y = -0.019x^2 + 1.09x - 15.07$, $R^2=0.48$). Vertical bars represent standard error of mean.

6.3.3 Sensitivity analysis of BIOTIC irrigation calls to temperature thresholds

The sensitivity of the stress canopy temperature threshold to the calculation of stress time and BIOTIC irrigation calls is shown in Table 6.1. 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 heavily 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 is expected, the implication for this is that the accuracy of the temperature threshold is highly 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 canopy temperature was compared to water application. The response of canopy temperatures measured during the stress time accumulation period at temperature thresholds of 26, 28 and 30°C to water application is shown in Figure 6.5. This regression was highly significant ($P < 0.001$) and accounted for 93% of the variation in the data with a standard error of observed stress time canopy temperatures of 0.36°C. It was hypothesised that average stress time canopy temperatures 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 canopy temperatures should not increase.

Table 6.1. Sensitivity analysis of the BIOTIC irrigation scheduling system to temperature thresholds and the average canopy temperature during stress time (ST) accumulation ($T_C > 28^\circ\text{C}$) 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% ET_C) WUE=4.6	Treatment 2 (93% ET_C) WUE=4.9	Treatment 3 (107% ET_C) WUE=4.3	Treatment 4 (123% ET_C) WUE=3.2	Treatment 5 (140% ET_C) 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% ET_C) WUE=1.8	Treatment 2 (67% ET_C) WUE=2.8	Treatment 3 (77% ET_C) WUE=3.2	Treatment 4 (92% ET_C) WUE=3.0	Treatment 5 (104% ET_C) 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}

The response of stress time canopy temperature to water application was characterised by the reduction of stress time canopy temperatures 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 canopy temperatures. At a temperature threshold of 26 and 30°C applications of water above 123% ET_C did not result in an

increase in average stress time canopy temperature, however at 28°C this occurred at water application of 107% ET_C. The deviation of average stress time canopy temperatures from the stress time threshold above water application is 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 hours in these treatments, suggesting no further increase in stress levels above sufficient water application. This suggests that well-watered plants attempt to keep their canopy temperatures at 28 to 30°C through transpiration. However, it is important to note that the average stress time canopy temperature values could be skewed by the decreasing amount of canopy temperature readings above the threshold as the temperature threshold is increased.

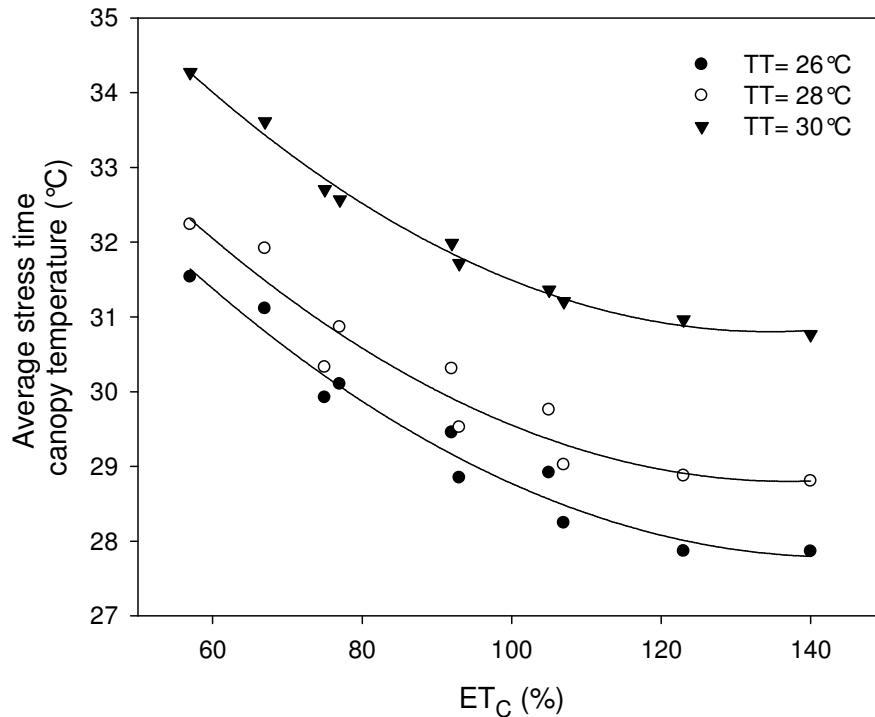


Figure 6.5. Calculated ET_c vs. average canopy temperature during the stress time (ST) period at temperature thresholds (TT) of 26 (●), 28 (○), and 30°C (▼). Note the reduced response of canopy temperature to an increase in ET_c above 100% ET_c application.

6.4 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 of 28°C to 30°C. This is consistent with existing research, predominantly conducted on US cotton cultivars (Burke 1990; Mahan 2000; Upchurch and Mahan 1988; Wanjura *et al.* 1990; 1992). 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. Sicot 70BRF is the result of a cross between Sicala V-1 (seed parent) and the

breeding line 84009-47 (pollen parent) in a planned breeding program at ACRI, Narrabri (Reid 2001). These parental lines were bred from US varieties from Texas (Tamcot SP37H and Paymaster 101–A lines) and Arizona (Delta Pine 90), as well as a Russian line (King Karajoski 1543), highlighting the strong US influence on Australian cotton germplasm (Constable, *Pers. Comm.* 2010).

Australian-bred cotton cultivars have historically been selected for phenotypes displaying desirable 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).

It is important to note that 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 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 (Burke 1995; Yancey and Somero 1978), 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. Isozymes are enzymes that differ in amino acid sequence, but catalyse the same chemical reaction. These enzymes usually display different kinetic parameters (apparent K_m values) 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 $25 \pm 5^{\circ}\text{C}$, and the optimum temperature was observed to be 28 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 moisture 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 moisture and thermal stress levels, the experiments conducted in the glasshouse were only allowed to acclimate to thermal treatments for eight days, 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) concludes 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 varieties display altered kinetic properties. However, most studies show that the response of enzyme kinetics to growth temperature (acclimation) do not occur (Björkman *et al.* 1978; Davidson and Simon 1981; Simon *et al.* 1984), 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 (Lutova *et al.* 1987; Simon *et al.* 1984) 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; 1995) suggests 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; 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 (Burke 1990; 1995; Steiner *et al.* 2001). 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 to 1869m, 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 6.1).

The peak in gas exchange parameters (both carbon assimilation and stomatal conductance) occurred at leaf temperatures of approximately 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 which 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 moisture deficits (number of irrigation calls) is very sensitive to the temperature threshold used to determine thermal stress (Table 6.1). 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 canopy temperatures and subsequent yields. The sensitivity of BIOTIC to canopy temperature thresholds suggests that BIOTIC is very responsive to changes in temperature thresholds. It also suggests that stress time canopy temperatures 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, canopy temperatures remain at approximately 28°C. However, these canopy temperatures may rise slightly above this threshold value, regardless of water availability.

A site-specific stress time calculator utilising 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 hr) 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 is used, treatments receiving in excess of 107% ET_C displayed similar average canopy temperatures during the stress time accumulation period and average daily stress times less than the calculated stress threshold. In water stressed plants, average stress time canopy temperatures 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 canopy temperatures 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 approximately 165 min produced the highest yielding crop in both Experiment 2 and 3. Changing the temperature threshold has 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 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 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 which received 93 and 77% ET_C , resulting in average stress time canopy temperatures of 29.5 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 water use efficiency.

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 200mm less irrigation water applied (Wanjura *et al.* 1992) or approximately 20 fewer BIOTIC irrigation calls (Table 6.1). 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.

6.5 Conclusion

The optimum temperature range for cotton metabolism has been extensively studied, with evolutionary, physiological, enzymatic and yield responses all indicating an optimal plant temperature of approximately 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 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 canopy temperatures at a preferred or optimal canopy temperature. 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 canopy temperatures exceed 28°C has consistently shown peak yields when compared to irrigation regimes based on higher or lower threshold canopy temperatures (Wanjura *et al.* 1990; 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 to 30°C using chlorophyll fluorescence recovery rates and between the range of 27 to 31°C using

photosynthetic and stomatal rates at discrete leaf temperatures. This value is within the TKW for cotton, 23.5 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 approximately 28°C ± 3°C.

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 canopy temperatures has also been used as an indicator of field crop water stress (Upchurch *et al.* 1996). The knowledge of plant canopy temperatures 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 moisture conditions, can result in canopy temperatures 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 canopy temperatures to detect water stress in that it uses a species-specific optimal plant temperature as the basis for determining when a canopy temperature is indicative of plant water deficit. Previous methods compared canopy temperatures 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 canopy temperatures 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 canopy temperature 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 crop canopy 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.

BIOTIC utilises infra-red thermometers 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 6). Therefore, stress time (ST) is defined as the cumulative sum of time that canopy temperatures exceed 28°C (time $T_C > 28^\circ\text{C}$). The

daily stress time-threshold (STT), which represents the period of time a fully irrigated crop canopy temperature is theoretically likely to exceed the optimal temperature in a given environment, is based on environmental variables (temperature, relative humidity, wind speed and radiation), and is specific to a particular region. STT differs from ST in that STT, under the BIOTIC protocol, is the recommended duration of time a canopy temperature 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 hr ST per day (165 min $> 28^{\circ}\text{C}$) 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 canopy temperature 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; 2004; 2006). These studies found a consistent relationship between the number of irrigation signals and the magnitude of temperature-time thresholds, where daily canopy temperature 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 yields were correlated with specific average daily stress times, they reported that similar 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 above 5.5 hours at Lubbock, Texas.

This chapter will explore 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. 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 stress time (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 6 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 hr (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 canopy temperature over an interval results in an irrigation that in turn determines the canopy temperature 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/canopy temperature 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 moisture deficits and irrigation treatments. This analysis was conducted to determine the stress time-canopy temperature, 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 net radiation was greater than 300 W m^{-2} .

Average daily stress time was related to irrigation treatment and average canopy temperature. Stress time followed the same trend as canopy temperatures, where stress time increased with corresponding increase in soil moisture 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.

Average canopy temperature and stress time displayed a positive linear relationship (Figure 7.1), where average stress time increased by approximately 0.8 hours for every one degree increase in average canopy temperature ($P<0.001$). It is evident from the canopy temperature and yield data that the plants experienced different degrees of water stress within and across years. The data in Figures 1-4 and Table 7.1 indicate that canopy temperature 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 4 and 5.

Although it is self evident that average canopy temperature and stress time 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 yield is related to crop canopy temperature (see Figure 4.14 and Figure 5.8), more information can be derived from stress time than canopy temperatures alone. Furthermore, the stress time 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 canopy temperature exceeds the

threshold temperature, which can occur at potential rates of more than once a day, as a canopy temperature threshold does.

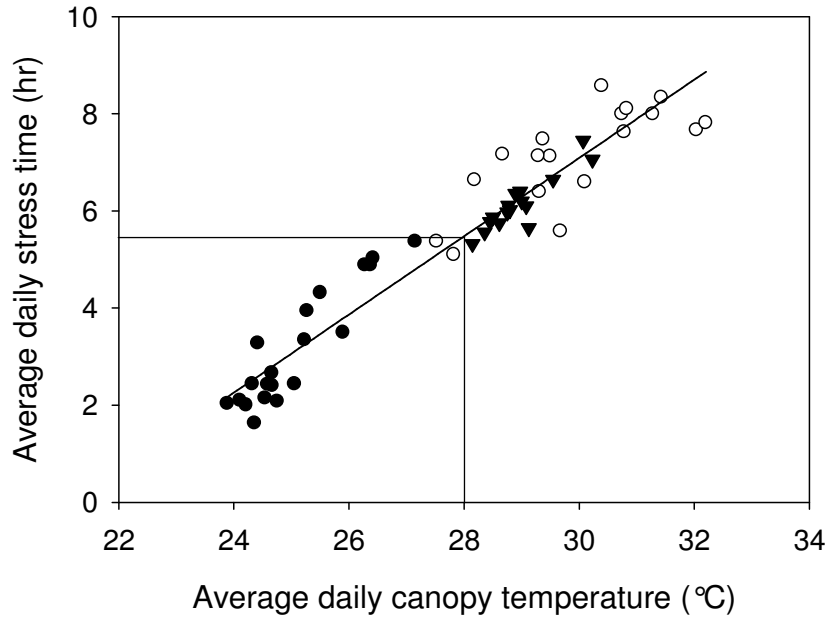


Figure 7.1. Average canopy temperature and average daily stress time regression in Experiment 2 (●), Experiment 3 (○) and Experiment 4 (▼) ($y = 0.8056x - 17.076$; $R^2 = 0.92$) ($P < 0.001$). When average daily canopy temperature is 28°C, average daily stress time equals 5.406 hr.

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 yields, and lowest average canopy temperatures and daily stress times. As soil moisture 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 (85-90% predicted 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.

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_n > 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_n > 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_n > 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}

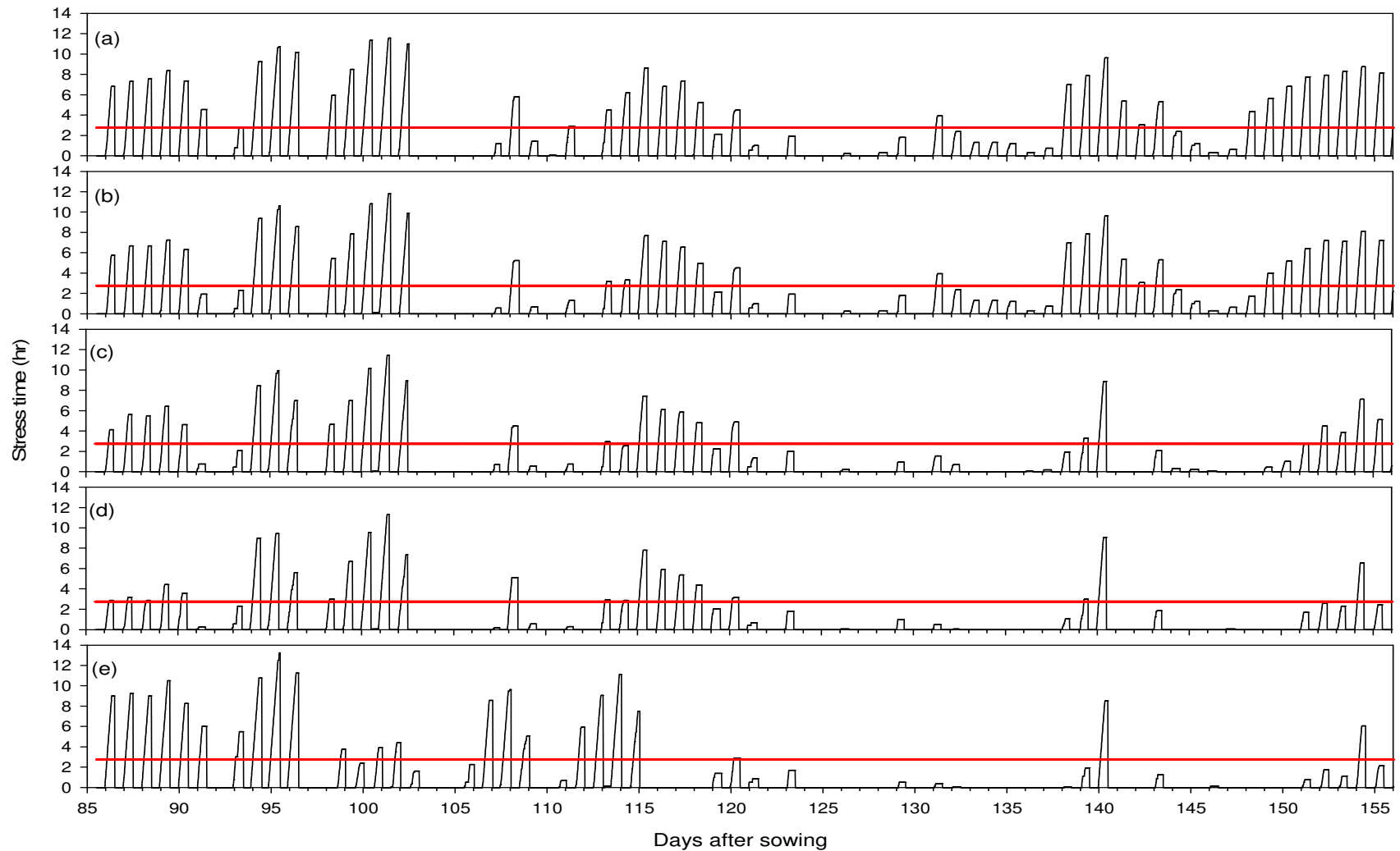


Figure 7.2. Average cumulative daily stress times in Experiment 2 experienced in (a) Treatment 1, (b) Treatment 2, (c) Treatment 3, (d) Treatment 4, (e) Treatment 5 irrigation treatments between 85 and 115 DAS. Peak daily values represent the daily sum of stress time. The red line at 2.75 hr represents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

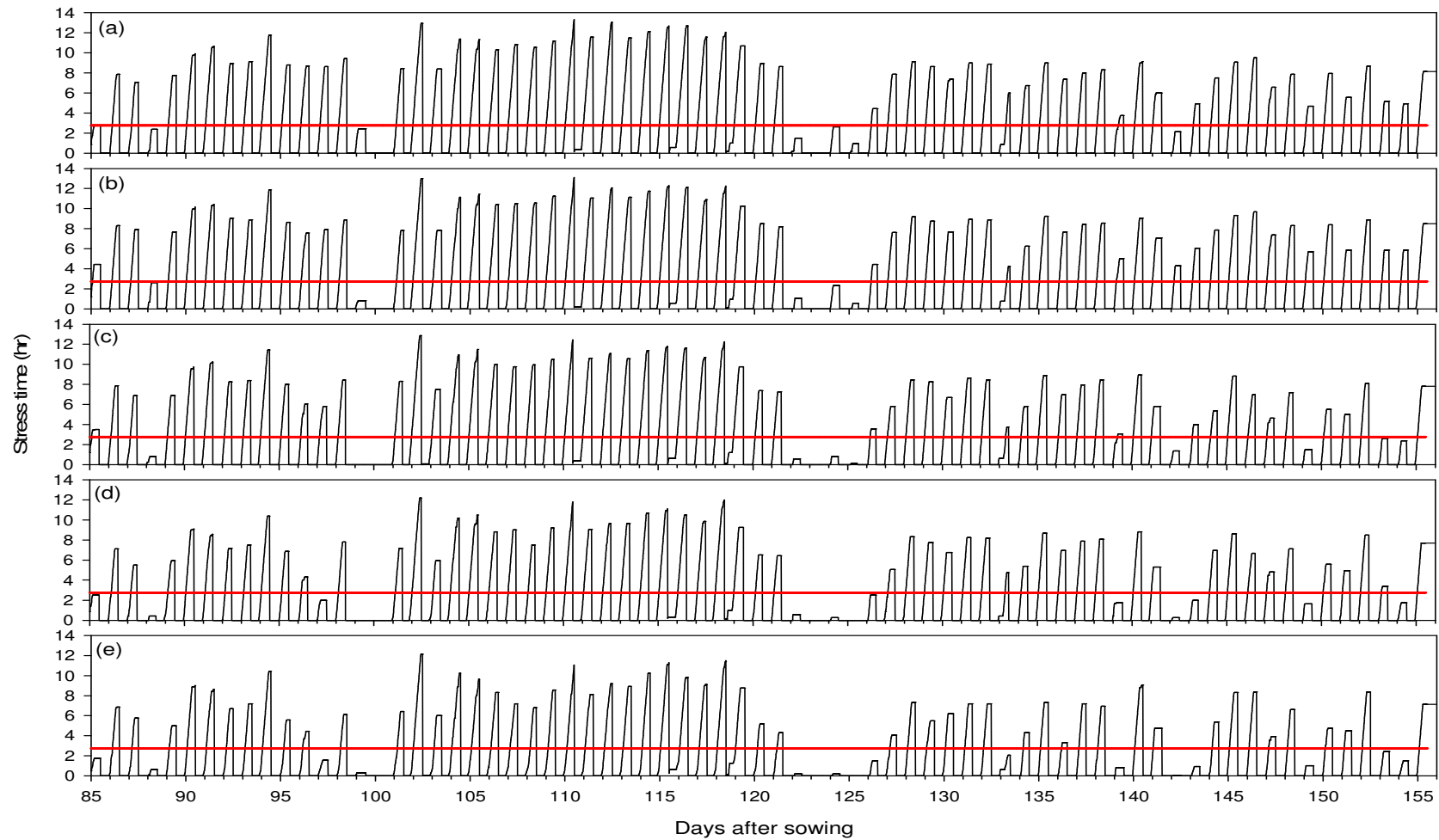


Figure 7.3. Average cumulative daily stress times in Experiment 3 experienced in (a) Treatment 1, (b) Treatment 2, (c) Treatment 3, (d) Treatment 4, (e) Treatment 5 irrigation treatments between 85 and 115 DAS. Peak daily values represent the daily sum of stress time. The red line at 2.75 hr represents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

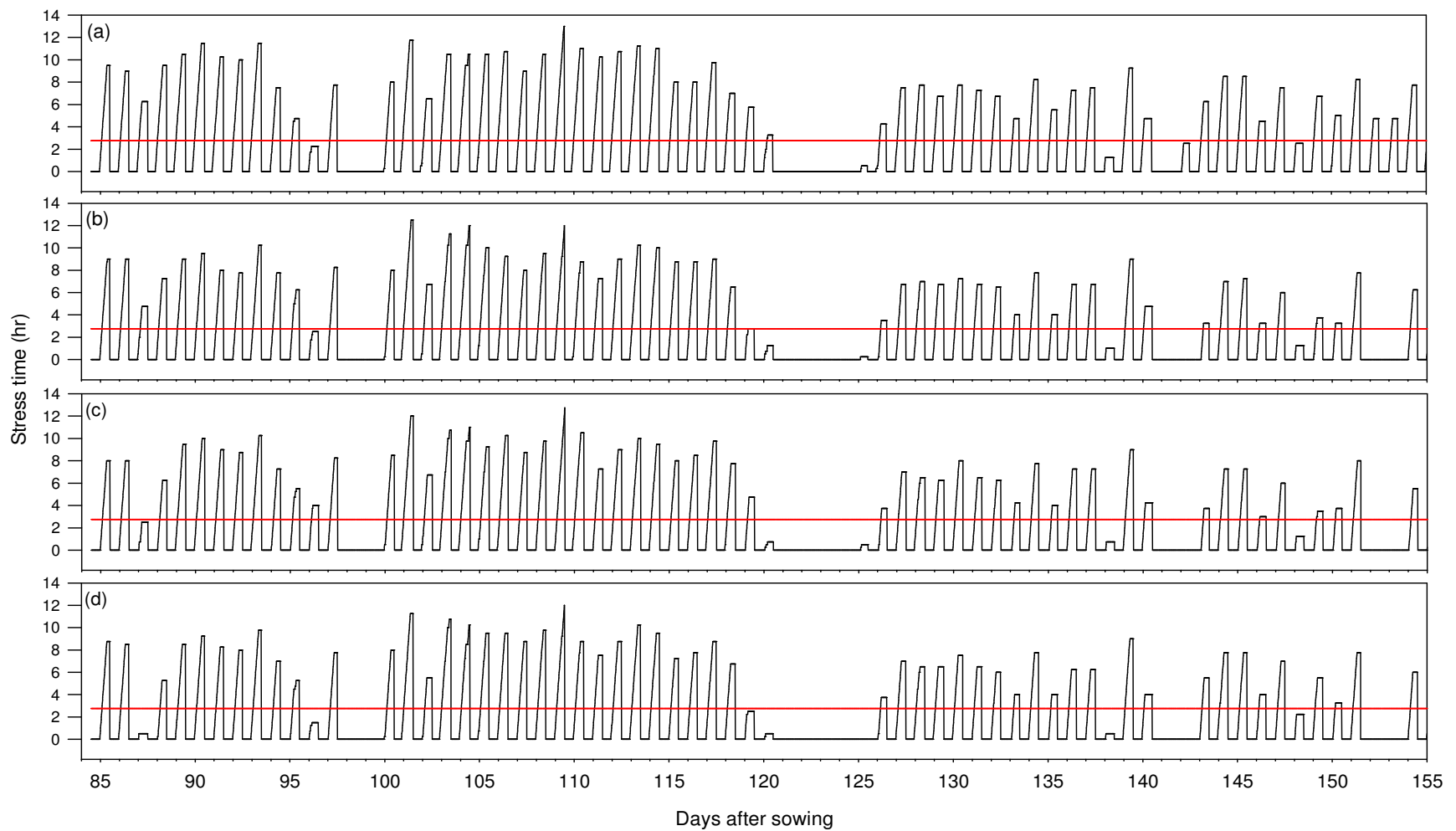


Figure 7.4. Average cumulative daily stress times in Experiment 4 experienced in (a) fully extended, (b) moderately extended, (c) control, and (d) frequently irrigated treatments between 85 and 115 DAS. Peak daily values represent the daily sum of stress time. The red line at 2.75 hr represents the calculated 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 yield (Table 7.1). A quadratic relationship was fitted to average daily stress time and final crop yield ($R^2=0.65$; $P<0.001$), where peak yields were observed between 1.8 – 5.2 hours stress time, with an average of 3.5 hours (Figure 7.5a). The difference between the average daily stress time and the calculated stress time-threshold (STT) was 0.75 hours (3.5 – 2.75 hours). This suggests that in practice, peak yields might be achieved at a slightly higher stress time-threshold than the calculated stress time-threshold. Therefore, according to this fitted regression, an average daily stress time-threshold of 4.45 hours (5.2 – 0.75 hours) should produce maximum 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 canopy temperature 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 hours ST in Treatment 3 of Experiment 2. This value is in agreement with the calculated STT of 2.75 hours, 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 hours ± 0.086 (95% CI of 3.55 - 6.00). Interestingly, the threshold value of ST resulting in 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 fit. The implications of this are explored in the discussion.

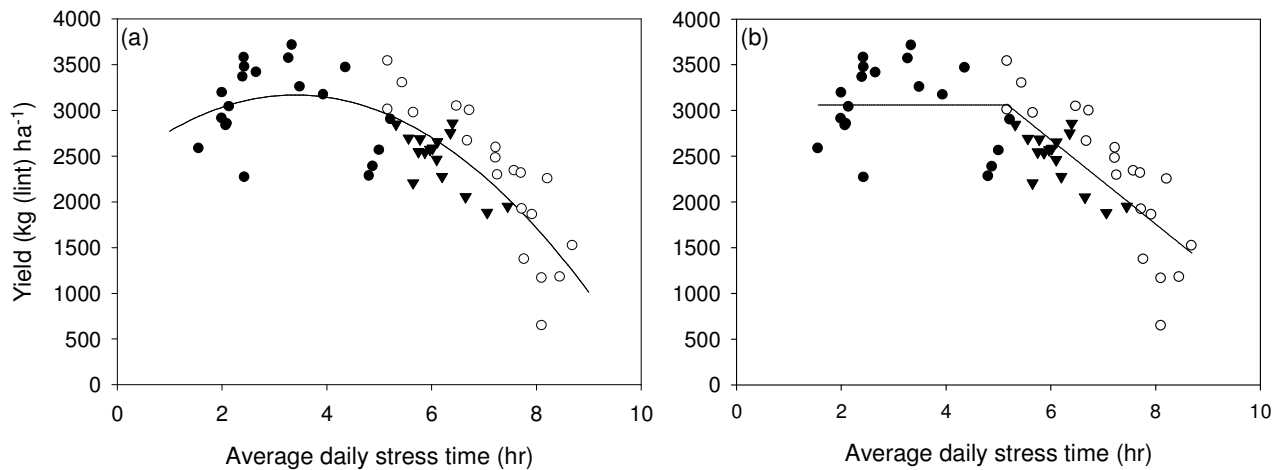


Figure 7.5. (a) Average daily stress time and yield quadratic polynomial regression in Experiment 2 (●), Experiment 3 (○) and Experiment 4 (▼) ($y = -68.697x^2 + 467.15x + 2372.8$, $R^2 = 0.65$) ($P < 0.001$); (b) Average daily stress time and yield broken linear regression in Experiment 2 (●), Experiment 3 (○) and Experiment 4 (▼) (when $x \leq 5.16$, $y = 3061.8$; 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 canopy temperatures under furrow irrigation can be warmer than those under drip irrigated conditions (see Chapter 5). The reason for this is the large fluctuations in soil moisture 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 canopy temperatures 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 moisture based scheduled furrow irrigation. Using the average cumulative stress time between scheduled furrow irrigation events (which were

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

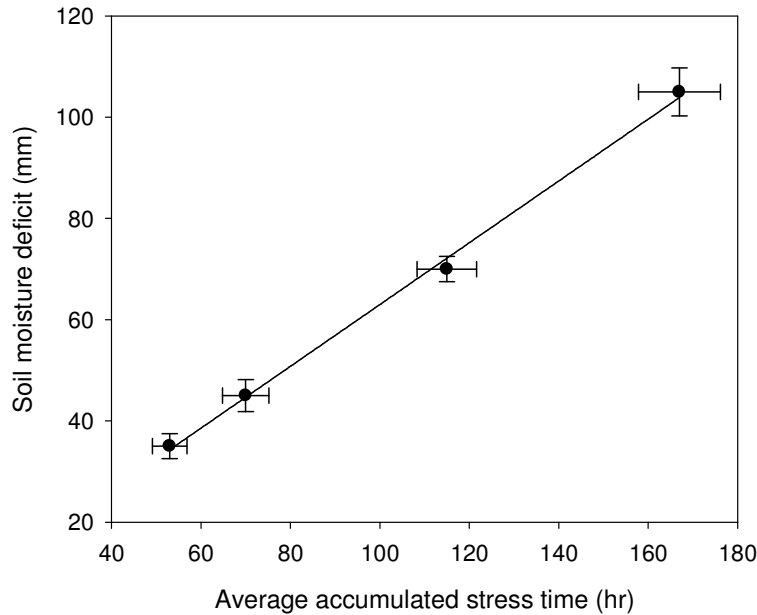


Figure 7.6. Regression model predicting the accumulated stress time between furrow irrigation events on a medium-heavy clay (Vertosol) at ‘Myall Vale’ Narrabri, at a given soil moisture deficit ($y = 0.6104x + 1.9482$, $R^2 = 0.99$) ($P=0.0011$). Bars represent standard error of mean.

The fitted regression model (Figure 7.6) shows that the average cumulative stress time increases linearly with an increase in soil moisture deficit. This relationship occurs over a physiologically viable range of water deficits and is characterised by one ST hour representing an additional 0.61mm soil water deficit. The measured soil moisture 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 predicted 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 (105mm) irrigation treatment. In this case an extra irrigation event was predicted with the modified thermal optimum protocol. However, this extra predicted irrigation event occurred after crop maturity, and would therefore be ignored in a commercial production setting. In all irrigation treatments the predicted 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 moisture deficits. This is advantageous as the thermal optimum protocol is easier to implement and less time consuming than existing soil moisture measurement techniques.

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 moisture deficit (mm)	35	45	70	105
(av. water applied/irrigation)				
Range of irrigation volumes applied (mm)	25 - 48	30 - 56	66 - 77	102 - 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 (hr)	53	70	115	167

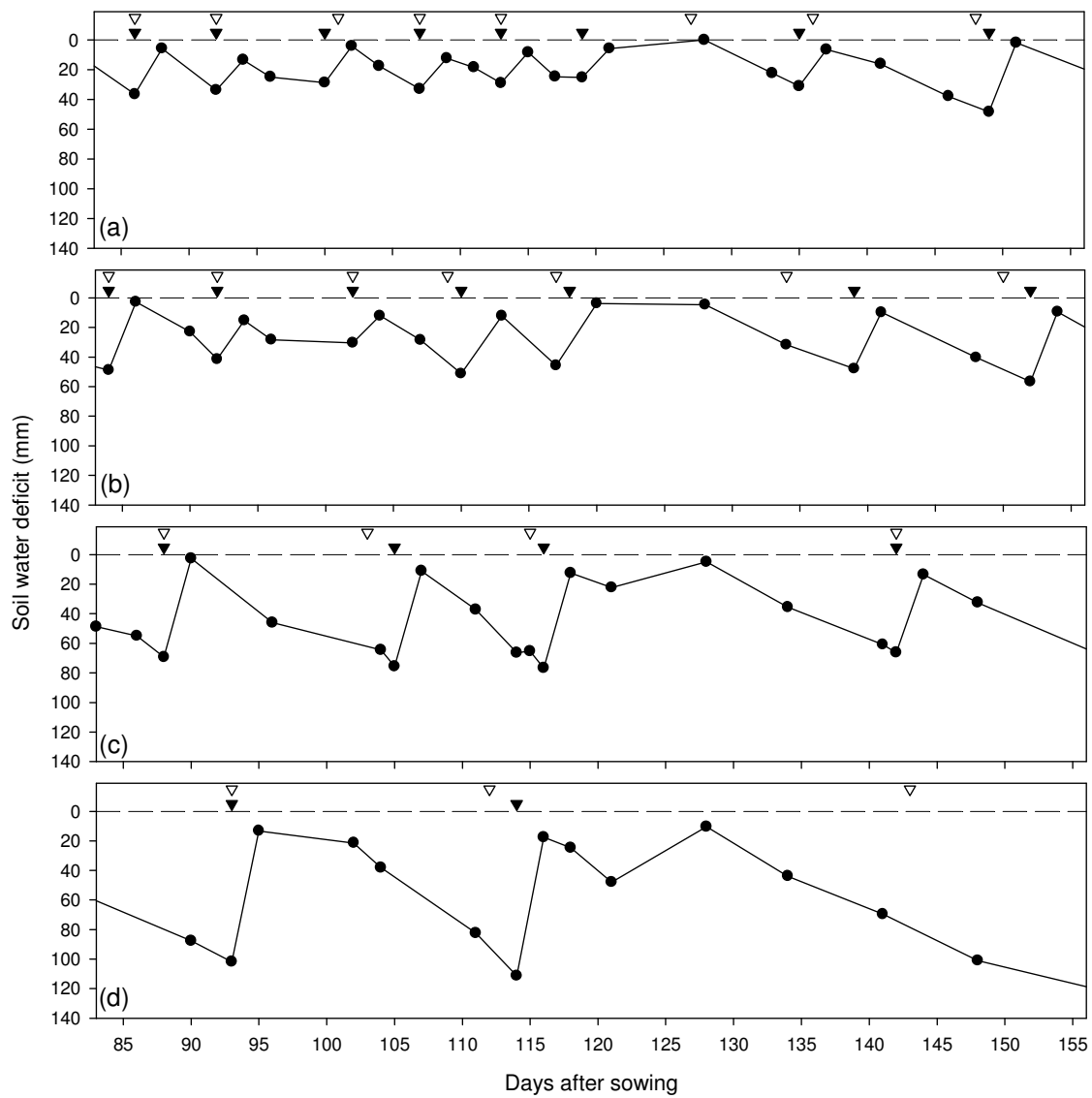


Figure 7.7. Soil moisture deficits in the (a) frequent, (b) control, (c) moderately extended, and (d) fully extended irrigation treatments with the scheduled irrigation events determined by a neutron moisture meter (▼) and irrigation events predicted with a modified thermal optimum protocol (▽) using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

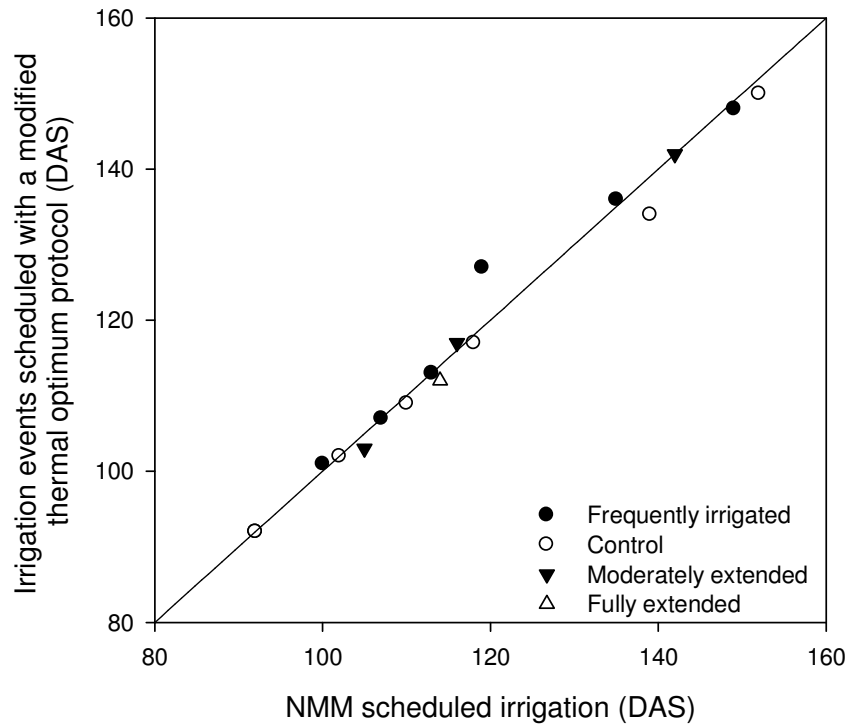


Figure 7.8. Irrigation events scheduled with neutron moisture meter (NMM) soil moisture deficit measurements vs. predicted irrigation events with the modified thermal optimum protocol. The regression represents a 1:1 line.

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 4). 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 hr increase in stress time (above a stress time of five hours) 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 hr increase in ST above 5.2 hours. This relationship saw peak yields at an average daily ST of 3.5 ± 1.7 hours, 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 approximately 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 hours. 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 predictions 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 yields that approached expected peak yields, were often larger than this threshold stress time of 2.75 hours (Table 7.1). As peak yields on the quadratic polynomial data fit between 1.8 and 5.2 hours ST, and yield reductions were observed at 5.2 hours ST on the broken linear equation fit, the calculated stress time of 2.75 hours 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 hours. Although the ST threshold could theoretically be extended to as long as 5.2 hours, 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 hr ST) and the calculated stress time-threshold (2.75 hr ST). As average daily stress time exceeded the time threshold by 0.75 hrs ($3.5 - 2.75$), a theoretical stress time-threshold of 4.45 hours is proposed ($5.2 - 0.75$ hours). 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 hours 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 predict the cumulative stress time calculated by the thermal optimum approach before a given soil moisture 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 0.61mm soil water depletion per stress time hour, and can be used as a guide for the desired soil moisture deficit to be scheduled by the thermal optimum approach to irrigation scheduling. This method appears to be robust as it consistently predicts irrigation events in a similar time frame as those determined from soil moisture 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 10-14mm, 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 moisture 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 moisture deficit treatment. Therefore, in order to increase the confidence of these average cumulative stress times at higher moisture 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 canopy temperatures 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 canopy temperatures 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 hours was similar to the amount of time over optimal temperature that was measured in optimally irrigated treatments (based on 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 minutes. The protocol has been validated using irrigation intervals of up to 5 days 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 canopy temperature 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 canopy temperature 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.

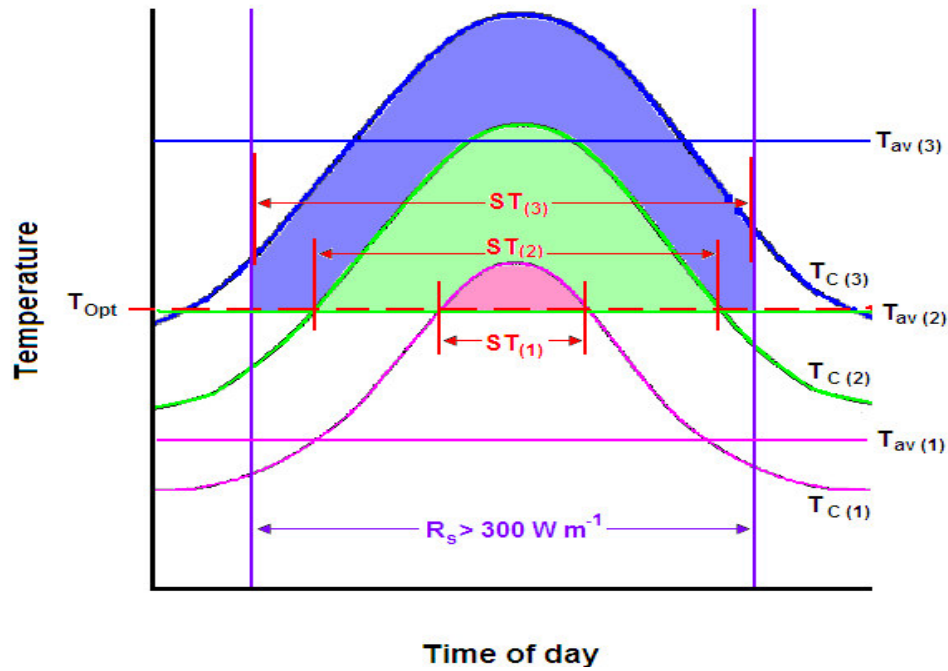


Figure 7.9. Sketch showing three possible outcomes for stress time accumulation. Option 1 is represented by the pink thermal trace, Option 2 by the green thermal trace, and option three by the blue thermal trace. Cumulative stress time accumulation is represented by the shaded areas between the optimal temperature and the daily thermal trace, when a net radiation is greater than 300 W m^{-1} . R_s = Net radiation, T_c = Canopy temperature, T_{av} = Average canopy temperature when net radiation levels are above 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 net radiation exceeds the lower limit of 300 W m^{-1} . The thermal environment and water use are driven by solar radiation. 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 in order to keep plant canopy temperature within a range that is conducive to biological processes. A potential limitation of the ST approach is that it treats all canopy temperatures 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 13, and has units of degree-days, similar to other responses to thermal experience such as germination and shoot elongation (Oryokot *et al.* 1997).

Equation 13. Cumulative sum of stress time approach to stress detection between the study period of 85 to 155 DAS

$$\sum_{\substack{85-155 \\ \text{DAS}}} \frac{(T_C - T_{Opt})(15)}{(60)(24)}$$

Where T_C is the average canopy temperature ($^{\circ}\text{C}$) for a 15 minute period as measured by BIOTIC infrared thermometers, 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 canopy temperature 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 6). 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 yield decreased as the sum of cumulative stress time increased. Using this regression, a theoretical maximum yield of approximately 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 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 R² 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 canopy temperature response to water stress.

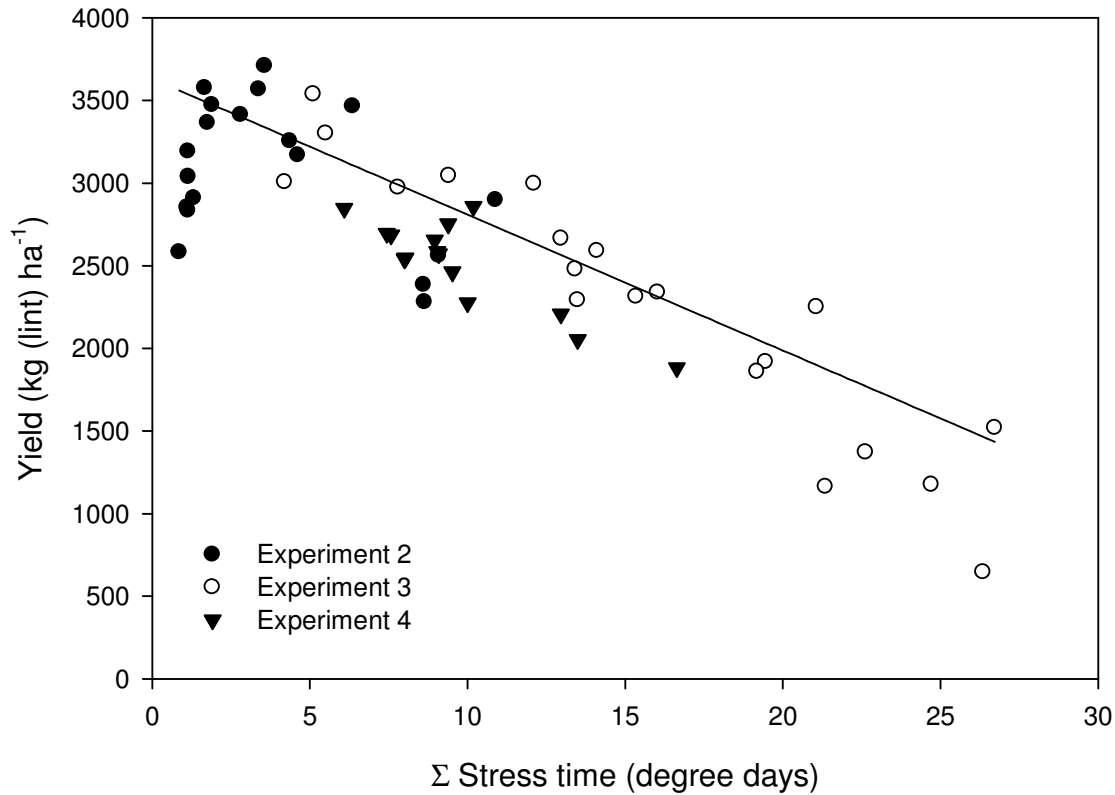


Figure 7.10. Sum of stress time and yield regression in Experiment 2 (●), Experiment 3 (○) and Experiment 4 (▼) ($y = -82.2x + 3431.6$, $R^2 = 0.75$) ($P < 0.001$) calculated based on an optimal temperature of 28°C. The R^2 value is significantly improved from 0.6 in Figure 7.5b and 0.65 in Figure 7.5a.

This response did not account for sum of cumulative stress time when average daily canopy temperature 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 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 yields (see Chapter 4). 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 (Jones 2007; Oryokot *et al.* 1997). 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 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 yield response and water use efficiency. 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 canopy temperatures before canopy closure and the effect of background soil temperatures, the effect of lower than optimal ambient temperatures on the canopy temperature 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 yield reductions were observed when average daily stress time exceeded 5.2 hours. 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 hours. This new threshold should produce similar yields to that of the calculated estimate of 2.75 hours, 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 moisture deficit, is proposed to adapt the thermal optimum approach to such irrigation systems. This adaptation to the

thermal optimum concept predicts a 0.61mm reduction in soil moisture 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 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 DISCUSSION

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 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. Presently, 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 predict 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 canopy temperature.

Although plant based measurements of water stress correlate the soil and atmospheric load contributing to plant moisture 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 moisture and atmospheric load. Therefore, these plant based measurements are theoretically advantageous (Jones 2004b; 2008). The advent of increasingly affordable and reliable infrared thermometers 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 canopy temperatures due to reduced evaporative cooling (Idso 1982; Jackson *et al.* 1981; Jones 2004a; Mahan *et al.* 2005). The BIOTIC (Biologically Identified Optimal Temperature Interactive Console) protocol uses the relationship between canopy temperature 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 canopy temperature 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 canopy temperature 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 canopy temperatures provide 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 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 yield, plant architecture, growth, biomass accumulation and canopy temperatures. 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 yield-water relations was constant across both experiments, where peak yields occurred at 822mm 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 canopy temperature-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 canopy temperatures were maintained close to 28°C. This observation is important in the context of the BIOTIC irrigation scheduling system, which utilises a threshold canopy temperature for stress detection and irrigation scheduling.

Similar experiments conducted in furrow irrigated cotton showed that average canopy temperatures of furrow irrigated cotton were warmer than those of drip irrigated cotton. However, further inspection of canopy temperatures in both furrow and drip irrigated cotton showed similar responses to water application with regards to lint yield-canopy temperature relations, regardless of the net volume of applied water per irrigation event and interval between irrigation events. This suggests that that canopy temperatures are dynamic predictors of water stress. The size of the soil water deficit and potential plant adaptation to previous moisture 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, canopy temperatures have potential utility for 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 water use efficiency.

The optimum temperature range for cotton metabolism has been extensively studied, with evolutionary, physiological, enzymatic and yield responses all indicating an optimal plant temperature of approximately 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, over a range of 23.5 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 tested. 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 approximately 28°C (27-31°C). This optimal plant temperature of 28°C is supported by the observation that yield benefits occur when average canopy temperatures are maintained as close to 28°C as possible (Chapters 4 and 5). 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 approximately 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 canopy temperature- stress time relations and stress time- yield relations were similar across all experiments. For an increase in stress time of one hour,

average daily canopy temperatures rose by 0.81°C which ultimately resulted in a 414 kg ha⁻¹ yield reduction (when average daily stress time exceeds 4 hours).

An increase in average daily canopy temperature 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 hours (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 hours by 0.75 hrs, a new stress time threshold of 4.45 hours (5.2 – 0.75 hours) 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 over 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 predicts a 0.61mm reduction in soil moisture 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 moisture 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 was 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 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 canopy temperatures are below the thermal optimum threshold.

8.1 Suggested future work

This study has 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 canopy temperatures, 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 moisture 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 canopy temperatures), 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 infrared thermometers 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 water use efficiency. Furthermore, the potential influence of lower than optimal canopy temperatures on this approach needs to be investigated and quantified.

8.2 Conclusion

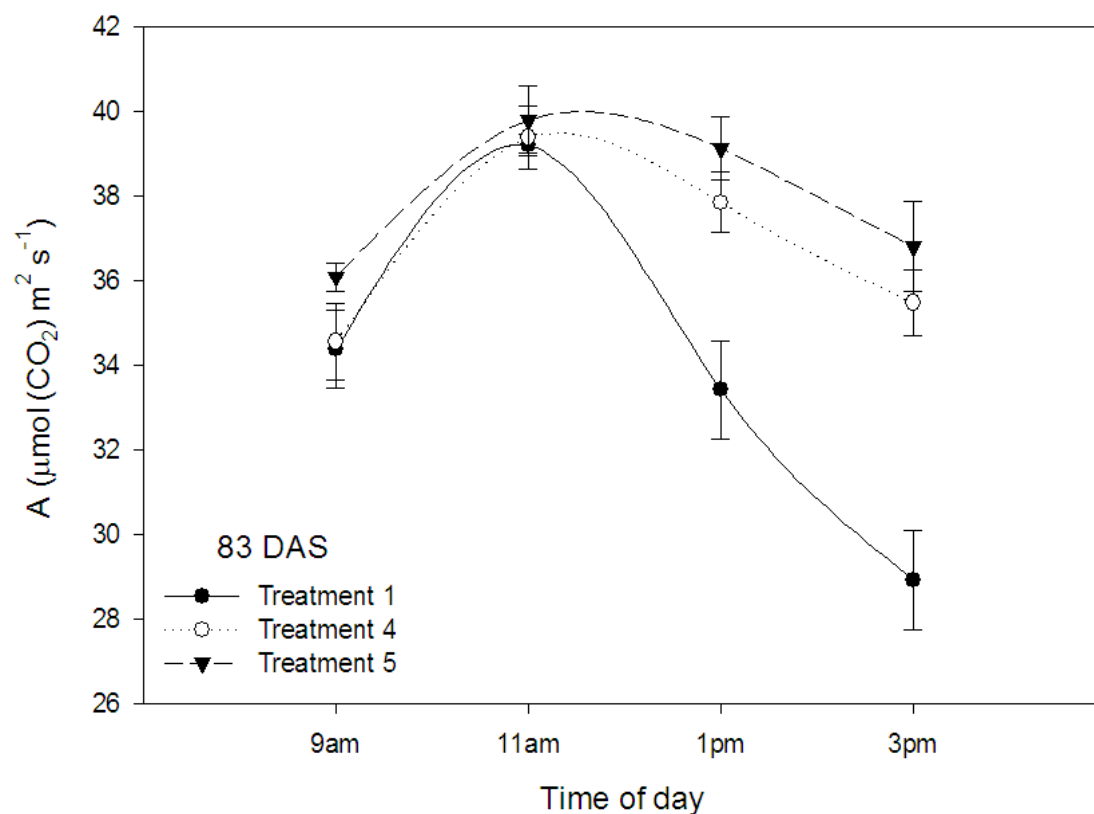
The utility and proposed modifications required to schedule irrigation in Australian cotton production systems using the BIOTIC protocol were assessed in this thesis. Plant performance, canopy temperature-yield and canopy temperature-water responses to soil water deficits in precision drip application irrigation systems (Chapter 4) and deficit furrow irrigation systems (Chapter 5) were assessed. The issue of plant adaptation, in terms of canopy temperature, in furrow irrigated systems was also investigated (Chapter 5). The data from these experiments displayed the potential utility of canopy temperatures 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 utility 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 6), 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 canopy temperatures as close to 28°C as possible is rewarded with peak plant

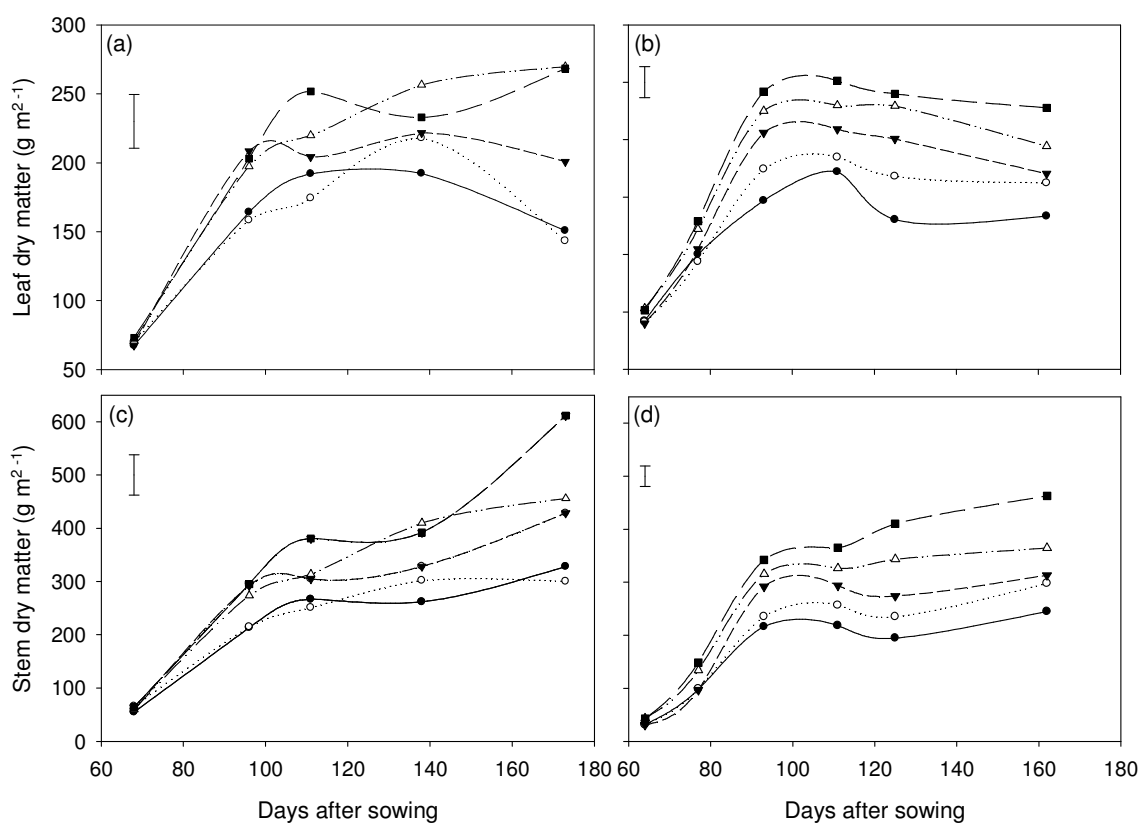
performance and yield. Due to their nature, drip irrigation systems have an increased ability to maintain average crop canopy temperatures at 28°C, producing a yield advantage with similar net water application. Scheduling drip irrigation with the proposed thermal optimal protocol is simple and effective. This is noteworthy as historically problems have been encountered scheduling irrigation in drip systems.

The temperature-time thresholds used to produce peak yield and water use efficiency at Narrabri are a temperature threshold of 28°C and a stress time threshold of 4.45 hours in drip irrigation, and 0.61mm 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) in (a) Experiment 2 and (b) Experiment 3; and stem dry matter accumulation (g.m⁻²) 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.

10. REFERENCE LIST

ABARE (2000) Australian Crop Report, 15 February 2000 no.113. http://www.abare.gov.au/publications_html/cr/cr_00/acr20_feb.pdf, accessed on 13/01/2010.

ABARE (2009) Australian Crop Report. 15 September 2009, no. 151. http://www.abare.gov.au/publications_html/cr/cr_09/cr09_Sept.pdf, accessed on 13/01/2010.

ABS (2009) Australian Bureau of Statistics: Principal Agricultural Commodities, Australia, Preliminary, 2008-09. <http://www.abs.gov.au/ausstats/abs@.nsf/Latestproducts/7111.0Main%20Features32008-09?opendocument&tabname=Summary&prodno=7111.0&issue=2008-09&num=&view=>, accessed on 10th November.

Ackerson RC, Krieg DR, Haring CL, Chang N (1977) Effects of plant water status on stomatal activity, photosynthesis, and nitrate reductase-activity on field-grown cotton. *Crop Science* **17**, 81-84.

Alderfasi AA, Nielsen DC (2001) Use of crop water stress index for monitoring water status and scheduling irrigation in wheat. *Agricultural Water Management* **47**, 69-75.

Allen RG, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration: guidelines for computing crop water requirements. In 'Irrigation and Drainage Paper no. 56'. (Food and Agricultural Organisation: Rome, Italy).

Amani I, Fischer RA, Reynolds MP (1996) Canopy temperature depression association with yield of irrigated spring wheat cultivars in a hot climate. *Journal of Agronomy and Crop Science* **176**, 119-129.

Ayars JE, Phene CJ, Hutmacher RB, Davis KR, Schoneman RA, Vail SS, Mead RM (1999) Subsurface drip irrigation of row crops: a review of 15 years of research at the Water Management Research Laboratory. *Agricultural Water Management* **42**, 1-27.

Ayars JE, Schoneman RA, Soppe RW, Mead RM (1998) Irrigating cotton in the presence of shallow ground water. In 'Proceedings of the 7th International Drainage Symposium-Drainage in the 21st century: Food production and the environment'. Orlando, FL pp. 82-89. (A.S.A.E.).

Baker JT, Gitz DC, Payton P, Wanjura DF, Upchurch DR (2007) Using leaf gas exchange to quantify drought in cotton irrigated based on canopy temperature measurements. *Agronomy Journal* **99**, 637-644.

Balota M, Payne WA, Evett SR, Lazar MD (2007) Canopy temperature depression sampling to assess grain yield and genotypic differentiation in winter wheat. *Crop Science* **47**, 1518-1529.

Balota M, William AP, Evett SR, Peters TR (2008) Morphological and physiological traits associated with canopy temperature depression in three closely related wheat lines. *Crop Science* **48**, 1897-1910.

Bange MP, Milroy SP (2004) Impact of short-term exposure to cold night temperatures on early development of cotton (*Gossypium hirsutum* L.). *Australian Journal of Agricultural Research* **55**, 655-664.

Bange MP, Milroy SP, Thongbai P (2004) Growth and yield of cotton in response to waterlogging. *Field Crops Research* **88**, 129-142.

Bastiaanssen WGM, Bos MG (1999) Irrigation performance indicators based on remotely sensed data: a review of literature. *Irrigation and Drainage Systems* **13**, 291-311.

Bhadula SK, Pandey OP, Purohit AN (1985) Thermostability and enzyme activation of P-glycolate phosphatase and 3-PGA phosphatase in *Selinum vaginatus* clerke grown at two altitudes. *Photosynthetica* **19**, 417.

Bhattarai SP, Midmore DJ, Pendergast L (2008) Yield, water-use efficiencies and root distribution of soybean, chickpea and pumpkin under different subsurface drip irrigation depths and oxygenation treatments in vertisols. *Irrigation Science* **26**, 439-450.

Bhattarai SP, Pendergast L, Midmore DJ (2006) Root aeration improves yield and water use efficiency of tomato in heavy clay and saline soils. *Scientia Horticulturae* **108**, 278-288.

Bielorai H, Hopmans PAM (1975) Recovery of leaf water potential, transpiration, and photosynthesis of cotton during irrigation cycles. *Agronomy Journal* **67**, 629-632.

Bielorai H, Mantell A, Moreshet S (1983) Water relations of cotton. In 'Water deficits and plant growth, Vol. VII Additional woody crop plants'. (Ed. TT Kozlowski). (Academic Press: New York).

Björkman O, Badger M, Armond PA (1978) Thermal acclimation of photosynthesis: Effect of growth temperature on photosynthetic characteristics and components of photosynthetic apparatus in *Nerium oleander*. In 'Year Book' p. 262. (Carnegie Institute: Washington).

Blum A, Shpiler L, Golan G, Mayer J (1989) Yield stability and canopy temperature of wheat genotypes under drought-stress. *Field Crops Research* **22**, 289-296.

BOM (2009) Bureau of Meteorology: Climate Data Online. www.bom.gov.au, accessed on September 2009.

Boyer JS (1968) Relationship of water potential to growth of leaves. *Plant Physiology* **43**, 1056-1062.

Boyer JS (1971) Nonstomatal inhibition of photosynthesis in sunflower at low leaf water potentials and high light intensities. *Plant Physiology* **48**, 532-536.

Boyer JS (1982) Plant productivity and environment. *Science* **218**, 443-448.

Bravdo BA (2005) Physiological mechanisms involved in the production of non-hydraulic root signals by partial rootzone drying - a review. In 'Proceedings of the VIIth International Symposium on Grapevine Physiology and Biotechnology, Davis, California, USA, 21-25 June, 2004.' pp. 267-276. (International Society for Horticultural Science (ISHS)).

Brown KW, Jordan WR, Thomas JC (1976) Water stress-induced alterations of stomatal response to decreases in leaf water potential. *Physiologia Plantarum* **37**, 1-5.

Bruce RR, Römken MJM (1965) Fruiting and growth characteristics of cotton in relation to soil moisture tension. *Agronomy Journal* **57**, 135-140.

Burke JJ (1990) Variation among species in the temperature dependence of the reappearance of variable fluorescence following illumination. *Plant Physiology* **93**, 652-656.

Burke JJ (1994) Enzyme adaptation to temperature. In 'Environment and plant adaptation'. (Ed. N Smirnov). (BIOS Scientific Publishers: Oxford, UK).

Burke JJ (1995) Enzyme adaptation to temperature. In 'Environment and plant adaptation'. (Ed. N Smirnov) pp. 63- 78. (BIOS Scientific Publishers: Oxford, UK).

Burke JJ (2001) Opportunities for improving cotton's tolerance to high temperature. In 'Beltwide Cotton Conference'. Memphis, TN. (Eds CP Dugger, DA Richter) p. 1453. (National Cotton Council of America).

Burke JJ, Hatfield JL, Klein RR, Mullet JE (1985) Accumulation of heat-shock proteins in field-grown cotton. *Plant Physiology* **78**, 394-398.

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

Burke JJ, Oliver MJ (1993) Optimal thermal environments for plant metabolic processes (*Cucumis sativus* L.) - Light-harvesting chlorophyll-a/b pigment-protein complex of photosystem-II and seedling establishment in cucumber. *Plant Physiology* **102**, 295-302.

Burke JJ, Upchurch DR (1989) Leaf temperature and transpirational control in cotton. *Environmental and Experimental Botany* **29**, 487-492.

Burke JJ, Velten J, Oliver MJ (2004) In vitro analysis of cotton pollen germination. *Agronomy Journal* **96**, 359-368.

Burke JJ, Wanjura DE (2010) Plant responses to temperature extremes. In 'Physiology of cotton'. (Eds JM Stewart, DM Oosterhuis, JJ Heitholt, JR Mauney). (Springer Science+Business Media: New York).

Cohen Y, Alchanatis V, Meron M, Saranga Y (2004) Mapping of leaf water potential using thermal images for site-specific irrigation. In 'Proceedings of the 7th International Conference on Precision Agriculture and Other Precision Resources Management, Hyatt Regency, Minneapolis, MN, USA, 25-28 July, 2004.' pp. 1090-1102. (Precision Agriculture Center, University of Minnesota, Department of Soil, Water and Climate).

Cohen Y, Alchanatis V, Meron M, Saranga Y, Tsipris J (2005) Estimation of leaf water potential by thermal imagery and spatial analysis. *Journal of Experimental Botany* **56**, 1843-1852.

Collins R (2004) Alternative irrigation systems: A case study. In 'WATERpak: A guide for irrigation management in cotton'. (Eds H Dugdale, G Harris, J Neilsen, D Richards, G Roth, D Williams). (Cotton Research and Development Corporation: Narrabri, Australia).

Conaty WC, Tan DKY, Constable GA, Sutton BS, Field DJ, Mamum EA (2008) Genetic Variation for Waterlogging Tolerance in Cotton. *Journal of Cotton Science* **12**, 53- 61.

Conroy JP, Seneweera S, Basra AS, Rogers G, Nissenwooller B (1994) Influence of rising atmospheric CO₂ concentrations and temperature on growth, yield and grain quality of cereal crops. *Australian Journal of Plant Physiology* **21**, 741-758.

Constable GA (1981) Carbon fixation and distribution in cotton: Implications of single leaf measurements to plant performance. Australian National University.

Constable GA (1991) Mapping the production and survival of fruit on field-grown cotton. *Agronomy Journal* **83**, 374-378.

Constable GA, Bange MP (2006) What is cotton's sustainable yield potential? *Australian Cottongrower* **26**, 6-10.

Constable GA, Hearn AB (1981) Irrigation for crops in a sub-humid environment. 6. Effect of irrigation and nitrogen-fertilizer on growth, yield and quality of cotton. *Irrigation Science* **3**, 17-28.

Constable GA, Rawson HM (1980) Effect of leaf position, expansion and age on photosynthesis, transpiration and water-use efficiency of cotton. *Australian Journal of Plant Physiology* **7**, 89-100.

Cothren JT (1999) Physiology of the cotton plant. In 'Cotton: Origin, history, technology, and production'. (Eds CW Smith, JT Cothren) pp. 207- 268. (John Wiley & Sons, Inc.: New York, USA).

Cottee NS (2009) Thermotolerance of cotton. Ph.D. diss. The University of Sydney, Sydney, Australia.

Cotton_Australia (2008) Cotton Australia Fact Sheet Booklet. http://www.cottonaustralia.com.au/media/Fact_Sheet_Booklet.183.pdf, accessed on 05/12/2009.

CRDC (2009) Australia's cotton and its markets <http://www.crdc.com.au/index.cfm?pageID=23>, accessed on October 2009.

Cremona MV, Stutzel H, Kage H (2004) Irrigation scheduling of Kohlrabi (*Brassica oleracea* var. *gongylodes*) crop using crop water stress index. *Hortscience* **39**, 276-279.

Crowther F (1934) Studies in growth analysis of the cotton plant under irrigation in the Sudan. I. The effects of different combinations of nitrogen applications and water-supply. *Annals of Botany* **48**, 877-913.

CSD (2008) 2008 Variety guide. Cotton Seed Distributors, Wee Waa.

CSIRO (2008) The Cotton Day-Degree Report: Based on the SILO Patched Point Dataset. <http://cottassist.cottoncrc.org.au/DDC/DDCTool.aspx>, accessed on 4th January 2009.

Cull PO, Hearn AB, Smith RCG (1981) Irrigation scheduling of cotton in a climate with uncertain rainfall. 1. Crop water requirements and response to irrigation. *Irrigation Science* **2**, 127-140.

Cutler JM, Rains DW (1977) Effects of irrigation history on responses of cotton to subsequent water stress. *Crop Science* **17**, 329-335.

Cutler JM, Rains DW, Loomis RS (1977) Role of changes in solute concentration in maintaining favourable water balance in field-grown cotton. *Agronomy Journal* **69**, 773-779.

Dahlhoff E, Somero GN (1993) Kinetic and structural adaptations of cytoplasmic malate dehydrogenase of eastern pacific abalone (Genus *Haliotis*) from different thermal habitats: Biochemical correlates fo biogeographical patterning. *Journal of Experimental Biology* **185**, 137-150.

Dane JH, Topp GC (2002) 'Methods of soil analysis. Part 4: Physical methods.' (American Society of Soil Science Madison, WI, USA).

Davidson D, Simon JP (1981) Thermal adaptation and acclimation of ecotypic populations of *Spirodela polyrhiza* (Lemnaceae): Thermostability and apparent activation energy of NAD⁺-malate dehydrogenase. *Canadian Journal of Botany* **59**, 1061.

Davidson D, Simon JP (1983) Thermal adaptation and acclimation of *Hepcotypis* populations of *Spirodella polyrhiza* L. Schleid (Lemnaceae): Temperature dependency of NAD malate dehydrogenase. *Journal of Thermal Biology* **8**, 289-296.

DeTar WR (2008) Yield and growth characteristics for cotton under various irrigation regimes on sandy soil. *Agricultural Water Management* **95**, 69-76.

Du YC, Kawamitsu Y, Nose A, Hiyane S, Murayama S, Wasano K, Uchida Y (1996) Effects of water stress on carbon exchange rate and activities of photosynthetic enzymes in leaves of sugarcane (*Saccharum* sp). *Australian Journal of Plant Physiology* **23**, 719-726.

Eaton FM (1955) Physiology of the cotton plant. *Annual Review of Plant Physiology* **6**, 299-328.

Ehlig CF, LeMert RD (1973) Effect of fruit load, temperature and relative humidity on boll retention of cotton. *Crop Science* **13**, 673-679.

Ehrler WL (1973) Cotton leaf temperatures as related to soil-water depletion and meteorological factors. *Agronomy Journal* **65**, 404-409.

Ehrler WL, Idso SB, Jackson RD, Reginato RJ (1978) Wheat Canopy Temperature - Relation to Plant Water Potential. *Agronomy Journal* **70**, 251-256.

Ephrath JE, Marani A, Bravdo BA (1990) Effects of moisture stress on stomatal-resistance and photosynthetic rate in cotton (*Gossypium hirsutum*). 1. Controlled levels of stress. *Field Crops Research* **23**, 117-131.

Epron D, Dreyer E, Breda N (1992) Photosynthesis of oak trees (*Quercus petraea* (Matt) Liebl.) during drought conditions under field conditions: diurnal course of net CO₂ assimilation and photochemical efficiency of photosystem-II. *Plant, Cell and Environment* **15**, 809-820.

Erdem T, Erdem AY, Orta AH, Okursoy H (2006) Use of a crop water stress index for scheduling the irrigation of sunflower (*Helianthus annuus* L.). *Turkish Journal of Agriculture and Forestry* **30**, 11-20.

Erdem Y, Erdem T, Orta AH, Okursoy H (2005) Irrigation scheduling for watermelon with crop water stress index (CWSI). *Central European Journal of Agriculture* **6**, 449-460.

Evelt SR, Howell TA, Schneider AD, Upchurch DR, Wanjura DF (1996) Canopy temperature based automatic irrigation control. In 'Evapotranspiration and irrigation scheduling. Proceedings of the International Conference, San Antonio, Texas, USA, November 3-6 1996.' pp. 207-213. (American Society of Agricultural Engineers (ASAE)).

Farrell T (2008) 'Cotton pest management guide 2008-09.' (NSW Department of Primary Industries: Narrabri, Australia).

Fereres E (1999) Irrigation scheduling and its impact on the 21st century. *International Water and Irrigation* **19**, 24-28.

Ferguson DL, Burke JJ (1991) Influence of Water and Temperature Stress on the Temperature-Dependence of the Reappearance of Variable Fluorescence Following Illumination. *Plant Physiology* **97**, 188-192.

Fitt GP (1994) Cotton pest-management. 3. An Australian perspective. *Annual Review of Entomology* **39**, 543-562.

Flexas J, Medrano H (2002) Drought-inhibition of photosynthesis in C-3 plants: Stomatal and non-stomatal limitations revisited. *Annals of Botany* **89**, 183-189.

Fuchs M (1990) Infrared Measurement of Canopy Temperature and Detection of Plant Water-Stress. *Theoretical and Applied Climatology* **42**, 253-261.

Gamon JA, Pearcy RW (1989) Leaf movement, stress avoidance and photosynthesis in *Vitis-califonica*. *Oecologia* **79**, 475-481.

Gardner B, Keener ME, DeSutter SC, Jagatich CT, Felice RA (1987) Apparatus for determining water stress in crops US Patent No. 4,876,647.

Garrot DJ, Kilby MW, Fangmeier DD, Husman SH, Ralowicz AE (1993) Production, Growth, and Nut Quality in Pecans under Water-Stress Based on the Crop Water-Stress Index. *Journal of the American Society for Horticultural Science* **118**, 694-698.

Garrot DJ, Ottman MJ, Fangmeier DD, Husman SH (1994) Quantifying Wheat Water-Stress with the Crop Water-Stress Index to Schedule Irrigations. *Agronomy Journal* **86**, 195-199.

Gates DM (1964) Leaf temperature and transpiration. *Agronomy Journal* **56**, 273-277.

Gerard CJ (1971) Influence of osmotic potential, temperature, and calcium on growth of plant roots. *Agronomy Journal* **63**, 555-558.

Gerard CJ, Cowley WR (1969) Interrelationship of growth and fruiting characteristics of cotton. *Agronomy Journal* **61**, 966.

Gibb D, Neilsen JE, Constable GA (2004) Cotton growth responses to water stress. In 'WATERpak: A guide for irrigation management in cotton'. (Eds H Dugdale, G Harris, J Neilsen, D Richards, G Roth, D Williams). (Cotton Research and Development Corporation: Narrabri, Australia).

Gimenez C, Mitchell VJ, Lawlor DW (1992) Regulation of photosynthetic rate of two sunflower hybrids under water stress. *Plant Physiology* **98**, 516-524.

Gonzalez-Dugo MP, Moran MS, Mateos L, Bryant R (2006) Canopy temperature variability as an indicator of crop water stress severity. *Irrigation Science* **24**, 233-240.

Grabham MK, Hornbuckle JW, Raine SR, Smith RJ (2009) Bankless channel irrigation systems: Irrigation performance assessment. In 'Irrigation and Drainage Conference'. Swall Hill, Vic, Australia. (Irrigation Australia Ltd.).

Grabham MK, Williams D (2005) Bankless channels: Irrigation without siphons. *Australian Cottongrower* **26**, 58-59.

Graham D, Hockley DG, Patterson BD (1979) Temperature effects on phosphoenolpyruvate carboxylase from chilling sensitive to chilling resistant plants. In 'Low temperature stress in crop plants'. (Eds JM Lyons, D Graham, JK Raison) pp. 453-461. (Academic Press: New York).

Graves JE, Somero GN (1982) Electrophoretic and functional enzymatic evolution in four species of eastern Pacific Barracudas from different thermal environments. *Evolution* **36**, 97-106.

Grimes DW, Dickens WL, Anderson WD (1969a) Functions for cotton (*Gossypium hirsutum* L.) production from irrigation and nitrogen fertilization variables. 2. Yield components and quality characteristics. *Agronomy Journal* **61**, 773-776.

Grimes DW, El-Zik KM (1990) Cotton. In 'Irrigation of agricultural crops'. (Eds BA Stewart, DR Neilsen). (American Society of Agronomy-Crop Science Society of America-Soil Science Society of America: Madison, USA).

Grimes DW, Miller RJ, Dickens L (1970) Water stress during flowering of cotton. *California Agriculture* **24**, 4-6.

Grimes DW, Yamada H, Dickens WL (1969b) Functions for cotton (*Gossypium hirsutum* L.) production from irrigation and nitrogen fertilization variables. 1. Yield and evapotranspiration. *Agronomy Journal* **61**, 769-773.

Guilioni L, Jones HG, Leinonen I, Lhomme JP (2008) On the relationships between stomatal resistance and leaf temperatures in thermography. *Agricultural and Forest Meteorology* **148**, 1908-1912.

Guy CL, Carter JV (1984) Characterisation of partially purified glutathione reductase from cold-hardened and non-hardened spinach leaf tissue. *Cryobiology* **21**, 454-464.

Hale MG, Orcutt DM (1987) 'The physiology of plants under stress.' (John Wiley and Sons: New York).

Hall AE, Hoffman GJ (1976) Leaf conductance response to humidity and water transport in plants. *Agronomy Journal* **68**, 876-881.

Hall JG (1985) Temperature-related differentiation of glucose phosphate isomerase alleoenzymes isolated from blue mussel, *Mytilus edulis*. *Biochemical Genetics* **23**, 705-727.

Hansen V, Israelsen O, Stringham G (1980) 'Irrigation principles and practices.' (John Wiley & Sons: New York).

Hatfield JL (1983) The utilisation of thermal infrared radiation measurements from grain-sorghum crops as a method of assessing their irrigation requirements. *Irrigation Science* **3**, 259-268.

Hatfield JL, Burke JJ, Mahan JR, Wanjura DE (1987a) Foliage temperature measurements: a link between the biological and physical environments. In 'Proceedings of international conference on measurement of soil plant and water status'. (Ed. RJ Hanks) pp. 99- 102. (Utah State University: Utah State University, Logan, Ut USA).

Hatfield JL, Quisenberry JE, Dilbeck RE (1987b) Use of canopy temperatures to identify water conservation in cotton germplasm. *Crop Science* **27**, 269-273.

Hearn AB (1969) Growth and performance of cotton in a desert environment. I. Morphological development of the crop. *Journal of Agricultural Science* **73**, 65-74.

Hearn AB (1975) Response of cotton to water and nitrogen in a tropical environment.1. Frequency of watering and method of application of nitrogen. *Journal of Agricultural Science* **84**, 407-417.

Hearn AB (1979) Water relationships in cotton. *Outlook on Agriculture* **10**, 159-166.

Hearn AB (1994) The principles of cotton water relations and their application in management. In 'Challenging the future- Proceedings of the world cotton research conference- 1'. (CSIRO, Melbourne: Brisbane, Australia).

Hearn AB, Constable GA (1984) Cotton. In 'The physiology of tropical field crops'. (Eds PR Goldsworthy, NM Fisher). (John Wiley & Sons Ltd.: New York).

Hearn AB, Da Roza GD (1985) A simple-model for crop management applications for cotton (*Gossypium hirsutum* L.). *Field Crops Research* **12**, 49-69.

Hearn AB, Fitt GP (1992) Cotton cropping systems. In 'Field crop ecosystems'. (Ed. CJ Pearson) pp. 85-142. (Elsevier: Amsterdam).

Hirayama M, Wada Y, Nemoto H (2006) Estimation of drought tolerance based on leaf temperature in upland rice breeding. *Breeding Science* **56**, 47-54.

Hochachka PW, Somero GN (1984) 'Biochemical adaptation.' (Princeton University Press: Princeton, New Jersey).

Hodges HF, Reddy KR, McKinion JM, Reddy VR (1993) Temperature effects on cotton. Mississippi Agricultural & Forestry Experiment Station Bulletin 990, Mississippi State, MS.

Hodgson AS, Constable GA, Duddy GR, Daniells IG (1990) A comparison of drip and furrow irrigated cotton on a cracking clay soil. 2. Water-use efficiency, waterlogging, root distribution and soil structure. *Irrigation Science* **11**, 143-148.

Hood S, Carrigan E (2006) Siphon-less irrigation systems: so how did they perform? *The Australian Cotton Grower* **27**, 44-46.

Howell TA, Hatfield JL, Yamada H, Davis KR (1984) Evaluation of cotton canopy temperature to detect crop water-stress. *Transactions of the A.S.A.E.* **27**, 84-88.

Hsiao TC (1973) Plant responses to water stress. *Annual Review of Plant Physiology* **24**, 519-570.

Huner NPA, Macdowall FDH (1979) The effect of low temperature acclimation of winter rye on catalytic properties of its ribulose biphosphate carboxylase-oxygenase. *Canadian Journal of Biochemistry* **57**, 155-164.

Huner NPA, Palta JP, Li PH, Carter JV (1981) Comparison of the structure and function of ribulose biphosphate carboxylase-oxygenase from a cold-hardy and nonhardy potato species. *Canadian Journal of Biochemistry* **59**, 280-289.

Idso SB (1982) Non-water-stressed baselines - a key to measuring and interpreting plant water-stress. *Agricultural Meteorology* **27**, 59-70.

Idso SB, Ehrlar WL (1976) Estimating soil moisture in the root zone of crops: A technique adaptable to remote sensing. *Geophysical Research Letters* **3**, 23- 25.

Idso SB, Jackson RD, Pinter PJ, Reginato RJ, Hatfield JL (1981a) Normalizing the Stress-Degree-Day Parameter for Environmental Variability. *Agricultural Meteorology* **24**, 45-55.

Idso SB, Jackson RD, Reginato RJ (1977) Remote-sensing of crop yields. *Science* **196**, 19-25.

Idso SB, Reginato RJ, Jackson RD, Pinter PJ (1981b) Foliage and Air Temperatures - Evidence for a Dynamic Equivalence Point. *Agricultural Meteorology* **24**, 223-226.

Idso SB, Reginato RJ, Jackson RD, Pinter PJ (1981c) Measuring yield-reducing plant water potential depressions in wheat by infrared thermometry. *Irrigation Science* **2**, 205-212.

Idso SB, Reginato RJ, Radin JW (1982) Leaf diffusion resistance and photosynthesis in cotton as related to a foliage temperature based plant water-stress index. *Agricultural Meteorology* **27**, 27-34.

Irmak S, Haman DZ, Bastug R (2000) Determination of crop water stress index for irrigation timing and yield estimation of corn. *Agronomy Journal* **92**, 1221-1227.

Isbell RF (1996) 'The Australian Soil Classification.' (CSIRO Publishing: Collingwood, Australia).

Jackson RD (1982) Canopy temperature and crop water stress. *Advances in Irrigation* **1**, 43-85.

Jackson RD, Idso SB, Reginato RJ, Pinter PJ (1981) Canopy Temperature as a Crop Water-Stress Indicator. *Water Resources Research* **17**, 1133-1138.

Jackson RD, Reginato RJ, Idso SB (1977) Wheat canopy temperature- Practical tool for evaluating water requirements. *Water Resources Research* **13**, 651-656.

Jones HG (1999) Use of thermography for quantitative studies of spatial and temporal variation of stomatal conductance over leaf surfaces. *Plant, Cell and Environment* **22**, 1043-1055.

Jones HG (2004a) Application of thermal imaging and infrared sensing in plant physiology and ecophysiology. In 'Advances in Botanical Research Incorporating Advances in Plant Pathology, Vol 41' pp. 107-163.

Jones HG (2004b) Irrigation scheduling: advantages and pitfalls of plant-based methods. *Journal of Experimental Botany* **55**, 2427-2436.

Jones HG (2007) Monitoring plant and soil water status: established and novel methods revisited and their relevance to studies of drought tolerance. *Journal of Experimental Botany* **58**, 119-130.

Jones HG (2008) Irrigation scheduling - comparison of soil, plant and atmosphere monitoring approaches. In 'Proceedings of the Fifth International Symposium on Irrigation of Horticultural Crops, Mildura, Australia, 28 August-2 September 2006.' pp. 391-403. (International Society for Horticultural Science (ISHS)).

Jordan WR (1986) Water deficits and reproduction. In 'Cotton Physiology'. (Eds JR Mauney, JM Stewart). (The Cotton Foundation: Memphis, TN, USA).

Jordan WR, Brown KW, Thomas JC (1975) Leaf age as a determinant in stomatal control of water loss from cotton during water stress. *Plant Physiology* **56**, 595-599.

Kanemasu ET, Thurtell GW, Tanner CB (1969) Design, calibration and field use of a stomatal diffusion porometer. *Plant Physiology* **44**, 881-885.

Karami E, Krieg DR, Quisenberry JE (1980) Water relations and C-14 assimilation of cotton with different leaf morphology. *Crop Science* **20**, 421-426.

Karlsen ÅK, Steiner JJ (2007) Scandinavian colonial bentgrass diversity described by RAPD, variable chlorophyll fluorescence, and collecting site ecogeography. *Acta Agriculturae Scandinavica, Section B - Plant Soil Science* **57**, 23- 34.

Kautsky H, Appel W, Amann H (1960) Chlorophyll fluorescence and carbonate assimilation. 13. The fluorescence curve and the photo chemistry of plant. *Biochemische Zeitschrift (Biochemical Journal- English Translation)* **332**, 277-292.

Kim K, Portis AR (2005) Temperature dependence of photosynthesis in Arabidopsis plants with modifications in Rubisco activase and membrane fluidity. *Plant and Cell Physiology* **46**, 522-530.

Krause GH, Weis E (1991) Chlorophyll fluorescence and photosynthesis - The basics. *Annual Review of Plant Physiology and Plant Molecular Biology* **42**, 313-349.

Kreidemann PE, Goodwin I (2003) Regulated deficit irrigation and partial rootzone drying. Irrigation Insights No 3, Land and Water Australia, Canberra.

Krieg DR (1986) Feedback control and stress effects on photosynthesis. In 'Cotton physiology'. (Eds JR Mauney, JM Stewart) pp. 227- 244. (The Cotton Foundation: Memphis, TN).

Krieg DR, Hutmacher RB (1986) Photosynthetic rate control in sorghum- Stomatal and nonstomatal factors. *Crop Science* **26**, 112-117.

Law RD, Crafts-Brandner SJ (1999) Inhibition and acclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5-bisphosphate carboxylase/oxygenase. *Plant Physiology* **120**, 173-181.

Leidi EO, Lopez JM, Lopez M, Gutierrez JC (1993) Searching for Tolerance to Water-Stress in Cotton Genotypes - Photosynthesis, Stomatal Conductance and Transpiration. *Photosynthetica* **28**, 383-390.

Leinonen I, Grant OM, Tagliavia CPP, Chaves MM, Jones HG (2006) Estimating stomatal conductance with thermal imagery. *Plant, Cell and Environment* **29**, 1508-1518.

Levitt J (1972) 'Responses of plants to environmental stresses.' (London, Academic Press, Inc. UK).

Li-COR (2004a) OPEN's system variables. In 'Using the Li-6400 portable photosynthesis system' pp. 14-17 to 14-18. (Li-COR Biosciences Inc.: Lincoln, Nebraska, USA).

Li-COR (2004b) System description. In 'Using the Li-6400 portable photosynthesis system' pp. 1-7 to 1-11. (Li-COR Biosciences Inc.: Lincoln, Nebraska, USA).

Longenecker DE, Lyster PJ (1969) Moisture content of cotton leaves and petioles as related to environmental moisture stress. *Agronomy Journal* **61**, 687-690.

Lovett S, Price P, Lovett J (2003) 'Managing riparian lands in the cotton industry.' (Cotton Research and Development Corporation: Narrabri, Australia).

Loveys B, McCarthy M, Jones HG, Theobald J, Skinner A (2005) When to water? Assessment of plant-based measurements to indicate irrigation requirements. Grape and Wine Research and Development Corporation, Adelaide, SA.

Lu ZM, Radin JW, Turcotte EL, Percy R, Zeiger E (1994) High yields in advanced lines of Pima cotton are associated with higher stomatal conductance, reduced leaf area and lower leaf temperature. *Physiologia Plantarum* **92**, 266-272.

Lu ZM, Zeiger E (1994) Selection for higher yields and heat resistance in Pima cotton has caused genetically determined changes in stomatal conductances. *Physiologia Plantarum* **92**, 273-278.

Lutova MI (1995) Thermostability and kinetic properties of enzymes during temperature adaptation in plants. *Russian Journal of Plant Physiology* **42**, 821-832.

Lutova MI, Kamentseva IE, Sharkova VE (1987) Effect of growth temperature on thermostability of enzymes from wheat leaves. *Fiziologicheskii Rastanii (Soviet Plant Physiology- English Translation)* **34**, 879.

Lyle WM, Brodovsky JP (1981) Low Energy Precision Application (LEPA) irrigation system. *Transactions of the A.S.A.E.* **24**, 1241-1245.

Mahan JR (2000) Thermal dependence of malate synthase activity and its relationship to the thermal dependence of seedling emergence. *Journal of Agricultural and Food Chemistry* **48**, 4544-4549.

Mahan JR, Burke JJ, Orzech KA (1987) The "thermal kinetic window" as an indicator of optimum plant temperature. *Plant Physiology (Supplement)* **83**, 87.

Mahan JR, Burke JJ, Orzech KA (1990) Thermal-Dependence of the Apparent-Km of Glutathione Reductases from 3 Plant-Species. *Plant Physiology* **93**, 822-824.

Mahan JR, Burke JJ, Upchurch DR, Wanjura DF (2000) Irrigation scheduling using biologically-based optimal temperature and continuous monitoring of canopy temperature. *Acta Horticulture* **537**, 375-379.

Mahan JR, Burke JJ, Wanjura DF, Upchurch DR (2005) Determination of temperature and time thresholds for BIOTIC irrigation of peanut on the Southern High Plains of Texas. *Irrigation Science* **23**, 145-152.

Mahan JR, Gitz DC (2007) A dynamic model of cotton emergence based on the thermal dependence of malate synthase. *Agronomy Journal* **99**, 1668-1674.

Mahan JR, McMichael BL, Wanjura DF (1995) Methods for reducing the adverse effects of temperature stress on plants: A review. *Environmental and Experimental Botany* **35**, 251-258.

Mahan JR, Upchurch DR (1988) Maintenance of constant leaf temperature by plants -1. hypothesis- limited homeothermy. *Environmental and Experimental Botany* **28**, 351-357.

Mahan JR, Yeater KM (2008) Agricultural applications of a low-cost infrared thermometer. *Computers and Electronics in Agriculture* **64**, 262-267.

Marani A, Amirav A (1971a) Effects of soil moisture stress on two varieties of upland cotton in Israel. III. Bet-Shean Valley. *Experimental Agriculture* **7**, 289-301.

Marani A, Amirav A (1971b) Effects of soil moisture stress on two varieties of upland cotton in Israel. I. Coastal plain region. *Experimental Agriculture* **7**, 213-224.

Martin B, Ruiztorres NA (1992) Effects of water-deficit stress on photosynthesis, its components and component limitations, and on water use efficiency in wheat (*Triticum aestivum* L.). *Plant Physiology* **100**, 733-739.

Maximov NA (1929) 'The plant in relation to water: A study of the physiological basis of drought resistance.' (Unwin Brothers Ltd.: London).

Maxwell K, Johnson GN (2000) Chlorophyll fluorescence - a practical guide. *Journal of Experimental Botany* **51**, 659-668.

McCree KJ (1974) Changes in stomatal response characteristics of grain-sorghum produced by water stress during growth. *Crop Science* **14**, 273-278.

McMichael BL, Hesketh JD (1982) Field investigations of the response of cotton to water deficits. *Field Crops Research* **5**, 319-333.

McMichael BL, Powell RD, Jordan WR (1972) Effect of water stress on ethylene production by intact cotton petioles. *Plant Physiology* **49**, 658-660.

Medrano H, Escalona JM, Bota J, Gulias J, Flexas J (2002) Regulation of photosynthesis of C-3 plants in response to progressive drought: Stomatal conductance as a reference parameter. *Annals of Botany* **89**, 895-905.

Meyer VG (1969) Some effects of genes cytoplasm and environment on male sterility of cotton (*Gossypium*). *Crop Science* **9**, 237-242.

Monteith JL (1973) 'Principles of environmental physics.' (Edward Arnold: London).

Moreshet S, Cohen Y, Fuchs M (1979) Effect of increasing foliage reflectance on yield, growth and physiological behavior of a dryland cotton crop. *Crop Science* **19**, 863-868.

Mutsaers HJW (1984) KUTUN - A Morphogenetic model for cotton (*Gossypium hirsutum*-L). *Agricultural Systems* **14**, 229-257.

Neilsen KF (1974) Roots and root temperature. In 'The plant root and its environment'. (Ed. EW Carson) pp. 293-333. (University Press Virginia: Charlottesville, VA).

Nielsen DC (1990) Scheduling Irrigations for Soybeans with the Crop Water-Stress Index (Cwsi). *Field Crops Research* **23**, 103-116.

O'Toole JC, Turner NC, Namuco OP, Dingkuhn M, Gomez KA (1984) Comparison of some crop water-stress measurement methods. *Crop Science* **24**, 1121-1128.

Oliveira EC, Jr. (1982) Growth and adaption of cotton in the field under water deficit conditions. Ph.D. diss. University of California, Davis, USA.

Oosterhuis DM (1999) Yield response to environmental extremes in cotton. In 'Proceedings of the 1999 Cotton Research Meeting'. Memphis, TN. (Eds CP Dugger, DA Richter) pp. 30-38. (National Cotton Council of America).

Orgaz F, Mateos L, Fereres E (1992) Season length and cultivar determine the optimum evapotranspiration deficit in cotton. *Agronomy Journal* **84**, 700-706.

Oryokot JOE, Murphy SD, Thomas AG, Swanton CJ (1997) Temperature- and moisture-dependent models of seed germination and shoot elongation in green and redroot pigweed (*Amaranthus powellii*, A-retroflexus). *Weed Science* **45**, 488-496.

Pankovic D, Sakac Z, Kevresan S, Plesnicar M (1999) Acclimation to long-term water deficit in the leaves of two sunflower hybrids: photosynthesis, electron transport and carbon metabolism. *Journal of Experimental Botany* **50**, 127-138.

Passioura JB (1988) Response to Dr P. J. Kramer's article 'Changing concepts regarding plant water relations'. *Plant, Cell and Environment* **11**, 569- 571.

Paulsen GM (1994) High temperature responses of crop plants. In 'Physiology and determination of crop yield'. (Eds KJ Boote, JM Bennett, TR Sinclair, GM Paulsen) pp. 365-389. (American Society of Agronomy: Madison, WIS, USA).

Peeler TC, Naylor AW (1988) The influence of dark-adaptation temperature on the reappearance of variable fluorescence following illumination. *Plant Physiology* **86**, 152-154.

Perry SW, Krieg DR, Hutmacher RB (1983) Photosynthetic rate control in cotton - photo-respiration. *Plant Physiology* **73**, 662-665.

Pettigrew WT (2004a) Moisture deficit effects on cotton lint yield, yield components, and boll distribution. *Agronomy Journal* **96**, 377-383.

Pettigrew WT (2004b) Physiological consequences of moisture deficit stress in cotton. *Crop Science* **44**, 1265-1272.

Pinter PJ, Zipoli G, Reginato RJ, Jackson RD, Idso SB, Hohman JP (1990) Canopy temperature as an indicator of differential water-use and yield performance among wheat cultivars. *Agricultural Water Management* **18**, 35-48.

Place AR, Powers DA (1984) Purification and characterization of the lactate dehydrogenase (LDH-B₄) allozymes of *Fundulus heteroclitus*. *Journal of Biological Chemistry* **259**, 1299-1308.

Polley HW (2002) Implications of atmospheric and climatic change for crop yield and water use efficiency. *Crop Science* **42**, 131-140.

Powell RD (1969) Effect of temperature on boll set and development of *Gossypium hirsutum*. *Cotton Growing Review* **46**, 29-36.

Puech-Suanzes I, Hsiao TC, Fereres E, Henderson DW (1989) Water-stress effects on the carbon exchange-rates of 3 upland cotton (*Gossypium hirsutum*) cultivars in the field. *Field Crops Research* **21**, 239-255.

Purcell J (2006) Irrigation and farm design. In 'Applied Cotton Production'. (University of New England: Armidale).

Qiu GY, Omasa K, Sase S (2009) An infrared-based coefficient to screen plant environmental stress: concept, test and applications. *Functional Plant Biology* **36**, 990-997.

Radin JW, Lu ZM, Percy RG, Zeiger E (1994) Genetic-variability for stomatal conductance in pima cotton and its relation to improvements of heat adaption. *Proceedings of the National Academy of Sciences of the United States of America* **91**, 7217-7221.

Radin JW, Reaves LL, Mauney JR, French OF (1992) Yield enhancement in cotton by frequent irrigations during fruiting. *Agronomy Journal* **84**, 551-557.

Rashid A, Stark JC, Tanveer A, Mustafa T (1999) Use of canopy temperature measurements as a screening tool for drought tolerance in spring wheat. *Journal of Agronomy and Crop Science* **182**, 231-237.

Ray JD, Gesch RW, Sinclair TR, Allen LH (2002) The effect of vapor pressure deficit on maize transpiration response to a drying soil. *Plant and Soil* **239**, 113-121.

Ray LL, Wendt CW, Roark B, Quisenberry JE (1974) Genetic modification of cotton plants for more efficient water use. *Agricultural Meteorology* **14**, 31-38.

Reddy AR, Reddy KR, Hodges HF (1998) Interactive effects of elevated carbon dioxide and growth temperature on photosynthesis in cotton leaves. *Plant Growth Regulation* **26**, 33-40.

Reddy KR, Hodges HF, McKinion JM (1995a) Carbon-dioxide and temperature effects on pima cotton development. *Agronomy Journal* **87**, 820-826.

Reddy KR, Hodges HF, McKinion JM (1995b) Cotton crop responses to a changing environment. In 'Climate change and agriculture: Analysis of potential international impacts'. (Eds C Rosenzweig, JT Ritchie, JW Jones, GY Tsuji, P Hilderbrand) pp. 3-30. (ASA Publishing: Madison, WI).

Reddy KR, Hodges HF, McKinion JM (1997a) A comparison of scenarios for the effect of global climate change on cotton growth and yield. *Australian Journal of Plant Physiology* **24**, 707-713.

Reddy KR, Hodges HF, McKinion JM (1997b) Crop modeling and applications: A cotton example. *Advances in Agronomy* **59**, 225-290.

Reddy KR, Hodges HF, McKinion JM, Wall GW (1992a) Temperature effects on pima cotton growth and development. *Agronomy Journal* **84**, 237-243.

Reddy KR, Hodges HF, Reddy VR (1992b) Temperature effects on cotton fruit retention. *Agronomy Journal* **84**, 26-30.

Reddy KR, Kakani VG, Zhao D, Koti S, Gao W (2004) Interactive effects of ultraviolet-B radiation and temperature on cotton physiology, growth, development and hyperspectral reflectance. *Photochemistry and Photobiology* **79**, 416-427.

Reddy KR, Reddy VR, Hodges HF (1992c) Temperature effects on early season cotton growth and development. *Agronomy Journal* **84**, 229-237.

Reddy VR, Baker DN, Hodges HF (1991a) Temperature effects on cotton canopy growth, photosynthesis, and respiration. *Agronomy Journal* **83**, 699-704.

Reddy VR, Reddy KR, Baker DN (1991b) Temperature effect on growth and development of cotton during the fruiting period. *Agronomy Journal* **83**, 211-217.

Reid P (2001) Sicot 70. *Plant Varieties Journal* **14**, 35-36.

Reynolds MP, Balota M, Delgado MIB, Amani I, Fischer RA (1994) Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. *Australian Journal of Plant Physiology* **21**, 717-730.

Ritchie JT (1981) Water dynamics in the soil-plant-atmosphere system. *Plant and Soil* **58**, 81-96.

Roth GW (1993) Agronomic measurements to validate airborne video imagery for irrigated cotton management. Ph.D. diss. University of Canberra, Canberra, Australia.

Rourke J (2004) Drip irrigation: design, installation and management. In 'WATERpak: A guide for irrigation management in cotton'. (Eds H Dugdale, G Harris, J Neilsen, D Richards, G Roth, D Williams). (Cotton Research and Development Corporation: Narrabri, Australia).

Sadras VO, Milroy SP (1996) Soil-water thresholds for the responses of leaf expansion and gas exchange: A review. *Field Crops Research* **47**, 253-266.

Sailsbury FB, Ross CW (1992) 'Plant Physiology.' (Wadsworth Inc.: Belmont, CA, U.S.A.).

Saleem MB, Buxton DR (1976) Carbohydrate status of narrow row cotton as related to vegetative and fruit development. *Crop Science* **16**, 523-526.

Salvucci ME, Crafts-Brandner SJ (2004) Inhibition of photosynthesis by heat stress: the activation state of Rubisco as a limiting factor in photosynthesis. *Physiologia Plantarum* **120**, 179-186.

Saranga Y, Menz M, Jiang C-X, Robert JW, Yakir D, Andrew HP (2001) Genomic dissection of genotype X environment interactions conferring adaptation of cotton to arid conditions *Genome Research* **11**, 1988-1995.

Scholander PF, Hammel HT, Bradstre ED, Hemmings EA (1965) Sap pressure in vascular plants - Negative hydrostatic pressure can be measured in plants. *Science* **148**, 339-346.

Schrader SM, Wise RR, Wacholtz WF, Ort DR, Sharkey TD (2004) Thylakoid membrane responses to moderately high leaf temperature in Pima cotton. *Plant, Cell and Environment* **27**, 725-735.

Shae JB, Steele DD, Gregor BL (1999) Irrigation scheduling methods for potatoes in the northern great plains. *Transactions of the A.S.A.E.* **42**, 351-360.

Shangguan Z, Shao M, Dyckmans J (1999) Interaction of osmotic adjustment and photosynthesis in winter wheat under soil drought. *Journal of Plant Physiology* **154**, 753-758.

Sharkey TD, Seemann JR (1989) Mild water stress effects on carbon-reduction-cycle intermediates, ribulose biphosphate carboxylase activity, and spatial homogeneity of photosynthesis in intact leaves. *Plant Physiology* **89**, 1060-1065.

Shimshi D, Marani A (1971) Effects of soil moisture stress on 2 varieties of upland cotton in Israel. 2. Northern Negev region. *Experimental Agriculture* **7**, 225-239.

Sikka MA, Dastur RH (1960) Climate and soils. In 'Cotton in India: A monograph'. (Eds RH Dastur, RD Asana, K Sawhney, SM Sikka, RS Vasudev, Q Khan, VP Rao, BL Setti). (Indian Central Cotton Committee: India).

Simon JP, Potvin C, Strain BR (1984) Effects of temperature and CO₂ enrichment on kinetic properties of phosphoenolpyruvate carboxylase in two ecotypes of *Echinochloa crus-galli* (L.) Beauv., a C₄ weed grass species. *Oecologia* **63**, 145.

Sinclair TR (2005) Theoretical analysis of soil and plant traits influencing daily plant water flux on drying soils. *Agronomy Journal* **97**, 1148-1152.

Sinclair TR, Ludlow MM (1986) Influence of soil-water supply on the plant water-balance of four tropical grain legumes. *Australian Journal of Plant Physiology* **13**, 329-341.

Singh RP, Prasad PVV, Sunita K, Giri SN, Reddy KR (2007) Influence of high temperature and breeding for heat tolerance in cotton: A review. *Advances in Agronomy* **93**, 313-385.

Smith KA, Mullins C (2001) 'Soil and environmental analysis: physical methods.' (Marcel Decker: New York, USA).

Smith RB, Oster JD, Phene CJ (1991) Subsurface drip produced the highest net return in the Westlands study area. *California Agriculture* **45**, 8-10.

Somero GN, Low PS (1976) Temperature: a "shaping force" in protein evolution. *Biochemical Society Symposium*, 33-42.

Steiner JJ, Brewer TG, Griffith SM (2001) Temperature effects on interspecific interference among two native wetland grasses and tall fescue. *Agronomy Journal* **93**, 1020- 1027.

Stockton JR, Doneen LD, Walhood VT (1961) Boll shedding and growth of the cotton plant in relation to irrigation frequency. *Agronomy Journal* **53**, 272-275.

Sung FJM, Krieg DR (1979) Relative sensitivity of photosynthetic assimilation and translocation of C-14 to water-stress. *Plant Physiology* **64**, 852-856.

Suy TB (1979) Contribution to the study of the growth of pollen tubes in *Gossypium hirsutum* L. in accordance with environmental conditions. *Coton et Fibres Tropicales (Cotton Fibers Tropical- English translation)* **34**, 295-300.

Tanner CB (1963) Plant Temperatures. *Agronomy Journal* **55**, 210-211.

Teeri JA (1980) Adaptation of enzymes to temperature variability. In 'Adaptation of plants to water and high temperature stress'. (Eds NC Turner, PJ Kramer) pp. 251- 260. (John Wiley and Sons: New York).

Teeri JA, Peet MM (1978) Adaptation of Malate-Dehydrogenase to Environmental-Temperature Variability in 2 Populations of *Potentilla glandulosa*-Lindl. *Oecologia* **34**, 133-141.

Tennakoon SB, Milroy SP (2003) Crop water use and water use efficiency on irrigated cotton farms in Australia. *Agricultural Water Management* **61**, 179-194.

Terri JA, Peet MM (1978) Adaptation of Malate-Dehydrogenase to Environmental-Temperature Variability in 2 Populations of *Potentilla-Glandulosa-Lindl.* *Oecologia* **34**, 133-141.

Thomas JC, Brown KW, Jordan WR (1976) Stomatal response to leaf water potential as affected by preconditioning water stress in field. *Agronomy Journal* **68**, 706-708.

Turner NC (1979) Drought resistance and adaptation to water deficits in crop plants. In 'Stress physiology in crop plants'. (Eds H Mussell, RC Staples) pp. 343-372. (Wiley-Interscience: New York).

Turner NC (1986) Crop water deficits - A decade of progress. *Advances in Agronomy* **39**, 1-51.

Turner NC, Begg JE, Tonnet ML (1978) Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its influence on water potential at which stomata close. *Australian Journal of Plant Physiology* **5**, 597-608.

Turner NC, Hearn AB, Begg JE, Constable GA (1986) Cotton (*Gossypium hirsutum* L) - Physiological and morphological responses to water deficits and their relationship to yield. *Field Crops Research* **14**, 153-170.

Turner NC, Jones MM (1980) Turgor maintenance by osmotic adjustment: a review and evaluation. In 'Adapation of plants to water and high temperature stress'. (Eds NC Turner, PJ Kramer) pp. 87-103. (Wiley: New York).

Upchurch DR, Mahan JR (1988) Maintenance of constant leaf temperature by plants. 2. Experimental observations in cotton. *Environmental and Experimental Botany* **28**, 359-366.

Upchurch DR, Wanjura DF, Burke JJ, Mahan JR (1996) Biologically-identified optimal temperature interactive console (BIOTIC) for managing irrigation., U.S Patent No. 5,539,637.

von Caemmerer S, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* **153**, 376-387.

Wanjura DE, Upchurch DR (2002) Water status response of corn and cotton to altered irrigation. *Irrigation Science* **21**, 45- 55.

Wanjura DF, Buxton DR (1972) Water uptake and radicle emergence of cottonseed as affected by soil moisture and temperature. *Agronomy Journal* **64**, 427-431.

Wanjura DF, Upchurch DR, Hatfield JL, Burke JJ, Mahan JR (1988) Cotton irrigation using the "thermal kinetic window" criteria. In 'Beltwide Cotton Conference' pp. 183-185.

Wanjura DF, Upchurch DR, Mahan JR (1990) Evaluating Decision Criteria for Irrigation Scheduling of Cotton. *Transactions of the A.S.A.E.* **33**, 512-518.

Wanjura DF, Upchurch DR, Mahan JR (1992) Automated Irrigation Based on Threshold Canopy Temperature. *Transactions of the A.S.A.E.* **35**, 1411-1417.

Wanjura DF, Upchurch DR, Mahan JR (1995) Control of Irrigation Scheduling Using Temperature-Time Thresholds. *Transactions of the A.S.A.E.* **38**, 403-409.

Wanjura DF, Upchurch DR, Mahan JR (2004) Establishing differential irrigation levels using temperature-time thresholds. *Applied Engineering in Agriculture* **20**, 201-206.

Wanjura DF, Upchurch DR, Mahan JR (2006) Behavior of temperature-based water stress indicators in BIOTIC-controlled irrigation. *Irrigation Science* **24**, 223-232.

Wanjura DF, Upchurch DR, Mahan JR, Burke JJ (2002) Cotton yield and applied water relationships under drip irrigation. *Agricultural Water Management* **55**, 217-237.

Ward WT, McTainsh G, McGarry D, Smith KJ (1999) The soils of the agricultural research station at 'Myall Vale', near Narrabri, NSW, with data analysis by fuzzy k-means. CSIRO, Land and Water Report 21/99, Griffith University, Qld.

Weisz R, Kaminski J, Smilowitz Z (1994) Water-deficit effects on potato leaf growth and transpiration: Utilizing fraction extractable soil-water for comparison with other crops. *American Potato Journal* **71**, 829-840.

White SC, Raine SR (2009) Physiological response of cotton to a root zone soil moisture gradient: implications for Partial Root Zone Drying irrigation. *Journal of Cotton Science* **13**, 67-74.

Widmoser P (2010) An alternative to define canopy surface temperature bounds. *Agricultural Water Management* **97**, 224-230.

Wiegand CL, Namken LN (1966) Influences of plant moisture stress, solar radiation and air temperature on cotton leaf temperature. *Agronomy Journal* **58**, 582-586.

Wise RR, Frederick JR, Alm DM, Kramer DM, Hesketh JD, Crofts AR, Ort DR (1990) Investigation of the limitations to photosynthesis induced by leaf water deficit in field-grown sunflower (*Helianthus annuus* L.). *Plant, Cell and Environment* **13**, 923-931.

Writeability W (2006) Cotton Research and Development Corporation Annual Report 2005-06. Narrabri.

Yancey PH, Somero GN (1978) Temperature dependance of intracellular pH: Its role in the conservation of pyruvate apparent K_m values of vertebrate lactate dehydrogenase.

Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology **125**, 129-134.

Zeihner C, Matumba N, Brown P, Silvertooth J (1995) Response of upland cotton to elevated night temperatures. II. Results of controlled environment studies. In 'Beltwide Cotton Conference'. Memphis, TN. (Eds CP Dugger, DA Richter) pp. 1129-1130.