

## Lincoln University Digital Thesis

### Copyright Statement

The digital copy of this thesis is protected by the Copyright Act 1994 (New Zealand).

This thesis may be consulted by you, provided you comply with the provisions of the Act and the following conditions of use:

- you will use the copy only for the purposes of research or private study
- you will recognise the author's right to be identified as the author of the thesis and due acknowledgement will be made to the author where appropriate
- you will obtain the author's permission before publishing any material from the thesis.

# Understanding the growth and development of maize (*Zea mays* L.)

---

A thesis  
submitted in partial fulfilment  
of the requirements for the Degree of  
Doctor of Philosophy

at  
Lincoln University  
by  
Annette Mwayawa

---

Lincoln University

2023

## Abstract

Abstract of a thesis submitted in partial fulfilment of the requirements for the Degree of Doctor of Philosophy  
Understanding the growth and development of maize (*Zea mays* L.)

by

Annette Mwayawa

A main constraint to maize production in New Zealand is yield variability due to the low rainfall supply and also the erratic distribution of rain in the summer which consequently affects crop N uptake and utilization. The aim of this study was to understand the influence of N and water on canopy development, crop growth, phenological development and yield formation. Crops with different yield potentials were created using different levels of N and water availability. Two experiments were carried out, marking the growing season, Experiment 1 in 2015/16 and Experiment 2 in 2016/17. The two experiments were carried out at two different locations at Lincoln University, Canterbury, New Zealand. Experiment 1 was arranged in a split-plot design with four nitrogen (N) levels under different water regimes. The N levels were N1- nil, N2 -75 kg N/ha, N3 – 150 kg N/ha and N4 – 300 kg N/ha, and water levels at Irr1- Irr4 as defined by the accumulated potential soil moisture deficit as 443 (rainfed), 367, 301 and 226 mm, respectively. These created grain yields that were not different in all the treatments which averaged 12.4 t/ha and only varied in total dry matter (DM) accumulated. To create more distinct differences in grain yield, this experiment was repeated at another location with a higher dose of N. Experiment 2 used two levels of water and N in a randomised block design. The treatments were for N1 –nil N and N2 - 500 kg N/ha, rainfed and irrigation (accumulated potential soil moisture deficit at 536 and 296 mm respectively).

In Experiment 1, grain yield was not different across the crops and average 12.4 t/ha. The total DM was 19.1 t/ha for the rainfed crop (Irr1) and averaged 22.4 t/ha for the irrigated crops. Grain yield and total DM as explained by intercepted photosynthetic radiation (iPAR) accumulated to 570 MJ/m<sup>2</sup> for Irr1 and was higher at 1082 MJ/m<sup>2</sup> for Irr2. All crops GAI reached a maximum at 3.7 m<sup>2</sup>/m<sup>2</sup> at a rate of 0.01 m<sup>2</sup>/m<sup>2</sup>/°Cd in the duration of 677 °Cd which justified the similarities in grain yield. After the linear phase, the intercepted light in Irr1 immediately reached an asymptote as the leaves withered quickly due to water stress. The radiation use efficiency (RUE) was 2.21 g/MJ for N1 and 2.49 g/MJ for N4 and mainly because of the specific leaf N (SLN). The SLN was highest at 2.1 g N/m<sup>2</sup> for the irrigated crop with N and lower at 1.66 g N/m<sup>2</sup> without N. The contribution of SLN to yield was reflected in total DM.

In Experiment 2, grain yield increased progressively from 0.98 t/ha under rainfed to 9.0 t/ha when irrigated and further to 16.3 t/ha with N. Total DM followed a similar response with rainfed accumulating only 4.10 t/ha and 14.3 t/ha under irrigation and doubling with N, creating total DM of 28.9 t/ha. The difference in total DM was explained by the differences in the total amount of iPAR. Under rainfed the total iPAR was 448 MJ/m<sup>2</sup> and increased to 551 MJ/m<sup>2</sup> with N, and when irrigated was 816 MJ/m<sup>2</sup> and further increased to 1005 MJ/m<sup>2</sup> with N. The rate and duration changed, indicating the capacity of the crop to capture light depended on the changes in pigment protein complexes, directly linked to development of the GAI as a process of leaf development and expansion. The maximum GAI was affected by the main effects of water and N where GAI increased from 2.14 to 3.49 m<sup>2</sup>/m<sup>2</sup> with water and from 2.48 to 3.14 m<sup>2</sup>/m<sup>2</sup> with N application.

In the contribution of RUE to grain yield, SLN was a key factor connecting leaf N concentration to DM production. The SLN was 1.23 g N/m<sup>2</sup> at 905 °Cd in all the crops, however, dissecting the canopy into cohorts, SLN varied. The main section of the canopy that supplied assimilates directly to ear development was the mid-cohort. This cohort was affected by both water and N, increasing SLN from 1.43 to 2.39 g N/m<sup>2</sup> with water and from 1.46 to 2.37 g N/m<sup>2</sup> with N. The changes at cohort levels were explained by GAI as parameter relating to canopy development and the allocation of N within the leaf, and light penetration through the hierarchical canopy arrangement.

The amount of water used to produce the given yield in Experiment 2 depended on crop water use which was converted to WUE. Only the crop under irrigation and N was efficiently converting water to DM at 47 kg DM/mm of water. The WUE for the rainfed crops was 17.9 kg DM/mm and did not differ from the irrigated crop without N which had a WUE of 25.7 kg DM/ha/mm.

Leaf and canopy photosynthesis has led to improvements in crop DM and yield through enhanced DM partitioning. In depth understanding into elements of SLN is essential for estimation of the SLN throughout the cropping season. The future of crop improvement strategies is dependent on maximising the leaf and canopy photosynthesis and converting DM accumulation into yield benefits.

**Keywords:** Maize, water, nitrogen, yield formation, Light interception, LAI, RUE, SLN, photosynthesis, plant soil water availability, LL, DUL, crop water use efficiency, *Zea mays* L.

## Acknowledgements

Completing my PhD has been a monumental achievement for me. I have reached this milestone! All praise and honour back to the Heavenly Father for his knowledge, understanding and wisdom. I want to raise a toast to everyone who has been a part of this incredible journey with me.

First and foremost, I thank the New Zealand Aid Scholarships (under Ministry of Foreign Affairs and Trade) who funded most of the duration of my studies. I also thank the PNG Central Provincial Administration team for their financial support in my last year of the program.

I owe a tremendous debt of gratitude to my supervisors Professor Derrick Moot, who has been the key person in putting this thesis together. I would also like to thank Dr Alistair Black who has been instrumental towards the setting up and running of all field work. He set the scene, all the field work, the technical support and academic grounding. I feel incredibly fortunate to have had the guidance and mentorship of such highly respected academics. Their constant support, guidance, and encouragement have been invaluable throughout the entire process. From the initial stages of refining my research proposal to the final submission of my thesis, their unwavering presence and wealth of wisdom have been instrumental in shaping my academic growth. I highly valued the biweekly meetings we held, which not only served as crucial checkpoints to keep me on track academically, but also provided me with plenty of encouragement. I am profoundly grateful for the immeasurable contributions they made to my development.

A special appreciation goes to my colleagues and peers at the Field Research Centre. Special mention to Dr Anna Mills and Dr Keith Pullock (late) who have provided a lot of technical advice and input. Engaging in stimulating academic exchanges with all of you while maintaining a personal connection has been truly enriching.

Lastly, I want to express my deepest gratitude to my family, PNG friends, Lincoln Union Church friends especially Miriam Pascoe, Erica Clealand and Rev. Phyllis Harris, whose belief in my abilities supported me through many difficult times. Special mention to Hellen David Moe, Arulmageswaran Shampasivam, ThinzarSoe Myint and my partner, Tommy Gareitz for their endless support during my last year and toughest times in achieving this milestone. Your encouragement played an integral role in my accomplishments. To my sister Naomi, Dad, and daughter, Natalie and son, Nathan: thank you for everything, this is for you all!!

I dedicate this PhD thesis to my Late Mother, Mrs Marilyn Mwayawa.

# Table of Contents

<b>Abstract</b> .....	<b>ii</b>
<b>Acknowledgements</b> .....	<b>iv</b>
<b>Table of Contents</b> .....	<b>v</b>
<b>List of Tables</b> .....	<b>viii</b>
<b>List of Figures</b> .....	<b>xi</b>
<b>Chapter 1 Introduction</b> .....	<b>1</b>
1.1 Importance of maize production in New Zealand’s dairy industry.....	1
1.2 Optimising N use.....	2
1.3 Research aim and objectives .....	2
1.4 Thesis layout and structure.....	4
<b>Chapter 2 Literature review</b> .....	<b>6</b>
2.1 Introduction .....	6
2.1 The physiological basis of yield potential .....	6
2.2 Crop growth and development and influence of thermal time.....	7
2.2.1 Vegetative growth and development .....	7
2.2.2 Thermal time effect.....	10
2.3 Light interception and canopy development.....	11
2.3.1 Leaf area expansion .....	12
2.3.2 Leaf expansion and senescence.....	13
2.4 Radiation use efficiency (RUE) and nitrogen .....	14
2.4.1 Crop nitrogen status .....	15
2.4.2 Leaf nitrogen and photosynthesis.....	15
2.4.3 Specific leaf nitrogen (SLN) .....	16
2.4.4 Photosynthesis in maize as a C <sub>4</sub> crop and photosynthesis under elevated CO <sub>2</sub> .....	16
2.4.5 Photosynthesis and water use efficiency (WUE) .....	17
2.5 Crop harvest index (CHI) .....	17
2.6 Crop water stress .....	18
2.6.1 Radiation use efficiency (RUE) and water stress.....	18
2.6.2 Leaf and canopy expansion and water stress .....	19
2.6.3 Water extraction and use .....	19
2.6.4 Water use efficiency (WUE) .....	20
2.7 Conclusion.....	20
<b>Chapter 3 Materials and methods.</b> .....	<b>22</b>
3.1 Introduction .....	22
3.2 Experimental design and treatments.....	22
3.2.1 Experiment 1 .....	22
3.2.2 Experiment 2 .....	25
3.2.3 Maize hybrid .....	27
3.3 Measurements.....	27
3.3.1 Dry matter .....	27
3.3.2 Phenological development .....	28
3.3.3 Leaf area.....	28

3.3.4	Soil moisture measurement.....	28
3.3.5	Canopy light interception.....	29
3.4	Climate and weather data .....	29
3.5	Calculations.....	31
3.5.1	Thermal time.....	31
3.5.2	Dry matter .....	31
3.5.3	Soil water calculations .....	32
3.5.4	Statistical Analysis.....	35

**Chapter 4 Dry matter accumulation and yield formation in maize under different N and water levels. ....36**

4.1	Introduction .....	36
4.2	Materials and Methods.....	37
4.2.1	Calculation.....	37
4.3	Results.....	38
4.3.1	Experiment 1.....	38
4.3.2	Experiment 2 .....	53
4.4	Discussion.....	63
4.4.1	Experiment 1.....	63
4.4.2	Experiment 2 .....	67
4.5	Conclusion.....	71

**Chapter 5 Light interception and canopy development .....73**

5.1	Introduction .....	73
5.2	Materials and methods.....	74
5.2.1	Measurement.....	74
5.2.2	Calculations .....	74
5.3	Results.....	76
5.3.1	Experiment 1.....	76
5.3.2	Experiment 2 .....	82
5.4	Discussion.....	97
5.4.1	Experiment 1.....	97
5.4.2	Experiment 2 .....	99
5.5	Conclusion.....	103

**Chapter 6 Radiation use efficiency (RUE) and nitrogen (N) .....104**

6.1	Introduction .....	104
6.2	Materials and methods.....	105
6.2.1	Measurement.....	105
6.2.2	Calculations .....	105
6.3	Results.....	106
6.3.1	Experiment 1.....	106
6.3.2	Experiment 2 .....	114
6.4	Discussion.....	124
6.4.2	Experiment 2 .....	128
6.5	Conclusion.....	133

**Chapter 7 Plant water use and dry matter production .....134**

7.1	Introduction .....	134
7.2	Materials and methods.....	135
7.2.1	Drained upper limits (DUL) and lower limits (LL) .....	135
7.3	Calculations.....	135
7.3.1	The critical limiting deficit ( $D_L$ ).....	135
7.4	Results.....	136
7.4.1	Plant available water content (PAWC).....	136
7.4.2	Actual soil moisture deficit (ASMD) .....	137
7.4.3	Critical limiting deficit ( $D_L$ ) .....	138
7.4.4	Crop water use and water use efficiency (WUE) .....	140
7.5	Discussion.....	142
7.5.1	Plant available water content (PAWC).....	142
7.5.2	Actual soil moisture deficit (ASMD) and Critical limiting deficit ( $D_L$ ) .....	142
7.5.3	Crop water use and water use efficiency (WUE) .....	143
7.6	Conclusion.....	144
<b>Chapter 8 General discussions.....</b>		<b>145</b>
8.1	Introduction .....	145
8.2	Rationale .....	145
8.3	Comparison between cropping seasons.....	146
8.4	Dry matter accumulation and yield formation. ....	147
8.5	Light interception and canopy development.....	148
8.6	Radiation use efficiency and nitrogen .....	149
8.7	Water use and dry matter production.....	150
8.8	Recommendations .....	151
8.9	Conclusion.....	152
<b>Appendix A Information on Urea fertilizer application .....</b>		<b>153</b>
A.1	Experiment 1.....	153
A.2	Experiment 2.....	153
<b>Appendix B Table of co-efficients for radiation use efficiency (RUE) regression.....</b>		<b>154</b>
B.1	Experiment 1.....	154
B.2	Experiment 2.....	154
<b>Appendix C Plant available water content .....</b>		<b>155</b>
<b>Appendix D Temperature in the growing seasons .....</b>		<b>156</b>
<b>References .....</b>		<b>157</b>

## List of Tables

Table 3-1 Soil fertility and N test results for Experiment 1, H9 at Horticulture area, 2015 at Lincoln University, Canterbury, New Zealand. The recommended N rates for comparison were extracted from Evanylo and Alley (1997). .....	23
Table 3-2 Soil fertility and N test results for Experiment 2, Iv 9 field, 2016 at Lincoln University, Canterbury, New Zealand. ....	26
Table 3-3 Temperature (°C) data obtained from Broadfields Meteorological Station showing the mean, minimum and maximum temperatures for 2015 to 2017, and long-term means (LTM) for 1999 to 2014 for Lincoln, Canterbury, New Zealand.....	30
Table 4-1 Grain yield, total dry matter (DM), and the crop harvest index (CHI) at harvest for maize in response to four N levels (0, 75, 150 and 300 kg N/ha) at each of the four water levels (Irr1 - 4) for the final harvest of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	39
Table 4-2 Total kernel dry weight per plant, individual kernel dry weight and total number grains per ear of maize in response to four N levels (0,75, 150, 300 Kg N/ha) at each of the four water levels (Irr1 - 4) for the final harvest of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	40
Table 4-3 The duration and rate of growth, and the final total dry matter (DM) accumulation for maize crops grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water regimes (Irr1 – 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	43
Table 4-4 The duration, rate and final ear dry matter (DM) accumulated for maize crop grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water regimes (Irr1 – 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	45
Table 4-5 Leaf dry matter accumulation duration and rate effect on final dry matter (DM) obtained for maize crop grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water regimes (Irr1 – 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	47
Table 4-6 The duration, rate and final stalk dry matter (DM) accumulation pattern for stalk DM for maize crop grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water regimes (Irr1 - 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	49
Table 4-7 Dry matter contribution from leaf and stalk dry matter (DM) remobilisation (t/ha) for maize crop grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water levels (Irr1 – 4) regimes in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	50
Table 4-8 Dry matter (DM) contribution from post-silking DM accumulation (t/ha) towards grain-filling for maize crop grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water levels (Irr1 – 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	51
Table 4-9 The ear partitioning rate and total dry matter (DM) at start of ear development for maize crops grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water levels (Irr1 – 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	53
Table 4-10 Grain yield, total dry matter (DM) and the crop harvest index (CHI) for maize in response to two N levels (0 and 500 kg N/ha) at water levels (rainfed and irrigated) for the final harvest of 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	54
Table 4-11 Number and dry weight of kernels, and individual grain dry weight for maize in response to two N levels (0 and 500 kg N/ha) at each of the two water levels (rainfed and irrigated) for the final harvest of 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	55
Table 4-12 The duration, rate and final dry matter (DM) for the pattern of total DM obtained for maize in response to two water levels (rainfed and irrigated) for each of the two N levels (0 and 500 kg N/ha) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	57
Table 4-13 The pattern of ear dry matter (DM) as quantified in duration, rate and final DM for maize in response to two N levels (0 and 500 kg N/ha) for each of the two water levels (rainfed and irrigated) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	58
Table 4-14 The rate, duration and final dry matter (DM) for the pattern of leaf DM accumulation for maize in response to two N levels (0 and 500 kg N/ha) for each of the two water levels (rain fed and irrigated) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	59
Table 4-15 Duration, rate and the final stalk dry matter (DM) accumulation for maize in response to two N levels (0 and 500 kg N/ha) for each of the two water levels (rainfed and irrigated) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	60
Table 4-16 Leaf, stalk and total dry matter (DM) remobilised for maize in response to two N levels (0 and 500 kg N/ha) for each of the two water levels (rainfed and irrigated) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	61

Table 4-17 Total dry matter (DM) (t/ha) production from post-silking current photosynthesis towards grain-filling for maize in response to two N levels (0 and 500 kg N/ha) for each of the two water levels (rainfed and irrigated) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.....	61
Table 4-18 The growth rate and total dry matter (DM) at start of ear development for maize grown at two N levels (at nil and 500 kg N/ha) and two levels of N (rainfed and irrigated) in 2015/16 at Lincoln University, Canterbury, New Zealand. ....	63
Table 5-1 The total intercepted PAR (MJ/m <sup>2</sup> ), rate of interception (MJ/m <sup>2</sup> /°Cd) and duration (°Cd) at initial PAR interception process for maize in response to nil N and 300 kg N/ha at Irr1 and Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	77
Table 5-2 Rate of linear increase in GAI, duration to reach critical GAI, duration of GAI above the critical GAI in thermal time and rate of linear increase in GAI for maize in response to two N levels (urea at 0 and 300 kg N/ha) for rainfed crops (Irr1) and irrigated crops (Irr4) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	80
Table 5-3 The total intercepted PAR (MJ/m <sup>2</sup> ), rate of interception (MJ/m <sup>2</sup> /°Cd) and duration of linear phase (°Cd) at initial PAR interception process for maize in response to two N levels (nil and 500 kg N/ha) for each of two water levels (rain fed and irrigated) for the final harvest of 2016/17 (Experiment 2) at Lincoln University. ....	83
Table 5-4 The maximum green area index (GAI), rate of linear increase in GAI, duration to reach maximum GAI, duration of maintaining GAI at and above the maximum GAI level in thermal time and rate of linear increase GAI for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	88
Table 5-5 The total and maximum leaf area per plant at each cohort in cm <sup>2</sup> /plant for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	90
Table 5-6 Duration of green area holding phase (°Cd) for the leaf area of lower, mid and upper canopy in °Cd for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	91
Table 5-7 The rate of linear decline in leaf area in cm <sup>2</sup> /°Cd for the three canopy cohorts (lower, mid and lower) for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	92
Table 5-8 The interval between leaf tips during Stage 1 (528 °Cd) and Stage 2 (528 -690 °Cd), the number of leaf tips at point of inflection, and total number of leaf tips per plant for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	94
Table 5-9 The phyllochron for expanded leaves during Stage 1 (498/597 °Cd) and Stage 2 (498/597 - 762 °Cd), the number of expanded leaves at point of inflection, and total number of expanded leaves per plant for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	96
Table 6-1 Radiation use efficiency (g/MJ iPAR) for maize in response to nil N and 300 kg N/ha under rainfed (Irr1) and irrigation (Irr4) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	107
Table 6-2 Total crop, leaf, kernel and stalk N (kg/ha) at early silking (679 °Cd) for maize in response to nil N and 300 kg N/ha under rainfed (Irr1) and under irrigation (Irr4) in 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	109
Table 6-3 Total crop, leaf, kernel and stalk N content (kg/ha) during grain-filling (1400 °Cd) for maize in response to nil N and 300 kg N/ha at Irr1 and Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	110
Table 6-4 Total crop, leaf, kernel and stalk N content (kg/ha) at crop maturity (1541 °Cd) for maize in response to nil N and 300 kg N/ha at Irr1 and Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	111
Table 6-5 Specific leaf nitrogen (SLN) (g/m <sup>2</sup> ) for post-silking samples at 679, 1400, 1541 °Cd for maize in response to nil N and 300 kg N/ha at Irr1 and Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	113
Table 6-6 Radiation use efficiency (g/MJ iPAR) for maize in response to two N levels (nil and 500 kg N/ha) for each of two water levels (rain fed and irrigated) when grown in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	115
Table 6-7 Total crop, leaf, kernel and stalk N (kg/ha) at late silking (905 °Cd) for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops in 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand. ....	116

Table 6-8 Total crop, leaf, kernel and stalk N (kg/ha) during grain-filling (1308 °Cd) for maize grown at two N levels (nil and 500 kg N/ha) either rainfed or irrigated in 2016/17 (Experiment 2) at Lincoln University, Canterbury New Zealand. ....	117
Table 6-9 Total crop, leaf, kernel and stalk N (kg/ha) at physiological maturity (1448 °Cd) for maize grown at two N levels (nil and 500 kg N/ha) and either rainfed or irrigated in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	118
Table 6-10 Specific leaf nitrogen (g N/m <sup>2</sup> ) around late silking stage (905 °Cd) for maize grown at two N levels (nil and 500 kg N/ha) and either rainfed or irrigated in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	120
Table 6-11 Specific leaf nitrogen (g N/m <sup>2</sup> ) during grain-filling (1308 °Cd) for maize grown at two N levels (nil and 500 kg N/ha) either rainfed or irrigated in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	121
Table 6-12 Specific leaf nitrogen (g N/m <sup>2</sup> ) around physiological maturity (1448 °Cd) for maize grown at two N levels (nil and 500 kg N/ha) either rainfed or irrigated in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	122
Table 7-1 Mean of the plant available water content (mm) to 1.5 m soil depth for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops in 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand. ....	136
Table 7-2 The maximum soil moisture deficit (mm) measured during the growing season for maize in response to two N levels (0 and 500 kg N/ha) for rainfed and irrigated crops in 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand. ....	138
Table 7-3 Total water use (mm) for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops in 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand. ....	140
Table 7-4 Water use efficiency (DM/mm) for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops in 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand. ....	141
Table 8-1 The accumulated number of days, degree day (°Cd), total intercepted photosynthetic active radiation (iPAR) and dry matter (DM) from emergence to silking for cropping season 2015/16 (Experiment 1) and 2016/17 (Experiment 2). ....	146
Table 8-2 Accumulated number of days, degree day (°Cd), total intercepted photosynthetic active radiation (iPAR), dry matter (DM), and from silking to crop maturity for cropping season 2015/16 (Experiment 1) and 2016/17 (Experiment 2). ....	147

## List of Figures

Figure 1-1 Schematic diagram of the thesis structure. ....	5
Figure 3-1 Total monthly total incident solar radiation data obtained from Broadfields meteorological station showing the totals for Experiment 1 from November 2015 to May 2016 (grey bar), Experiment 2 from November 2016 to May 2017 (striped bar) and long term means (LTM) (solid line) for 1999 to 2014 for Lincoln, Canterbury, New Zealand. ....	30
Figure 3-2 Soil water budget for maize crops in Experiment 1 for the growing season of 2015/16 at Lincoln University, New Zealand. Soil moisture deficit is represented by the line graph above the graph (Irr1 (—), Irr2 (.....), Irr3 (---), Irr4 (----), accumulated total Penman evapotranspiration shown in line graph (—), irrigation shown as shaded bar graph Irr2 (■), Irr3 (■) and Irr4 (■)) and unshaded bars indicate weekly rainfall. ....	34
Figure 3-3 Soil water budget for maize crops grown in Experiment 2 for the growing season of 2016/17 at Lincoln University, New Zealand. Soil moisture deficit is represented by the line graph above: Rainfed (—), irrigated (—), total Penman evapotranspiration (---), irrigation shown as shaded bars and rainfall as unshaded bars. ....	35
Figure 4-1 Total dry matter (DM) accumulation for maize in response to four N levels (0, 75,150, 300 kg N/ha) at each of four water levels (Irr1 (a), Irr2 (b), Irr3 (c) and Irr4 (d)) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Dotted line indicates silking at 790 °Cd. Error bars indicate the standard deviation of the mean across the points. ....	42
Figure 4-2 Ear dry matter (DM) accumulated against thermal time for maize in response to four N levels (0, 75,150, 300 kg N/ha) at each of four water levels (Irr1 (a), Irr2 (b), Irr3 (c) and Irr4 (d)) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard deviation of the mean across the points. ....	44
Figure 4-3 Leaf dry matter (DM) accumulation against thermal time for maize in response to four N levels (0, 75,150, 300 kg N/ha) at each of four water levels (Irr1 (a), Irr2 (b), Irr3 (c) and Irr4 (d)) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	46
Figure 4-4 The pattern of stalk dry matter (DM) accumulation against thermal time for maize in response to four N levels (0, 75,150, 300 kg N/ha) at each of four water levels (Irr1 (a), Irr2 (b), Irr3 (c) and Irr4 (d)) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	48
Figure 4-5 Ear dry matter against total dry matter (DM) for maize in response to four N levels (0, 75,150, 300 kg N/ha) at each of four water levels (Irr1 (a), Irr2 (b), Irr3 (c) and Irr4 (d)) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. ....	52
Figure 4-6 Dry matter (DM) accumulation of total (a), ear (b), stalk (c) and leaf (d) dry matter of maize in response to two N levels (0 and 500 kg N/ha) at each of two water levels (rainfed (●,○ (nil 500 kg N/ha N)) and irrigated (▲, △ (nil and 500 kg N/ha)) for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard error. ....	56
Figure 4-7 Total ear dry matter (DM) against total DM increase during grain-filling for crops grown under two N levels (nil and 500 kg N/ha) at each of two water levels ((a) rainfed (●,○) and (b) irrigation (▲, △)) for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	62
Figure 5-1 Total intercepted PAR (MJ/m <sup>2</sup> ) against the thermal time for maize to nil N (●) and 300 kg N/ha (○) under Irr1 and nil N (▲) and 300 kg N/ha (△) under Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard error of the mean across the points. ....	76
Figure 5-2 Natural log of R/R <sub>0</sub> versus green area index (GAI) measuring light attenuation through the maize canopy in response to two N levels of urea at 0 and 300 kg N/ha for each of two water levels, Irr1 (0 (●) and 300 kg N/ha (○)) and Irr4 (0 (▲) and 300 kg N/ha (△)) for the sampling dates of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. The solid lines represent linear regression at $y=0.838x$ (●&○) and $y=0.871x$ (▲&△). ....	78
Figure 5-3 Fraction of light intercepted versus green area index (GAI) for maize in response to nil N (●) and 300 kg N/ha (○) under Irr1 and nil N (▲) and 300 kg N/ha (△) under Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. The solid lines represent exponential curves at $y=1-\exp -0.84 *LAI$ (●&○) and $y=1-\exp -0.87 *LAI$ (▲&△). The dotted lines indicate 95% light interception when the critical LAI is at 3.5 and 3.6. ....	79
Figure 5-4 Leaf area development per plant in thermal time for maize in response to nil N (●) and 300 kg N/ha (○) under Irr1 and nil N (▲) and 300 kg N/ha (△) under Irr4 for the sampling dates of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bars represent standard deviation of the means of the leaf area at each harvest date. ....	81

Figure 5-5 Total accumulated PAR (MJ/m <sup>2</sup> ) against thermal time for maize in response to two N levels ((○, ▲) and 500 kg N/ha (○,△)) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bar indicate the standard error of the means. ....	82
Figure 5-6 The linear relationship between the natural log of R/R <sub>0</sub> and the GAI from the destructive harvest for maize in response to two N levels at 0 and 500 kg N/ha for each of two water levels (rainfed (●,○) and irrigated (▲,△)) for the sampling dates of 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	84
Figure 5-7 The fraction of light intercepted versus green area index (GAI) for maize in response to two N levels at nil and 500 kg N/ha for each of two water levels, nil irrigation (nil (●) and 500 kg N/ha (○)) and irrigated crop (nil (▲) and 500 kg N/ha (△)) for the sampling dates of 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. The solid lines represent exponential curves at $y=1-\exp^{-0.75 \cdot LAI}$ . The dotted lines indicate the critical LAI at 4.0. ....	85
Figure 5-8 Green area index (GAI) versus accumulated thermal time (°Cd) for maize in response to nil N (●) and 300 kg N/ha (○) under Irr1 and nil N (▲) and 300 kg N/ha (△) under Irr4 for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	87
Figure 5-9 Leaf area per plant versus thermal time for the three cohorts: the lower (a), mid (b) and top (c) leaf layers for maize in response to nil N (●) and 500 kg N/ha (○) under rainfed and nil N (▲) and 500 kg (△) with irrigation for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....	89
Figure 5-10 Number of visible leaf tips versus thermal time for maize in response to two N levels ((●) and 500 kg N/ha (○)) for rainfed and irrigated crops (nil N (▲) and 500 kg N/ha (△)) for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. The first linear phase indicating the phyllochron at Stage 1 and the later indicating the phyllochron at Stage 2.....	93
Figure 5-11 Number of fully expanded leaves versus thermal time for maize in response to two N levels (urea at 0 (●) and 500 kg N/ha (○)) for rainfed and irrigated crops (nil N (▲) and 500 kg N/ha (△)) for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. The first linear phase determines the phyllochron for Stage 1 and the later for the phyllochron at Stage 2. ....	95
Figure 6-1 Total crop dry matter (g/m <sup>2</sup> ) against intercepted PAR (MJ/m <sup>2</sup> ) for maize in response to nil N (●) and 300 kg N/ha (○) under rainfed (Irr1) and nil N (▲) and 300 kg N/ha (△) under irrigation (Irr4) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bar indicates the standard error. ....	106
Figure 6-2 Crop N content against thermal time for the total crop (a), kernel (b), stalk (c) and leaf (d) for maize in response to nil N (●) and 300 kg N/ha (○) under rainfed (Irr1) and nil N (▲) and 300 kg N/ha (△) under irrigation (Irr4) for three silking/post-silking sampling dates of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bars represent standard error of the means at each harvest date.....	108
Figure 6-3 Specific leaf nitrogen against thermal time for silking/post-silking sampling dates for maize in response to nil N (●) and 300 kg N/ha (○) under rainfed (Irr1) and nil N (▲) and 300 kg N/ha (△) under irrigation (Irr4) for three silking/post-silking sampling dates of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bars represent standard error of the means of the SLN at each harvest date. ....	112
Figure 6-4 Total crop dry matter against (g/m <sup>2</sup> ) against total PAR intercepted (MJ/m <sup>2</sup> ) for maize in response to nil N (●) and 500 kg N/ha (○) under rainfed and nil N (▲) and 500 kg N/ha (△) with irrigation for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bar indicates the standard error. ....	114
Figure 6-5 Crop N against thermal time for the total crop (a), kernel (b), stalk (c) and leaf (d) for maize in response to nil N (●) and 500 kg N/ha (○) under rainfed and nil N (▲) and 500 kg (△) with irrigation for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard error of the means.....	115
Figure 6-6 SLN against thermal time for post-silking sampling points for maize in response to nil N (●) and 500 kg N/ha (○) under rainfed and nil N (▲) and 500 (△) kg N/ha with irrigation for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard error of the means. ....	119
Figure 6-7 Leaf number/position versus size for different maize canopy structure in response to nil N (unshaded bar) and 500 kg N/ha (shaded bar) under rainfed (a) and nil N (unshaded) and 500 (shaded) kg N/ha with irrigation (b) for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard error of the means. ....	123
Figure 7-1 The LL (○) and DUL (●) of the available soil water content (mean of plots) for rainfed maize in response to nil N and 500 kg N/ha for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.....	136

- Figure 7-2 Actual soil moisture deficit (ASMD) (mm) from 0.0 - 1.5 m soil depth against accumulated thermal time for maize in response to nil N (●) and 500 kg N/ha (○) under rainfed and nil N (▲) and 500 (△) kg N/ha with irrigation for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Dotted lines indicate the  $D_L$  for yield at 100 mm without N and 77 mm with 500 kg N/ha. Error bars indicate the standard error of the means.....137
- Figure 7-3 Decrease in relative GAI of (a) irrigation without N (▲) relative to rainfed without N (●) and (b) irrigation with 500 kg N/ha (△) relative to rainfed with 500 kg N/ha (○) for maize during 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. ....138
- Figure 7-4 Decrease in relative yield of (a) irrigation without N (▲) relative to rainfed without N (●) and (b) irrigation with 500 kg N/ha (△) relative to rainfed with 500 kg N/ha (○) for maize during 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Dotted lines indicate slope and DL for under rainfed and solid lines are under irrigated conditions. ....139
- Figure 7-5 Accumulated DM yield (kg DM/ha) against cumulative annual water use (mm) for maize in response to nil N (●) and 500 kg N/ha (○) under rainfed and nil N (▲) and 500 (△) kg N/ha with irrigation for 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand. Error bar indicates the standard error. ....141

# Chapter 1

## Introduction

### 1.1 Importance of maize production in New Zealand's dairy industry

Maize (*Zea mays* L.) is used for forage, silage and grain for supplementary feed in the New Zealand Dairy Industry. The Dairy Industry uses around 99% of the country's maize production for as silage (Booker, 2009). Maize provides a feed source that maintains high-quality and the quantity of milk production to overcome any shortfall in the main pasture species of perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.). The shortfalls in feed availability occur due to cold temperatures in spring and during periods of lower than expected rainfall in summer/autumn. It may also be used in the cold winter season but feed deficits at this time may also be filled by specialist forage crops including, brassicas, annual ryegrasses (*L. multiflorum* L.), cereals and lucerne (*Medicago sativa* L.) baleage. These forage crops are grazed *in situ* or as conserved hay or ensiled (Valentine and Kemp, 2007) to support year round outside grazing of livestock. Even so, maize feed is one of the supplementary forage options that compliment pasture intake for the dairy industry.

The production area for maize has been estimated at 71,000 ha (Arable Industry Marketing Initiative, 2018). Maize silage yields have improved over the years at rate of 1.7 t/ha in every 10 year period (Morris et al., 2016). This has supported herd numbers which have observed dairy cattle numbers more than doubled from 2.44 million to nearly 5 million between 1990 and 2015 (Ma et al., 2019). For maize production to continue to meet this demand, improved selection of introduced hybrids and agronomic practices are key areas of emphasis (Stone et al., 1997).

Yield variability can be related to environmental factors, particularly in the temperate conditions of New Zealand. The duration of growth is limited by the cool conditions in spring which lower the soil temperature and delay the planting to avoid the risk of late frosts, while early autumn frosts may reduce yields at the other end of the season (Fletcher et al., 2008; Wilson et al., 1994 ). Recurrent and variable drought is the main factor contributing to the seasonal fluctuations in grain yields. Summer droughts are common throughout the cereal-growing region (Jamieson et al., 1995b). Soil moisture under these dry conditions also affects crop responses to N uptake from the soil and remobilisation thus resulting in inconsistent plant response and variability in productivity (Stone et al., 2001; Wang et al., 2017). Attaining consistent high yields to improve maize nutritive quality requires understanding the factors that cause yield variability and their influence on the yield formation processes.

## 1.2 Optimising N use

Nitrogen is a limiting nutrient in the production of many cereals, including maize. The intensification of production has correspondingly led to an increase in the application levels of N over the years (Ciampitti and Vyn, 2012). The main environmental concern is N leaching as the projected contribution to nitrogen leaching losses from nitrogen fertilisers in New Zealand witnessed an increase from 10% to 18% of the overall N losses during the period spanning from 1990 to 2012 (Tsimba et al., 2020). Maize crops are grown to effectively absorb and utilise N from soils that have received excessive effluent (Stevenson et al., 2022).

Attaining consistent high yields and improved maize nutritive quality requires an ample amount of N. Therefore, understanding the physiological mechanism and processes of the contribution of N to yield formation is essential to the proper use of N in maximising yield. Photosynthesis serves as a significant contributor to the production of DM, a crucial factor directly associated with the formation of grain yield (Li et al., 2021). The relationship between photosynthetic characteristics and N and time is evident, as N has a direct impact on both the leaf area index (LAI) and chlorophyll levels (El Hallof and Sárvári, 2006). In well-watered maize crops, N from SLN is diluted and photosynthesis decreases, however when there is N deficiency is severe enough, leaf area will decrease (Lemaire et al., 2008). An increased supply of N enhances chlorophyll content, thus increasing supply of photoassimilates, which in turn results in higher growth rates and yield (Bassi et al., 2018). Moreover, N is needed for the synthesis of enzymes, structures, and regulatory proteins that are essential for the process of photosynthesis and various other metabolic activities (Zhang et al., 2020). Increased N availability results in higher net photosynthetic rate and consequently higher maize dry weight (Uribelarrea et al., 2009). In order to effectively meet the crop's N needs and guarantee a satisfying yield at the agronomic maximum, N rate and timing of application are important (Stevens et al., 2005). A thorough understanding of crop and leaf N dynamics is essential to maximise N allocation into photosynthesis, and how this process affects total DM and the yield formation process.

## 1.3 Research aim and objectives

The aim of this thesis is to understand the influence of N and water on canopy development and how it affects crop growth and development into the yield formation processes. The maize crop strategy of N allocation in the leaf is explored as is the utilisation of N for photosynthesis and ultimately RUE verses leaf area expansion and light interception.

The objectives are as follows:

1. Create crops with different yield potential with different levels of N and water availability at vegetative, silking and grain-filling stages, and use these to explain yield formation as shown by the total DM accumulation and partitioning.
2. Quantify yield differences in relation to total intercepted photosynthetically active radiation (iPAR) and its effects on yield formation (i.e at silking and grain filling) and describe the development of crop canopies that contribute to different DM accumulation patterns.
3. Quantify the N dynamics at the turnover of vegetative stage, N for kernel development and grain-filling, and N retention at leaf senescence stage for crops with these different yield scenarios.
4. Explain the impact of crop water use on canopy expansion growth and the different yield scenarios.
5. To make recommendations for management and use of N and water for optimum yield and make suggestions for crop modelling purposes.

## 1.4 Thesis layout and structure

This thesis is written in eight chapters (Figure 1-1). This first chapter is the general introduction which provides context to the study and outlines our understanding of yield formation as affected by N allocation in maize. It also gives an overview of the study and outlines the layout of the thesis.

Chapter 2 is a literature review that draws understanding on the physiology of yield as linked to the known process of crop growth and development. This chapter examines the relationship between iPAR, canopy expansion and DM accumulation and more importantly the formation of yield. It discusses temperature, light, N and water as the fundamental basis of determining DM accumulation and partitioning.

Chapter 3 describes the materials and methods, including the techniques and instruments used, the site and the overall experiments. Specifically, there were two experiments: Experiment 1 had four levels of water and N, and Experiment 2 focused on the extreme treatments i.e., with and without water and N. The aim of the experiments was to generate crops with a wide range of maize yields. Understanding how those yield differences were created is then explored based on the physiological processes (Equation 2-1). The main results are provided in Chapter 4, in which DM accumulation and yield are described. The following results chapters (Chapter 5 to 7) then aim to describe and explain the physiological mechanisms behind the yield differences.

Chapter 5 concentrates on the assimilate supply/DM accumulation with relation to kernel sink requirement. The process of DM production is the essence of this chapter. Specifically, it concentrates on canopy development and leaf expansion, and light interception. These aspects are central to the initial and the final processes of yield formation.

The intermediate processes of N and water function in kernel development and their role in the overall canopy development processes are examined in Chapters 6 and 7. These aim to show how the different yield results from Chapter 4 are caused by changes in N uptake and remobilisation and how this was affected by crop water use.

Finally, Chapter 8 is the general discussion which combines all the results draw conclusions. This chapter relates the physiological processes to management inputs for improved agronomic strategies and recommendations for crop modelling purposes.

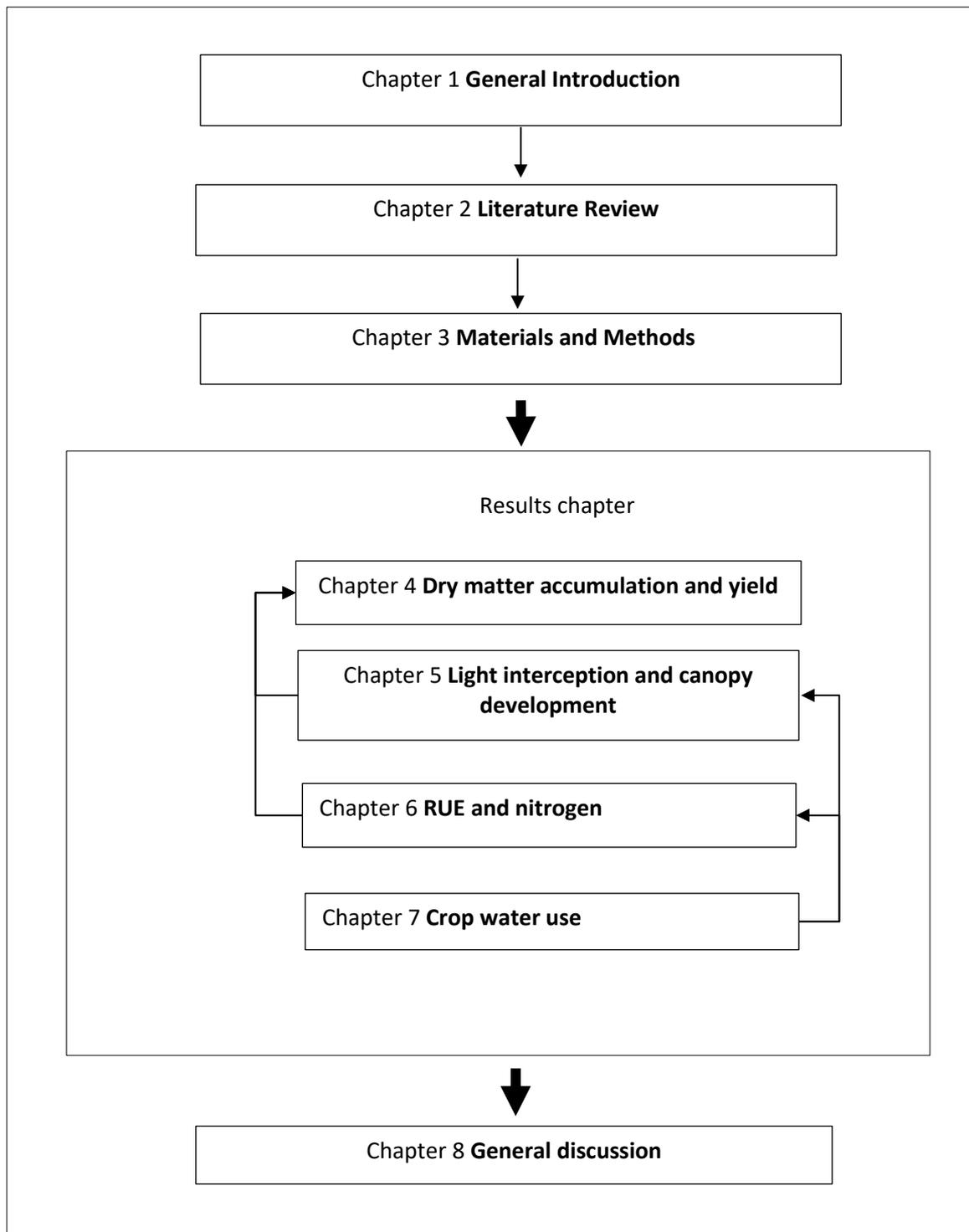


Figure 1-1 Schematic diagram of the thesis structure.

## Chapter 2

### Literature review

#### 2.1 Introduction

This literature review focuses on the effect of N on canopy development and its influence on yield. Maize canopy development is a critical aspect of maize growth and productivity and plays a crucial role in intercepting solar radiation and photosynthesis. Understanding the key biophysical factors that influence canopy development and factors attributed to yield formation is essential to addressing yield variability in the production of maize. The literature reviewed in this chapter is focused on the mechanisms and factors that contribute to maize yield formation. It emphasizes on crop, canopy and leaf N dynamics and the partitioning of N within the leaf in the canopy as affected by water and N inputs.

#### 2.1 The physiological basis of yield potential

An understanding of resource capture and efficiency can be explained by its influence on crop physiological characteristics. The concept of light interception is the key aspect of the yield formation process. It is facilitated by crop growth and development which are dependent on resource capture and efficiency. Crop yield and its component parameters are primarily determined by radiation conditions and a collection of environmentally induced variables (Hay and Porter, 2006).

Yield is represented by the equation from Monteith (1977);

$$\text{Equation 2-1} \quad Y = Q * RI * RUE * CHI$$

The yield determinants are identified in the equation where Y is the yield, Q is the total quantity of solar radiation received in the growing season ( $\text{MJ}/\text{m}^2$ ), RI is the fraction of light intercepted by the crop (iPAR); RUE ( $\text{g}/\text{MJ}$ ) is the radiation use efficiency of the crop which is the conversion of intercepted radiation into biomass and CHI is the harvest index, indicating the efficiency of partitioned biomass into grain yield.

The availability of N and water are essential parts of light interception and RUE in their function in canopy development and photosynthesis. Hence, yield potentials are recognised in the absence of stress caused by water, nutrients and biotic factors, allowing DM yield to be dependent on the capacity of the crop to intercept light.

## **2.2 Crop growth and development and influence of thermal time**

### **2.2.1 Vegetative growth and development**

Phenological development refers to the process of initiating, differentiating, expanding, and ultimately losing plant structures (Bonhomme, 2000; Hay and Porter, 2006). It comprises of a series of distinct stages, each lasting a specific period of time (Thornley and France, 2007), and is influenced by both genotype and environment (Birch et al., 2003). Growth, on the other hand, is defined as a permanent increase in plant dry weight (Hunt, 1982; Richards, 1969), and it is intricately associated with the process of development. Nevertheless, plant development can happen irrespective of growth (Angus et al., 1980; Hay and Porter, 2006). However, it is important to highlight that growth is optimised when the plant intercepts the most amount of radiation throughout each phase of development, assuming that temperatures remain over a certain threshold ( $T_b$ ) (Angus et al., 1980; Stone et al., 1999).

The life cycle of maize may be categorised into two distinct phases: the vegetative phase, which covers from emergence to flag leaf appearance, and the reproductive phase, which extends from silking to physiological maturity (Nleya et al., 2016). The vegetative development phase occurring between emergence (VE) and tasseling (VT) are often determined by the count of visible leaf collars, sometimes referred to as V stages. The phase occurring between the V6 stage, characterised by the presence of six leaves with visible collars, and the VT stage, marked by the emergence of the tassel, is often denoted as the time of accelerated growth. At VT, the plant has attained its maximum vertical extent, and all foliage is visible. The impact of water stress on crop yield is relatively minimal during the V4 to V5 growth stages, assuming the plants are able to survive. However, as the plants reach the V6 stage and begin to develop tassels and ears, water stress can lead to more significant damage compared to the seedling stage. Furthermore, the severity of damage increases as the occurrence of water stress approaches the tasseling period (Edwards, 2009).

#### **Emergence and germination**

The anatomical examination demonstrated that desiccated dry maize seed encompasses four to five embryonic leaves at various stages of development (Liu et al., 2013). The process of germination starts being imbibed by the seed (Brito et al., 2015). The presence of water is crucial for cellular metabolism during the process of germination. It plays a significant role in several internal mechanisms within the seed, such as the activation of enzymes and the dissolution and transportation of reserve chemicals. The utilisation of accumulated reserves occurs subsequent to seed hydration, namely during the second stage of germination, which initiates heightened

metabolic processes, including respiration and alterations in the composition of proteins, lipids, and carbohydrates (Ali and Elozeiri, 2017; Han et al., 2013).

The majority of stored chemicals are used during the latter stages of germination to support the growth of seedlings until they become capable of producing their own energy via photosynthesis. It should be noted that energy is allocated towards the growth and development of the radicle and plumule prior to the completion of germination (Bewley, 2001). The process of seed hydration is negatively affected by a water shortage, resulting in changes that restrict the movement of stored reserves to the developing tissue and leads to a delay in the germination process (Nonogaki, 2008).

The duration of the pre-emergence phase is mostly affected by temperature. Millner et al. (2005) demonstrated that the practise of planting seeds at an early stage in New Zealand, may encounter challenges due to the presence of low spring soil temperatures. These low temperatures have the potential to negatively impact seed germination, the rate at which seedlings emerge, and the overall establishment of the plants (Hayhoe et al., 1996). The occurrence of delayed and suboptimal emergence may have a substantial negative impact on crop output, perhaps leading to the need of re-sowing paddocks in severe scenarios. Moreover, the rate of growth in maize crops is influenced by soil temperature until the six leaf stage due to the fact that the plant meristem remains below the soil surface until its emergence (Stone et al., 1999). According to current guidelines in New Zealand, it is advised to seed maize only when the soil temperature is continuously over 10 °C (White et al., 1999).

### **Leaf initiation and appearance rate**

Leaf initiation takes place on the leaf primordia located at the apical dome of vegetative shoots (Hay and Porter, 2006). The final number of leaves is based upon the rate and duration of leaf initiation. The rate is typically determined by dividing the number of leaves emerged from the time of sowing until tassel initiation by the duration between these occurrences, with consideration to the initial number of leaves in the embryo, which is commonly assumed to be either five (Hunter et al., 1977) or six (Aitken, 1980).

Between emergence and the start of the reproductive phase, maize develops on a phenological scale based on the sequential appearance and collaring of new leaves (Abendroth et al., 2011; Ritchie et al., 1986). Developmental phases are identified by the letter V followed by the number of visible collars, starting at the first visible collar. The developmental stage V1 would be indicated by the first visible collar, and the developmental stage V15 would be indicated by the fifteenth visible collar (Ritchie et al., 1986).

Temperature is the environmental factor that has greatest effect on phenological development (Vinocur and Ritchie, 2001). The phyllochron ( $^{\circ}\text{Cd}$  per leaf tip) is obtained by taking the reciprocal of the regression between thermal time and the number of visible leaf tips (Birch et al., 1998b). In the absence of nutritional or water stress, there is a consistent pace of phyllochron from emergence to flowering, indicating a linear correlation between the number of leaves and the accumulation of thermal time under field settings (Birch et al., 1998). Nevertheless, prior studies have used exponential and bilinear relationships to elucidate the association between leaf numbers and thermal time (Muchow and Carberry, 1989). The bilinear relationship is characterised by a relatively high phyllochron value during the first phase of the crop's lifecycle, which corresponds to the slow development of leaves (Phase I). This is then followed by a subsequent period (Phase II) characterised by low phyllochron values, indicating a rapid appearance of leaves. Phase II starts when stem elongation takes place and the tassel is pushed towards the top of the plant. The phyllochron values for phases I and II of maize are often reported as 52 and  $36^{\circ}\text{Cd}$  per leaf tip, respectively, with a base temperature of  $8^{\circ}\text{C}$  (Birch et al., 1998; Van Esbroeck et al., 2008).

Padilla and Otegui (2005) reported a range of published values for maize phyllochron, typically ranging from 37 to 42 degree days ( $^{\circ}\text{Cd}$ ), with a base temperature of  $8^{\circ}\text{C}$  (Hesketh and Warrington, 1989; Otegui and Melón, 1997). However, Birch et al. (1998) observed variations in phyllochron values, ranging from 35 to  $50^{\circ}\text{Cd}$ , across different maize hybrids and populations, although the primary source of variation was attributed to environmental factors. Verheul et al. (1996) observed a somewhat higher range of phyllochron values, ranging from 38 to  $52^{\circ}\text{Cd}$  among inbred lines compared with the values reported for hybrids. However, it is challenging to make meaningful comparisons due to the utilisation of a base temperature of  $6^{\circ}\text{C}$  in their study. Further investigations by Giauffret et al. (1995) observed variations in both the phyllochron and base temperature among different inbred lines. The phyllochron values ranged from 33 to  $62^{\circ}\text{Cd}$ , while the base temperature values ranged from  $7$  to  $12.5^{\circ}\text{C}$ . The measurements were derived from air temperature measurements. It should be noted that the apical meristem remains beneath the soil surface in the early stages of development (Ritchie and Nesmith, 1991; Vinocur and Ritchie, 2001).

A study conducted by Baumont et al. (2019) showed that growth rate imposes limitations on the phyllochron of wheat. Dos Santos et al. (2022) confirmed a similar correlation between relative growth rate and leaf appearance rate in maize. The conclusions drawn from their study were derived from estimations obtained during the in-season period, in contrast to the comprehensive season-long assessments conducted by Baumont et al. (2019). Further investigation is required in this area, since establishing direct connections between plant development and growth has the potential to facilitate advances in mechanistic crop modelling (Dos Santos et al., 2022).

The emergence of fully developed leaves in maize, in contrast to leaf tips, increases exponentially with thermal time (Muchow and Carberry, 1989). The higher leaves develop at a faster rate as the stem lengthens and the staminate apex of the plant emerges from the soil. The response exhibits an early approximation to linearity but increases its rate due to the fast emergence of the last leaves (Muchow and Carberry, 1989). The onset of rapid stem elongation occurs after seven leaves have completely developed, regardless of the hybrid's eventual leaf numbers or water availability (Robertson, 1994).

### **2.2.2 Thermal time effect**

Temperature is a key environmental factor regulating crop ontogeny. Thermal time is used to estimate the progress of crop development and phenological stages based on temperature. This approach accounts for the impact of temperature change and enables more accurate treatment comparisons between studies than those based entirely on time (Bonhomme, 2000; Coelho and Dale, 1980). Additionally, thermal time seems to be more constant than days in terms of the interval between two phenological stages (Hay and Porter, 2006).

The rates of plant developmental processes are mostly influenced by temperature, although it should be noted that the temperature relationships of these processes are not uniform (Porter and Gawith, 1999). It enables the characterisation of temperature-dependent responses in plant growth processes by the establishment of linear associations between the accumulation of degrees above a specific threshold per day (Bonhomme, 2000). There exist multiple meteorologically derived metrics for quantifying thermal time, which are specifically developed to evaluate the phenological progression of crops. The growing degree day (GDD) refers to the average daily temperature, which exceeds a specific base temperature that is appropriate for plant growth (Shaykewich, 1995). However, beyond the optimal temperature, there is a significant decline in plant developmental rates (Porter and Gawith, 1999). The concept of a thermal time unit has been developed to more accurately simulate the rate of plant development in response to temperature, particularly at temperatures that exceed the optimal range. In the calculation of thermal time three cardinal temperatures are used. These temperatures are utilised to determine the rate of development, within a specified temperature range or temperature threshold. The rate of development increases linearly from a base temperature ( $T_b$ ) until it reaches the optimum temperature, after which it progressively decreases until it reaches a maximum temperature, beyond which development ceases.

Understanding the theoretical basis of the thermal time concept is essential to justifying its use for developmental duration estimate or projection. The rate of development is positively correlated with the mean temperature, as indicated by Equation 2.2.

$$\text{Equation 2-2} \quad Td(^{\circ}\text{C} \cdot \text{d}) = \sum_{i=1}^n (T_a - T_b)$$

Where  $T_a$  is hourly air temperature for a 24 hour period and the sum of  $(T_a - T_b)$  provides daily thermal time accumulation of the  $(Td)$ . These are then further summed to calculate accumulated thermal time for a specific period of time or the growing season.

In their study, Birch et al. (1998) investigated the development of five different hybrids of maize, focusing on their sensitivity to temperature in the time of emergence until tassel initiation. The temperature response exhibited uniformity across all cultivars, and its characterisation was most accurately captured by a three-stage broken-stick linear function. The temperatures recorded ranged from a low of 8°C to an optimum of 34°C, with a high of 44°C. However, according to Willson et al. (1995) the accumulation of growing degree days using a base temperature of 10 °C was insufficient to forecast maize growth under unusually warm or temperate conditions. These findings prompted a modification of the accumulating thermal time between 0 and 18 °C in temperate cold conditions like New Zealand, during the maize emergence to silking period.

## 2.3 Light interception and canopy development

The capacity of the canopy to intercept light depends relatively on the leaf green area index (GAI). This relationship is represented by an exponential function (Hippis, 1983; Jones et al., 1986; Monsi M and T., 1953; Trápani et al., 1992);

$$\text{Equation 2-3} \quad \text{RI} = a(1 - e^{-k \cdot \text{GAI}})$$

The fraction of photosynthetically active light intercepted by the crop, RI is determined by  $k$  which is the attenuated coefficient of light moving through the canopy and affected by the leaf surface area, the GAI and its ability to capture that light. The function of  $a$  represents the plateau value of the curve when the crop reaches its maximum light interception limit.

The main influencing factors on RI are highlighted by Maddonni and Otegui (1996) caused by genotype differences and ontogenetic stages of the maize crop. Several studies (Jones et al., 1986; Muchow et al., 1990) have derived exponential equations to describe the association between RI

and GAI in maize. However, these studies have reported variations in the estimated attenuation coefficient ( $k$ ) and the maximum value of RI (referred to as the plateau value,  $a$ ). In their study, Muchow et al. (1990) used the values  $a = 1$  and  $k = 0.4$ , but Gallo et al. (1993) achieved a more optimal fit by using the values  $a = 0.95$  and  $k = 0.52$ . The disparities in coefficients might potentially be attributed to variations in cultivars, specifically in terms of plant height (Edmeades and Lafitte, 1993), leaf number (Dwyer et al., 1992a), leaf angle (Loomis et al., 1968; Pepper et al., 1977), and leaf area index (Dwyer et al., 1992a), which impact the interception of radiation over time. The timing of sowing (Cirilo and Andrade, 1994), the density of plants (Giauffret et al., 1991; Loomis et al., 1968), and the amount of water provided (Matthews et al., 1988; Muchow, 1989b) all might potentially alter the structure of the crop canopy, leading to a distinct pattern of development in fractional photosynthetically active radiation. Neglecting variations in the parameters ' $k$ ' and ' $a$ ' might potentially lead to erroneous conclusions (Maddoni and Otegui, 1996).

### 2.3.1 Leaf area expansion

The amount of intercepted radiation is also greatly influenced by the function of the pattern and extent of leaf area development. Leaf area is a crucial factor in determining the crops growth. The use of crop growth models in both research and management has seen a notable rise, with the effectiveness of these models being heavily reliant on the precision of leaf area projections (Keating and Wafula, 1992).

The area-per-leaf profile of a variety of maize crops was described by (Dwyer and Stewart, 1986) using a slightly skewed bell-shaped function:

$$\text{Equation 2-4} \quad LA_n = Y_0 * \exp(a * (x_n - X_0)^2 + b * (x_n - X_0)^3)$$

In this context, the amplitude ( $Y_0$ ) signifies the magnitude of the greatest leaf, while the point of inflection ( $X_0$ ) corresponds to the leaf number ( $x_n$ ) at which the largest leaf occurs,  $a$  and  $b$  are used as constants.

The function for maize was investigated by Muchow and Carberry (1989) who ultimately rejected it in favour of a set of four discontinuous linear and non-linear functions. In a subsequent study conducted by Muchow and Carberry (1990), it was shown that the bell-shaped function had a greater ability to explain the variance in leaf area in sorghum plants compared to discontinuous functions. The bell-shaped model was further developed by the authors via establishing a relationship between two of its parameters, namely  $Y_0$  and  $X_0$ , and total leaf number (TLNO). Keating and Wafula (1992) have shown that variations in growing conditions have the potential to modify

the parameters of the bell-shaped curve and their associations with TLNO. Therefore, the bell-shaped function's parameters must be related to TLNO if they are to be useful for defining fully expanded leaf area across diverse genotypes and environments.

### **2.3.2 Leaf expansion and senescence**

A significant body of literature exists that provides quantitative data on the occurrence of leaf tips and the length of the expansion phase in maize (Birch et al., 1998a; Wilson et al., 1995).

Nevertheless, there is a notable limitation of published evidence on duration of the maximum leaf size and senescence phases (Teixeira et al., 2011). Lizaso et al. (2003) identified several approaches have been used to quantify green leaf area. Early attempts described the growth in leaf area from emergence to silking using the Gompertz function or logistic functions (Baker et al., 1975). Later, regression analysis was used to fit discontinuous functions (Dale et al., 1980) or polynomials (Hunt and Parsons, 1974) to explain whole-season leaf area on daily or thermal time scales. A set of discontinuous equations is used by simulation models like APSIM-Maize (Birch et al., 1998a; Carberry et al., 1989) and CERES-Maize (Jones et al., 1986) to forecast canopy leaf area. Others use the idea of specific leaf area to extrapolate leaf area from the biomass distributed to the leaves (De Vries, 1989). More recently, methods have been created to simulate the processes of leaf expansion (Arkebauer et al., 1995) and/or leaf senescence separately (Birch et al., 1998a; Stewart and Dwyer, 1994; Yin et al., 2000); in some cases, on a per-leaf basis (Arkebauer et al., 1995; Stewart and Dwyer, 1994).

A leaf area model was created by Stewart and Dwyer (1994) to forecast leaf growth and senescence. Temperature and water stress functions were included to allow for yearly change. The authors used data from selected hybrids for several years to calibrate their model. Eight parameters were to be optimised as part of the model calibration process to take into consideration hybrid-specific responses that limited the model's applicability (Dwyer et al., 1992a).

While there is a comprehensive understanding of canopy growth processes such as leaf emergence and expansion, there is a lack of quantitative knowledge on the dynamics of leaf senescence, which explains why leaf expansion is simulated at the individual leaf level while leaf senescence is modelled at the canopy level. Teixeira et al. (2011) identified a pattern of differential leaf expansion and senescence for individual leaf positions and explained the progression of LAI senescence in two distinct phases. The first phase, from final leaf expansion until approximately the onset of senescence in the 7th leaf, showed a slow rate of LAI decline with negligible changes in light interception. After that, LAI declined at approximately 0.08% per day causing a steep reduction in light interception. In his work, Teixeira et al. (2011) monitored individual maize leaves (i.e. from leaf

tip appearance to physiological maturity) in a fully irrigated field maize crop at Lincoln, Canterbury, New Zealand. The thermal-time requirement for leaf appearance (phyllochron) was constant after the 4th leaf position at 46 °Cd/leaf. Total leaf expansion, characterised by the appearance of leaf ligules, showed a bi-linear pattern at a rate of 65 °Cd/leaf until the 7th leaf position and 26 °Cd/leaf after that. The rate of senescence onset was 135 °Cd/leaf until the 7th leaf position and 25 °Cd/leaf after that. Finally, the rate of complete senescence was 115 °Cd/leaf until the 7th leaf. The findings and parameterization obtained from this work can enhance the accuracy of maize LAI predictions, possible through facilitating the modelling of leaf growth and senescence on a per-leaf basis.

## 2.4 Radiation use efficiency (RUE) and nitrogen

Radiation use efficiency (RUE) is a measure of the conversion efficiency of a canopy's capacity to use solar radiation to convert CO<sub>2</sub> into DM through photosynthesis. RUE may be calculated using either absorbed or intercepted radiation, total solar radiation, or PAR (wavelength 400–700 nm). Except where specified, RUE values are based on the photosynthetic active radiation (PAR) which is 50% of the available solar radiation (Sinclair and Muchow, 1999).

Radiation use efficiency is quantified as the amount of DM (g) accumulated per MJ of photosynthetically active radiation (PAR). Several prospective RUE values for maize have been reported in the literature. Values ranging between 3.3 and 3.8 g/MJ were reported by Tewes and Schellberg (2018) whilst Fletcher (2004) reported ranges between 2.4 and 3.4 g/MJ. The reported values reflect the range of genotypes, N and water supply and environments of growth (Stockle and Kemanian, 2009). Essentially, the range of RUE values reflect the impact of these factors on the photosynthetic rate and its relationship with respiration.

There have been differences reported among cultivars for RUE but this is not expected among modern hybrids (Major et al., 1991). There are reports that the RUE of a modern hybrid was higher than that of an early hybrid (Tollenaar and Aguilera, 1992). There are also numerous reports of lower RUE after silking than before (Bonhomme et al., 1982; Muchow, 1989a; Muchow and Sinclair, 1994). This contradicts Major et al. (1991) who suggested that in non-limiting conditions RUE was constant for the whole crop cycle. Also, Muchow (1994) and Andrade (1995) found no reduction in RUE at least until just before physiological maturity. Thus, RUE appears to be constant until close to physiological maturity for crops grown under non-limiting conditions. The implication is that changes in RUE related to crop maturity may actually reflect a limitation in other factors. For example, RUE may decline under inadequate N supply during grain filling as senescence occurs. This is because most values of RUE are calculated from above-ground DM, so would be expected to increase once root growth stops. The proportion of total DM allocated to roots is rarely reported but has been

shown to affect assessment of RUE particularly for the perennial lucerne (Moot et al., 2003). Indeed, Tollenaar (1989) reported partitioning to root growth represented 47% of carbon allocation at the 4-leaf stage, 40% at the 8 leaf, and 30% at the 12 leaf stage. Fairey and Daynard (1978) reported that the allocation to root DM was 16% at silking and 13% two weeks after silking. These changes in allocation of carbon would also affect RUE values based solely on shoot growth.

(Muchow and Davis, 1988) related RUE to specific leaf N (SLN) ( $0.51.6 \text{ g N/m}^2$  of leaf) for grain sorghum and maize. They speculated that theoretically there is a point beyond which a further increase in SLN will not increase RUE but they did not find it and the highest RUE in their study was close to the highest reported. Understanding the physiological basis of these variables will be the emphasis of the discussion below.

#### **2.4.1 Crop nitrogen status**

Crop N nutritional status is never stable and continuously changes with N uptake and plant interactive processes. Throughout the process of crop growth and development, the plant's level of nitrogen gradually decreases (Gonzalez-Dugo et al., 2010). The "N dilution" phenomenon, which was first described by Salette and Lemaire (1981), was brought on by changes in the dry matter ratio of roots to shoots at different crop stages and leaf self-shading effects (Cassman et al., 1998; Sims and Gamon, 2002). Since plant N is mostly found in the metabolically active aerial plant portions, it is more directly connected to plant surface than to plant volume. Crop N concentration decreases as N moves from high N tissues into building storage and structural components that are relatively low in N which results in the decrease in average plant N concentration (Greenwood et al., 1990; Lemaire and Gastal, 1997). There is also variation in N concentration within the canopy because of leaf modification with acclimatization to changing light condition (Gastal and Lemaire, 2002; Hardwick, 1987). Leaf exposed to high light intensity increase the number of chloroplasts and the amount of photosynthetic enzymes (Urban et al., 2021). The concentration of N and its distribution of N in crop organs is an essential part on the in-plant physiological mechanism (Bradford and Hsiao, 1982; Fischer and Hagan, 1965).

#### **2.4.2 Leaf nitrogen and photosynthesis**

Understanding the governing mechanism driving crop N demand has shifted the paradigm away from N and DM accumulation into a more physiological approach of the leaf and photosynthesis. The growth of leaves plays a crucial role in determining the N requirement, as the photosynthetic process of leaves requires a significant amount of reduced N in comparison with other structures (Novoa and Loomis, 1981). Approximately 75% of the overall reduced N within the leaf is attributed

with the process of photosynthesis (Field, 1986). The two main N compounds include the soluble proteins (primarily the enzymes present in CO<sub>2</sub> fixation and regeneration of the CO<sub>2</sub> acceptor molecule ribulose 1,5-bisphosphate) and the compounds found in the chloroplast thylakoid membranes that are used in the light reactions, including chlorophyll, chlorophyll proteins, and various enzymes (Field, 1986). The enzyme responsible for initiating CO<sub>2</sub> is ribulose-1,5-bisphosphate carboxylase. It has been observed to make up approximately 10-30% of the total N content in leaves (Evans, 1989).

Given the significant presence of nitrogenous compounds in leaves, which are closely linked to the process of photosynthesis, it is reasonable to anticipate a relationship between photosynthesis and leaf N levels. Numerous studies demonstrate a correlation between the N content of the leaf and the net photosynthetic rate, which is the rate of CO<sub>2</sub> uptake net of respiration, in a particular environmental setting. A variety of techniques may be used to alter the N content of leaves to explore connections with photosynthetic rates, and they all generally provide comparable results (Evans, 1983; Field, 1986). The N content in leaves vary, based on canopy location, leaf maturity, the intensity of photosynthetic photon flux density (PPFD) during plant growth, N availability in the soil, the specific time of year, and cultivars (Grindlay, 1997).

### **2.4.3 Specific leaf nitrogen (SLN)**

An indicator of the amount of N in the leaf that is attributed to source N is the SLN. This variable measures the photosynthetic capacity of the leaf and also becomes an evitable indicator to N requirements of N sink organs and tissues. The majority of the reduced N in leaves is linked to photosynthetic structures and enzymes, which is the basis for the SLN method ((Dangl, 2000; Grindlay, 1997). Since photosynthesis and light interception are area-based processes, it is also preferable to describe the estimate of leaf N requirement as a function of leaf area. The maximum rate of photosynthesis occurs at approximately 1.0 g m<sup>-2</sup> SLN in maize, where the rate of light-saturated net photosynthesis and the radiation use efficiency (RUE) increase with SLN (Muchow and Sinclair, 1994; Sinclair and Horie, 1989). This is most likely the point when enzyme activity starts to restrict the CO<sub>2</sub> fixation rate. Based around the critical SLN, the maximum and minimal levels are established independently of the crop ontogeny (Van Oosterom et al., 2010).

### **2.4.4 Photosynthesis in maize as a C<sub>4</sub> crop and photosynthesis under elevated CO<sub>2</sub>**

Maize is a C<sub>4</sub> crop that has originated from the tropics and is well adapted to warm dry areas. The photosynthesis process in C<sub>4</sub> plants is designed to maximise the abundance of irradiance and the warm temperatures (Leegood, 2002). The main characteristics of C<sub>4</sub> photosynthesis process is the large reduction in photorespiration, and lower mesophyll resistance to CO<sub>2</sub>, an attribute that lowers

water use per unit of DM produced (Zhao et al., 2013). There is much interest in the C<sub>4</sub> photosynthesis process to increase crop yields in C<sub>3</sub> plants, however, it is well understood that C<sub>4</sub> photosynthesis does not produce consistently high yields under different climatic conditions (Gowik and Westhoff, 2011). The C<sub>3</sub> photosynthesis pathway is more suited to temperate conditions and in such environment produces higher yields compared with C<sub>4</sub> photosynthesis.

#### **2.4.5 Photosynthesis and water use efficiency (WUE)**

Water use efficiency can be defined as the ratio of CO<sub>2</sub> fixed by photosynthesis to water lost through transpiration (Evans and Sadler, 2008). Leaf transpiration is driven by the vapour pressure difference between inside and outside the leaf, which encounters stomatal, cuticular, and boundary layer resistances. The transpiration rate increases linearly with stomatal conductance ( $g_s$ ) and net CO<sub>2</sub> assimilation, but the latter saturates at high  $g_s$  due to an enzymatic (Rubisco) limitation (Drake et al., 1997). There are different possibilities to improve WUE which include: reducing stomatal density and stomatal aperture, cuticular transpiration, and boundary layer conductance, the latter being related to leaf surface size and shape, roughness and presence of trichoma. The canopy is also highly dependent on the microclimate environment of each leaf position and that WUE values of upper locations were double those of lower ones. These variations were similar or even higher under moderate and severe water stress. In fact, daily leaf WUE proved to be highly determined by the daily intercepted light at each leaf position (with a  $R^2$  of 0.98 for irrigated plants). Elevated CO<sub>2</sub> levels increases photosynthesis and also has a subtle effect of decreasing water lose and stress through a decrease in stomatal conductance to water vapour.

### **2.5 Crop harvest index (CHI)**

Crop harvest index, or the grain as the proportion of above ground DM, has also been used to predict grain yield (Kiniry et al., 2004). Harvest indices reported for tropically adapted genotypes (0.30-0.40) are generally lower than those for temperate genotypes (0.50-0.55) (Aluko and Fischer, 1988). The rate of increase in harvest index as grain is filled can also be considered to predict the terminal crop harvest index. A linear increase in harvest index has been used in models of maize (Muchow et al., 1990), sorghum (Hammer and Muchow, 1994), and sunflower (Chapman et al., 1993). This rate is reported in maize and grain sorghum grown in a limited range of environments (Muchow, 1990). However, it was variable for sunflowers, especially when temperature was low (Bange et al., 1997). This variability in the rate of increase in harvest index makes it useful as a tool, however, questionable unless it can be related to another plant characteristic, e.g. crop ontogeny.

## 2.6 Crop water stress

There are three primary ways in which soil moisture deficit lowers the yield of maize through the reduction in GAI, at RUE level and through changes in CHI. Initially, the overall absorption of incident PAR by the entire canopy may decrease due to drought-induced constraints on leaf area expansion, temporary leaf withering or rolling under extreme stress, or premature leaf senescence (Xianshi et al., 1998). Also, the efficiency at which the crop utilises absorbed PAR to generate DM (RUE) is reduced under drought stress. This can be observed by a reduction in the quantity of DM accumulated by the crop per unit of PAR absorbed over a period of time (Stone et al., 2001). Jones et al. (1986) found that this could occur as a decrease in the instantaneous whole-canopy net CO<sub>2</sub> exchange rate per unit absorbed PAR (Egball and Maranville, 1991). Furthermore, drought stress has the potential to restrict maize grain yield through a decrease in the CHI, which represents the proportion of DM in the crop that is allocated to the grain. This can happen even without a significant decrease in overall crop dry matter accumulation, provided a short period of stress corresponds with the crucial developmental stage during silking. Ovarian development appears to have poor sink for photosynthate; if insufficient new (concurrent) photosynthate is available to sustain their growth (Schussler and Westgate, 1991). Water stress may also inhibit the receptivity of silk (Bassetti and Westgate, 1993), thereby impeding ovary fertilisation; conversely, a diminished water potential in the kernel can prematurely halt the development of the kernel (Grant et al., 1989). This effect results in decreased CHI even if water stress occurs towards the end of the grain filling stage (Westgate, 1994).

### 2.6.1 Radiation use efficiency (RUE) and water stress

Reduction in RUE is the main contributor to maize yield loss under water deficit. Destructive measurements of aboveground DM combined with continuous (Muchow, 1994; Tollenaar and Aguilera, 1992; Tollenaar and Bruulsema, 1988) or periodic (Kiniry et al., 1998; Otegui et al., 1995; Westgate et al., 1997) assessments of canopy absorption of incident PAR are well-established techniques for determining RUE of maize in the field, typically over several weeks (Earl and Davis, 2003). The direct measurement of changes in whole crop DM cannot always be achieved, as this would necessitate evaluating changes in RUE over brief time periods (hours or days) (Earl and Davis, 2003). Short-term measurements at the whole canopy level can only be achieved by measuring net CO<sub>2</sub> exchange using canopy enclosures or micrometeorological techniques like eddy flux covariance (Rochette et al., 1996). However, these methods are usually not suitable for small plot field experiments with multiple treatments (Earl and Davis, 2003). Decreases in overall canopy RUE are

caused by decreases in RUE at the individual leaf level. Therefore, measuring leaf gas exchange (net photosynthesis) can serve as a valuable, somewhat quantitative indication of immediate changes in crop RUE, provided that a thorough sampling of leaf position throughout the canopy is conducted. The utilisation of these leaf gas exchange measurements has contributed to a greater comprehension of the immediate physiological responses exhibited by maize in response to water stress and various stresses encountered in the field (Ceulemans et al., 1988; Dwyer et al., 1992b). To assess instantaneous leaf RUE under current PAR, chlorophyll fluorometry may be used in place of leaf gas exchange measurements for C4 species such as maize (Edwards and Baker, 1993). Due to the brief duration of each fluorescence measurement, usually only a few seconds, numerous measurements can be conducted daily using a single instrument, significantly enhancing the sampling resolution compared to leaf gas exchange approaches (Earl and Tollenaar, 1999).

### **2.6.2 Leaf and canopy expansion and water stress**

The decrease in cell turgor leads to a decrease in cell growth, a process that is particularly susceptible to water stress (Pugnaire et al., 1999). The findings presented by Brown and Tanner (1983) demonstrated a significant drop in leaf and stem growth rates of lucerne by 90% when the water potential declined from -0.8 to -2.5 MPa. The combination of lower growth that hinders leaf expansion results in a decrease in GAI and subsequently decreases the ratio of leaf mass to root mass of the crop. Illustrating this phenomenon Jamieson et al. (1995a) demonstrated that barley plants subjected to severe water deficits had a 50% reduction in the maximum GAI compared with control plants under irrigation. The reduction of ratio of leaf mass to root mass has two impacts. The level of water stress escalates while a crop undergoes growth and development, resulting in an expansion of its leaf area and an accompanying rise in its evapotranspiration requirement.

### **2.6.3 Water extraction and use**

The water content of a certain layer of soil may decrease due to processes such as soil evaporation, root uptake, or water movement towards a neighbouring layer (Kuhlmann et al., 2012). The potential crop water extraction is influenced by the plant available water capacity (PAWC) within which it is cultivated. The PAWC is dependent upon the soil depth, as well as the drained upper limit (DUL) and the permanent wilting point of the soil profile (Scotter, 1977). The DUL and permanent wilting point are influenced by the distribution of soil pore sizes and are assessed by extracting soil samples and conducting measurements of soil water content at certain soil water potentials (Scotter, 1977). The estimation of PAWC may also be derived by observing the corresponding effects between soil texture and pore characteristics (Watt and Brugham, 1991). Webb et al. (2000) provided data on the physical parameters of Wakanui silt loam soil in the vicinity of Lincoln

University. The authors reported an average PAWC of 0.22 mm<sup>3</sup>/mm<sup>3</sup> for the topsoil and 0.17 mm<sup>3</sup>/mm<sup>3</sup> for the subsoil.

The plant accessible water capacity indicates how much of the water in the soil is available to a crop, and is mostly dependent on the root features of the crop (Jamieson and Ewert, 1999). Although the lower limit (LL) may sometimes be greater than the permanent wilting point depending on the root characteristics (Ritchie, 1981). By monitoring profile DUL before a crop is sown and LL after the crop gets very dry, the PAWC may be expressed for a given crop/soil combination (Hochman et al., 2001). An increase in extraction depth or a decrease in LL at that depth may have the potential to improve water supply. The PAWC makes no allowance for the pattern of water extraction between DUL and LL. The daily pattern of water extraction determines how water limitations dynamically affect crop growth (Brown et al., 2009).

#### **2.6.4 Water use efficiency (WUE)**

Water use efficiency (WUE) is also considered a determining factor in crop productivity under stress conditions and is also seen as a characteristic of crop tolerance to drought stress. The majority studies determine WUE by analysing above-ground yield, neglecting to account for partitioning to the roots (De Haan et al., 2021). WUE is defined in this study as the slope of the regression between above-ground DM yield and the amount of water (mm) utilised to produce that yield. WUE can also be determined using the evapotranspiration and transpiration efficiency estimates (Tanner and Sinclair, 1983). The increase in yield is attributed to the higher utilisation of water for transpiration rather than for soil or leaf evaporation in evapotranspiration. During drought stress, changes in water use efficiency (WUE) may indicate the inaccuracy of potential evapotranspiration (PET) as a measure of evapotranspiration. The study will calculate WUE using Equation 2-7, where ET represents transpiration (mm), which is the actual water use recorded in the field (Section 5.2).

$$\text{Equation 2-5} \quad \text{WUE} = \text{DM}/\text{ET}$$

## **2.7 Conclusion**

Due to the physiological relevance of temperature as a process driver, the use of thermal time to describe crop growth and development provides a distinct benefit over the conventional method of incorporating time. Thermal time provides a standardised approach to accurately predict timing of important developmental stages such as silking and physiological maturity.

Literature shows that there has been more effort put into studying the maize from leaf initiation from emergence to leaf appearance rate and the area of individual leaf up until the canopy is fully

developed but there is not much around the time when the canopy is fully developed and the process into senescence suggesting a lack of quantitative knowledge on the dynamics of leaf senescence.

Although there is a comprehensive literature around understanding of canopy growth processes on a per-leaf basis, the phenomenon of crop N dilution suggest there is a holistic crop and canopy level response to increase in organ size and leaf response exposure to light and leaf self-shading that shifts the N dynamics. Dissecting the canopy per-leaf basis disadvantages accurate crop response to varying N conditions.

Water availability regulates N availability to fulfil shoot N demand. The interaction between N and water on leaf growth and photosynthesis is intricate due to simultaneous activities. Water availability at the plant level regulates N demand, absorption, and distribution, affecting metabolic activities such as transpiration, carbon supply, and growth potential. This is reflected in the changes in RI and RUE which affect CHI.

## Chapter 3

### Materials and methods.

#### 3.1 Introduction

Two experiments were carried out with the explicit intent to meet Objective 1 which was to create maize crops with different yield potential by changing water and N availability. The maize hybrid, row spacing and management practices were common between the experiments. This chapter provides details of the experiments, measurements, environmental conditions, and statistical analysis used to quantify the treatment effects.

#### 3.2 Experimental design and treatments

There were two seasons of maize, cropped at two locations at Lincoln University. In the first season maize was grown in 2015/16 at H9, Horticulture Research Fields. The second 2016/17 season used the Iversen Field, still within the vicinity of the University on low N soils. This thesis considers the two crops as individual experiments that both aimed to meet Objective 1. Throughout this thesis, Experiment 1 refers to the 2015/16 maize crops and Experiment 2 to the 2016/17 maize crops.

##### 3.2.1 Experiment 1

###### Site

Experiment 1 was situated in field H9 (GPS coordinates: 43°38'54.97"S, 172°27'14.86"E) at Lincoln University. The landform is flat with a row of windbreak, hybrid poplar trees (*Populus deltoides x nigra*) on the northeast side of the field which were almost 10 – 20 m away from the headlands. Apart from the tree hedge, there were no other noticeable obstructions that would have affected the experiment. This land had been grazed as a ryegrass and white clover pasture for the previous two years (2013-14).

Manaaki whenua Landcare Research New Zealand (2016) describes the soil as Mottled Immature Pallic. These are silty loam soils of alluvium origin. Gravel is found at layers more than 1.0 m deep. The New Zealand Soil Bureau (1986) previously classified them as Templeton silt loam soils and they are Udic Ustrochrepts soils based on the UDSA classification system (Cox, 1978).

A general soil analysis and N testing were carried out to assess the fertility of the soil at the start of the cropping (one month after planting). Soil samples were taken at 150 mm depth for the general soil analysis and 600 mm for the N tests on the 21<sup>st</sup> of November 2015. Samples were analysed by

Hill Laboratory's soil test procedures. Table 3-1 shows a medium range of most of the soil nutrients but the nitrate level was 26 mg/kg of soil which was close to the recommended nitrate levels.

**Table 3-1 Soil fertility and N test results for Experiment 1, H9 at Horticulture area, 2015 at Lincoln University, Canterbury, New Zealand. The recommended N rates for comparison were extracted from Evanylo and Alley (1997).**

Nutrient	pH	Olsen P mg/L	SO <sub>4</sub> -S mg/kg	Ca <sup>++</sup>	K <sup>+</sup>	Mg <sup>++</sup>	Na <sup>+</sup>
				me/ 100g			
	6.0	13	8	5.5	0.36	0.65	0.16
Recommended		14-22	5	-	<5	5	-
N content	Potentially available N kg/ha	Anaerobically mineralisable N μg/g	Ammonium N	Nitrate N	Mineral N		
			mg/kg				
600 mm	38	23	4	26	30		
Recommended	-	-	-	18	22		

## Field layout

The design was a split-plot in four randomised blocks (replicates). Four levels of irrigation and four levels of N fertiliser were used in Experiment 1 to create a wide range of yield potentials. Irrigation levels were assigned at random to the main plots within each block, and nitrogen levels were assigned at random to the subplots within each main plot. Each block (62.4 × 15.6 m) was divided along its longest axis into the four main plots (each 12.6 × 12.0 m), allowing a 3 m guard row space between each main plot, and each main plot was divided into the four equal subplots (each 6.3 × 6.0 m). Any bias due to the hedge trees were taken care of by allocating the blocks parallel to the hedge trees.

## Treatments

### 1. Water

The main plot treatment comprised of four water regimes. Initially, the treatments were based on the changes in soil moisture as taken from field measurements and calculated according to water use. The water treatments were set to meet evapotranspiration rates at nil (rain fed), 0.25, 0.5 and 1 of evapotranspiration (Et). However, post experiment analyses of soil water deficit calculations from daily Penman evapotranspiration readings from Broadfields Meteorological Stations, number 17603 (National Institute of Water and Atmospheric Research [NIWA], New Zealand, <http://cliflo.niwa.co.nz>) showed the treatments met evapotranspiration rates at 0.3, 0.4, 0.5 and 0.7 of Et (Figure 3-2). The irrigation treatments are referred to as Irr1, Irr2, Irr3 and Irr4, respectively.

The soil moisture level was monitored using Neutron tubes (Troxler 4300 Neutron Probe) and Time Domain Reflectometry (TDR) rods. The Neutron tubes were installed in all plots to a depth of 1.55 m into the soil profile and measured soil moisture at every 0.1 m increment depth. The TDR rods measured soil moisture in the topsoil at 0.2 m into the soil surface.

The irrigation system used soaker hoses to deliver water to the plants. The set-up was connected from the main valves with PVC pipes which diverted water to regular garden hoses and eventually discharges from the soaker hoses. The amount of water discharged was monitored by a gauge at the main valves using a flow meter. Plots were irrigated in grouped schedules based on the main plot treatment.

## **2. Nitrogen**

Nitrogen was applied as Urea fertilizer (containing 46% N) with N calculated at four rates: 0, 75, 150 and 300 kg N/ha. The application was split across five dates (Appendix A). Each application had an actual N rate of 0, 0.087, 0.175 and 0.350 kg per subplot basis. There was a two-week interval between each application from one month after seedling emergence. When Urea fertilizer was applied, the plants were at leaf 6 stage. Fertilizer was applied manually by hand to provide an even distribution of the granules within each plot.

## **Cultural practices**

### **Seed bed**

The land for Experiment 1 was prepared by the 20<sup>th</sup> of October 2015. The soil was ploughed to a depth of 20 cm and later harrowed before sowing. The seed bed was flat and sowing reflected the common practices used on commercial maize farms.

### **Crop establishment**

Seed drilling occurred on the 5<sup>th</sup> of November 2015 using a Stanhay S870 precision seeder. The seeds were sown at a spacing of 0.7 x 0.15 m. Seeds were sown to one seed per planting hole. Missing plants were transplanted from the outer headlands to fill in the gaps in the guard rows. The transplanted seedlings grew slower than the sown crop and were not sampled. Transplanting was carried out on the 23<sup>rd</sup> to 27<sup>th</sup> November 2015 to guard row plants. A population count of each plot was done 37 days (14<sup>th</sup> December 2015) after planting. From actual counts the population was 8.7 plants/m<sup>2</sup>. Commercial production of maize for silage is recommended at 11 -12 plants/m<sup>2</sup> (Pioneer Brand Products, 2016).

### **Fertiliser application**

At four weeks after planting, the young maize plants had purple tints on the margins, veins and stems which spread over the whole leaf blade. This may have been a response to the cold temperatures from cool nights which averaged a minimum of 8.1 °C (Section 3.4). However, to ensure it wasn't a nutrient deficiency basal fertilizer was applied as Triple superphosphate at 250 kg/ha and Potassium chloride at 200 kg/ha on the 8<sup>th</sup> of December 2015 and the purpling disappeared.

### **Weed control**

Broadleaf weeds were obvious in the fourth week after planting and included fathen (*Chenopodium murale* L), black nightshade (*Solanum nigrum* Linn.) and thistles (*Cirsium vulgare*). A post planting herbicide application of atrazine (2-chloro-4-ethylamino-6-isopropylamino 4,3,5-triazine) at 1.5 litres ha<sup>-1</sup> was sprayed on the 18<sup>th</sup> of December 2015. No further herbicide or insecticide was required.

### **3.2.2 Experiment 2**

Experiment 2 had the same objective as Experiment 1, to create crops of different yield potential and assess the yield components. In this experiment only two different levels of water and N were used on a soil with a lower N content (Table 3.2) than in Experiment 1. This was done to create different growing conditions which would produce different grain yields.

#### **Site**

Experiment 2 was carried out in Iversen field (Iv 9) at the Field Research Centre, Lincoln University, Canterbury, New Zealand (GPS coordinates: 43°38'54.2"S, 172°28'01.1"E) at 12 m above sea level. These fields are situated on the flat plains of Canterbury.

The soil was the same as that used in Experiment 1, being a Mottled Immature Pallic Soil (Landcare Research New Zealand, 2016). Similarly, the soil in this area has a silty loam texture, however, the colour of the soil was lighter than that of H9. Soil samples were collected on the 3<sup>rd</sup> of November 2016 for general analysis and N levels. The soil test results are presented in Table 3-2. Soil nutrient levels (150 mm) were similar to those of Experiment 1 however, at this site N-nitrate levels to 600 mm were 11 mg/kg.

**Table 3-2 Soil fertility and N test results for Experiment 2, Iv 9 field, 2016 at Lincoln University, Canterbury, New Zealand.**

Nutrient	pH	Olsen P mg/L	SO <sub>4</sub> -S mg/kg	Ca <sup>++</sup>	K <sup>+</sup>	Mg <sup>++</sup>	Na <sup>+</sup>
				me/ 100g			
	5.8	15	-	5.4	0.39	0.90	0.15
N content	Potentially available N kg/ha	Anaerobically mineralisable N µg/g	Ammonium N	Nitrate N	Mineral N		
				mg/kg			
150 mm	74	42	2	7	10		
600 mm	23	13	3	11	15		

### Field layout

Experiment 2 was a two-factor factorial in a completely randomised block design. The two treatments were water and N applied at two regimes (four treatment combinations). There were five blocks with treatments replicated once, in a randomized arrangement. Blocks measured 40.2 x 6.0 m and had a 3.0 m guard row between each plot. Plot size was equivalent to Experiment 1 at 6.3 x 6.0 m length.

### Treatment

#### 1. Water

The two water regimes applied were with and without irrigation. The nil irrigation treatments were rainfed and the irrigated treatment had 106 mm of water applied per plot/application/month (see Section 3.5.3). The irrigation requirement was calculated from the soil moisture measurements at one month after planting. The irrigation system was the same as described in Experiment 1. Soaker hoses laid at alternating rows supplied distributed water to the plants. The soil moisture levels at different profiles were monitored using Neutron tubes to 1.55 m depth and TDR rods at 0.2 m depth, stationed in each plot.

#### 2. Nitrogen

There were two treatments of N and it was applied as Urea fertilizer (46% N) with N calculated at 500 kg/ha and nil N. The fertilizer was applied by hand on 6th and 20th of December 2016 with 250 kg/ha applied each time.

### Crop establishment

The same soil cultivation practices were applied as in Experiment 1. Soil was prepared by mid-October and seeds were drilled into the soil on the 1<sup>st</sup> of November 2016. The Stanhay S870 precision seeder was used to drill the seeds. The machine spaced the seeds at 0.7 m between rows

and 0.15 m between plants. The actual plant population count was 11.5 plants/m<sup>2</sup> and achieved the targeted 11-12 plants/m<sup>2</sup> (Pioneer Brand Products, 2016). The obvious gaps in the rows from the drilling and these were filled in with transplanted seedlings from the outer headlands.

## **Weeds**

The weeds found in the maize field mainly included: fathen, wireweed (*Polygonum heterophyllum* Sol.) perennial ryegrass (*Lolium perenne*), thistle and chicory (*Cichorium intybus* Linn.). The diversity and population of the weed was more in this area compared with Experimental 1.

Atrazine (2-chloro-4-ethylamino-6-isopropylamino 4,3,5-triazine) was applied at 1.5 litres/ha on the 6th of December 2017, and no further weed control was necessary.

### **3.2.3 Maize hybrid**

The maize seeds used in both experiments were from hybrid P7524 supplied by Pioneer®. This hybrid is reported to have high grain and silage yields (Pioneer, 2017). The hybrid is known to have early maturity with early vigour growth and tall stands. It is recommended for the cooler growing regions of north and mid Canterbury (2018 Genetic Technology Ltd, 2018). The Wisconsin Comparative Relative Maturity (CRM) approach is typically used in New Zealand to grade the relative maturity of hybrid maize. For this hybrid the CRM was 75 which indicates intermediate maturity period. This hybrid is planted early November and should mature in mid-autumn (2018 Genetic Technology Ltd, 2018).

## **3.3 Measurements**

The same measurements were taken for each experiment unless otherwise stated.

### **3.3.1 Dry matter**

Plant DM was measured at 2 - 3 week intervals from sowing in November to final harvest in April. Two selected plants from each plot were harvested at ground level. The leaves, stem, cobs and tassels were separated before being oven dried. Plant material was dried to a constant weight in a forced draft oven at 65 °C. Only plants representative of the overall main plots were selected with transplants avoided. Plants were selected randomly but avoided the four middle rows at the centre of the plots as these were left undisturbed for light interception measurements.

### **3.3.2 Phenological development**

Before sampled whole maize plants were dissected for oven drying, phenological and morphological measurements were taken. The physical characteristics noted included: the number of green and senesced leaves and node at which the cobs emerge. The number of cobs was noted, and the cob was de-husked for grain count. The product of the number of grains lengthwise down the cob and around the circumference was used to calculate the number of grains per cob. Grain count was taken on both the main and any secondary cobs.

### **3.3.3 Leaf area**

Individual leaf area measurements were taken every second day, from establishment until the plants reached a maximum leaf area, after which measurements were taken weekly. Five marked plants at the centre of each plot were used for these leaf measurements. The leaf length and maximum width were measured from first leaf appearance through to maturity. Senescence on each leaf was scored as a percentage of the leaf area by giving a score ranking out of five. A score of 1 meant individual leaf senescence (yellowing) was 10 - 20% and a score of 5 indicated 80 – 100% senescence.

Additional leaf area measurements were carried out on the sample plants harvested for biomass measurements. From the two plants harvested per plot, the leaf dimensions were measured using a ruler for all leaves with green area present. The same scoring system out of five was used to quantify the proportion of green area remaining on senesced leaves.

During the destructive harvest, leaf area measurements were also taken using the LI-COR 3,100 Area Meter. All the leaves of the harvested plant were measured. This was done to calibrate the accuracy of the LI-COR 3,100 Area Metre against the physical measurements taken. Only the green area for each leaf was scanned and measured. The dead, dried and discoloured leaf areas were excluded.

### **3.3.4 Soil moisture measurement**

Weekly soil moisture measurements were taken from 0 – 0.2 m from the soil surface using the TDR rods. Weekly soil moisture measurements throughout the soil profile were taken with Neutron probe from 0.25 m depth at an interval of 0.1 m to a depth of 1.55 m.

### **3.3.5 Canopy light interception**

The amount of photosynthetic active radiation entering through the canopy was measured using the Sun-Scan SS1 - SunScan Canopy Analysis System. Measurements were taken weekly and measured on markedly clear days or fully overcast days. The most suitable part of the day when the measurements were taken was between 11:00 am and 2:00 pm during which the sun was at its highest zenith angle. Radiation transmitted through the canopy was measured with the scanning rod placed at ground level and to 50 cm above ground level when the crop had all its leaves fully emerged. The scanning rod was raised to avoid the dried, senescent leaves at the base of the plant and weeds. As maize is a row crop, the rod was placed diagonally at about 45° from the row of maize plants. Measurements were taken from the centre of the plots and repeated eight times to obtain an average reading.

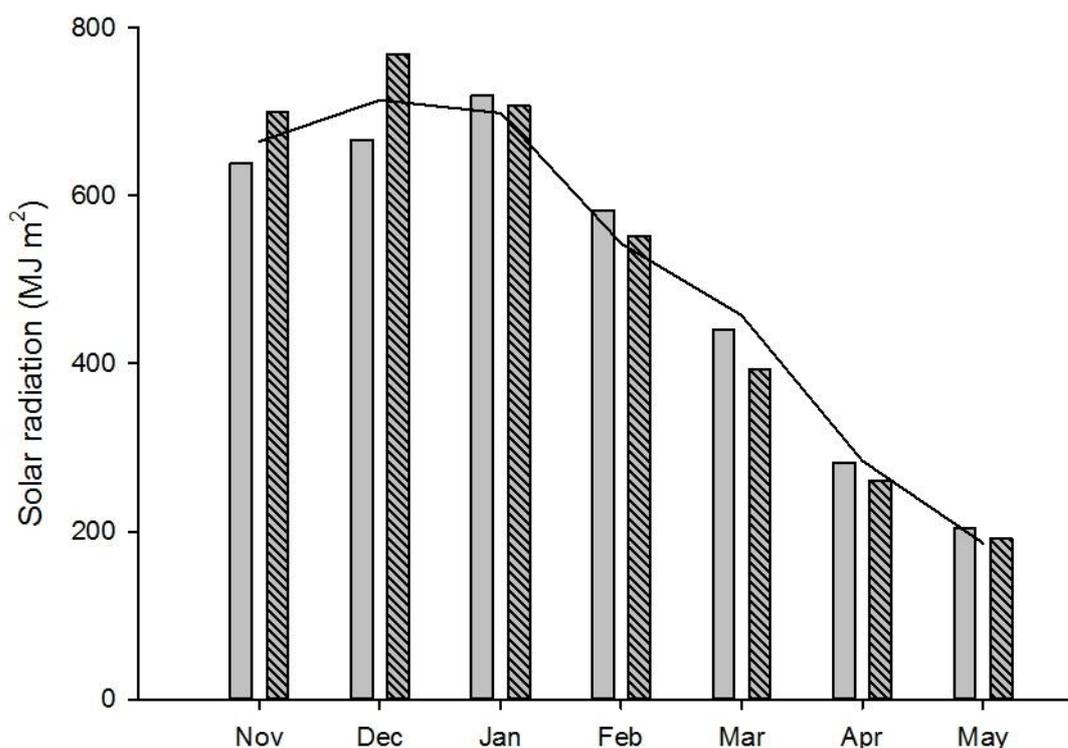
## **3.4 Climate and weather data**

Meteorological data were obtained from Broadfields Meteorological Stations, number 17603 (National Institute of Water and Atmospheric Research [NIWA], New Zealand, <http://cliflo.niwa.co.nz>) weather station, approximately 3 km east of the experiments. The mean temperatures were higher than the long-term mean (LTM) in January in 2016 and February of 2015 and 2016 (Table 3-3). In May of 2016 the mean temperature was warmer at 12.5 °C than the LTM. The minimum temperature for December 2015 was lower than the LTM but increased in January, February and March 2016 to temperatures higher than the LTM. The maximum temperatures for 2015 to 2017 were higher than the LTM except for December 2015 and March to May 2017.

**Table 3-3 Temperature (°C) data obtained from Broadfields Meteorological Station showing the mean, minimum and maximum temperatures for 2015 to 2017, and long-term means (LTM) for 1999 to 2014 for Lincoln, Canterbury, New Zealand.**

Month	Mean Temp (°C)			Minimum Temp (°C)			Maximum Temp (°C)		
	2015/16	2016/17	LTM	2015/16	2016/17	LTM	2015/16	2016/17	LTM
Nov	13.7	14.1	13.3	8.1	8.7	8.1	19.2	19.5	18.5
Dec	15.4	15.7	15.6	9.7	10.6	10.7	21.1	20.9	20.6
Jan	16.2	17.2	16.7	12.1	11.3	11.5	20.3	23.2	21.8
Feb	19.2	17.2	16.7	13.5	11.4	11.8	24.8	23.0	21.7
Mar	16.2	15.0	15.0	10.8	10.7	9.9	21.5	19.4	20.1
Apr	13.1	12.3	12.4	7.0	8.1	7.5	19.2	16.5	17.3
May	12.5	8.3	9.8	7.4	3.3	5.0	17.5	13.2	14.6

The monthly solar radiation was lower at the start of Experiment 1 in November and December 2015 but higher for Experiment 2 during these two months in 2016 when compared with the LTM (Figure 3-1). After this period, the incident solar radiation was close to the LTM for both experiments.



**Figure 3-1 Total monthly total incident solar radiation data obtained from Broadfields meteorological station showing the totals for Experiment 1 from November 2015 to May 2016 (grey bar), Experiment 2 from November 2016 to May 2017 (striped bar) and long term means (LTM) (solid line) for 1999 to 2014 for Lincoln, Canterbury, New Zealand.**

## 3.5 Calculations

### 3.5.1 Thermal time

The daily thermal time was calculated from air temperatures and used a bilinear model determined on an hourly basis for 24 hours. This model as adapted from Cutforth and Shaykewich (1990) uses the cardinal temperatures for base, optimum and maximum at 0, 34 and 44 °C respectively (Birch et al., 1998c). Thermal time was accumulated by summing the daily thermal time at crop emergence. However, the thermal time accumulation for temperatures below 10 °C inadequately predicts maize development in New Zealand. Therefore, Wilson et al. (1995) proposed the use of a broken-stick relationship to quantify this curvilinear response between 0 - 18 °C. This method was used in the thermal time calculations.

### 3.5.2 Dry matter

The pattern of DM accumulation was described using a logistic function with high coefficients of determination (Clewer and Scarisbrick, 2001). The logistic curve was segmented into three main parts that describe the pattern of dry matter accumulation which starts with the lag phase (0 – 5% of the maximum DM) which signifies the establishment phase (Wilson et al., 1995). This is followed by a rapid growth phase represented by the exponential (5 -95% of the maximum DM) increase and finally the asymptote as resource availability decreases and the biological mechanism of the plant slowly halts (Thornley and France, 2007). The logistic equation can be rearranged to quantify aspects of pattern of growth (Weaich et al., 1996). This is a four-parameter logistic curve that is asymmetrical in nature around the inflection point.

The logistic curve as expressed by Loss et al. (1989) is represented below:

$$\text{Equation 3-1} \quad Y = A + \frac{C}{(1+e^{(-B(X-M))})}$$

Dry matter (Y) is a function of thermal time (x), and the logistic curve is represented by A, the starting point, B is the slope during the linear exponential phase and indicates the rate of dry matter increase, M is the point of inflection where maximum growth rate occurs, and C is the ceiling or maximum dry matter value.

The duration (DUR) and rate of DM or yield accumulation is calculated to reflect the growth process. The duration (DUR) at which the slope B progresses indicates the time between 5 -95% DM accumulation as described by Robert et al. (1999) in the following equation:

$$\text{Equation 3-2} \quad \text{DUR} = \frac{1}{B} \left( \text{BM} - \ln \left( \frac{0.05(C+A)}{0.95C-0.05A} \right) \right)$$

The maximum rate (R) of DM accumulation is expressed as:

$$\text{Equation 3-3} \quad R = \frac{CB}{6}$$

### 3.5.3 Soil water calculations

#### Total soil moisture content

The amount of water required for each irrigation treatment was calculated after soil moisture measurements were obtained. Soil moisture measurements were taken from TDR rods at the top 0 - 0.2 m of soil and neutron probe from 0.25 to 1.55 m depth at 0.1 m intervals. Volumetric soil water content, known as  $\Theta$  ( $\text{mm}^3/\text{mm}^3$ ), was calculated for each soil depth measurement. Soil moisture at each 0.1 m layer was attained by converting volumetric soil water content to mm of water/depth layer. The total soil moisture content ( $\text{SMC}_T$ ) was attained by accumulating soil moisture content to 1.55 m depth.

#### Soil water extraction

Water available for plant use is supplied from the stored soil water. This is calculated by finding the drained upper limit (DUL) and the lower limits (LL) for the soil capacity to hold water in correspondence to the field capacity (FC) and wilting point (WP). The data used for the upper limit were obtained from the soil moisture measurements from the average of second and third highest soil water measurements after drainage was accounted for. The lower limits were averaged from second and third lowest soil water measurements of the Rainfed treatment.

The soil water extraction (SWE) was calculated at each soil depth layer by subtracting the upper from the lower limits. The total soil water extraction for each profile was obtained by summing the difference at each depth layer to 1.55 m as described:

$$\text{Equation 3-4} \quad \text{SWE} = \sum(\text{DUL} - \text{LL}) * 1.55 \text{ m depth}$$

#### Actual soil moisture deficit (ASMD)

The actual soil moisture deficit (ASMD) was obtained by subtracting the total soil moisture content of the DUL from the given total soil moisture content ( $\text{SMC}_{Tx}$ ) at the time measurements was taken:

$$\text{Equation 3-5} \quad \text{SMD}_{\text{actual}} = \text{DUL} - \text{SMC}_{\text{Tx}}$$

The calculated soil moisture deficit ( $\text{SMD}_{\text{cal}}$ ) assumes that the soil water storage when used by plant water uptake has to be continuously replaced to avoid depletion. The existing soil moisture deficit ( $\text{SMD}_{\text{cal}}$ ) can be calculated from the previous soil moisture deficit ( $\text{SMD}_{\text{prev}}$ ). Plant water use also regarded as  $E_t$  will usually contribute to further depletion of stored soil water whilst precipitation ( $P$ ) and irrigation recharge the soil water. This is represented as Equation 3.6.

$$\text{Equation 3-6} \quad \text{SMD}_{\text{cal}} = \text{SMD}_{\text{prev}} + E_t - (P + I_r)$$

### **Water use and irrigation requirements**

In the experiments, irrigation was based on the plant water use. Plant water requirement is supplied from the stored soil water, and through  $P$  and  $I_r$ . Adding up these parameters, gives water used as:

$$\text{Equation 3-7} \quad \text{WU} = (\text{SMC}_{\text{TF}} - \text{SMC}_{\text{TS}}) - (P + I_r)$$

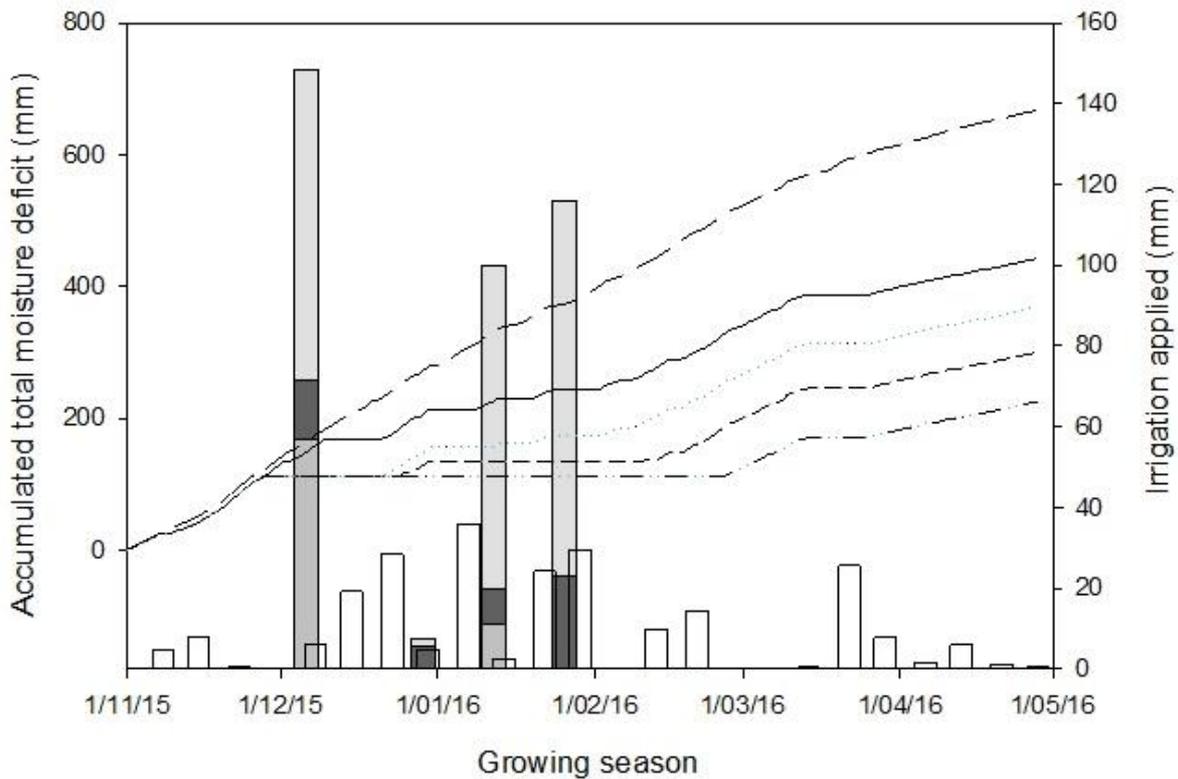
Water supplied from the stored soil water was determined from the difference between the total soil moisture content at the finish ( $\text{SMC}_{\text{TF}}$ ) and ( $\text{SMC}_{\text{TS}}$ ) start of measurement period.

### **Water use efficiency (WUE)**

The amount of water required to produce a given quantity of DM ( $\text{kg DM/h/mm}$ ) was derived by calculating the WUE. The WUE was derived from the linear regression between the cumulative DM at each harvest time and corresponding amount of water use over the period.

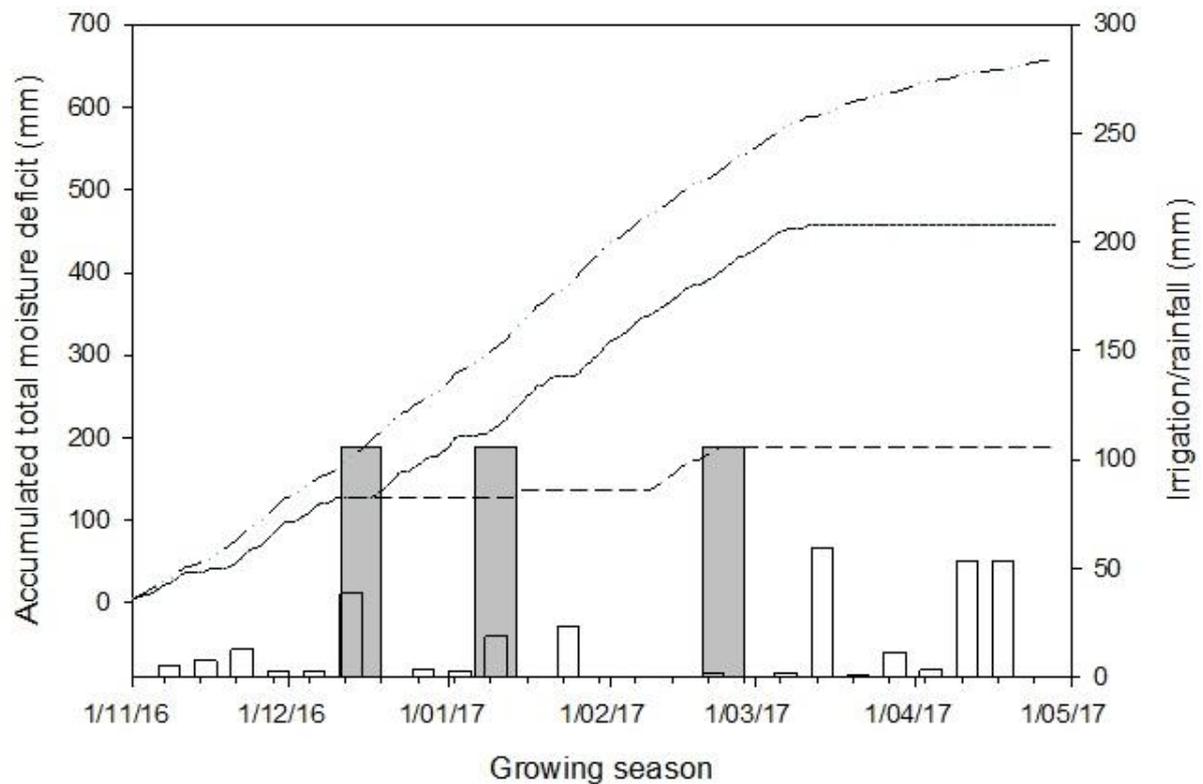
### **Soil water budget**

The potential moisture deficit for the irrigation treatments for Experiment 1 are shown in Figure 3-2. Total accumulated PET for the growing season was 668 mm. Irrigation treatments produced soil moisture deficits between 226 and 369 mm by the end of the season.



**Figure 3-2 Soil water budget for maize crops in Experiment 1 for the growing season of 2015/16 at Lincoln University, New Zealand. Soil moisture deficit is represented by the line graph above the graph (Irr1 (—), Irr2 (.....), Irr3 (---), Irr4 (-.-.-)), accumulated total Penman evapotranspiration shown in line graph (— —), irrigation shown as shaded bar graph Irr2 (■), Irr3 (■) and Irr4 (■)) and unshaded bars indicate weekly rainfall.**

The two irrigation treatments in Experiment 2 were with and without irrigation (Figure 3-3). The treatments with irrigation received a standard rate of water at 106 mm per plot for each monthly application date (15th of December 2016, 16th of January 2017 and 23rd of February 2017). Soil moisture deficit for the irrigation treatments was 188 mm by the 22<sup>nd</sup> of February 2017. For the rainfed treatments the potential soil moisture deficit reached 457 mm in mid-March. Rainfall amounted to 73 mm in March and 111 mm in April which maintained a constant deficit for both treatments to the end of the growing season.



**Figure 3-3 Soil water budget for maize crops grown in Experiment 2 for the growing season of 2016/17 at Lincoln University, New Zealand. Soil moisture deficit is represented by the line graph above: Rainfed (—), irrigated (---), total Penman evapotranspiration (— · — · —), irrigation shown as shaded bars and rainfall as unshaded bars.**

### 3.5.4 Statistical Analysis

All statistical analyses were done in GenStat, release 16.1. The analysis performed included ANOVA and curve fitting for linear, bilinear, and logistic curves. The ANOVA followed the respective experimental designs. The results include the significance level of the Fisher's protected test for means separation. The standard error of differences of means were used for all data represented. For the logistic curves, the rate and duration of the DM accumulation were calculated on plot basis and analysed through ANOVA assess differences in the treatments.

## Chapter 4

# Dry matter accumulation and yield formation in maize under different N and water levels.

### 4.1 Introduction

Objective 1 of this research was to create crops with different yield potentials, and this is described and quantified in this chapter. These yield differences are then assessed in relation to differences in the coefficients in Equation 2-1 (Monteith, 1977). Total yield is also analysed in relation to DM partitioning and the amount that ends up as grain yield. Therefore, the three main components assessed in this chapter are final grain yield, total DM accumulated and partitioning patterns of DM into the grain constituents defined as CHI. This chapter quantifies the different yield scenarios to enable the mechanisms responsible for yield differences to be investigated in the following chapters.

Grain yield is quantified by the product of the number of kernels and their individual weight at harvest per plant (Chapman and Edmeades, 1999) multiplied by plant population (DeBruin et al., 2018). Grain yield is set by three physiological mechanisms, (i) the total DM accumulated at silking, (ii) the rate of DM partitioned to the reproductive structure bearing the kernels (ear) during the kernel growth and development period, and (iii) the total DM partitioned into kernel filling.

These physiological mechanisms are reflected in kernel development by the shape of the lag, linear and maturity phases. Kernel set is further governed by assimilate supply, which in turn is influenced by N and water availability. Firstly, kernel numbers per plant is determined by the total assimilate available at the final stage of the lag phase in the DM accumulation curve. Depending on total assimilate available, a defined number of kernels is set (Kiniry et al., 1990). Concurrent to this event, the potential kernel weight is mainly determined by N availability as endosperm and granule starch cells develop (Severini et al., 2011). The availability of water is important to maximise rapid water accumulation in endosperm expansion in the lag phase through to the middle of the linear phase of grain filling (Borrás et al., 2003). It is during this critical period that the potential number of kernels and their maximum size are set. After this phase, the final stages of kernel weight gain are dependent on assimilate supply which determines the actual yield (Ouattar et al., 1987). Therefore, the treatments imposed with different water and nitrogen supplies were designed to give yield differences. The reduction in the final yield can then be attributed to one or more of these factors.

The main influence of stay-green is on the final yield where the assimilate supply at grain-filling is mostly influenced by the rate of senescence. Stay-green contribution is evident in yield contribution

when kernel set is maximised. Otherwise, it is only effective in providing sustenance to the grain filling process. These experiments do not seek to assess the stay-green component of the hybrid used, merely note that it may affect the results produced.

## 4.2 Materials and Methods

Samples were obtained from destructive harvests as described in Section 3.3.1. Dry matter was measured at 2-to-3-week intervals.

### 4.2.1 Calculation

Dry matter production was calculated on a tonnes per hectare basis. This came from individual DM per plant in grams, converted to kg and multiplied by plant population. A logistic curve was fitted to the pattern of DM accumulation (Section 3.5.2) to determine the rate and duration of growth.

For Experiment 1, the leaves for one plant were weighed together and packed into one bag. Whereas in Experiment 2, the green leaves were bagged separately and numbered in ascending order from the base of the crop to top with the flag leaf being the final leaf. This was done to monitor changes in leaf green area in more detail in the second cropping season.

The weight for each kernel was measured by detaching a subsample of kernels from the middle part of the cobs, weighing them and counting the number of kernels to determine the average weight for a kernel. The kernel weight per ear was attained by multiplying the number of kernels per cob (Section 3.3.2) by the mean weight per kernel.

However, due to the disparities in grain-filling and final grain weight across different positions on the ear there are evident differences kernel weight in basal-middle and apical grains of maize ear (Wu et al., 2022). To avoid these disparities, total grain weight per hectare basis was calculated from ear weight minus the cob, shank and husk.

The CHI is the weight of grain DM divided by the weight of total DM.

Decreases in DM of the leaf and stem weights were considered to result from the remobilisation of DM between successive harvests and assumed that there was no loss from respiration. Any decline after maximum leaf and stalk DM accumulation was totalled to provide an estimate of the amount of DM remobilised to meet the sink demand of the kernels.

The amount of DM accumulated at post-silking was calculated by subtracting the total DM at final harvest from the total DM around silking, and further subtracting the estimated amount of leaf and stalk DM remobilised.

## 4.3 Results

### 4.3.1 Experiment 1

#### Crop yield and its components

Unless otherwise stated there was no interaction between water and nitrogen.

Unexpectedly, there was no difference in grain yield among crops. Grain yield showed no influence of water ( $P=0.162$ ) or N ( $P=0.085$ ) and averaged 12.4 t/ha (Table 4-1). However, differences were observed in the total DM yield which was affected by both water ( $P=0.012$ ) and N ( $P=0.022$ ). The total DM was 19.1 t/ha for Irr1 and increased to 23.2 t/ha for Irr4. Moreover, the total DM was 19.9 t/ha for crops without N and increased to 22.3 t/ha with 75 kg N/ha and then there was no further increase. This affected the CHI with the influence of water ( $P=0.003$ ) being more prominent. Crop harvest index was 0.61 for crops under Irr1 and dropped to 0.56 with higher irrigation at Irr3.

**Table 4-1 Grain yield, total dry matter (DM), and the crop harvest index (CHI) at harvest for maize in response to four N levels (0, 75, 150 and 300 kg N/ha) at each of the four water levels (Irr1 - 4) for the final harvest of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Irrigation				Mean
	Irr1	Irr2	Irr3	Irr4	
<u>Grain yield (t/ha)</u>					
0	12.1	10.6	11.0	12.9	11.6
75	11.2	13.1	14.1	13.3	12.9
150	11.8	12.3	13.5	12.2	12.4
300	11.4	13.1	12.5	13.1	12.5
Mean	11.6	12.3	12.8	12.8	12.4
SED <sub>N</sub> =0.481, SED <sub>W</sub> =0.542, SED <sub>N*W</sub> =0.993, P <sub>N</sub> =0.085, P <sub>W</sub> =0.162, P <sub>N*W</sub> =0.112					
<u>Total DM yield (t/ha)</u>					
0	18.4	18.6	19.9	22.6	19.9 <sub>b</sub>
75	18.7	21.9	23.7	24.8	22.3 <sub>a</sub>
150	20.0	21.6	25.1	20.4	21.8 <sub>a</sub>
300	19.1	22.8	23.0	25.1	22.5 <sub>a</sub>
Mean	19.1 <sub>b</sub>	21.2 <sub>ab</sub>	22.9 <sub>a</sub>	23.2 <sub>a</sub>	21.6
SED <sub>N</sub> =0.882, SED <sub>W</sub> =1.059, SED <sub>N*W</sub> =1.858, P <sub>N</sub> =0.022, P <sub>W</sub> =0.012, P <sub>N*W</sub> =0.135					
<u>CHI</u>					
0	0.65	0.58	0.56	0.57	0.59
75	0.60	0.60	0.59	0.54	0.58
150	0.59	0.60	0.54	0.55	0.57
300	0.60	0.61	0.54	0.52	0.57
Mean	0.61 <sub>a</sub>	0.60 <sub>a</sub>	0.56 <sub>b</sub>	0.54 <sub>b</sub>	0.58
SED <sub>N</sub> =0.017, SED <sub>W</sub> =0.014, SED <sub>N*W</sub> =0.032, P <sub>N</sub> =0.582, P <sub>W</sub> =0.003, P <sub>N*W</sub> =0.566					

Main effect means within the same row or column with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

The grain yield is made up of the total kernel dry weight per plant and derived from the individual kernel dry weight and the total number of kernels per plant. These components are examined in Table 4-2.

Total kernel dry weight per plant was not affected by water ( $P=0.394$ ) or N ( $P=0.485$ ). The mean grain yield was 151 g per plant for all water and N levels. There was no response to water ( $P=0.968$ ) and N ( $P=0.485$ ) of the crop to increase number of kernels per plant with an indication of an upper limit at

423 kernels per plant. However, individual grain dry weight was affected by both N ( $P=0.034$ ) and water ( $P=0.015$ ), whereby mean weight increased from 333 mg for nil N to ~364 mg for N fertilised crops, and from 320 mg for rainfed crop (Irr1) to ~376 mg for crops under Irr3 and Irr4.

**Table 4-2 Total kernel dry weight per plant, individual kernel dry weight and total number grains per ear of maize in response to four N levels (0,75, 150, 300 Kg N/ha) at each of the four water levels (Irr1 - 4) for the final harvest of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Irrigation				Mean
	Irr1	Irr2	Irr3	Irr4	
<u>Kernel dry weight per plant (g)</u>					
0	136	126	144	151	139
75	133	159	163	171	156
150	146	166	180	113	151
300	139	154	154	184	158
Mean	138	151	160	154	151
SED <sub>N</sub> =18.48, SED <sub>W</sub> =20.14, SED <sub>N*W</sub> =37.81, P <sub>N</sub> =0.485, P <sub>W</sub> =0.394, P <sub>N*W</sub> =0.489					
<u>Number of kernels per plant</u>					
0	425	392	415	424	414
75	420	431	424	429	426
150	435	466	452	312	416
300	434	425	414	465	435
Mean	429	429	426	408	423
SED <sub>N</sub> =20.03, SED <sub>W</sub> =21.52, SED <sub>N*W</sub> =40.83, P <sub>N</sub> =0.469, P <sub>W</sub> =0.968, P <sub>N*W</sub> =0.933					
<u>Individual kernel dry weight (mg)</u>					
0	309	322	346	355	333 <sub>b</sub>
75	316	369	384	399	367 <sub>a</sub>
150	335	356	398	363	363 <sub>a</sub>
300	321	362	372	395	362 <sub>a</sub>
Mean	320 <sub>b</sub>	352 <sub>ab</sub>	374 <sub>a</sub>	378 <sub>a</sub>	356
SED <sub>N</sub> =12.36, SED <sub>W</sub> =15.30, SED <sub>N*W</sub> =26.31, P <sub>N</sub> =0.034, P <sub>W</sub> =0.015, P <sub>N*W</sub> =0.781					

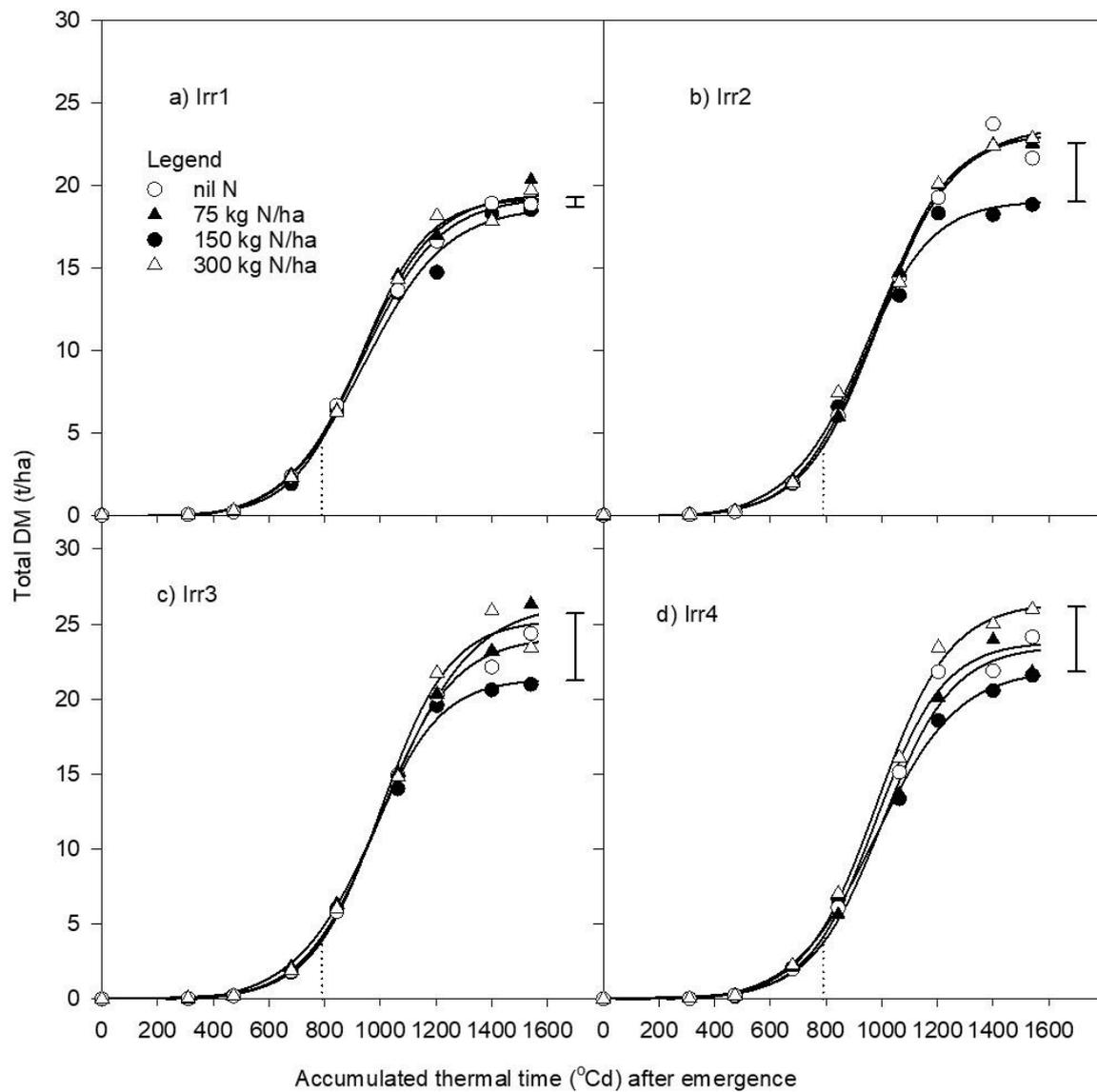
Means within the same row or column with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### **Pattern of dry matter accumulation**

Logistic curves were used to describe the pattern of DM accumulation. The logistic curves show the pattern of DM accumulation, final yield, and DM components at the final harvest. Grain yield and DM accumulation are expressed as the rate and duration of growth.

The pattern of the total DM accumulation only differed at the upper asymptote as observed in Figure 4-1. This is shown in Table 4-3 where the duration ( $P=0.404$ ) and rate ( $P=0.361$ ) did not differ.

Although statistically the duration and rate did not differ, from visual observations suggest there were differences in the duration which caused the final DM to be different. The differences in the total DM accumulated were affected by water ( $P=0.01$ ) and N ( $P=0.003$ ). Without irrigation (Irr1) the total DM estimated from the fitted curves was 18.7 t/ha and increased to 21.4 and 23.1 t/ha with irrigation (Irr2 – Irr4). The final DM was lowest at 19.7 t/ha for nil N and averaged 22.2 t/ha for N fertilised crops.



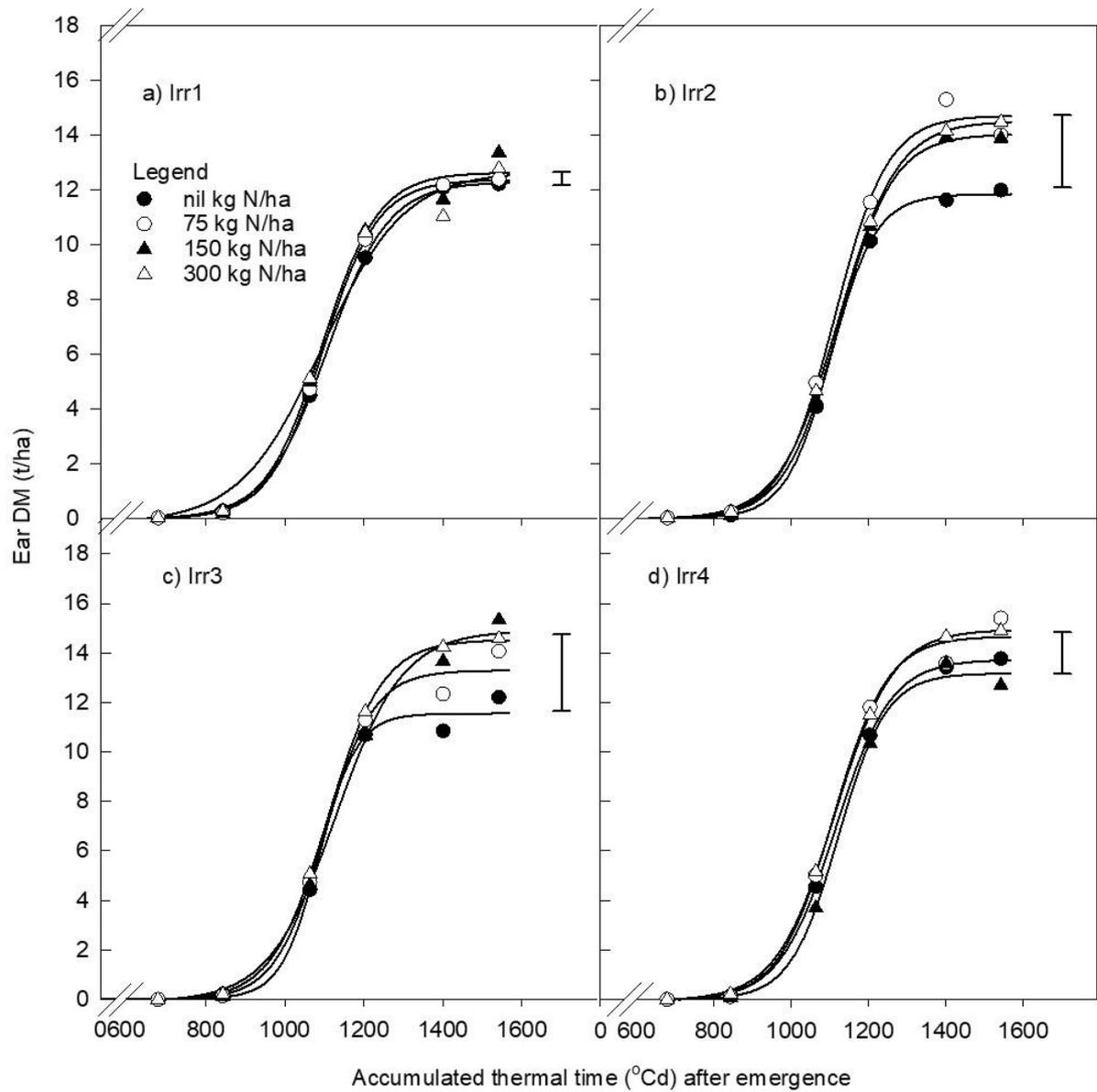
**Figure 4-1 Total dry matter (DM) accumulation for maize in response to four N levels (0, 75,150, 300 kg N/ha) at each of four water levels (Irr1 (a), Irr2 (b), Irr3 (c) and Irr4 (d)) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Dotted line indicates silking at 790 °Cd. Error bars indicate the standard deviation of the mean across the points.**

**Table 4-3 The duration and rate of growth, and the final total dry matter (DM) accumulation for maize crops grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water regimes (Irr1 – 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Irrigation				Mean
	Irr1	Irr2	Irr3	Irr4	
<u>Duration of total DM accumulation (°Cd)</u>					
0	856	750	611	886	776
75	797	768	778	731	769
150	770	750	925	791	809
300	738	899	732	775	786
Mean	790	792	762	796	785
SED <sub>N</sub> =65.3, SED <sub>W</sub> =85.5, SED <sub>W*N</sub> =141.8, P <sub>N</sub> =0.932, P <sub>W</sub> =0.976, P <sub>N*W</sub> =0.404					
<u>Rate of total DM accumulation (kg/ha/°Cd)</u>					
0	22.7	24.3	28.3	23.2	24.6
75	22.9	27.2	28.8	29.4	27.1
150	23.8	27.7	26.0	29.2	26.7
300	24.7	24.5	31.4	31.0	27.9
Mean	23.5	25.9	28.6	28.2	26.6
SED <sub>N</sub> =3.99, SED <sub>W</sub> =4.67, SED <sub>N*W</sub> =8.34, P <sub>N</sub> =0.884, P <sub>W</sub> =0.235, P <sub>N*W</sub> =0.361					
<u>Final DM (t/ha)</u>					
0	18.6	18.5	20.1	21.4	19.7 <sub>b</sub>
75	18.7	22.1	23.0	22.7	21.6 <sub>a</sub>
150	18.7	22.0	25.3	23.0	22.3 <sub>a</sub>
300	18.7	23.0	24.1	25.2	22.8 <sub>a</sub>
Mean	18.7 <sub>b</sub>	21.4 <sub>a</sub>	23.1 <sub>a</sub>	23.1 <sub>a</sub>	22.7
SED <sub>N</sub> =0.823, SED <sub>W</sub> =1.118, SED <sub>W*N</sub> =1.811, P <sub>N</sub> =0.003, P <sub>W</sub> =0.01, P <sub>N*W</sub> =0.469					

Means within the same row or column with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

The pattern of the total ear DM accumulation (Figure 4-2) followed the pattern of total DM in Figure 4-1 but with more variability in the upper asymptote. The lower part of the logistic curve, as represented by the rate and duration of DM of growth, was non-responsive to water and N (Table 4-4). The rate of ear DM accumulation averaged 32 kg/ha/°Cd ( $P=0.696$ ) and occurred for a mean duration of 437 °Cd ( $P=0.409$ ). Again, there were visual differences from the graph in the duration which caused differences in the final ear DM. The final ear DM estimated from the asymptote showed a response to water ( $P=0.038$ ) and N ( $P=0.005$ ) with an increase from 11.8 t/ha for rainfed crops to a mean of 13.3 t/ha for irrigated crops. For N it was 11.8 t/ha for nil N crop and 13.3 t/ha for N fertilised crops.



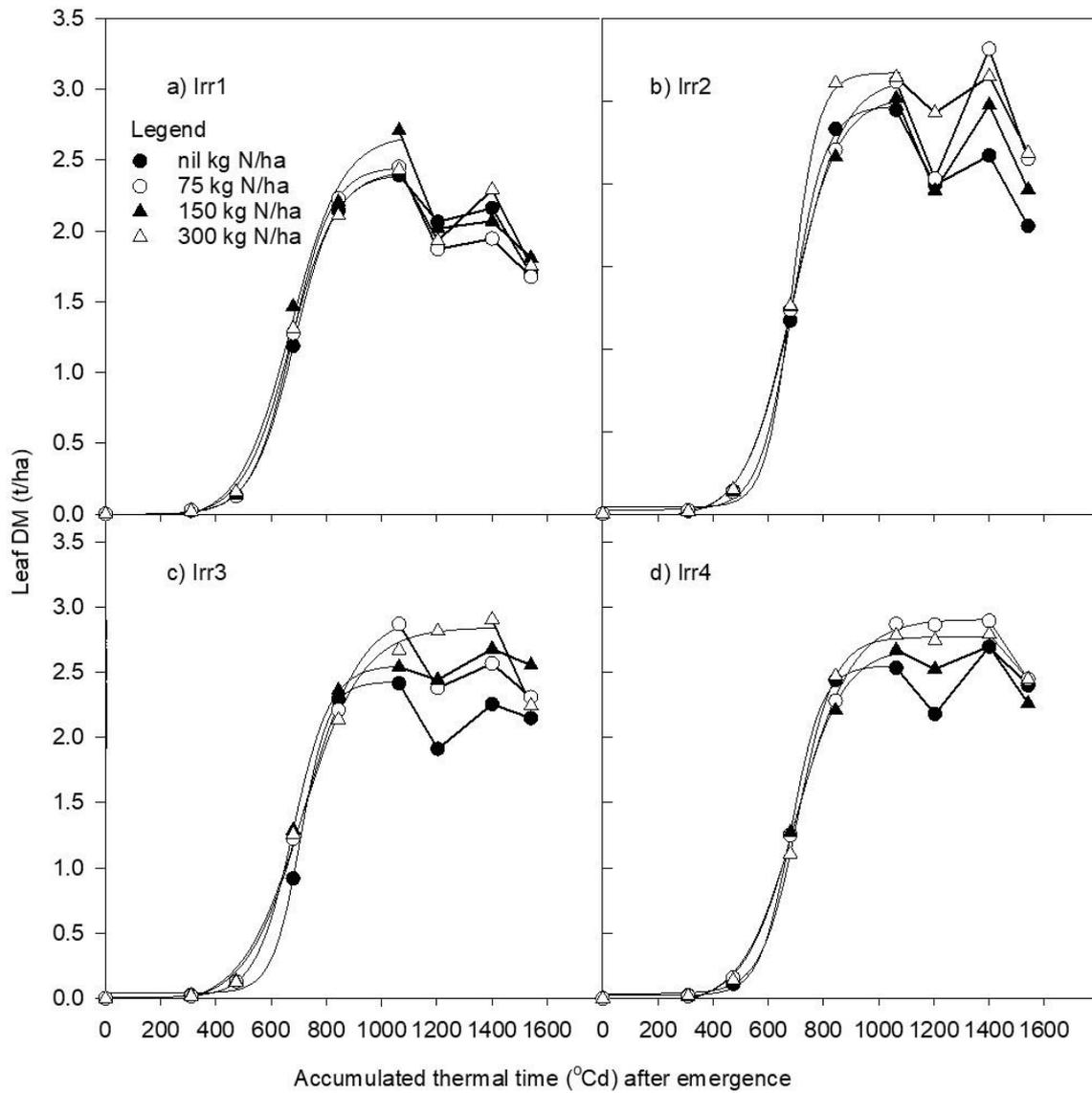
**Figure 4-2 Ear dry matter (DM) accumulated against thermal time for maize in response to four N levels (0, 75,150, 300 kg N/ha) at each of four water levels (Irr1 (a), Irr2 (b), Irr3 (c) and Irr4 (d)) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard deviation of the mean across the points.**

**Table 4-4 The duration, rate and final ear dry matter (DM) accumulated for maize crop grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water regimes (Irr1 – 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water				Mean
	Irr1	Irr2	Irr3	Irr4	
<u>Duration ear DM accumulation (°Cd)</u>					
0	435	332	282	440	372
75	353	408	397	422	395
150	423	421	514	430	447
300	365	439	432	456	423
Mean	394	400	406	437	409
SED <sub>N</sub> =37.7, SED <sub>W</sub> =48.0, SED <sub>N*W</sub> =81.1, P <sub>N</sub> =0.234, P <sub>W</sub> =0.815, P <sub>N*W</sub> =0.409					
<u>Rate of ear accumulation (kg/ha/°Cd)</u>					
0	28.0	38.0	39.3	30.8	34.0
75	49.1	34.6	32.6	34.1	37.6
150	29.0	32.8	29.2	31.4	30.6
300	39.4	35.5	33.8	31.7	35.1
Mean	36.4	35.2	33.7	32.0	34.3
SED <sub>N</sub> =4.57, SED <sub>W</sub> =5.18, SED <sub>N*W</sub> =9.45, P <sub>N</sub> =0.496, P <sub>W</sub> =0.848, P <sub>N*W</sub> =0.696					
<u>Final ear DM (t/ha)</u>					
0	11.7	11.3	11.0	13.2	11.8 <sub>b</sub>
75	11.8	14.0	12.7	14.0	13.1 <sub>a</sub>
150	12.1	13.4	14.4	12.8	13.1 <sub>a</sub>
300	11.6	14.0	13.9	14.3	13.4 <sub>a</sub>
Mean	11.8 <sub>b</sub>	13.2 <sub>a</sub>	13.0 <sub>a</sub>	13.6 <sub>a</sub>	12.9
SED <sub>N</sub> =0.473, SED <sub>W</sub> =0.525, SED <sub>N*W</sub> =0.973, P <sub>N</sub> =0.005, P <sub>W</sub> =0.038, P <sub>N*W</sub> =0.126					

Means within the same row or column with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

The pattern of leaf DM accumulation was also assessed with a logistic curve fitted to the successively increasing DM and ended when leaf DM started to decline (Figure 4-3). Leaf DM accumulation is shown in Table 4-5. The duration of leaf DM accumulation indicates an interaction between water and N ( $P=0.052$ ), with main differences observed for crops under Irr3, however, there is no obvious pattern. The rate of DM accumulation was influenced by N ( $P=0.025$ ) with DM decreasing from 8.98 kg/ha/°Cd for the control to ~5.29 kg/ha/°Cd for crops with 75 – 150 kg N/ha. The final leaf DM was also affected by N ( $P=0.032$ ), indicating 2.46 t/ha for nil N crops and increasing to 2.71 t/ha for N fertilised crop. After the period of leaf DM accumulation there was a decline in leaf DM. This was considered as when DM remobilisation occurred.



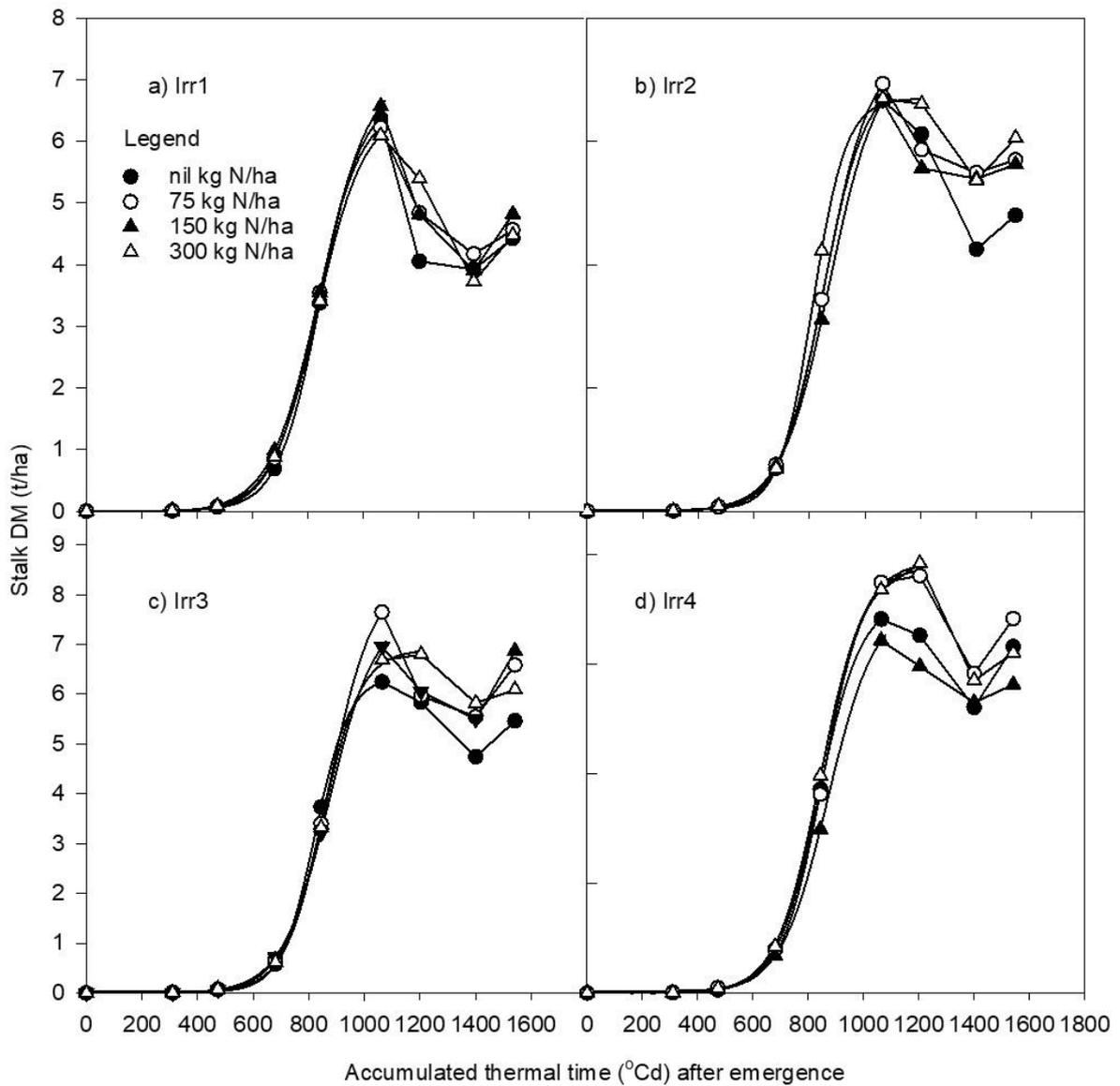
**Figure 4-3 Leaf dry matter (DM) accumulation against thermal time for maize in response to four N levels (0, 75,150, 300 kg N/ha) at each of four water levels (Irr1 (a), Irr2 (b), Irr3 (c) and Irr4 (d)) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

**Table 4-5 Leaf dry matter accumulation duration and rate effect on final dry matter (DM) obtained for maize crop grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water regimes (Irr1 – 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water				Mean
	Irr1	Irr2	Irr3	Irr4	
<u>Duration of leaf DM accumulation (°Cd)</u>					
0	399 <sub>bcde</sub>	302 <sub>de</sub>	270 <sub>e</sub>	379 <sub>cde</sub>	338 <sub>b</sub>
75	411 <sub>bcde</sub>	516 <sub>abcd</sub>	618 <sub>ab</sub>	566 <sub>abc</sub>	527 <sub>a</sub>
150	567 <sub>abc</sub>	492 <sub>abcde</sub>	393 <sub>cde</sub>	495 <sub>abcd</sub>	487 <sub>a</sub>
300	478 <sub>bcde</sub>	295 <sub>de</sub>	712 <sub>a</sub>	404 <sub>bcde</sub>	472 <sub>a</sub>
Mean	464	401	498	461	456
SED <sub>N</sub> =56.9, SED <sub>W</sub> =51.4, SED <sub>N*W</sub> =111.1, P <sub>N</sub> =0.012, P <sub>W</sub> =0.357, P <sub>N*W</sub> =0.052					
<u>Rate of leaf DM accumulation (kg/ha/°Cd)</u>					
0	7.98	9.88	9.99	7.19	8.98 <sub>a</sub>
75	5.76	4.90	4.71	5.01	5.12 <sub>b</sub>
150	5.01	4.95	6.61	5.23	5.45 <sub>b</sub>
300	4.91	13.75	4.25	8.06	7.75 <sub>ab</sub>
Mean	5.92	8.37	6.39	6.39	6.77
SED <sub>N</sub> =1.336, SED <sub>W</sub> =1.154, SED <sub>N*W</sub> =2.585, P <sub>N</sub> =0.025, P <sub>W</sub> =0.219, P <sub>N*W</sub> =0.162					
<u>Final leaf DM (t/ha)</u>					
0	2.43	2.45	2.39	2.59	2.46 <sub>b</sub>
75	2.44	2.67	3.01	2.93	2.76 <sub>a</sub>
150	2.80	2.55	2.55	2.70	2.65 <sub>a</sub>
300	2.45	2.70	2.99	2.79	2.73 <sub>a</sub>
Mean	2.53	2.59	2.73	2.75	2.65
SED <sub>N</sub> =0.099, SED <sub>W</sub> =0.111, SED <sub>N*W</sub> =0.205, P <sub>N</sub> =0.032, P <sub>W</sub> =0.226, P <sub>N*W</sub> =0.220					

Means within the same row or column with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

There were no differences in the pattern of DM accumulation in the stalk (Figure 4-4). The duration of stalk DM accumulation averaged 480 °Cd at a rate of 25.4 kg/ha/°Cd (Table 4-6). The duration and rate of DM accumulation resulted in an average maximum DM of 7.6 t/ha. After the period of stalk DM accumulation, there was a decline which indicates remobilisation, followed by an increase in the last measurement of each crop.



**Figure 4-4** The pattern of stalk dry matter (DM) accumulation against thermal time for maize in response to four N levels (0, 75, 150, 300 kg N/ha) at each of four water levels (Irr1 (a), Irr2 (b), Irr3 (c) and Irr4 (d)) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.

**Table 4-6 The duration, rate and final stalk dry matter (DM) accumulation pattern for stalk DM for maize crop grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water regimes (Irr1 - 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water				Mean
	Irr1	Irr2	Irr3	Irr4	
<u>Duration of stalk DM accumulation (°Cd)</u>					
0	460	465	388	479	448
75	501	514	489	419	481
150	583	517	544	539	546
300	510	345	425	503	446
Mean	513	460	462	485	480
SED <sub>N</sub> =56.0, SED <sub>W</sub> =42.5, SED <sub>N*W</sub> =105.8, P <sub>N</sub> =0.263, P <sub>W</sub> =0.583, P <sub>N*W</sub> =0.922					
<u>Rate of stalk DM accumulation (kg/ha/°Cd)</u>					
0	22.8	26.4	27.6	24.3	25.3
75	21.3	24.9	26.8	28.2	25.3
150	26.9	21.7	24.6	29.6	25.7
300	19.6	29.9	26.2	25.3	25.3
Mean	22.7	25.7	26.3	26.8	25.4
SED <sub>N</sub> =2.459, SED <sub>W</sub> =2.617, SED <sub>N*W</sub> =4.999, P <sub>N</sub> =0.884, P <sub>W</sub> =0.235, P <sub>N*W</sub> =0.361					
<u>Final stalk DM (t/ha)</u>					
0	6.61	7.82	6.27	7.06	6.94
75	6.43	8.05	8.21	7.25	7.49
150	11.2	7.13	7.71	11.4	9.36
300	6.24	6.41	6.64	7.73	6.76
Mean	7.62	7.35	7.21	8.36	7.64
SED <sub>N</sub> =1.445, SED <sub>W</sub> =1.005, SED <sub>N*W</sub> =2.7, P <sub>N</sub> =0.274, P <sub>W</sub> =0.663, P <sub>N*W</sub> =0.887					

Means within the same row or column with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### **Remobilised DM and post-silking photosynthesised DM contribution to grain-filling**

The remobilisation of DM was responsive to water (Table 4-7). Leaf DM was influenced by water ( $P=0.002$ ) with 1.66 t/ha DM remobilised from the nil irrigated crops (Irr1) but only ~0.66 t/ha for crops under Irr3 and Irr4. Stalk DM was also affected by water ( $P=0.047$ ) with more stalk DM remobilised at 2.38 t/ha for Irr1 but only 1.38 for crop under Irr3 and Irr4. The total DM showed water ( $P=0.014$ ) decreased remobilised DM from 4.04 t/ha in the rainfed crops to a mean of 2.26 t/ha for the irrigated crops.

**Table 4-7 Dry matter contribution from leaf and stalk dry matter (DM) remobilisation (t/ha) for maize crop grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water levels (Irr1 – 4) regimes in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water				Mean
	Irr1	Irr2	Irr3	Irr4	
<u>Leaf DM remobilised (t/ha)</u>					
0	1.88	1.08	0.93	0.65	1.13
75	1.78	1.59	0.96	0.45	1.20
150	1.55	1.07	0.35	0.8	0.94
300	1.45	0.68	0.43	0.69	0.81
Mean	1.66 <sub>a</sub>	1.11 <sub>ab</sub>	0.67 <sub>b</sub>	0.65 <sub>b</sub>	1.02
SED <sub>N</sub> =0.2292, SED <sub>W</sub> =0.2916, SED <sub>N*W</sub> =0.4926, P <sub>N</sub> =0.330, P <sub>W</sub> =0.022, P <sub>N*W</sub> =0.811					
<u>Stalk DM remobilised (t/ha)</u>					
0	2.44	2.41	1.50	1.61	1.99
75	2.05	1.44	2.10	1.66	1.81
150	2.67	1.25	1.46	0.14	1.38
300	2.37	1.33	0.86	1.65	1.55
Mean	2.38 <sub>a</sub>	1.61 <sub>ab</sub>	1.48 <sub>b</sub>	1.27 <sub>b</sub>	1.68
SED <sub>N</sub> =0.495, SED <sub>W</sub> =0.346, SED <sub>N*W</sub> =0.924, P <sub>N</sub> =0.616, P <sub>W</sub> =0.047, P <sub>N*W</sub> =0.787					
<u>Total DM remobilised (t/ha)</u>					
0	4.32	3.49	2.43	2.26	3.13
75	3.83	3.04	3.07	2.11	3.01
150	4.21	2.32	1.81	0.93	2.32
300	3.81	2.01	1.29	2.35	2.37
Mean	4.04 <sub>a</sub>	2.72 <sub>b</sub>	2.15 <sub>b</sub>	1.91 <sub>b</sub>	2.71
SED <sub>N</sub> =0.540, SED <sub>W</sub> =0.567, SED <sub>N*W</sub> =1.121, P <sub>N</sub> =0.359, P <sub>W</sub> =0.014, P <sub>N*W</sub> =0.909					

Means within the same row or column with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

Dry matter contribution from post-silking photosynthesis was estimated as the difference between DM accumulation and DM remobilisation (Table 4-8). During kernel growth and towards grain-filling this was affected by both water ( $P=0.032$ ) and N ( $P=0.016$ ). Photosynthesised DM increased from 8.61 t/ha for rainfed crops to an average of 11.5 t/ha for irrigated crops. Similarly, the addition of N increased the contribution from current photosynthesis from 9.3 t/ha for crops with nil N to an average of 11.5 t/ha for crops receiving 150 and 300 kg N/ha.

**Table 4-8 Dry matter (DM) contribution from post-silking DM accumulation (t/ha) towards grain-filling for maize crop grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water levels (Irr1 – 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

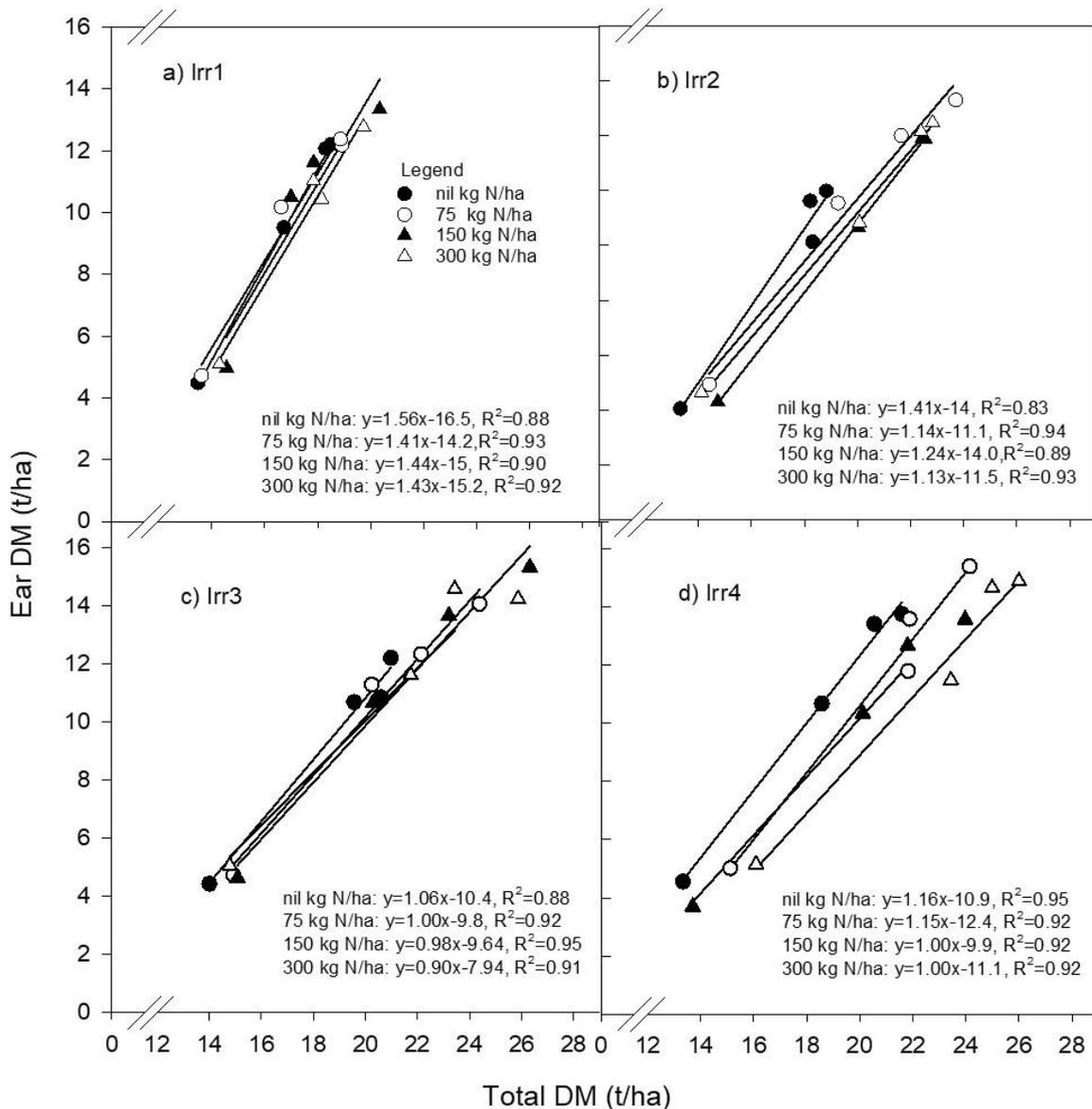
N (kg/ha)	Water				Mean
	Irr1	Irr2	Irr3	Irr4	
	<u>Post-silking DM (t/ha)</u>				
0	7.64	8.64	9.56	11.4	9.30 <sub>a</sub>
75	8.86	10.7	10.9	13.2	10.9 <sub>ab</sub>
150	8.97	11.4	13.4	11.7	11.4 <sub>b</sub>
300	8.96	12.2	13.1	12.3	11.7 <sub>b</sub>
Mean	8.61 <sub>b</sub>	10.8 <sub>a</sub>	11.7 <sub>a</sub>	12.1 <sub>a</sub>	10.8

SED<sub>N</sub>=0.823 SED<sub>W</sub>=0.916, SED<sub>N\*W</sub>=1.645, P<sub>N</sub>=0.016, P<sub>W</sub>=0.032, P<sub>N\*W</sub>=0.798

Means within the same row or column with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### Total DM influence on ear DM

A linear relationship between ear and total DM is shown in Figure 4-5. This linear relationship represents the rate of partitioning of total DM into ear. The rate of ear DM partitioning was only affected by water ( $P<0.001$ ) (Table 4-9). It decreased from 1.4 ear DM/total DM (40% greater than the increase in total DM) for Irr1 to 1.2 ear DM/total DM (20% more ear DM than total DM) for Irr2 and 1.1 ear DM/total DM for Irr3 and Irr4. There was no indication ( $P=0.485$ ) that total DM at silking and/or at the start of ear development was different for the crops. The total DM available at silking averaged 10.1 t/ha.



**Figure 4-5 Ear dry matter against total dry matter (DM) for maize in response to four N levels (0, 75, 150, 300 kg N/ha) at each of four water levels (Irr1 (a), Irr2 (b), Irr3 (c) and Irr4 (d)) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

**Table 4-9 The ear partitioning rate and total dry matter (DM) at start of ear development for maize crops grown under four levels of N (0, 75, 150, 300 kg N/ha) at four water levels (Irr1 – 4) in 2015/2016 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water				Mean
	Irr1	Irr2	Irr3	Irr4	
<u>Ear partitioning rate (Ear DM/total DM)</u>					
0	1.32	1.35	1.01	1.20	1.22
75	1.41	1.12	1.04	1.21	1.20
150	1.43	1.21	1.09	0.99	1.18
300	1.44	1.10	0.90	0.98	1.11
Mean	1.40 <sub>a</sub>	1.20 <sub>b</sub>	1.01 <sub>c</sub>	1.10 <sub>c</sub>	1.18
SED <sub>N</sub> =0.139, SED <sub>W</sub> =0.063, SED <sub>W*N</sub> =0.187, P <sub>N</sub> =0.864, P <sub>W</sub> <0.001, P <sub>W*N</sub> =0.464					
<u>Total DM at start of ear development (t/ha)</u>					
0	8.91	10.4	9.82	9.41	9.64
75	10.0	9.69	9.81	10.8	10.0
150	10.4	11.3	9.90	9.91	10.4
300	10.6	10.1	8.84	11.1	10.2
Mean	10.0	10.4	9.59	10.3	10.1
SED <sub>N</sub> =0.506, SED <sub>W</sub> =0.486, SED <sub>N*W</sub> =1.772, P <sub>N</sub> =0.551, P <sub>W</sub> =0.375, P <sub>W*N</sub> =0.485					

Means within the same row or column with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### 4.3.2 Experiment 2

Experiment 2 was carried out to ensure yield differences because of the lack of differences in Experiment 1. Therefore, only the extreme treatments were included to create differences in the canopy using the two water regimes at two N levels with maize grown under low soil N conditions. The two water regimes included rain-fed and irrigation (106 mm per plot monthly application) under which two N levels were imposed at nil and 500 kg N/ha. This section describes the results for grain yield and the DM partitioning.

#### Grain yield and its components

There was an interaction between water and N (Table 4-10) for grain yield ( $P=0.004$ ) and total DM yield ( $P<0.001$ ) but only a main effect of water for CHI ( $P<0.001$ ). Grain yield averaged 0.98 t/ha for the rainfed crop and increased from 9.0 to 16.3 t/ha in response to 500 kg N/ha for the irrigated crop. Total DM gave a mean yield of 4.1 t/ha for the rainfed crop and increased from 14.3 to 28.9 t/ha in response to 500 kg N/ha with irrigation. Crop harvest index increased from 0.24 to 0.60 with irrigation.

**Table 4-10 Grain yield, total dry matter (DM) and the crop harvest index (CHI) for maize in response to two N levels (0 and 500 kg N/ha) at water levels (rainfed and irrigated) for the final harvest of 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
<u>Grain DM yield (t/ha)</u>			
0	0.81 <sub>c</sub>	9.00 <sub>b</sub>	4.91
500	1.15 <sub>c</sub>	16.3 <sub>a</sub>	8.73
Mean	0.98	12.7	6.82
SED <sub>N and W</sub> =0.565, SED <sub>N*W</sub> =0.799, P <sub>N</sub> =0.003, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.004			
<u>Total DM yield (t/ha)</u>			
0	3.80 <sub>c</sub>	14.3 <sub>b</sub>	9.00
500	4.40 <sub>c</sub>	28.9 <sub>a</sub>	17.7
Mean	4.10	21.6	12.8
SED <sub>N and W</sub> =0.621, SED <sub>N*W</sub> =0.878, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> <0.001			
<u>Crop harvest index</u>			
0	0.22	0.64	0.43
500	0.25	0.56	0.41
Mean	0.24 <sub>b</sub>	0.60 <sub>a</sub>	0.42
SED <sub>N and W</sub> =0.0345, SED <sub>N*W</sub> =0.0488, P <sub>N</sub> =0.522, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.194			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

In this experiment, grain yield was influenced by both the number and weight of kernels. For the components of grain yield (Table 4-11), there were consistent effects of N ( $P<0.001$ ) and water ( $P<0.001$ ) for the number of kernels/ear, and interactions between N and water in their effects on kernel weight/ear ( $P=0.020$ ) and individual kernel weight ( $P=0.023$ ). The mean number of kernels increased from 187 to 267/plant with 500 kg N/ha, and from 117 to 337/plant with irrigation. Kernel dry weight per ear increased from 13.4 to 34.9 g in response to N without irrigation, to 69.8 g with irrigation and no N, and to 124.4 g with both N and irrigation. Individual grain weight was not affected ( $P=0.193$ ) by N without irrigation, averaging 207 mg, but increased to 253 mg with irrigation and no N and to 322 mg with both N and irrigation.

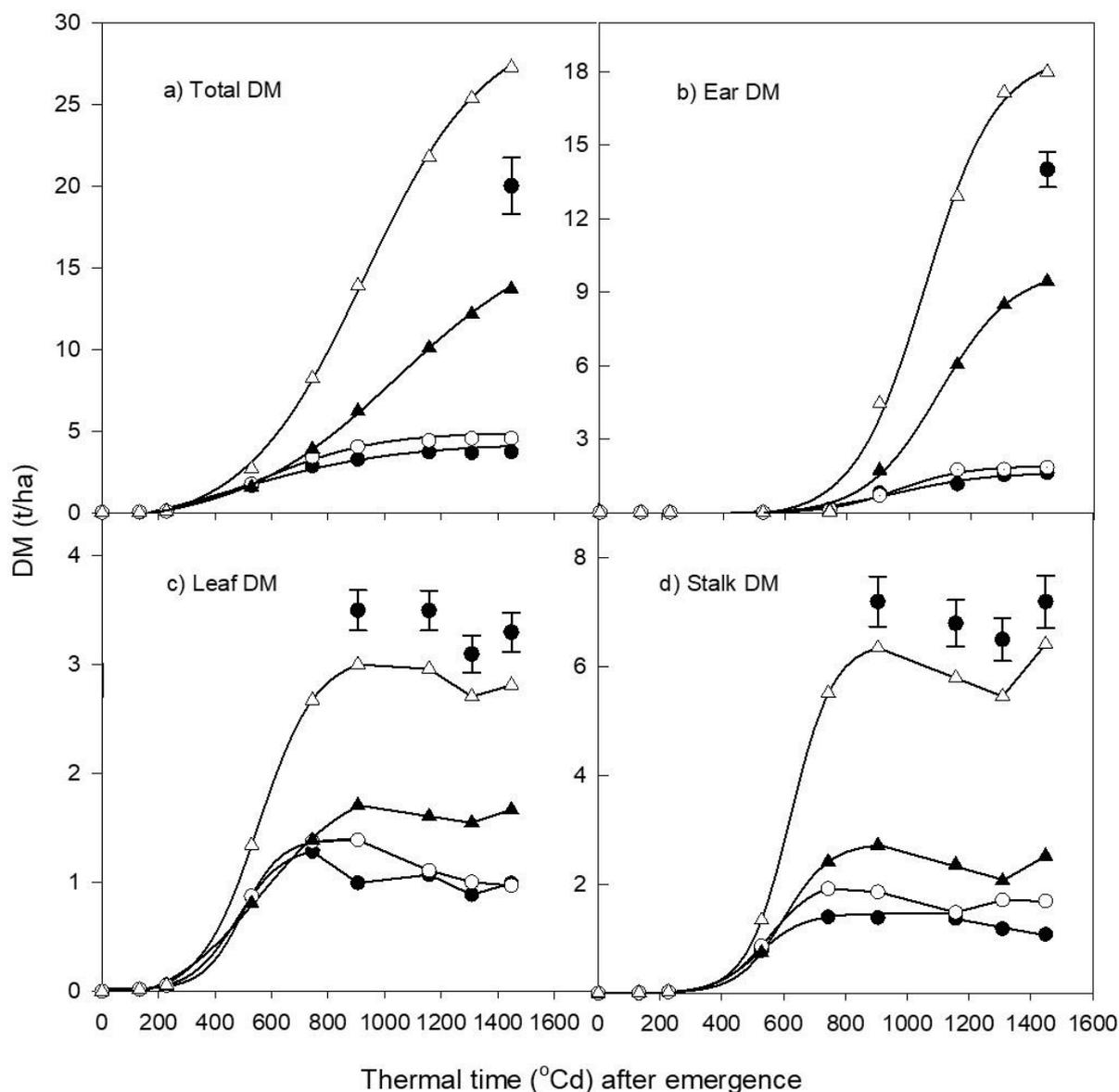
**Table 4-11 Number and dry weight of kernels, and individual grain dry weight for maize in response to two N levels (0 and 500 kg N/ha) at each of the two water levels (rainfed and irrigated) for the final harvest of 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
	<u>Kernel dry weight per plant (g)</u>		
0	13.4 <sub>d</sub>	69.8 <sub>b</sub>	41.6
500	34.9 <sub>c</sub>	124 <sub>a</sub>	79.7
Mean	26.7	97.1	60.7
SED <sub>N and W</sub> =4.42, SED <sub>N*W</sub> =6.26, P <sub>N</sub> =0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.020			
	<u>Number of kernels per plant</u>		
0	84.0	289	187 <sub>b</sub>
500	149	384	267 <sub>a</sub>
Mean	117 <sub>b</sub>	337 <sub>a</sub>	227
SED <sub>N and W</sub> =15.00, SED <sub>N*W</sub> =21.21, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.345			
	<u>Individual dry kernel weight (mg)</u>		
0	221 <sub>c</sub>	253 <sub>b</sub>	237
500	194 <sub>c</sub>	322 <sub>a</sub>	258
Mean	207	288	248
SED <sub>N and W</sub> =13.45, SED <sub>N*W</sub> =19.02, P <sub>N</sub> =0.193, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.023			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### Pattern of dry matter accumulation

Logistic curves determined the difference in DM accumulation patterns. The parameters of the logistic curve were used to indicate the rate and duration of DM accumulation. The patterns of DM accumulation for the total, ear, leaf and stalk are shown in Figure 4-6. The accumulation rate is quantified against thermal time to indicate growth rate of different organs.



**Figure 4-6** Dry matter (DM) accumulation of total (a), ear (b), stalk (c) and leaf (d) dry matter of maize in response to two N levels (0 and 500 kg N/ha) at each of two water levels (rainfed (●,○ (nil 500 kg N/ha N)) and irrigated (▲, △ (nil and 500 kg N/ha)) for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard error.

The pattern of the total DM showed there were consistent effects of water ( $P=0.002$ ) on the duration of DM accumulation and an interaction between water and N on the final DM yield. There was no effect of water and N ( $P=0.201$ ) for the rate of DM accumulation and interactions ( $P=0.003$ ) between N and water in their effects on the final DM (Table 4-12). The duration of DM accumulation increased from 618 to 1487 °Cd with irrigation. The rate of DM accumulation averaged 15.7 kg/ha/°Cd for all crops, but from visual observations of the graph there were differences in the rate. The final DM averaged 4.8 t/ha for the rain fed crop, and for irrigated crops increased from 18.6 to 29.1 t/ha with 500 kg N/ha.

**Table 4-12 The duration, rate and final dry matter (DM) for the pattern of total DM obtained for maize in response to two water levels (rainfed and irrigated) for each of the two N levels (0 and 500 kg N/ha) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
	<u>Duration of total DM accumulation (°Cd)</u>		
0	540	1723	1132
500	695	1252	973.0
Mean	618 <sub>b</sub>	1487 <sub>a</sub>	1053
SED <sub>N and W</sub> =216.2, SED <sub>N*W</sub> =305.7, P <sub>N</sub> =0.478, P <sub>W</sub> =0.002, P <sub>N*W</sub> =0.173			
	<u>Rate of total DM accumulation (t/ha/°Cd)</u>		
0	14.6	11.4	13.0
500	13.6	23.3	18.4
Mean	14.1	17.3	15.7
SED <sub>N and W</sub> =0.005, SED <sub>N*W</sub> =0.007, P <sub>N</sub> =0.276, P <sub>W</sub> =0.506, P <sub>N*W</sub> =0.201			
	<u>Final DM accumulated (t/ha)</u>		
0	4.11 <sub>c</sub>	18.6 <sub>b</sub>	11.4
500	5.40 <sub>c</sub>	29.1 <sub>a</sub>	17.3
Mean	4.80	23.4	14.3
SED <sub>N and W</sub> =1.223, SED <sub>N*W</sub> =1.729, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.003			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

The final ear DM was only influenced by the rate of DM accumulation. The pattern of ear DM accumulation is shown in Figure 4-6b. There was no effect of water or N ( $P=0.538$ ) on the duration of DM accumulation, but an interaction between water and N in their effects on the rate ( $P=0.002$ ) and the final ( $P<0.001$ ) amount of DM accumulated (Table 4-13). The duration of ear DM accumulation averaged 661 °Cd for all crops. The rate of DM accumulation averaged 3.94 kg/ha/°Cd for the rain fed and increased from 14.5 to 26.8 kg/ha/°Cd in response to N with irrigation. The final ear DM averaged 1.82 t/ha under rain fed, and when irrigated increased from 9.61 to 18 t/ha in response to N.

**Table 4-13 The pattern of ear dry matter (DM) as quantified in duration, rate and final DM for maize in response to two N levels (0 and 500 kg N/ha) for each of the two water levels (rainfed and irrigated) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
<u>Duration of ear DM accumulation (°Cd)</u>			
0	727	688	708
500	549	678	614
Mean	638	683	661
SED <sub>N and W</sub> =132.7, SED <sub>N*W</sub> =187.6, P <sub>N</sub> =0.492, P <sub>W</sub> =0.740, P <sub>N*W</sub> =0.538			
<u>Rate of ear DM accumulation (t/ha/°Cd)</u>			
0	2.87 <sub>c</sub>	14.5 <sub>b</sub>	8.69
500	5.01 <sub>c</sub>	26.8 <sub>a</sub>	15.9
Mean	3.94	20.6	12.3
SED <sub>N and W</sub> =0.001, SED <sub>N*W</sub> =0.002, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.002			
<u>Maximum ear DM accumulated (t/ha)</u>			
0	1.71 <sub>c</sub>	9.61 <sub>b</sub>	5.66
500	1.93 <sub>c</sub>	18.0 <sub>a</sub>	9.97
Mean	1.82	13.8	7.81
SED <sub>N and W</sub> =0.511, SED <sub>N*W</sub> =0.723, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> <0.001			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

As in Experiment 1, there were declines in leaf and stalk DM when grain filling commenced. The logistic curve was fitted to the data up to the last 2-3 harvest dates before leaf and stalk DM started to decline. These declines were assumed to indicate the amount of DM remobilisation from these organs into grain filling.

The leaf component of the DM accumulation showed consistent effects of water for the duration of DM accumulation ( $P=0.021$ ) and the final DM accumulated ( $P<0.001$ ). There was an interaction between water and N ( $P=0.019$ ) on the rate of leaf DM accumulation (Table 4-14). The duration increased from 524 to 988 °Cd with irrigation. The rate was between 2.52 kg/ha/°Cd under rain fed and at nil N for irrigated crops. This rate of leaf DM accumulation increased to 5.53 kg/ha/°Cd with 500 kg N/ha with irrigation. The final leaf DM increased from 1.38 to 3.01 t/ha with irrigation.

**Table 4-14 The rate, duration and final dry matter (DM) for the pattern of leaf DM accumulation for maize in response to two N levels (0 and 500 kg N/ha) for each of the two water levels (rain fed and irrigated) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
<u>Duration of leaf DM accumulation (°Cd)</u>			
0	502	1256	879
500	546	720	633
Mean	524 <sub>b</sub>	988 <sub>a</sub>	756
SED <sub>N and W</sub> =174.4, SED <sub>N*W</sub> =246.7, P <sub>N</sub> =0.183, P <sub>W</sub> =0.021, P <sub>N*W</sub> =0.122			
<u>Rate of leaf DM accumulation (t/ha/°Cd)</u>			
0	2.72 <sub>b</sub>	2.30 <sub>b</sub>	2.51
500	2.73 <sub>b</sub>	5.53 <sub>a</sub>	4.13
Mean	2.73	3.91	3.32
SED <sub>N and W</sub> =0.0006, SED <sub>N*W</sub> =0.0008, P <sub>N</sub> =0.019, P <sub>W</sub> =0.070, P <sub>N*W</sub> =0.019			
<u>Total leaf DM accumulated (t/ha)</u>			
0	1.32	2.81	2.07
500	1.43	3.21	2.32
Mean	1.38 <sub>b</sub>	3.01 <sub>a</sub>	2.20
SED <sub>N and W</sub> =0.334, SED <sub>N*W</sub> =0.472, P <sub>N</sub> =0.381, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.653			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

The stalk DM accumulated showed no effect of N ( $P=0.888$ ) on the duration of accumulation but there was an interaction between water and N on the rate ( $P=0.005$ ) and total stalk DM accumulated ( $P<0.001$ ) (Table 4-15). The duration of stalk DM accumulation averaged 489°Cd for all crops. The rate of DM accumulation was 3.30 kg/ha/°Cd for nil N under rain fed, but when irrigated increased from 7.10 to 14.7 t/ha/°Cd in response to 500 kg N/ha. The total stalk DM showed the same response, with an average of 1.8 t/ha for nil and 500 kg N/ha under rainfed, and with irrigation increasing from 3.45 to 6.72 t/ha in response to 500 kg N/ha.

**Table 4-15 Duration, rate and the final stalk dry matter (DM) accumulation for maize in response to two N levels (0 and 500 kg N/ha) for each of the two water levels (rainfed and irrigated) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
<u>Duration of stalk DM accumulation (°Cd)</u>			
0	528	488	508
500	482	460	471
Mean	505	474	489
SED <sub>N and W</sub> =63.4, SED <sub>N*W</sub> =89.7, P <sub>N</sub> =0.567, P <sub>W</sub> =0.637, P <sub>N*W</sub> =0.888			
<u>Rate of total stalk DM accumulation (t/ha/°Cd)</u>			
0	3.30 <sub>c</sub>	7.10 <sub>b</sub>	5.20
500	4.28 <sub>bc</sub>	14.7 <sub>a</sub>	9.51
Mean	3.79	10.9	7.35
SED <sub>N and W</sub> =0.001, SED <sub>N*W</sub> =0.001, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.005			
<u>Total stalk DM accumulated (t/ha)</u>			
0	1.61 <sub>c</sub>	3.45 <sub>b</sub>	2.53
500	1.98 <sub>c</sub>	6.72 <sub>a</sub>	4.35
Mean	1.80	5.09	3.44
SED <sub>N and W</sub> =0.265, SED <sub>N*W</sub> =0.374, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> <0.001			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### **Remobilised DM and photosynthesised DM contribution to grainfilling**

The decline in leaf and stalk DM (Figure 4-6c & d) were assumed to indicate remobilisation to grains. Both of these DM components were combined to attain the total DM remobilised (Table 4-16). Dry matter remobilised showed leaf DM was not affected by water and N ( $P=0.986$ ). However, the stalk remobilisation was influenced by water ( $P=0.039$ ). Leaf DM remobilised averaged 0.34 t/ha for the crop. Stalk DM remobilised 0.08 t/ha of DM for the rainfed crop and this increased to 0.77 t/ha for the irrigated crop. This influenced the total DM remobilised, increasing from 0.32 when rainfed to 1.18 t/ha with irrigation.

**Table 4-16 Leaf, stalk and total dry matter (DM) remobilised for maize in response to two N levels (0 and 500 kg N/ha) for each of the two water levels (rainfed and irrigated) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
<u>Leaf DM remobilisation (t/ha)</u>			
0	0.15	0.40	0.28
500	0.28	0.51	0.40
Mean	0.22	0.46	0.34
SED <sub>N and W</sub> =0.1003, SED <sub>N*W</sub> =0.1481, P <sub>N</sub> =0.078, P <sub>W</sub> =0.317, P <sub>N*W</sub> =0.986			
<u>Stalk DM remobilisation (t/ha)</u>			
0	0.02	0.65	0.33
500	0.15	0.90	0.52
Mean	0.08 <sub>b</sub>	0.77 <sub>a</sub>	0.43
SED <sub>N and W</sub> =0.298, SED <sub>N*W</sub> =0.421, P <sub>N</sub> =0.536, P <sub>W</sub> =0.039, P <sub>N*W</sub> =0.857			
<u>Total DM remobilised (t/ha)</u>			
0	0.18	0.94	0.56
500	0.45	1.41	0.93
Mean	0.32 <sub>b</sub>	1.18 <sub>a</sub>	0.99
SED <sub>N and W</sub> =0.335, SED <sub>N*W</sub> =0.473, P <sub>N</sub> =0.244, P <sub>W</sub> =0.035, P <sub>N*W</sub> =0.868			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

Source availability was determined from the amount of DM derived from current photosynthesis post-silking during the grain-filling stage, differed with resource availability (Table 4-17). The contribution of DM from photosynthesis showed an interaction of water and N. The amount of DM for grain filling from photosynthesis averaged 0.15 t/ha for rainfed crops, and with irrigation increased from 7.06 t/ha to 14.8 t/ha in response to 500 kg N/ha.

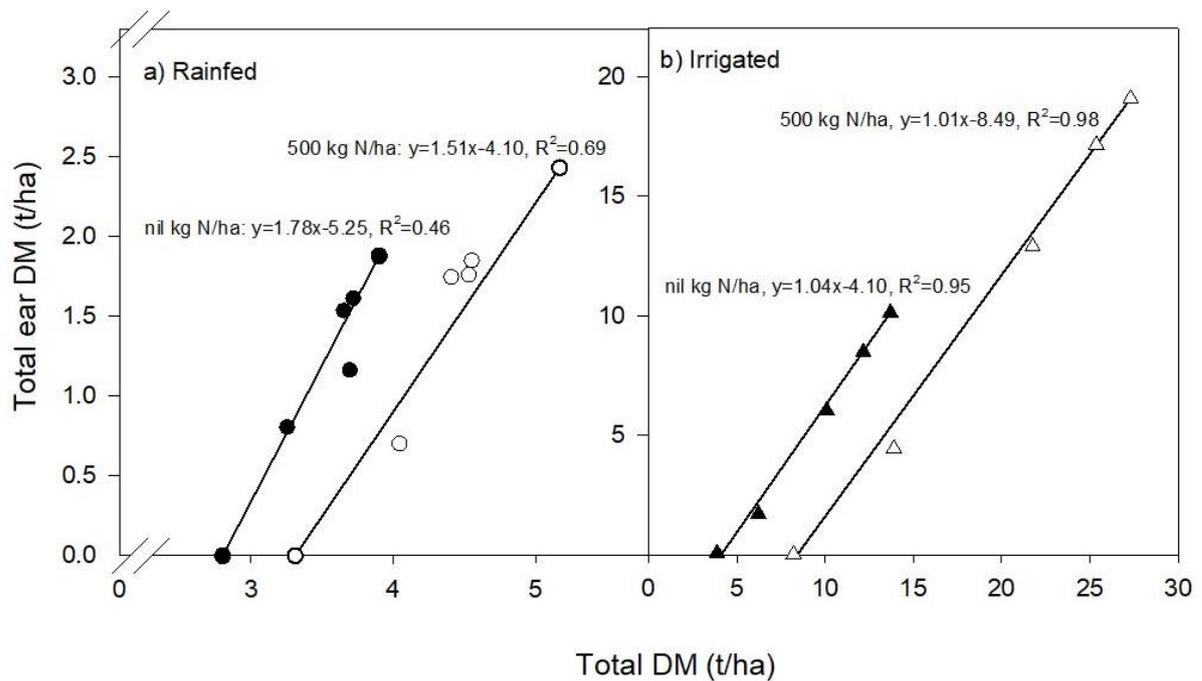
**Table 4-17 Total dry matter (DM) (t/ha) production from post-silking current photosynthesis towards grain-filling for maize in response to two N levels (0 and 500 kg N/ha) for each of the two water levels (rainfed and irrigated) in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
0	0.05 <sub>c</sub>	7.06 <sub>b</sub>	3.56
500	0.25 <sub>c</sub>	14.8 <sub>a</sub>	7.53
Mean	0.15	10.93	5.54
SED <sub>N and W</sub> =0.552, SED <sub>N*W</sub> =0.781, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> <0.001			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### Total and ear DM accumulation

The linear relationship between the ear and total DM accumulated was stronger for the irrigated crop when compared with rain fed crops (Figure 4-7). Ear development and growth are shown in Table 4-18. The rate of total DM partitioning to the ear responded to irrigation ( $P=0.03$ ), and the amount of DM at the start of kernel development (silking) was affected by the interaction between N and water ( $P<0.001$ ). The partitioning rate decreased from 1.65 ear DM/total DM for rain fed to 1.03 ear DM/total DM for irrigated crops. Total DM at the start of ear filling was 2.73 t/ha for rainfed crops without N and increased from 4.1 to 8.6 t/ha for irrigated crops when N was supplied.



**Figure 4-7 Total ear dry matter (DM) against total DM increase during grain-filling for crops grown under two N levels (nil and 500 kg N/ha) at each of two water levels ((a) rainfed (●,○) and (b) irrigation (▲, △)) for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

**Table 4-18 The growth rate and total dry matter (DM) at start of ear development for maize grown at two N levels (at nil and 500 kg N/ha) and two levels of N (rainfed and irrigated) in 2015/16 at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
	<u>Ear partitioning rate (Ear DM/total DM)</u>		
0	1.78	1.04	1.41
500	1.51	1.01	1.26
Mean	1.65 <sub>a</sub>	1.03 <sub>b</sub>	1.34
SED <sub>N and W</sub> =0.266, SED <sub>N*W</sub> =0.376, P <sub>N</sub> =0.511, P <sub>W</sub> =0.033, P <sub>N*W</sub> =0.546			
	<u>Total DM at start of ear development (t/ha)</u>		
0	2.73 <sub>c</sub>	4.12 <sub>b</sub>	3.43
500	3.31 <sub>bc</sub>	8.59 <sub>a</sub>	5.95
Mean	3.02	6.36	4.69
SED <sub>N and W</sub> =0.344, SED <sub>N*W</sub> =0.486, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> <0.001			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

## 4.4 Discussion

### 4.4.1 Experiment 1

Objective 1 was to create maize crops with different yield potentials. Unfortunately, the high initial soil N levels in Experiment 1 did not create the range expected. Therefore, Experiment 2 was set up in a different soil to ensure yield differences and so between them Objective 1 was achieved. This discussion compares the different yield outcomes from each experiment and explains the different yield responses through the main variables of grain yield, total dry matter and CHI. The grain yield is the final yield at crop maturity. Despite the lack of grain yield differences in Experiment 1, the crop growth strategies which contributed to that yield did differ amongst treatments.

#### Grain yield

The grain yield is the product of the total DM produced by the crop and the proportion of that DM that is partitioned into the grain component, quantified as the CHI. The consistent grain yield results across treatments in Experiment 1 suggests that all crops approached the maximum grain yield capacity for this particular stay-green hybrid in this year (Table 4-1). Essentially the genetic component of the hybrid and the environment set the yield potential and this was unaffected by management. Specifically, total DM increased from 19.1 to 23.1 t/ha with irrigated crops under Irr3 and Irr4 and increased from 19.9 – 22.2 t/ha with N. However, this increase in total DM did not result in higher grain yields because there was a decrease in CHI for irrigated crops under Irr3 and Irr4 and this did not affect the N fertilised crops. This hybrid reached its maximum grain yield under these field conditions so there was no impact of water and N on grain-filling. There is evidence that once the crops completed kernel filling, and therefore had met the sink requirements, they diverted

excess assimilate to other DM pools (stem) which caused an increase in total DM but no additional grain yield.

### **Grain yield components**

The total kernel sink size, which determines the demand during grain-filling, involves establishing the number of kernels, and their potential kernel weight which is then met through endosperm expansion enduring and into the middle of the linear kernel growth phase. Kernel growth occurs through assimilate supply from post-silking photosynthate and remobilization from vegetative organs. By assessing the grain components, the influence of water and N on kernel growth and development can be identified.

In Experiment 1, kernel dry weight per plant and number of kernels per plant did not differ among crops (Table 4-2) but the individual kernel weight was lowest for crops without N and water (Irr1 & nil N) indicating a lower sink size. The number of kernels for crops under Irr1 with nil N did not differ from the other crops. This suggests that the time when crop growth was affected was after the final kernel number was set. This implies no limitation in assimilate supply up to this point but after this there were indications of restrictions in kernel growth shown by the decrease in average kernel weight (Tollenaar, 1977). Kernel weight increased by 13% when the crops were irrigated and by 9% when crops were fertilized with N. Crops under Irr2 and 75 kg N/ha were at the maximum point for utilising the water and N for kernel development and growth. Further increases in water and N did not increase the kernel sink size which indicates that in this season the sink capacity was reached with minimal irrigation (Irr2) and with only 75 kg N/ha applied. The maximum number of endosperm cells were established at 75 kg N/ha and the cell could expand to its limit under Irr2 for this maize hybrid in this year. This treatment therefore established the sink capacity for this hybrid and will be used for comparative purposes.

### **Pattern of DM accumulation and partitioning**

The temporal pattern of the total DM accumulation (Figure 4-1) did not differ among crops. There was some difference in the upper asymptote with lower total DM in the nil N treatment associated with reduced individual kernel growth rates. The duration of DM accumulation averaged 785 °Cd across treatments which suggests crop development processes were completed within the same period (Table 4-3). The rate of total DM accumulation for all crops was conservative at 27.8 kg/ha/°Cd for the structural developmental. However, from visual observation of the pattern of DM accumulation suggest there were differences in the duration which was the reason for differences in the final DM. The final DM was lowest for the control (rain fed, nil N) and showed the same response pattern as individual kernel weight gain. The result was therefore that total DM accumulated at the

upper asymptote was 19.7 t/ha and lower than all the N fertilized crops. The same response was observed for irrigated crops, that averaged the lowest total DM at 18.7 t/ha.

The ear is the organ that contains the kernels, and thus the pattern of DM accumulation of the ear (Figure 4-2) represents kernel growth. This is based on the assumption that the non-grain (structural) components of the ear do not change weight during grain-filling. Total crop DM at the start of ear development had no influence on grain-filling and averaged 10.1 t/ha for all the crops (Table 4-9). Dry matter available at this stage is utilised to set the number of kernels (development) rather their size for filling. Therefore, the lack of difference in DM reflects the uniformity in the number of kernels in all crops. Equally, the duration of the period of ear DM accumulation was not different and averaged 409 °Cd. This indicates that all kernel development progressed for the same duration and at the same rate of 34.4 kg/ha/°Cd (Table 4-4). However, visual inspection of the ear DM accumulation pattern indicated differences in the duration which is the reason for the differences in final ear DM. Kernel developmental processes start from the setting of the number of kernels, followed by endosperm establishment through to the middle of rapid linear grain-filling stage. During this period there is rapid water accumulation in granules to accommodate DM for grain-filling. The differences in the final ear DM represents the differences in individual kernel dry weight from grain-filling.

Leaves and stems act as both sink and source organs. The pattern of DM accumulation of the leaf (Figure 4-3) during the vegetative stage did not affect the sink during grain-filling and indicates there was adequate resources to fulfil all structural developmental requirements up to this point in time. The changes in duration, rate and final leaf DM were mainly due to changes in the duration of increasing leaf weight during grain-filling (Table 4-5). Increases in stalk weight ceased at 1064 °Cd which coincided with completion of rapid ear development of kernel structures (Figure 4-4). The duration, rate and final DM of the stalk at the end of the logistic phase show that crop growth and kernel development were consistent for all crops (Table 4-6) up to kernel-filling.

However, the results also suggest that there were differences amongst crops in the amount of remobilized assimilates from vegetative components during grain-filling.

### **Remobilised DM and photosynthesised DM contribution to grain-filling**

The pattern of DM accumulation in the leaf and stalk (Figure 4-3 and Figure 4-4) were consistent until ear development initiated the sink demand from kernels. The drop in stalk DM indicates the kernel sink demand started at ~1064 °Cd and ended at ~1541 °Cd. During this period of rapid ear DM increase, the drop in stalk and leaf DM indicates the ears (kernels) are the main sink for DM and that DM (stored assimilate) is being remobilised to meet the ear demand. Leaf DM was also remobilised to kernel growth, however, at around 1210 °Cd the leaf DM increased again. This coincided with the end of grain-filling and suggests that the demand from kernels had stopped. Thus, the leaves were

probably still photosynthesising, potentially due to the “stay-green” trait. The implication is that excess assimilate was available, so leaf weight increased. Indeed, once the leaf DM had recovered there was also some recovery in stalk DM. Thus, it seems likely that the leaf sink was also met and then the stem became a sink again. The combination of leaf and stalk increases suggests there was photosynthate produced after kernel-filling had ceased. This could be advantageous if the crop was ensiled but also suggests the crop did not set-up sufficient sink capacity in the kernels to fully exhaust the available supply in this season.

The low individual kernel weight in rainfed crops supports the idea that excess assimilate was produced in the irrigated and N fertilized crops. These control crops remobilised leaf and stalk DM that totalled to 4.04 t/ha and was 56% higher than the irrigated crops (Table 4-8). This suggests that the contribution to kernel filling from current photosynthesis was 8.61 t/ha for rain fed crops and 34% lower than the irrigated crops. The lack of grain yield difference was therefore due to the remobilisation of the stalk DM for the control crops and the inability of the irrigated and fertilized crops to increase their sink capacity to fully exploit the available assimilate.

Thus, the results from Experiment 1 showed that supply of DM for grain-filling was initially from the DM reserve pools. The leaves displayed the stay-green trait and maintained green leaf area as the leaf and stalk pools were depleted but the impact of the stay-green trait was minimal in terms of total DM and grain yield because any response was seen after ear DM had reached its peak yield.

### **Total DM influence on ear DM**

The rate of DM accumulation in the ear supports the described changes in dry matter sinks and sources. A rate of one or less means DM was all acquired from current photosynthesis, while a rate higher than one means remobilisation must have occurred from storage organs.

The rainfed crop was most dependent on remobilised DM from the reserve pools and did not replenish these reserves once kernel filling ceased. Figure 4-5 shows the rate of total DM partitioning to the ear was higher than in the irrigated crops at 1.4 ear DM/total DM (Table 4-9). Crops under Irr2 showed an intermediate response with a ratio of 1.2 ear DM/total DM. This also indicates about a 20% dependency on remobilised DM to meet the sink demand from kernel filling. However, irrigated crops did replenish reserve pools because of the active green canopy, post kernel filling. In contrast the rainfed crops experienced water stress at the canopy level and thus the earliest decline and to the lowest levels of leaf and stalk DM.

## 4.4.2 Experiment 2

In Experiment 2 there were yield differences created by the treatments, so Objective 1 was met. In the second year both irrigation and nitrogen affected grain yield and total DM but only irrigation affected CHI (Table 4.10). The discussion will explain which aspects of dry matter accumulation and partitioning were conservative and consistent with Experiment 1 and which components differed.

### Grain yield

The differences in grain yield were larger for Experiment 2 (Table 4-10). The grain yield for the rainfed crop was 0.98 t/ha and increased with irrigation and nil N to 9.0 t/ha, and further to 16.3 t/ha with 500 kg N/ha. The total DM response was consistent, with rainfed crops increasing their total DM at 4.1 t/ha to 14.3 to 28.9 t/ha with irrigation 500 kg N/ha. In both Experiments 1 and 2, water had more effect on the CHI than N. For example, in Experiment 2 water increased CHI from 0.24 to 0.60 but it was  $0.42 \pm 0.01$  for N. Also, pre-silking DM was reduced by the lack of N (Figure 4.6) which also affected total DM and CHI of the rainfed crops (Table 4.10). Post-silking water and N resulted in the highest yields. In the discussion that follows, pre and post silking phases are considered separately.

#### 4.4.2..1 Grain yield components

The mean kernel dry weight per plant in Experiment 2 was 60.7 g/plant (Table 4-11) which was lower than in Experiment 1. However, mean kernel weight was affected by the water and N interaction with the control at 13.4 g/plant, about 10x lighter than the irrigated plus N crops at 124 g/plant. Equally there was a 3x difference in the number of kernels per plant from the rainfed at 177 kernels/plant with 337 kernels per plant for the fully irrigated and fertilised crops. The difference in individual kernel weight was smaller but again affected by the interaction of water and N. The absolute kernel weights attained were lower than in Experiment 1 which suggests there may have been potential for more grain-filling even though the maximum yield of 16.3 t/ha of grain was 25% higher than Experiment 1. This higher yield response to N was expected because the initial N in the soil was lower than in Experiment 1. The site for Experiment 1 had nitrate and mineral N content at 150 mm depth that was within the recommended N levels for maize production (Table 3-1). In contrast to Experiment 2, the nitrate and mineral N content at 150 mm and 600 mm depth was below the requirement for maize (Table 3-2). However, the organic N (potentially available N and anaerobic mineralizable N) was much higher than that of the site in Experiment 1.

In contrast to Experiment 1, both the number of kernels and their individual weight differed in Experiment 2 (Table 4-11). The number of kernels was affected by both water and N as main effects, while water caused a greater response to kernel size with N than without. These combined to give differences in the kernel dry weight per plant that was also affected by the interaction of water and

N. The results also suggest that water stress occurred earlier in Experiment 2. Moisture deficit for rainfed crops were 382 mm while irrigated crops were at 170 mm at silking stage (6<sup>th</sup> February 2017, 781 °Cd) as shown in Figure 3-3. In contrast, crops in Experiment 1 reached silking on the 7<sup>th</sup> of February 2016 (790 °Cd), when the water deficit was 256 mm for the rainfed crops (Irr1) and only accumulated to 369 mm by the end of the growing season. Thus, the water stress was more severe for the rainfed crops in Experiment 2. Both water and N affected resource availability and the assimilate supply during vegetative growth up to the silking stage which had an adverse effect on the number of kernels set.

Individual kernel weight in Experiment 2 was affected by the interaction of water and N. For the rainfed crops, the kernel weight did not differ which is consistent with previous reports (Li et al. (2018) that showed kernel weight does not differ under water stress. It seems the effect of water stress was greater on the number of kernels, which sets the potential yield. Fewer kernels were set when water stress occurred although this was alleviated to some extent by the presence of N. However, the difference between the fertilised and non-fertilised (nil N and 500 kg N/ha) crops was only realised when irrigated. The rainfed crops increased in kernel weight from 207 mg to 253 mg with water and further to 322 mg when fertilised. This is explained by the number of endosperm cells established at silking. The crop without N (irrigated crop with nil N) had fewer endosperm cells thus when irrigated the cells only expanded to cater for the starch accumulated (in assimilate supply). Whereas in the fertilised crop (irrigated crop with 500 kg N/ha), the application of N increased the number of endosperm cells and therefore created more sites for starch deposition. This indicated the importance of N in developing the number of endosperm cells (Reddy and Daynard, 1983) which allows water uptake to facilitate cell expansion (Borrás et al., 2003).

Therefore, in Experiment 2, the main factors affecting yield was the assimilate supply which affected the number of kernels set and then the limitations in N and water for kernel starch cell growth which was evident in the individual kernel weights.

#### **4.4.2.2 Pattern of dry matter accumulation and partitioning**

The pattern of total DM accumulation in Experiment 2 (Figure 4-6a) showed the rainfed crops reached an asymptote earlier, with only a short linear phase compared with the irrigated crops. The irrigated crops had a long linear phase that did not reach an asymptote. The duration of total DM accumulation (Table 4-12) averaged 1487 °Cd for the irrigated crops but the rate of accumulation averaged 20 kg/ha/°Cd for all the crops. However, visual inspection of the total DM accumulation graph suggest there were also differences in the rate. The low DM production of 3.8 t/ha in the non-fertilized rainfed crops indicates a shortage in resource availability. In contrast, the fertilized irrigated crops accumulated 28.9 t DM/ha which was higher than the 23.4 t/ha in Experiment 1. Soil N content

was low in mineral N but high in both potentially available N and anaerobic mineral N (Table 3-2) which suggests the utilisation of this N component in the soil to support the prolonged growth in Experiment 2.

Ear DM accumulation also followed a logistic pattern but showed an indication of reaching an asymptote (Figure 4-6b). In the linear phase the rate of DM accumulation, rather than the duration, affected the grain yield. The implication was that the duration of ear DM accumulation or phenological phase of grain-filling was not affected by the availability of resource. In contrast the rate of kernel filling was the sole contributor to differences in the weight of kernels, or growth of the organ (at developmental stage). It seems likely that the rate of DM accumulation to the ear was influenced by size of the sink reached by the kernels (Table 4-11) which was dependent on resource availability at silking. The ear DM in both irrigated crops peaked at final harvest, indicating that ear growth reached its limit as the kernel sink potential was achieved.

The final ear DM of 18.6 t/ha in Experiment 2 for the irrigated crops with 500 kg N/ha was higher than the average ear DM of 12.9 t/ha in Experiment 1. This supports the idea of a surplus in the supply of assimilate for grain filling in Experiment 1 that was not used to fill kernels (as they were limited by the kernel sink size; mentioned in Section 4.1). This explanation of sink limitation is further supported by comparison of the number of kernels and individual kernel weight per plant in Experiment 1 (Table 4-2).

In Experiment 2, the pattern of DM accumulation in the leaf (Figure 4-6 (c)) showed differences in the linear phase of leaf growth which can be interpreted in relation to the availability of resources. The duration of leaf DM accumulation was only affected by water availability (Table 4-14). This suggests that water stress reduced leaf area development through reduced expansion rate (organ development) or premature senescence. The rate of leaf DM accumulation was affected by the water and N interaction, with no effect of N when water was not available but trebling with N when it was. The result was that total leaf DM was more than double in the irrigated compared with rainfed crops. Overall, the irrigated crops were advantaged by the longer duration of the linear phase and the irrigated crop with 500 kg N/ha by the high rate of leaf DM accumulation. This meant the leaf photosynthetic capacity of the irrigated crops was enhanced, especially when irrigated.

The pattern of stalk DM accumulation followed that of leaf and total DM (Figure 4-6d). The duration of stalk growth was not different for all crops averaging 661 °Cd, which suggests phenology was not affected (including kernel development). However, the rate of stalk DM accumulation was affected by resource availability and influenced potential size of individual kernels (kernel development). Total stalk DM was influenced by the rate of stalk DM accumulation and reflects increases in the weight of

individual kernel weight per plant (Table 4-11). The final stalk DM accumulated at the beginning of grain-filling is an indication of the total DM pool available for DM remobilisation for kernel growth.

#### **4.4.2.3 Remobilised DM and photosynthesised DM contribution to grain-filling**

The pattern of DM remobilised from the leaf and stalk (Figure 4-6c & d) differed from Experiment 1. This was caused by lower soil moisture availability during grain-filling for the irrigated crops (Figure 3-3). In contrast to Experiment 1, there was only evidence of an increase in leaf DM at the end of grain-filling. The leaf DM only increased for the final harvest point which would indicate the sink capacity was reached as ear DM accumulation reduced so excess photosynthate accumulated as DM in leaves and suggest benefits from stay green.

The rainfed crops showed no increase in leaf DM at the end of the season and had a similar pattern of response to that of Experiment 1. For these crops the implication is that leaf DM was not required to meet kernel demand during the grain-filling process. The rainfed crops with N also showed no sign of leaf sink demand. The available DM in its reserve pools was sufficient to supply the demand from the established kernel sink size. There was also excess DM after grain-filling which was adequate to replenish the stalk reserves (Figure 4.6d). Unlike the rainfed crops without N, there was adequate N levels to sustain leaf photosynthesis therefore there was no demand for leaf DM movement due to the small sink size.

Even though results suggest differences in leaf DM remobilisation, the overall amount of leaf DM remobilised was consistent (Table 4-16). The leaf DM remobilised averaged 0.34 t/ha. However, there were differences in the stalk DM remobilisation patterns. Specifically, the irrigated crops, with higher grain sink potential initially lost dry matter during grain-filling. However, as in Experiment 1 this was replenished once ear DM accumulation began to slow. The implication of these two results is that the stalk was the primary source for remobilisation followed by the leaves. If the stalk had sufficient DM to meet the sink demand, then the leaf DM was unaffected, as occurred for the crops which had low total grain yield potentials. The importance of the stalk as a storage organ is shown by the irrigated and fertilized crops when stalk DM was up to 6.72 t/ha then dropped about 1 t/ha to support grain-filling. Once there was a reduction in grain-filling this enabled the stalk to once again become a sink and increase in DM. Therefore, the stalk had the greatest influence on total DM remobilised to meet the sink created by the kernels.

Concurrent with remobilisation, current photosynthesis is the main contributor to meeting the sink demand of growing kernels. For the rainfed crops the contribution from current photosynthate was <0.25 t DM/ha, suggesting crops under severe stress (Table 4-17). In contrast, with water over 7 t DM/ha was attained from the irrigated crop and this doubled when N was added. Thus, the

photosynthetic apparatus of the irrigated crops was able to provide the majority of the assimilate to meet the demand of grain-filling.

#### **4.4.2.4 Total DM influence on ear DM accumulation**

The amount of remobilisation to aid kernel filling was higher for the unirrigated crops that were severely water stressed (Figure 4-7). This was consistent with Experiment 1 that also showed the capacity to compensate for the lack of current photosynthates through remobilisation. However, because the yield potential of the crops rainfed in Experiment 2 was low, and the water stress more severe, the amount remobilised was greater. The amount of DM at silking is indicative of the assimilate supply at that point and was affected by the interaction of water and N (Table 4-18). This was directly related to the soil moisture and soil N conditions around silking. The rate of DM partitioning to the ear was then influenced by the differences in kernel sink size and source capacity. The rate of DM partitioning was influenced by water. The rainfed crop was source limited and thus had the highest rate of 1.65 ear DM/total DM for grain growth being remobilised without replenishing reserves. This may actually represent an upper limit to remobilisation as crops were severely stressed. In contrast, the irrigated crops had a moisture stress free canopy and were able to meet all of the kernel sink demand directly through photosynthesis, with an ear partitioning rate of 1.03 ear DM/total DM and they replenished all stalk reserves. The implication being that there was assimilate left in the stalk that could have been used for kernel growth if needed and thus, that the crops grown under non-limiting conditions were sink limited. In contrast, those grown under water stress were source limited and thus remobilised more reserves.

## **4.5 Conclusion**

Objective 1 was to create crops with different yield potentials and then examine the physiological basis of those differences. However, in Experiment 1 there were no differences in grain yield because the nitrogen and water availability up until ear emergence was not different. This meant that all crops had the same grain yield potential. This was shown by the duration and rate of canopy and kernel development being conservative until kernel growth. At this point differences in water and N availability affected the grain-filling processes but crops achieved the same number and weight of grains by using different mechanisms. This plasticity meant there was only a difference in individual kernel weights of the rainfed crop. Thus, the rainfed crops utilised more of their stalk dry matter to meet the demand for grain-filling. In contrast the irrigated and fertilized plots had a greater supply of current photosynthates and remobilised less of their stalk and leaf dry matter to meet the sink created by grain demand. A feature of this experiment was the increase in leaf and then stalk DM after grain-filling ceased. This showed that there was a continuing supply of assimilate after grain-

filling which may have been the result of the stay-green trait, particularly in the irrigated crops. However, the impact of the trait was too late to affect grain-filling and was therefore only apparent when examining the total DM.

In Experiment 2, there were large differences in grain yield because the duration and rate of canopy and kernel development was affected by water and N limitations. For the rainfed crop the limitation in water and N continued into kernel growth severely affecting the grain-filling process. The differences between the irrigated crops were caused by N which affected kernel number and therefore predetermined the sink size. The irrigated crops that were limited by N enabled kernel growth by fulfilling all kernel DM sink requirements and fully replenished stalk sink reserves. This again highlighted that there was assimilate available after the grain-filling was complete which supports the idea that yield was sink limited, potentially due to the expression of the stay-green trait.

In both experiments, the kernel growth utilised both the DM pool reserves and current photosynthate to satisfy kernel sink demand. The grain-filling process indicated that stalk reserves were remobilised before leaf reserves to meet grain demand. When grain demand was met by current photosynthate then stalk DM was replenished even late in the crop cycle. As expected, the highest yield was produced by the fully irrigated crop with nitrogen, but the implication was that this crop was able to meet grain-filling demand predominantly through current photosynthate and did not expend all of the reserves in the stalk and stem. The implications of the results from both experiments are that the same grain yield can be achieved using reduced N and water rates because grain-filling is sink limited. Alternatively, if the sink can be increased there was probably sufficient reserves to meet the demand. The results of this chapter will be explored further in Chapter 5 where the impact of N and water on light interception and radiation use efficiency will be examined in relation to these different crops with different yield potentials.

## Chapter 5

# Light interception and canopy development

### 5.1 Introduction

Objective 2 of the thesis is to explain yield differences in relation to total iPAR captured and its effects on yield formation (i.e. at silking and grain filling), and describe the development of crop canopies that contribute to different DM accumulation patterns.

By assessing light interception, the yield outputs can be explained by the changes in the canopies that created the different responses in yield onset and post-silking growth. In particular, the total DM at the start of ear development and the rate of DM diverted to kernel growth that affect grain yield. These two variables are investigated by quantifying light interception, particularly through any differences in the time to canopy closure, and crop development (both canopy and kernel) stages. These affect the total DM available to establish kernel sink potential, and the duration and rate of kernel filling.

Light interception is the major determinant of the total DM accumulated. The extinction co-efficient represents the transmission of light through the canopy and thus its ability to intercept light. However, only the green portion of the canopy or green area index (GAI) is effective at capturing light for photosynthesis. Senescing or dead leaves intercept light but do not contribute to DM accumulation so must be accounted for when measuring light interception. The GAI is compromised of the green leaf area, as used in this thesis. In this chapter, the yield scenarios reported in Chapter 4 are explained according to changes in green leaf area of the different crops.

It is the photosynthetic capacity that provides the source that determines the ability and timeliness to supply assimilate to meet kernel sink requirements. In addition, the expression of stay-green traits starts well before senescence (Adhikari et al., 2015). This is exhibited in three phases: firstly, in the chlorophyll build-up in the leaf green area (at vegetative stage) and followed by the extent to which the leaf holds this chlorophyll content prior to initiation of senescence, and finally descending into chlorophyll degradation (the actual senescence process). The commencement, timeliness and rate of progress of each phase affects the lag and rapid linear grain-filling phase of the kernel development process which predetermines assimilate supply to fulfil kernel sink requirement. This GAI pattern and its association with grain development was demonstrated by (Teixeira et al., 2011). If the canopy development and assimilate supply to the kernel development process is well synchronised, then the crop is capable of meeting yield potentials, particularly if the photosynthetic capacity is fully established prior to kernel set. In this chapter, the different yield scenarios are interpreted according

to the rate and duration of green leaf area development, longevity of green leaf area maintenance and timeliness of green leaf area deterioration. Therefore, the patterns of leaf activity are matched against crop capacity to intercept light at kernel developmental stages and growth to meet kernel sink size.

## 5.2 Materials and methods

### 5.2.1 Measurement

For all measurements refer to Chapter 3, Section 3.3.3 and 3.3.5.

### 5.2.2 Calculations

#### Canopy extinction coefficient

Canopy extinction coefficient is determined from  $R_0$  as the incident light above the canopy and  $R$  as the light transmitted, measured below the canopy. The light penetrating through the canopy changes with GAI. The  $k$  value is derived from arranging Equation 2 to make  $k$  the subject.

$$\text{Equation 5-1} \quad k = \frac{\ln \frac{R_0}{R}}{\text{GAI}}$$

This transforms the exponential equation into a linear function from which the  $k$  value is derived from the slope intercepting at zero (Robertson et al., 2001).

#### Light Interception

The fraction of light intercepted is calculated from Equation 2-3. It uses the derived  $k$  values and the GAI from photosynthetically active leaf material. The fraction of light intercepted by the plants is total global solar radiation of which 0.5 is considered to be photosynthetically active radiation (PAR) (Ge et al., 2011). The total light intercepted by the canopy is accumulated from the sum of daily light interception interpolated linearly between measured GAI and light interception readings.

#### GAI

Green area index (GAI) in this study is defined as the photosynthetically active area of the leaf. It is a measure of the green leaf area per unit of ground area. The upper surface area of the green leaf material ( $\text{m}^2$ ) increases with the leaf mass ( $\text{g}$ ), and enables a linear relationship to be determined which quantifies the specific leaf area (SLA) (Hammer et al., 2010). The total green leaf DM or mass of leaf per  $\text{m}^2$  is then used to calculate the GAI ( $\text{m}^2/\text{m}^2$ ) expressed as:

$$\text{Equation 5-2} \quad \text{GAI} = \frac{\text{Leaf DM} \left( \frac{\text{g}}{\text{m}^2} \right)}{\text{SLA} \left( \frac{\text{m}^2}{\text{g}} \right)}$$

Leaf area measurements were taken from physical measurements and LI-COR 3,100 Area Meter as described in Section 3.3.3. Measurements from LI-COR 3,100 Area Meter were used to measure the accuracy of the physical measurements taken. Both types of leaf area measurements were carried out on the sample plants harvested for biomass measurements.

### **Duration of green area**

The time to reach critical GAI (95% light interception) and also the maximum GAI were obtained from rearranging the logistic function fitted to GAI from emergence to pre-senescence stage. This function is expressed to make thermal time the subject as shown in Equation 5.3:

$$\text{Equation 5-3} \quad X = \left[ \frac{\ln\left(\frac{c}{y}-1\right)}{-b} \right] + m$$

The parameter X represents the thermal time, y as the GAI, b is the rate of linear increase for GAI per unit thermal time, m is the inflection point from the linear growth reaching an asymptote and c is the maximum GAI value.

### **Duration of green area holding phase**

The time GAI reached its maximum value to the last harvest measurement before senescence occurred was identified as the 'duration of the green area holding phase'.

### **Green leaf area at cohort level**

The canopy was separated into cohorts to measure the changes in GAI at different levels of the canopy. This was a non-destructive approach with two sample plants tagged and monitored per plot. Measurements were taken on a weekly basis. Leaves were separated into three cohorts depending on the leaf location from the cob bearing leaf. The leaf/leaves which had sheath(s) wrapped around the cob(s) plus the two leaves below and above were referred to as the mid cohort. The lower and upper cohorts are separated by the mid cohort. Green leaf area was measured as described in Section 3.3.3

### **Phyllochron**

The phyllochron was measured for both the leaf tips and fully expanded leaves (ligule visible). Both variables showed a bilinear relationship over time: leaf tip count and leaf expansion measurements were measured against thermal time. The regressed slopes represent the interval between leaf appearance/full leaf development which defines the phyllochron. The point of inflection is the

connecting point where thermal time and leaf tip/expanded leaf are equal for the two linear regressions. Experiment 1 had insufficient data to show this relationship.

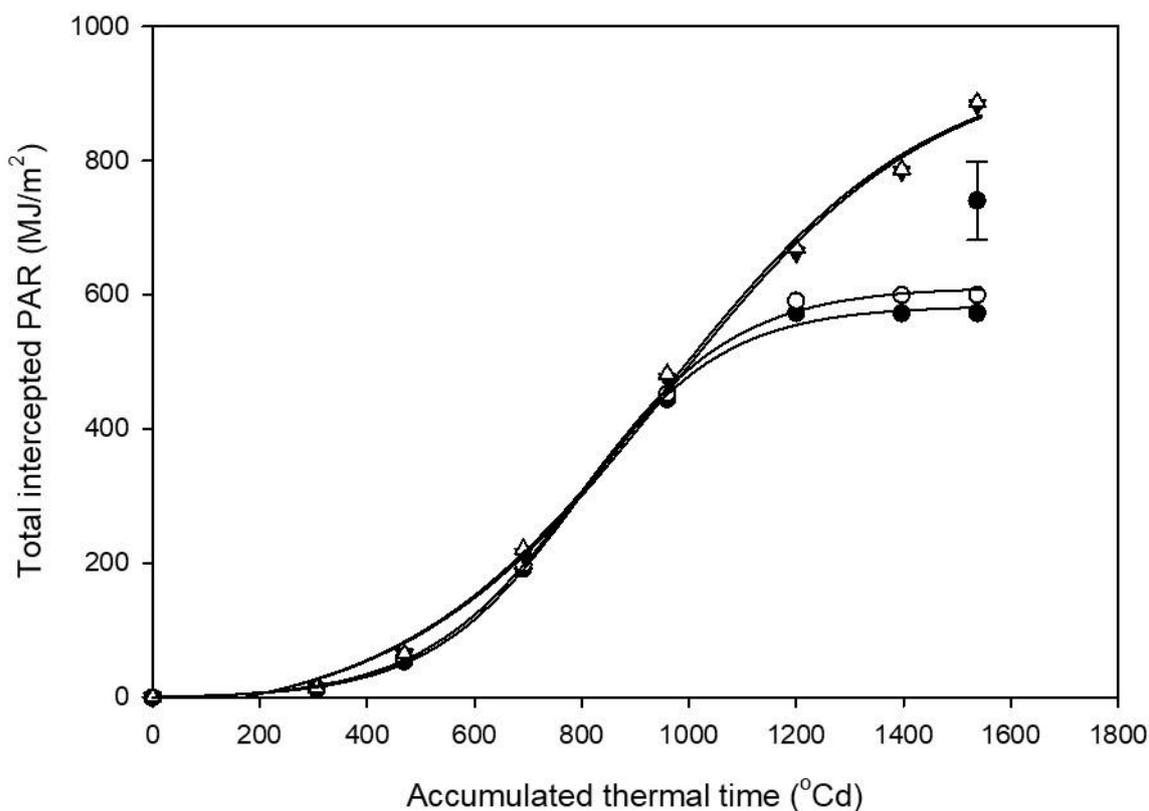
## 5.3 Results

### 5.3.1 Experiment 1

Since there were no grain yield differences in Experiment 1, the results of the light interception will focus on the lowest and highest water treatments i.e. Irr1 and Irr4.

#### Total intercepted PAR

The intercepted PAR for the crops with nil N and 300 kg N/ha at Irr1 and Irr4 were examined to assess canopy expansion. The intercepted PAR followed a logistic curve with a lag phase followed by a linear phase and finally reaching an asymptote (Figure 5-1). From the observed pattern in the graph, the total intercepted PAR reached an asymptote earlier than the last field measurement dates with no irrigation (nil N and 300 kg N/ha at Irr1) but continued the linear response with irrigation.



**Figure 5-1** Total intercepted PAR ( $\text{MJ}/\text{m}^2$ ) against the thermal time for maize to nil N (●) and 300 kg N/ha (○) under Irr1 and nil N (▲) and 300 kg N/ha (△) under Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard error of the mean across the points.

Total PAR intercepted was affected by water ( $P=0.003$ ) but not N ( $P=0.764$ ) (Table 5-1) or their interaction. There was also a consistent effect of water on the rate ( $P<0.001$ ) and duration ( $P=0.006$ ) of the total PAR intercepted. The accumulated PAR increased from 570 to 1082 MJ/m<sup>2</sup> with irrigation. This was caused by slow rate at 0.59 MJ/m<sup>2</sup>/°Cd and longer duration at 1831 °Cd of intercepted PAR with irrigation in contrast to the faster rate at 0.67 but shorter duration at 849°Cd of intercepted PAR without irrigation. The main attribute of the irrigated crop was the prominent linear phase as projected by the logistic curve extended to 1831 °Cd (Logistic curve fit:  $P= 98.1$  se  $\pm 41.1$ , linear curve:  $P= 97.9$  se  $\pm 43.2$ ). The rainfed crops showed a more distinct logistic response and also had a closer fit than the linear curve ( $P= 99.3$  se  $\pm 18.5$ ). The rainfed crops had a longer lag phase of 377 °Cd and consequently shorter time (849 °Cd) to reach its asymptote.

**Table 5-1 The total intercepted PAR (MJ/m<sup>2</sup>), rate of interception (MJ/m<sup>2</sup>/°Cd) and duration (°Cd) at initial PAR interception process for maize in response to nil N and 300 kg N/ha at Irr1 and Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Irr1	Irr4	
	<u>Total intercepted PAR (MJ/m<sup>2</sup>)</u>		
0	556	1089	822
300	586	1076	830
Mean	570 <sub>b</sub>	1082 <sub>a</sub>	827
SED <sub>N</sub> =27.8 SED <sub>W</sub> =58.5, SED <sub>N*W</sub> =64.8, P <sub>N</sub> =0.764, P <sub>W</sub> =0.003, P <sub>N*W</sub> =0.472			
	<u>Rate of PAR intercepted (MJ/m<sup>2</sup>/°Cd)</u>		
0	0.67	0.59	0.63
300	0.67	0.59	0.63
Mean	0.67 <sub>a</sub>	0.59 <sub>b</sub>	0.63
SED <sub>N</sub> =0.007 SED <sub>W</sub> =0.006, SED <sub>N*W</sub> =0.009, P <sub>N</sub> =0.641, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.919			
	<u>Duration of PAR intercepted (°Cd)</u>		
0	849	1837	1330
300	874	1826	1350
Mean	849 <sub>a</sub>	1831 <sub>b</sub>	1340
SED <sub>N</sub> =25.7, SED <sub>W</sub> =48.7, SED <sub>N*W</sub> =55.1, P <sub>N</sub> =0.981, P <sub>W</sub> =0.006, P <sub>N*W</sub> =0.496			

Means with different letters are significantly different  $\alpha=0.05$ .

### Canopy extinction coefficient

The exponential relationship between the fraction of PAR intercepted and GAI was converted into a linear relationship to attain the k value (Equation 5-1). This is the relationship between the natural log of transmitted light and GAI as derived from the SunScan canopy analyser and destructive harvests (Figure 5-2). The line of best fit indicated there was a response to irrigation ( $P=0.035$ ) which gave k values of 0.838, showing an erect leaf projection without irrigation, and flatter leaves at k values of 0.871 with irrigation.

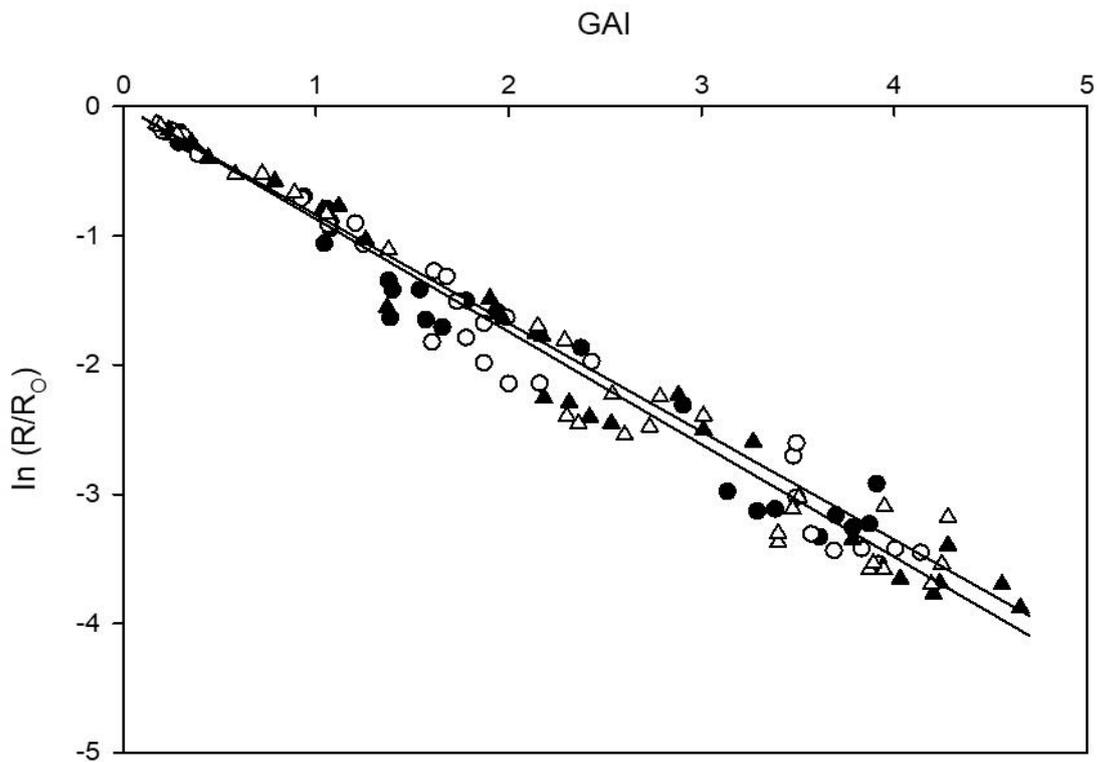


Figure 5-2 Natural log of  $R/R_0$  versus green area index (GAI) measuring light attenuation through the maize canopy in response to two N levels of urea at 0 and 300 kg N/ha for each of two water levels, Irr1 (0 (●) and 300 kg N/ha (○)) and Irr4 (0 (▲) and 300 kg N/ha (△)) for the sampling dates of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. The solid lines represent linear regression at  $y=0.838x$  (●&○) and  $y=0.871x$  (▲&△).

### Critical LAI

The critical LAI was derived at 95% light interception from the exponential relationship between the fraction of light intercepted and the GAI (Figure 5-3). At 95% light interception, the critical LAI was 3.5 for rainfed crops (nil and 300 kg N/ha) and 3.6 for irrigated crops (nil and 300 kg N/ha at Irr4).

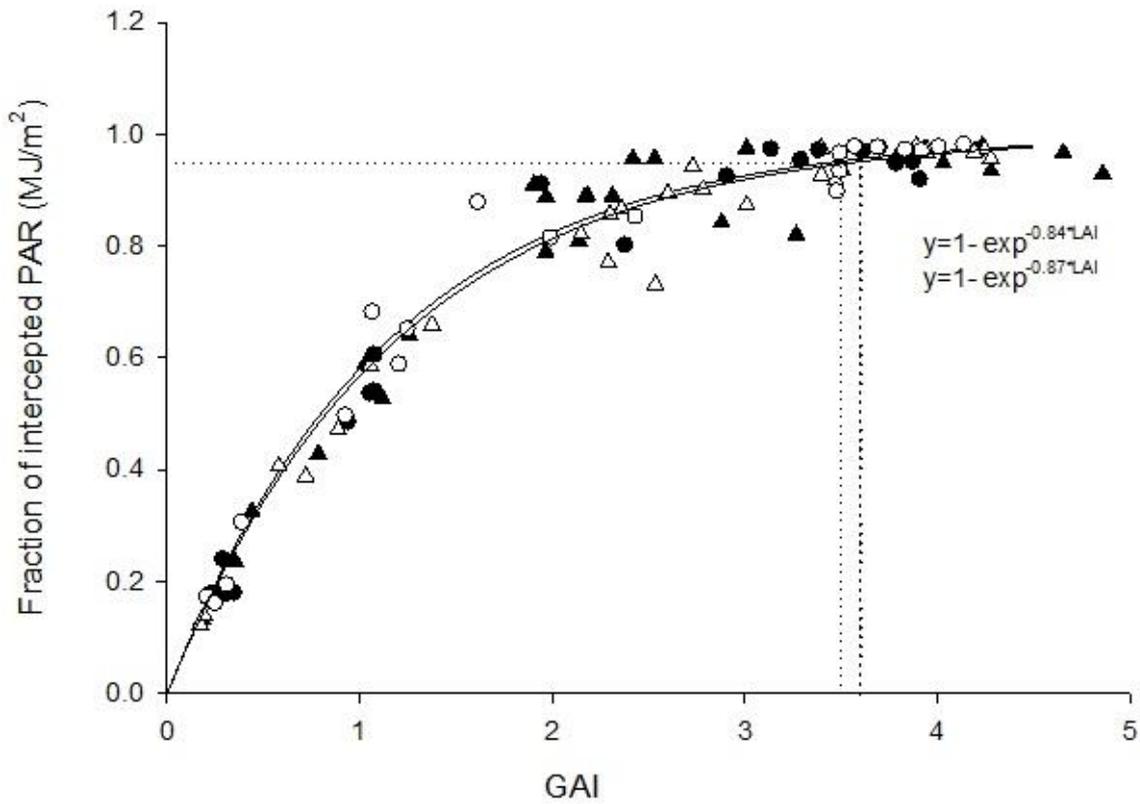


Figure 5-3 Fraction of light intercepted versus green area index (GAI) for maize in response to nil N (●) and 300 kg N/ha (○) under Irr1 and nil N (▲) and 300 kg N/ha (△) under Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. The solid lines represent exponential curves at  $y=1-\exp^{-0.84 \cdot LAI}$  (●&○) and  $y=1-\exp^{-0.87 \cdot LAI}$  (▲&△). The dotted lines indicate 95% light interception when the critical LAI is at 3.5 and 3.6.

## Green area development

### 5.3.1..1 Green area index

The pattern of green area expansion showed three phases: an increase in green area, attainment of the critical GAI and then a decline with senescence. The rate and duration of these three phases were analysed (Table 5-2). In the first phase, there were no differences in the rate ( $P=0.177$ ) and duration ( $P=0.200$ ) of GAI increase to reach the critical GAI. A similar response was seen in the second phase where there were also no differences in the duration of maintaining the GAI at and above the critical GAI level ( $P=0.200$ ). However, in the third phase, the decline in GAI was evident as water ( $P=0.003$ ) influenced the rate of GAI decrease. This explains the differences in the total intercepted PAR (Table 5-1).

**Table 5-2 Rate of linear increase in GAI, duration to reach critical GAI, duration of GAI above the critical GAI in thermal time and rate of linear increase in GAI for maize in response to two N levels (urea at 0 and 300 kg N/ha) for rainfed crops (Irr1) and irrigated crops (Irr4) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N	Water		Mean
	Irr1	Irr4	
<u>Maximum GAI (m<sup>2</sup>/m<sup>2</sup>)</u>			
0	3.41	3.59	3.50
300	3.72	4.10	3.91
Mean	3.57	3.85	3.71
SED <sub>N</sub> =0.132, SED <sub>W</sub> =0.339, SED <sub>N*W</sub> =0.363, P <sub>N</sub> =0.074, P <sub>W</sub> =0.403, P <sub>N*W</sub> =0.551			
<u>Rate of linear increase in GAI (m<sup>2</sup>/m<sup>2</sup>/ °Cd)</u>			
0	0.007	0.015	0.011
300	0.010	0.007	0.009
Mean	0.008	0.011	0.010
SED <sub>N</sub> =0.003 SED <sub>W</sub> =0.004, SED <sub>N*W</sub> =0.005, P <sub>N</sub> =0.509, P <sub>W</sub> =0.541, P <sub>N*W</sub> =0.177			
<u>Time to reach critical GAI (°Cd)</u>			
0	722	632	677
300	662	691	676
Mean	692	662	677
SED <sub>N</sub> =41.47 SED <sub>W</sub> =42.66, SED <sub>N*W</sub> =59.50, P <sub>N</sub> =0.989, P <sub>W</sub> =0.535, P <sub>N*W</sub> =0.200			
<u>Duration of maintaining GAI at and above the Critical GAI level (°Cd)</u>			
0	232	327	283
300	298	268	283
Mean	286	298	392
SED <sub>N</sub> =41.47 SED <sub>W</sub> =42.66, SED <sub>N*W</sub> =59.50, P <sub>N</sub> =0.989, P <sub>W</sub> =0.535, P <sub>N*W</sub> =0.200			
<u>Rate of linear decrease in GAI (m<sup>2</sup>/m<sup>2</sup>/ °Cd)</u>			
0	0.014	0.001	0.008
300	0.014	0.001	0.008
Mean	0.014 <sub>a</sub>	0.001 <sub>b</sub>	0.010
SED <sub>N</sub> =0.001 SED <sub>W</sub> =0.002, SED <sub>N*W</sub> =0.002, P <sub>N</sub> =0.812, P <sub>W</sub> =0.003, P <sub>N*W</sub> =0.881			

Means with different letters are significantly different  $\alpha=0.05$ .

### 5.3.1..2 Green leaf area

The pattern of leaf area development is shown in Figure 5-4. A corresponding pattern is observed in the leaf area development displaying leaf area expansion, maximum and decline phases.

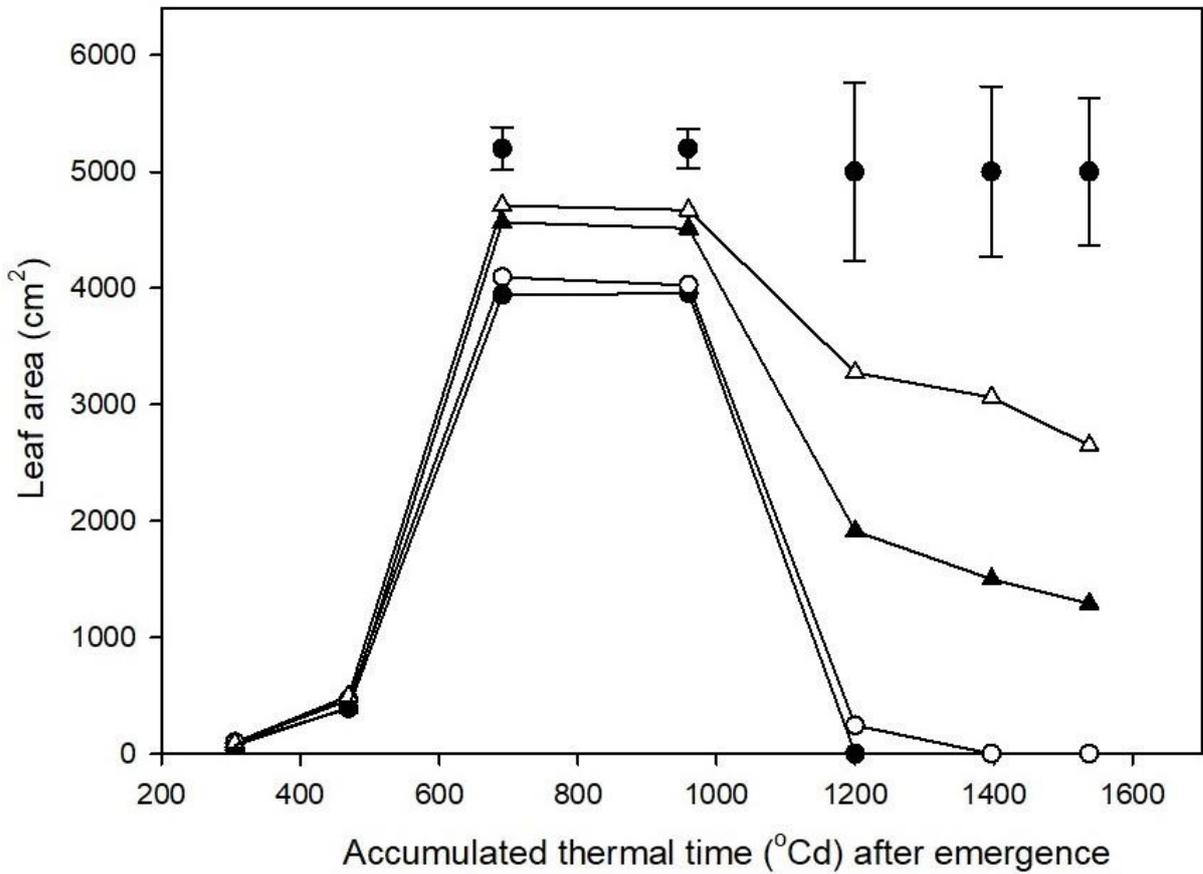
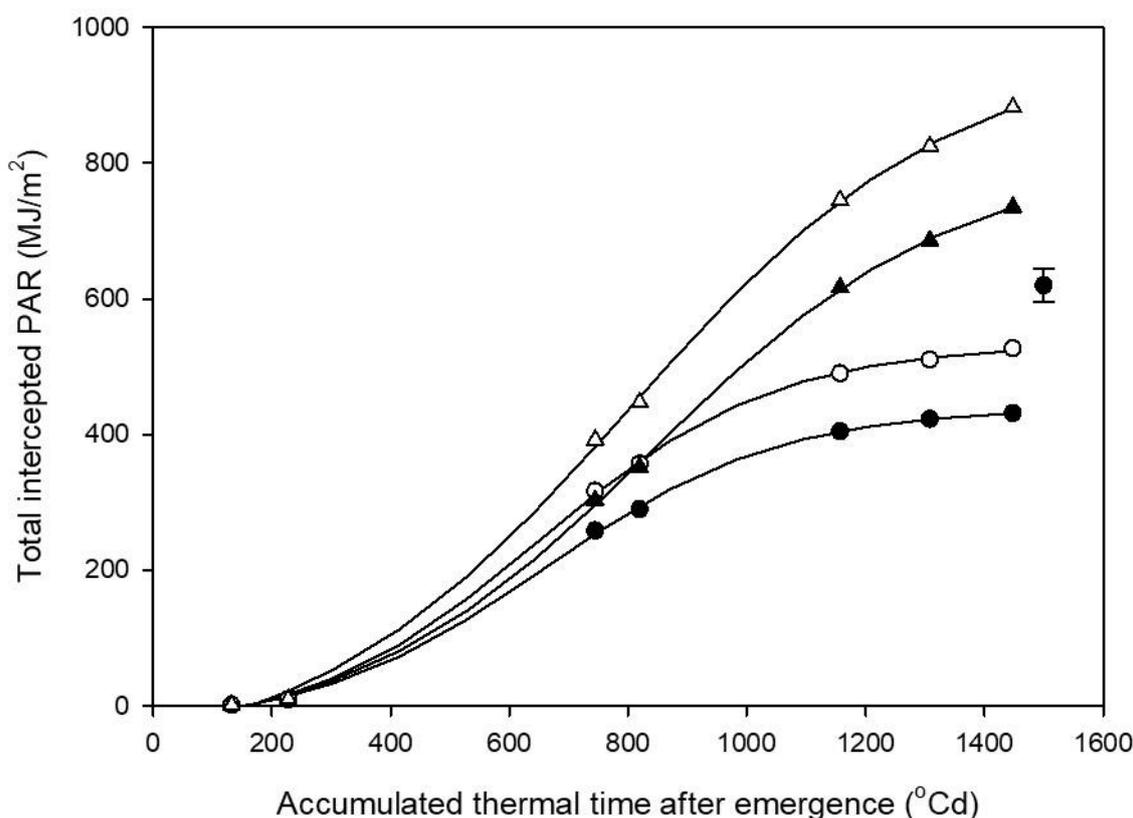


Figure 5-4 Leaf area development per plant in thermal time for maize in response to nil N (●) and 300 kg N/ha (○) under Irr1 and nil N (▲) and 300 kg N/ha (△) under Irr4 for the sampling dates of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bars represent standard deviation of the means of the leaf area at each harvest date.

### 5.3.2 Experiment 2

#### Total intercepted PAR

The relationship between light interception and thermal time also followed a logistic response in Experiment 2 (Figure 5-5). The lag phase (time to 5% of maximum) of low light capture lasted less than 200 °Cd and then there was a linear increase before the upper asymptote.



**Figure 5-5 Total accumulated PAR (MJ/m<sup>2</sup>) against thermal time for maize in response to two N levels ((○, ▲) and 500 kg N/ha (○,△)) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bar indicate the standard error of the means.**

The total intercepted PAR was influenced by an interaction between water and N ( $P=0.029$ ) (Table 5-3). The total intercepted PAR increased from 448 to 551 MJ/m<sup>2</sup> in response to N without irrigation, but N increased the amount of light intercepted from 816 to 1005 MJ/m<sup>2</sup> with irrigation. Crops showed treatment effects through increased total intercepted PAR from 500 to 910 MJ/m<sup>2</sup> with irrigation and from 632 to 778 MJ/m<sup>2</sup> with N. This effect was due to the rate of intercepted PAR as influenced by water ( $P<0.001$ ) and N ( $P<0.001$ ). The rate of intercepted PAR increased from 0.42 MJ/m<sup>2</sup>/°Cd without water to 0.58 MJ/m<sup>2</sup>/°Cd with water. N increased the rate from 0.46 MJ/m<sup>2</sup>/°Cd to 0.55 MJ/m<sup>2</sup>/°Cd. The duration of the linear phase was affected by water ( $P<0.001$ ), increasing from 1183 °Cd without irrigation to 1563°Cd with irrigation.

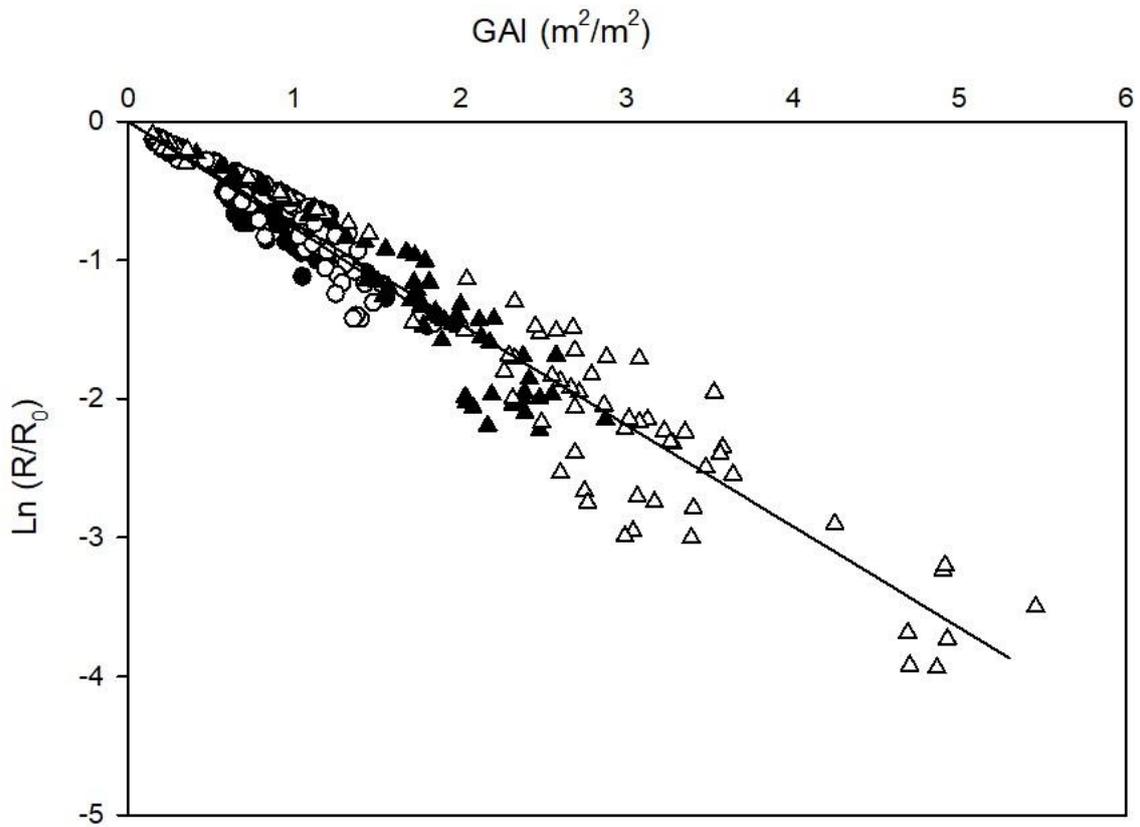
**Table 5-3 The total intercepted PAR (MJ/m<sup>2</sup>), rate of interception (MJ/m<sup>2</sup>/°Cd) and duration of linear phase (°Cd) at initial PAR interception process for maize in response to two N levels (nil and 500 kg N/ha) for each of two water levels (rain fed and irrigated) for the final harvest of 2016/17 (Experiment 2) at Lincoln University.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
	<u>Total intercepted PAR (MJ/m<sup>2</sup>)</u>		
0	448 <sub>d</sub>	816 <sub>b</sub>	632
500	551 <sub>c</sub>	1005 <sub>a</sub>	778
Mean	500	910	705
SED <sub>N and W</sub> =17.25, SED <sub>N*W</sub> =24.39, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.029			
	<u>Rate of intercepted PAR (MJ/m<sup>2</sup>/°Cd)</u>		
0	0.38	0.54	0.46 <sub>b</sub>
500	0.47	0.62	0.55 <sub>a</sub>
Mean	0.42 <sub>b</sub>	0.58 <sub>a</sub>	0.50
SED <sub>N and W</sub> =0.015, SED <sub>N*W</sub> =0.021, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.957			
	<u>Duration of linear phase (°Cd)</u>		
0	1174	1513	1344
500	1191	1612	1402
Mean	1183 <sub>a</sub>	1563 <sub>b</sub>	1374
SED <sub>N and W</sub> =1.361, SED <sub>N*W</sub> =33.6, P <sub>N</sub> =0.199, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.361			

Means with different letters are significantly different  $\alpha=0.05$ .

### Extinction coefficient

The extinction co-efficient (Figure 5-6) showed no influence of water ( $P=0.162$ ) or N ( $P=0.085$ ) and averaged a  $k$  value of 0.75 for all the treatments.



**Figure 5-6** The linear relationship between the natural log of  $R/R_0$  and the GAI from the destructive harvest for maize in response to two N levels at 0 and 500 kg N/ha for each of two water levels (rainfed (●,○) and irrigated (▲,△)) for the sampling dates of 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.

### Critical LAI

The critical GAI at 95% light interception from a full canopy was reached for the irrigated crop with N as shown in Figure 5-7. The exponential function indicated: a critical GAI of 4.0 for all the crops.

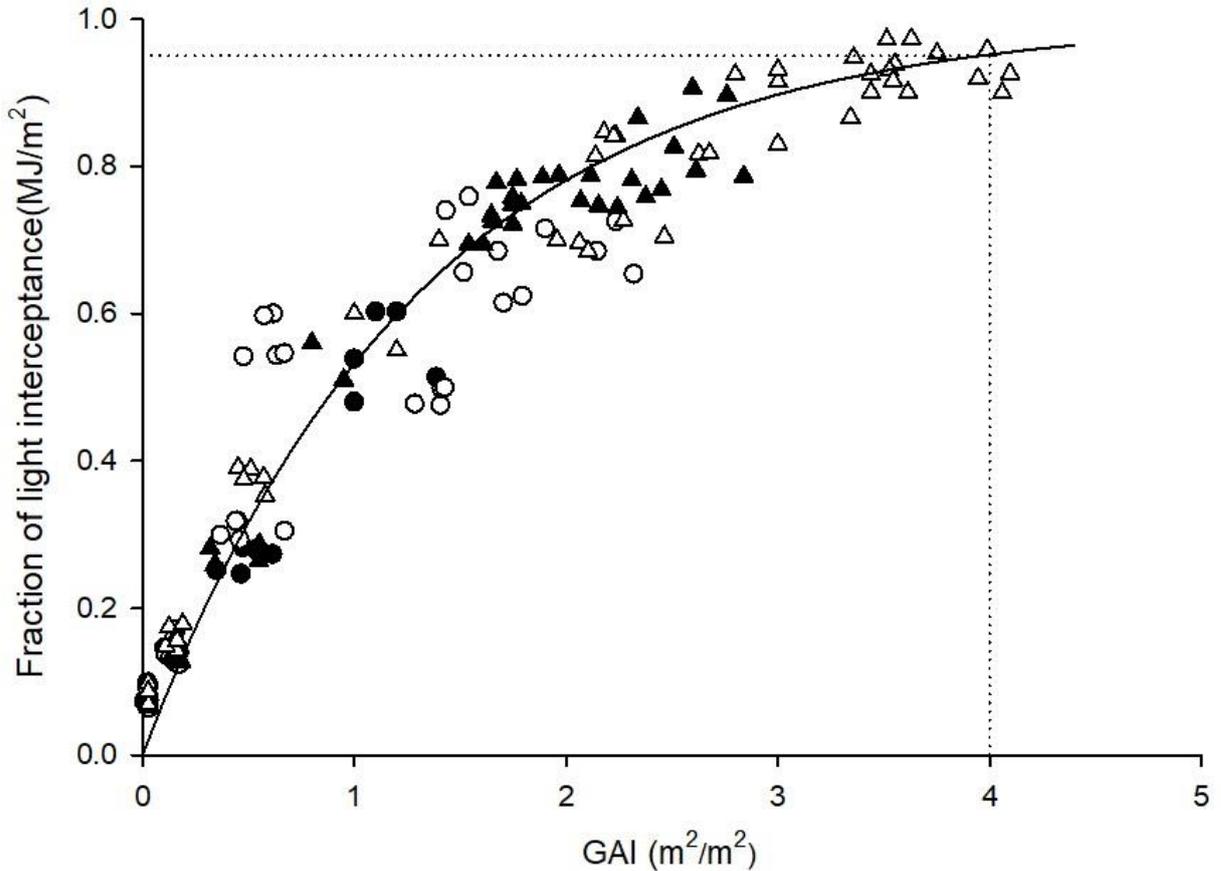


Figure 5-7 The fraction of light intercepted versus green area index (GAI) for maize in response to two N levels at nil and 500 kg N/ha for each of two water levels, nil irrigation (nil (●) and 500 kg N/ha (○)) and irrigated crop (nil (▲) and 500 kg N/ha (△)) for the sampling dates of 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. The solid lines represent exponential curves at  $y = 1 - \exp^{-0.75 * LAI}$ . The dotted lines indicate the critical LAI at 4.0.

## Green area development

### 5.3.2..1 *Green area index*

The derived variables of GAI from Figure 5-8 are shown in Table 5-4. The maximum GAI was influenced by the water and N treatments. The irrigated crops increased in maximum GAI from 2.14 to 3.49 m<sup>2</sup>/m<sup>2</sup> and when fertilised with N increased from 2.48 to 3.14 m<sup>2</sup>/m<sup>2</sup>. Based on the maximum GAI, the green area build-up phase; indicated by the rate and duration of linear phase showed an interaction between water (P<0.001) and N (P=0.004). The rate of linear increase in GAI increased from 0.003 m<sup>2</sup>/m<sup>2</sup>/ °Cd for the rainfed crop without N to 0.024 m<sup>2</sup>/m<sup>2</sup>/°Cd when irrigated with 500 kg N/ha (Table 5-9). The duration to reach maximum GAI was shortest at 166 °Cd for the irrigated crop with 500 kg N/ha and averaged 558 °Cd for rainfed crops with the longest duration of 958 °Cd for the irrigated crop without N.

The duration of maintaining GAI (at and above the maximum GAI), was influenced by water (P<0.001). The duration for irrigated crops was 332 °Cd and without irrigation this phase was not evident.

The rate of the decline in green area was affected by the interaction between water and N (P<0.001). The irrigated crop delayed senescence which brought about a sharper decline of 0.009 m<sup>2</sup>/m<sup>2</sup>/°Cd for crops with N and 0.005 m<sup>2</sup>/m<sup>2</sup>/°Cd without N. The rate of decline for the rainfed crop was 0.002 m<sup>2</sup>/m<sup>2</sup>/ °Cd.

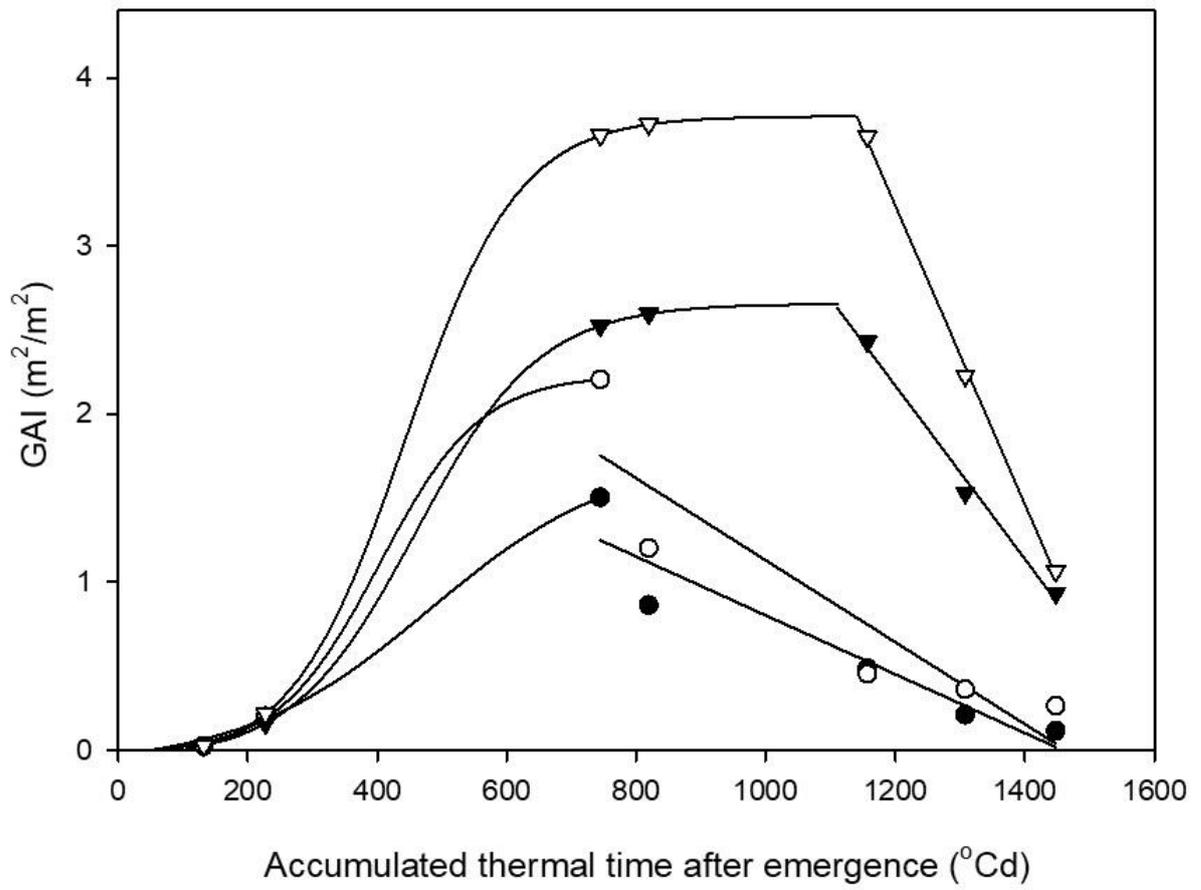


Figure 5-8 Green area index (GAI) versus accumulated thermal time (°Cd) for maize in response to nil N (●) and 300 kg N/ha (○) under Irr1 and nil N (▲) and 300 kg N/ha (△) under Irr4 for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.

**Table 5-4 The maximum green area index (GAI), rate of linear increase in GAI, duration to reach maximum GAI, duration of maintaining GAI at and above the maximum GAI level in thermal time and rate of linear increase GAI for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
<u>Maximum GAI (m<sup>2</sup>/m<sup>2</sup>)</u>			
0	1.75	3.21	2.48 <sub>b</sub>
500	2.52	3.76	3.14 <sub>a</sub>
Mean	2.14 <sub>b</sub>	3.49 <sub>a</sub>	2.81
SED <sub>N and w</sub> =0.221, SED <sub>N*W</sub> =0.312, P <sub>N</sub> =0.012, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.397			
<u>Rate of linear increase in GAI (m<sup>2</sup>/m<sup>2</sup>/ °Cd)</u>			
0	0.003 <sub>b</sub>	0.003 <sub>b</sub>	0.003
500	0.005 <sub>b</sub>	0.024 <sub>a</sub>	0.014
Mean	0.004	0.013	0.008
SED <sub>N and w</sub> =0.002, SED <sub>N*W</sub> =0.002, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> <0.001			
<u>Duration to reach maximum GAI (°Cd)</u>			
0	598 <sub>b</sub>	958 <sub>a</sub>	778
500	519 <sub>b</sub>	166 <sub>c</sub>	342
Mean	558	562	560
SED <sub>N and w</sub> =100.3, SED <sub>N*W</sub> =141.9, P <sub>N</sub> <0.001, P <sub>W</sub> =0.970, P <sub>N*W</sub> =0.004			
<u>Duration at green area holding phase (°Cd)</u>			
0	0 <sub>c</sub>	250 <sub>b</sub>	125
500	0 <sub>c</sub>	415 <sub>a</sub>	207
Mean	0	332	166
SED <sub>N and w</sub> =26.2, SED <sub>N*W</sub> =37.1, P <sub>N</sub> =0.009, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.009			
<u>Rate of decline in GAI (m<sup>2</sup>/m<sup>2</sup>/°Cd)</u>			
0	0.002 <sub>c</sub>	0.005 <sub>b</sub>	0.003
500	0.002 <sub>c</sub>	0.009 <sub>a</sub>	0.006
Mean	0.002	0.007	0.005
SED <sub>N and w</sub> =26.2, SED <sub>N*W</sub> =37.1, P <sub>N</sub> =0.009, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.09			

Means with different letters are significantly different  $\alpha=0.05$ .

### 5.3.2.2 Cohort leaf area

An assessment of the leaf area components provides a dissection of the canopy structure (Figure 5-8). The response of the maximum GAI was consistent with the total leaf area where crops responded to water and N. The increase in leaf area was from 2978 to 3568 cm<sup>2</sup>/plant when irrigated and from 2829 to 3717 cm<sup>2</sup>/plant when N was applied (Table 5-5). The maximum leaf area for the lower cohort was influenced by water (P=0.317), which increased leaf area from 955 cm<sup>2</sup> to 1339 cm<sup>2</sup>. The mid cohorts were affected by both water (P=0.011) and N (P<0.001). Their leaf area of 1095 cm<sup>2</sup> without irrigation and larger area of 1320 cm<sup>2</sup> with water, and 934 cm<sup>2</sup> without N increasing to 1481 cm<sup>2</sup> with N. A similar response was observed in the upper canopy where leaf area was responsive to both water (P=0.013) and N (P<0.001). The maximum leaf area was 563 cm<sup>2</sup> without irrigation and 737 cm<sup>2</sup> with irrigation, and 428 cm<sup>2</sup> without N and 873 cm<sup>2</sup> with N.

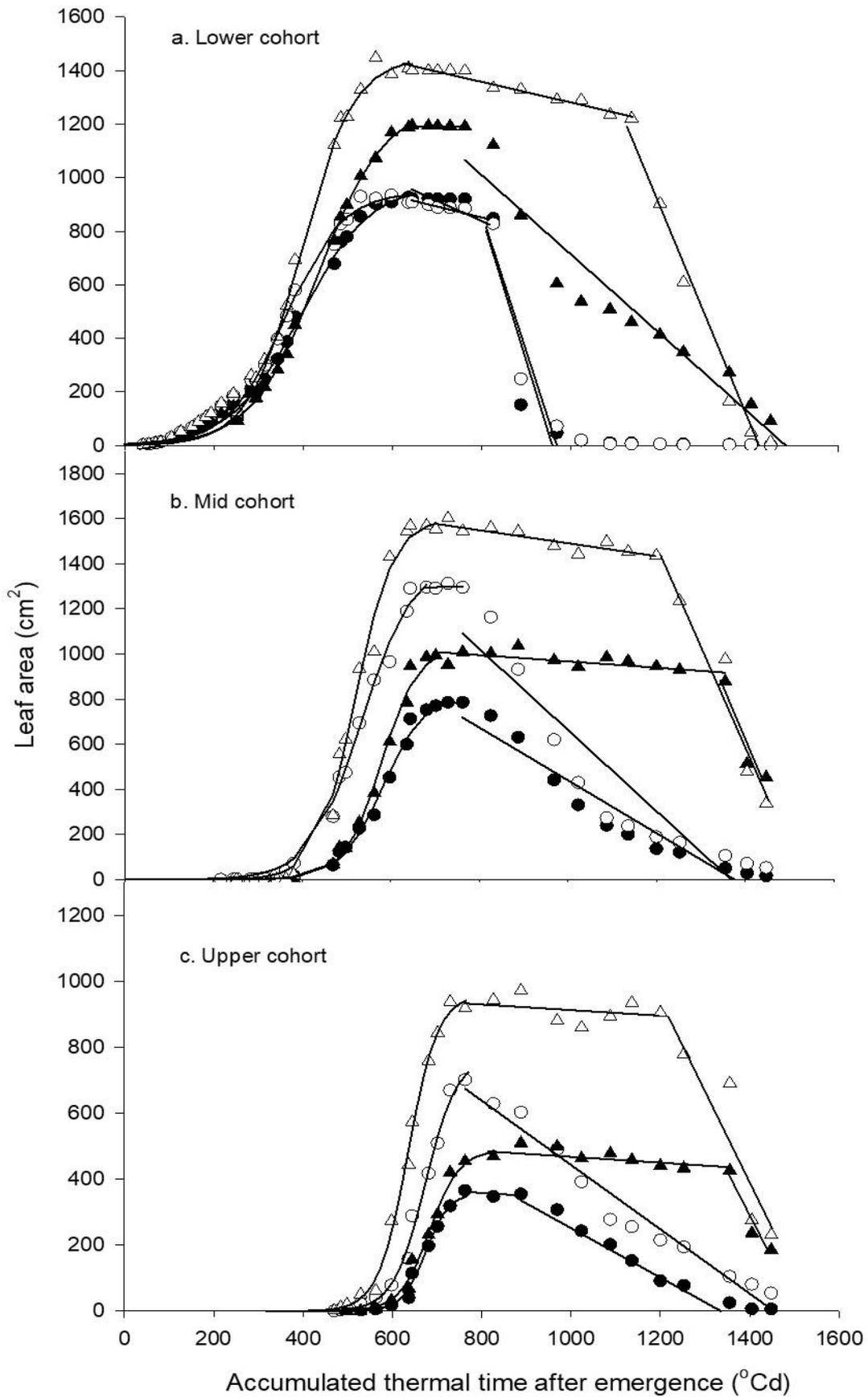


Figure 5-9 Leaf area per plant versus thermal time for the three cohorts: the lower (a), mid (b) and top (c) leaf layers for maize in response to nil N (●) and 500 kg N/ha (○) under rainfed and nil N (▲) and 500 kg (△) with irrigation for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.

**Table 5-5 The total and maximum leaf area per plant at each cohort in cm<sup>2</sup>/plant for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
	<u>Total leaf area</u>		
0	2654	3004	2829 <sub>b</sub>
500	3301	4133	3717 <sub>a</sub>
Mean	2978 <sub>b</sub>	3568 <sub>a</sub>	3273
SED <sub>N and W</sub> =202.9, SED <sub>N*W</sub> =287.0, P <sub>N</sub> <0.001, P <sub>W</sub> =0.013, P <sub>N*W</sub> =0.257			
	<u>Lower cohort</u>		
0	974	1258	1116
500	936	1419	1178
Mean	955 <sub>b</sub>	1339 <sub>a</sub>	1147
SED <sub>N and W</sub> =95.5, SED <sub>N*W</sub> =135.1, P <sub>N</sub> =0.533, P <sub>W</sub> =0.002, P <sub>N*W</sub> =0.317			
	<u>Mid cohort</u>		
0	836	1031	934 <sub>b</sub>
500	1353	1610	1481 <sub>a</sub>
Mean	1095 <sub>b</sub>	1320 <sub>a</sub>	1207
SED <sub>N and W</sub> =74.8, SED <sub>N*W</sub> =105.8, P <sub>N</sub> <0.001, P <sub>W</sub> =0.011, P <sub>N*W</sub> =0.684			
	<u>Upper cohort</u>		
0	357	500	428 <sub>b</sub>
500	770	975	873 <sub>a</sub>
Mean	563 <sub>b</sub>	737 <sub>a</sub>	650
SED <sub>N and W</sub> =59.5, SED <sub>N*W</sub> =84.2, P <sub>N</sub> <0.001, P <sub>W</sub> =0.013, P <sub>N*W</sub> =0.609			

Means with different letters are significantly different  $\alpha=0.05$ .

The ability of the canopy to maintain green leaf area was examined at the different cohorts (Table 5-6). The duration of green area in the asymptotic phase for the leaf area of lower canopy showed an interaction ( $P=0.038$ ) between water and N. The green leaf area was maintained for 227 °Cd for crops without water and N and was extended to 476 °Cd with water and N. The mid cohort also showed an interaction ( $P=0.008$ ) between water and N, increasing the green area holding period from 87 °Cd for rainfed crops to 557 °Cd for crops with water and N and further to 648 °Cd for crops with water but without N. The upper canopy was only affected by water ( $P<0.001$ ); the duration of the asymptotic phase for crops without irrigation was 56 °Cd and increased to 478 °Cd for irrigated crops.

**Table 5-6 Duration of green area holding phase ( $^{\circ}\text{Cd}$ ) for the leaf area of lower, mid and upper canopy in  $^{\circ}\text{Cd}$  for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
<u>Lower cohort</u>			
0	227 <sub>b</sub>	231 <sub>b</sub>	229
500	213 <sub>b</sub>	476 <sub>a</sub>	344
Mean	220	353	287
SED <sub>N and W</sub> =55.5, SED <sub>N*W</sub> =78.6, P <sub>N</sub> =0.060, P <sub>W</sub> =0.034, P <sub>N*W</sub> =0.038			
<u>Mid cohort</u>			
0	67 <sub>c</sub>	648 <sub>a</sub>	358
500	108 <sub>c</sub>	557 <sub>b</sub>	333
Mean	87	603	345
SED <sub>N and W</sub> =20.7, SED <sub>N*W</sub> =29.3, P <sub>N</sub> =0.247, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.008			
<u>Upper cohort</u>			
0	20	498	259
500	91	458	285
Mean	56 <sub>b</sub>	478 <sub>a</sub>	267
SED <sub>N and W</sub> =39.8, SED <sub>N*W</sub> =56.2, P <sub>N</sub> =0.185, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.705			

Means with different letters are significantly different  $\alpha=0.05$ .

The senescence phase was assessed as the decline in green area after the asymptotic phase (Table 5-7). The rate of decline in green leaf area at the lower cohort showed an interaction ( $P=0.035$ ) between water and N. It declined at a rate of  $3.83 \text{ cm}^2/^{\circ}\text{Cd}$  without water and N but at  $1.48 \text{ cm}^2/^{\circ}\text{Cd}$  for irrigated crops with 500 kg N/ha. Senescence at the mid and upper cohorts was affected by water ( $P<0.001$ ). The decline in rate for the mid cohort was at  $1.45 \text{ cm}^2/^{\circ}\text{Cd}$  for the rainfed crop with a steeper but later decline at  $4.55 \text{ cm}^2/^{\circ}\text{Cd}$  for the irrigated crop. In the upper cohort, the rate was  $0.82 \text{ cm}^2/^{\circ}\text{Cd}$  for the rainfed crop and faster at  $2.70 \text{ cm}^2/^{\circ}\text{Cd}$  for the irrigated crop.

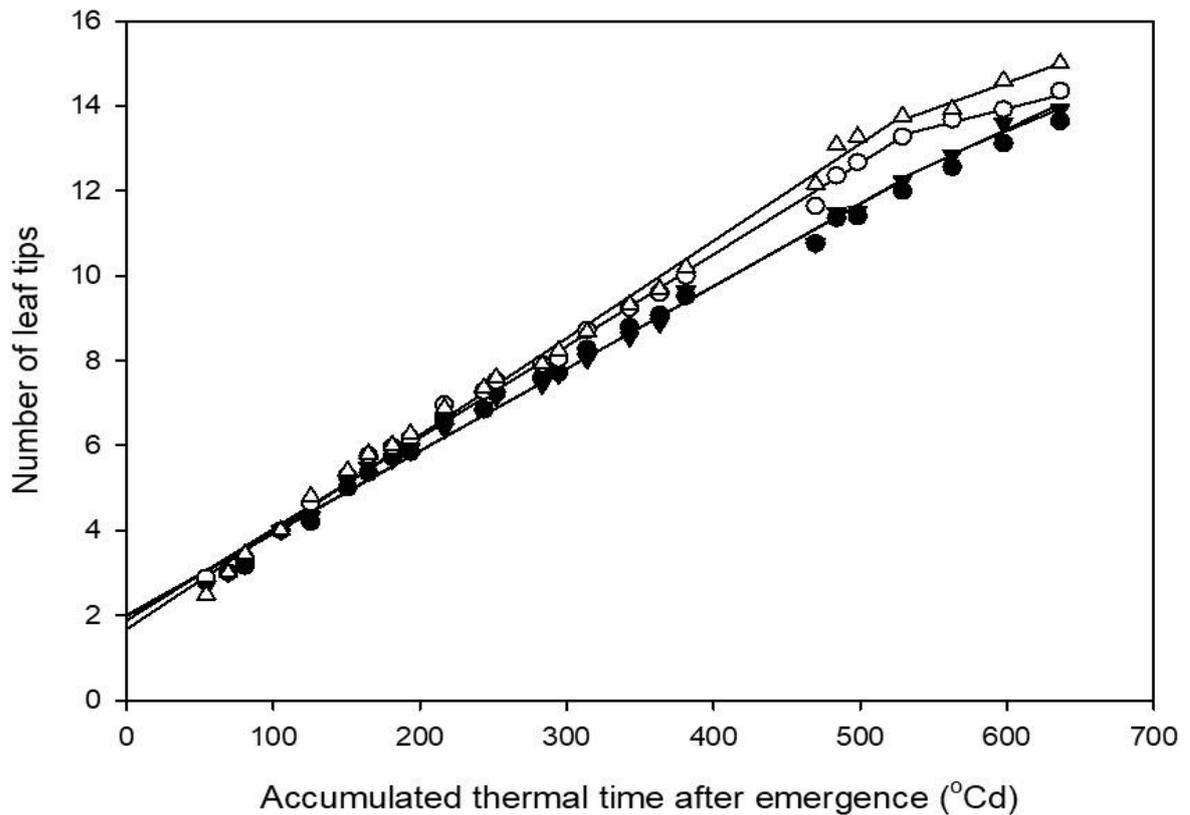
**Table 5-7 The rate of linear decline in leaf area in cm<sup>2</sup>/°Cd for the three canopy cohorts (lower, mid and lower) for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
<u>Lower cohort</u>			
0	3.83 <sub>a</sub>	1.48 <sub>b</sub>	2.66
500	3.86 <sub>a</sub>	4.02 <sub>a</sub>	3.94
Mean	3.85	2.75	3.30
SED <sub>N and W</sub> =0.531, SED <sub>N*W</sub> =0.751, P <sub>N</sub> =0.062, P <sub>W</sub> =0.033, P <sub>N*W</sub> =0.035			
<u>Mid cohort</u>			
0	1.11	4.65	2.88
500	1.80	4.46	3.13
Mean	1.45 <sub>b</sub>	4.55 <sub>a</sub>	3.00
SED <sub>N and W</sub> =0.271, SED <sub>N*W</sub> =0.383, P <sub>N</sub> =0.376, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.132			
<u>Upper cohort</u>			
0	0.65	2.63	1.64
500	0.98	2.76	1.87
Mean	0.82 <sub>b</sub>	2.70 <sub>a</sub>	1.76
SED <sub>N and W</sub> =0.1733, SED <sub>N*W</sub> =0.2451, P <sub>N</sub> =0.216, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.597			

Means with different letters are significantly different  $\alpha=0.05$ .

### 5.3.2.3 Leaf appearance

Leaf initiation and appearance of leaves reflect the changes in leaf area. These events relate to the green area accumulation phase (Figure 5-10 and Figure 5-11). There was a bilinear response with the faster rate of leaf appearance related to the upper leaf cohort.



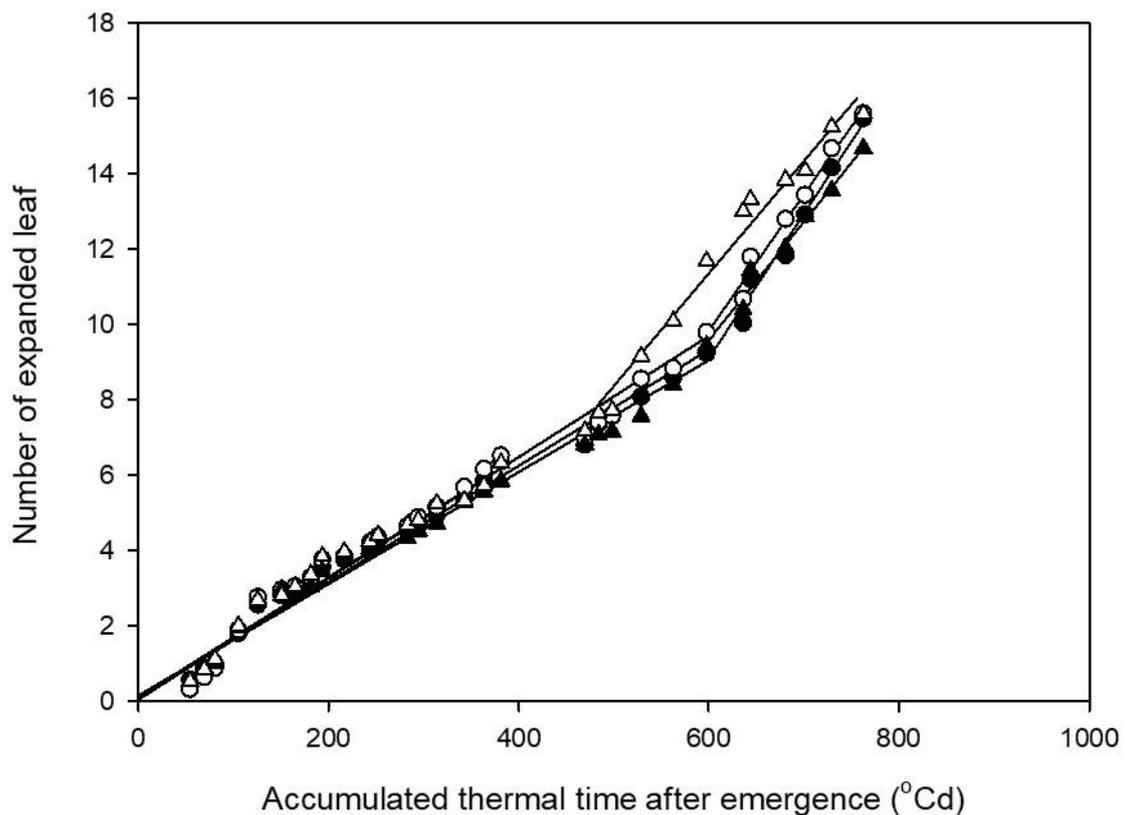
**Figure 5-10** Number of visible leaf tips versus thermal time for maize in response to two N levels ((●) and 500 kg N/ha (○)) for rainfed and irrigated crops (nil N (▲) and 500 kg N/ha (△)) for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. The first linear phase indicating the phyllochron at Stage 1 and the later indicating the phyllochron at Stage 2.

The coefficients related to leaf initiation are presented in Table 5-8. The initiation of leaf tips at Stages 1 and 2 was affected by N ( $P=0.001$  and  $P=0.016$ , respectively). Leaf initiation for Stage 1 took  $43.8\text{ }^{\circ}\text{Cd}/\text{leaf}$  for crops without N and  $39.2\text{ }^{\circ}\text{Cd}/\text{leaf}$  with 500 kg N/ha. The duration of leaf initiation at Stage 2 was  $67.8\text{ }^{\circ}\text{Cd}/\text{leaf}$  for crops without N and was longer at  $101.2\text{ }^{\circ}\text{Cd}/\text{leaf}$  with 500 kg N/ha. The total leaf tips per plant at the point of inflection was also affected by N ( $P=0.016$ ). There were 4.7 leaves without N and 9.7 with 500 kg N/ha. The overall number of leaf tips per plant was influenced by N ( $P=0.009$ ) and not water ( $P=0.514$ ). Leaf tips per plant for crops without N was 14.8 and increased to 15.7 with 500 kg N/ha.

**Table 5-8 The interval between leaf tips during Stage 1 (528 °Cd) and Stage 2 (528 -690 °Cd), the number of leaf tips at point of inflection, and total number of leaf tips per plant for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
<u>Phyllochron (leaf tips) Stage 1 (°Cd/leaf)</u>			
0	44.3	43.2	43.8 <sub>a</sub>
500	40.0	39.2	39.2 <sub>b</sub>
Mean	42.1	40.8	41.5
SED <sub>N and W</sub> =1.079, SED <sub>N*W</sub> =1.526, P <sub>N</sub> =0.001, P <sub>W</sub> =0.290, P <sub>N*W</sub> =0.899			
<u>Phyllochron (leaf tips) Stage 2 (°Cd/leaf)</u>			
0	70.0	65.6	67.8 <sub>b</sub>
500	113.8	88.5	101.2 <sub>a</sub>
Mean	91.9	77.0	84.5
SED <sub>N and W</sub> =11.98, SED <sub>N*W</sub> =16.95, P <sub>N</sub> =0.016, P <sub>W</sub> =0.239, P <sub>N*W</sub> =0.399			
<u>Number of leaf tips per plant at the point of inflection</u>			
0	4.71	4.64	4.68 <sub>b</sub>
500	10.4	9.09	9.74 <sub>a</sub>
Mean	7.55	6.87	7.21
SED <sub>N and W</sub> =1.032, SED <sub>N*W</sub> =1.460, P <sub>N</sub> <0.001, P <sub>W</sub> =0.514, P <sub>N*W</sub> =0.565			
<u>Total number of leaf tips per plant</u>			
0	14.6	14.9	14.8 <sub>b</sub>
500	15.4	16.0	15.7 <sub>a</sub>
Mean	15.0	15.5	15.2
SED <sub>N and W</sub> =0.290, SED <sub>N*W</sub> =0.411, P <sub>N</sub> =0.009, P <sub>W</sub> =0.139, P <sub>N*W</sub> =0.547			

Means with different letters are significantly different  $\alpha=0.05$ .



**Figure 5-11** Number of fully expanded leaves versus thermal time for maize in response to two N levels (nil (●) and 500 kg N/ha (○)) for rainfed and irrigated crops (nil N (▲) and 500 kg N/ha (△)) for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. The first linear phase determines the phyllochron for Stage 1 and the later for the phyllochron at Stage 2.

Quantification of leaf appearance is given in Table 5-9. Phyllochron at Stage 1 was influenced by N ( $P=0.027$ ) taking 65.4 °Cd/leaf for crops without N and 62.0 °Cd/leaf for crops with 500 kg N/ha. There was no effect of water ( $P=0.173$ ) and N ( $P=0.074$ ) on the phyllochron at Stage 2 which averaged 49.8 °Cd/leaf. The number of expanded leaves at point of inflection per plant was affected by water ( $P<0.001$ ) with a leaf number of 9.5 without irrigation and fewer at 8.0 with irrigation. The final number of expanded leaves per plant was not influenced by water and N and had an average leaf count of 15.3.

**Table 5-9 The phyllochron for expanded leaves during Stage 1 (498/597 °Cd) and Stage 2 (498/597 - 762 °Cd), the number of expanded leaves at point of inflection, and total number of expanded leaves per plant for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
	<u>Phyllochron - Stage 1 (°Cd/leaf)</u>		
0	64.5	66.3	65.4 <sub>a</sub>
500	62.1	61.9	62.0 <sub>b</sub>
Mean	63.3	64.1	63.7
SED <sub>N and W</sub> =1.347, SED <sub>N*W</sub> =1.905, P <sub>N</sub> =0.027, P <sub>W</sub> =0.561, P <sub>N*W</sub> =0.465			
	<u>Phyllochron - Stage 2 (°Cd/leaf)</u>		
0	49.3	52.1	50.7
500	49.0	48.9	48.9
Mean	49.2	50.5	49.8
SED <sub>N and W</sub> =0.919, SED <sub>N*W</sub> =1.300, P <sub>N</sub> =0.074, P <sub>W</sub> =0.173, P <sub>N*W</sub> =0.149			
	<u>Number of expanded leaves per plant at the point of inflection</u>		
0	9.53	8.34	8.94
500	9.55	7.68	8.62
Mean	9.54 <sub>a</sub>	8.01 <sub>b</sub>	8.78
SED <sub>N and W</sub> =0.292, SED <sub>N*W</sub> =0.413, P <sub>N</sub> =0.406, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.240			
	<u>Total number of expanded leaves per plant</u>		
0	15.5	14.7	15.1
500	15.6	15.6	15.6
Mean	15.5	15.1	15.3
SED <sub>N and W</sub> =0.273, SED <sub>N*W</sub> =0.386, P <sub>N</sub> =0.081, P <sub>W</sub> =0.168, P <sub>N*W</sub> =0.168			

Means with different letters are significantly different  $\alpha=0.05$ .

## 5.4 Discussion

In this discussion, yield differences in Chapter 4 are examined in relation to total iPAR captured to meet Objective 2. Specifically, yield is related to attributes of the canopies that contributed to the different DM accumulation patterns.

### 5.4.1 Experiment 1

In Experiment 1, Section 4.4.1 outlined no grain yield differences among crops but the mechanism through which DM was partitioned to the ear differed. For the rainfed crop, grain-filling was dependent on DM pool reserves. In comparison, the crop at Irr3 was mainly reliant on post-silking photosynthesis to supply current assimilates. The implication being that there were reserves in the leaves and stalk that were not drawn into the grain. This section explores how the canopy developed for each crop influenced the crop strategies that enabled the demand of grain-filling to be met.

#### Total intercepted PAR

The fitted model to the light interception curve was a logistic curve (Figure 5-1). In the fitted logistic curve, the canopy establishment and leaf senescence phase were signified by the upper and lower asymptote, respectively. The linear canopy growth was marked by the rapid vegetative growth phase. The bi-linear curve as used by Kosgey (2011) did not account for a reduction in light interception caused by the decrease in GAI as a result of the senescence process. The crop with delayed senescence portrayed a more linear response. The linear phase was more consistent between the irrigated and rainfed crops than at the asymptote phase.

The total intercepted PAR was 570 MJ/m<sup>2</sup> for the rainfed crops and almost doubled to 1082 MJ/m<sup>2</sup> when irrigated (Table 5-1). The duration of light interception was the main reason for differences in the total intercepted PAR. The duration of the irrigated crop was 982 °Cd and more than double the rainfed crop which explains the differences in total DM. However, this doubling effect of the duration on the total iPAR did not affect the grain yield.

The rate of light interception was 0.59 MJ/m<sup>2</sup>/°Cd for the irrigated crops and 8% higher than the rainfed crops. However, this difference appears to be an artefact of the analysis. The curve fitting process shows a longer lag phase for the rainfed crop and lower rate but the accuracy of the rate calculation may have been affected by the low number of sample points in the linear phase of the rainfed crop. Specifically, there were only three sample points in the linear phase of the rainfed crop (Figure 5-1), compared with 5-6 in the irrigated crops. Between 500 and 1000 °Cd the lines were parallel suggesting the rate was conservative at its maximum. This indicates a biological maximum rate for the environment in this season.

### **Canopy extinction coefficient**

The extinction coefficient differed between the irrigated and rainfed crops which indicates a difference in the efficiency of light interception. The extinction coefficient was lower at 0.838 for the rainfed crop (Figure 5-2) and indicated a more erect leaf projection. The higher extinction coefficient of 0.8711 for the irrigated crop reflects the prostrate leaf arrangement of the canopy, which may occur with longer leaves that droop. The canopy extinction coefficient determines the efficiency of interception per unit of leaf area. Therefore, despite different canopy extinction coefficients, the total iPAR is most affected by GAI.

### **Critical GAI**

The rainfed crop achieved 95% canopy cover at a GAI of 3.5 GAI whereas larger more watered canopy of the irrigated crop was at 3.6 GAI (Figure 5-3). The canopy structure of the rainfed crop appears to have been more efficient in capturing light which may be related to the leaf cohort development and their leaf area.

### **Green area index**

As a main function that influences the light intercepted, GAI is used to explain the differences in the light interception curve. Table 5-2 shows that there was no difference in the canopy expansion, with the maximum GAI of 3.7 m<sup>2</sup>/m<sup>2</sup>. The rate of linear increase in GAI averaged 0.01 m<sup>2</sup>/m<sup>2</sup>/ °Cd. This indicates that canopy development was not different across treatments and explains the uniform crop growth rate which resulted in no differences in the amount of DM accumulated at the start of ear development (Table 4-9). Additionally, grain-filling is associated with the duration for which GAI is maintained above the critical level or at maximum GAI. This duration averaged 392 °Cd for all the crops, which is consistent with the no differences in final total grain yields.

The senescence phase mainly affected the remobilised DM pools. The slow rate of senescence at 0.001 m<sup>2</sup>/m<sup>2</sup>/ °Cd with irrigation suggests current assimilate was a sufficient source to meet the demand or sink of grain-filling during this phase and once grain-filling ceased also replaced all DM that was previously diverted to grain-filling. The faster rate of 0.014 m<sup>2</sup>/m<sup>2</sup>/ °Cd in the rainfed crops explains the low assimilate supply off-setting DM reserve pools after remobilisation of DM to grain-filling reflected in the low total DM. The consequence was 4 t/ha lower total DM yield but no difference in grain yield (Table 4.1).

### **Leaf area**

The temporal pattern of response from GAI was reflected in the response of the leaf area (Figure 5-4). The initial phase of linear increase was consistent amongst treatments with no differences in the maximum leaf area during the period when the number of kernels was set. However, the sink

demand from the grains has resulted in an earlier and more rapidly decline in green leaf area of the rainfed crops to meet that demand. Thus, total DM differed but not grain yield.

### **5.4.2 Experiment 2**

In Experiment 2, the main differences in yield were caused at the start of ear development stage where limitations in availability of resources in some crops limited DM at the kernel development stage. The grain-filling phase for the rainfed crops was predominantly dependent on DM reserves (Section 4.4.2) whereas the source for irrigated crops appeared to have met the sink post-silking, through current photosynthesis, which also replenished all DM reserve pools.

#### **Total intercepted PAR**

The relationship between total iPAR and thermal time was represented by a logistic curve as presented in Figure 5-5. This is consistent with Experiment 1 where the reduction in PAR interception due to senescence was not captured in a bi-linear curve. The temporal pattern of response is the result of different aspects of canopy development.

The total PAR intercepted was 448 MJ/m<sup>2</sup> for the rainfed (control) crop and increased with application of water and N, being doubled to 1005 MJ/m<sup>2</sup> for the irrigated crop with 500 kg N/ha (Table 5-3). This increase was caused by differences in both the rate and duration of PAR interception. The rate was 0.42 MJ/m<sup>2</sup>/°Cd for the rainfed crops and increased by 6% with application of water and 9% to 0.46 MJ/m<sup>2</sup>/°Cd when fertilised with N. The rate of PAR intercepted impacts on crop development especially the ear formation. Water increased the duration of the linear phase from 1183 to 1563 °Cd which highlights the importance of water in maintaining the longevity of canopy functions.

#### **Canopy extinction coefficient**

Figure 5-6 shows the rate of light attenuation through the canopy averaged 0.75 k value for all the crops. These values are within the normal range of extinction coefficient values reported for maize of 0.45- 0.90 (Stockle and Kemanian, 2009). The erect leaves have a lower k value while prostate leaves perceive a higher k value. In this experiment the treatments did not alter canopy angle which indicates the extinction coefficient as a constant variable, as found in Experiment 1, and the differences in total iPAR were therefore mainly due to changes in GAI.

#### **Critical GAI**

The crop irrigated crop with N achieved Critical GAI of 95% crop cover at 4.0 m<sup>2</sup>/m<sup>2</sup> (Figure 5-7). For the other crops resource availability restricted full plant growth and development and impaired leaf growth from reaching critical LAI. The inability to reach critical GAI affected ear development especially kernel setting (number of kernels).

## **Green area index**

The maximum GAI was affected by water and N (Table 5-4)(Figure 5-8) but was not reflected in the differences in the grain yield. Rather, the maximum GAI was influenced by the rate and duration of GAI linear increase which dictated the amount of light intercepted and thus grain yield.

For the rainfed crop, the GAI build-up progressed at a rate of  $0.004 \text{ m}^2/\text{m}^2/^\circ\text{Cd}$  lasting for a duration of  $558^\circ\text{Cd}$ . This comprised of a slow rate and short duration and explains the low maximum GAI attained of  $2.14 \text{ m}^2/\text{m}^2$  which is consistent with its low total DM and grain yields.

Irrigation increased the efficiency of the canopy to intercept light, not necessarily by the rate of linear increase in GAI but by the longer duration of  $958^\circ\text{Cd}$ . This resulted in the intermediate yields. Nitrogen accelerated the rate of linear increase in GAI to  $0.024 \text{ m}^2/\text{m}^2/^\circ\text{Cd}$ . However, this rapid rate resulted in a shorter period of  $166^\circ\text{Cd}$  of linear GAI increase. The shorter duration probably restricted the period of kernel setting. The response to N also doubled the duration of the GAI maximum (plateau) phase, increasing the duration from  $250$  to  $415^\circ\text{Cd}$ . This is consistent with the higher total light interception and yields. A consequence of this delayed senescence, was a more rapid rate of decline at  $0.005 \text{ m}^2/\text{m}^2/^\circ\text{Cd}$  without N and at  $0.009 \text{ m}^2/\text{m}^2/^\circ\text{Cd}$  with N. Irrigation appears to have also provided the crops with a sufficiently wide window at the end of grain-filling to restore DM reserves in the leaves and stalk (Table 4-17) that were previously remobilised to satisfy kernel sink demand.

In contrast, the rainfed crops, proceed straight into senescence after their GAI build-up phase and showed no response to N. The GAI build-up progressed at a rate of  $0.004 \text{ m}^2/\text{m}^2/^\circ\text{Cd}$  lasting for a duration of  $558^\circ\text{Cd}$ . Without irrigation, the crop did not show a plateau at maximum GAI instead it proceeded into a more gradual decline in GAI at  $0.002 \text{ m}^2/\text{m}^2/^\circ\text{Cd}$ . This pattern of response is consistent with the poor kernel set in this crop (Table 4-11). The low rates meant less DM was available for kernel development and after the reserve DM was remobilised into grain-filling, the canopy was unable to restore the reserve DM pools because the source had been exhausted and the green area senesced.

## **Green leaf area**

The temporal pattern of leaf area development in Figure 5-9 highlights the green area plateau phase. The maximum leaf area (Table 5-5) indicates the total surface area for photosynthesis at completion of canopy development. Almost three quarters of the leaf area came from the lower and mid plant cohorts. The total leaf area per plant for the rainfed crop was  $2978 \text{ cm}^2$  and water increased leaf area by 20% to  $3568 \text{ cm}^2$ . This increase was seen across all the cohorts. Nitrogen acted independently of water to increase the total leaf area by 31% from  $2829$  to  $3717 \text{ cm}^2$ . This was mainly due to the larger leaf size in the mid and upper cohorts of the plants. It is at the maximum leaf area that the crop shift

from vegetative to reproductive development. This switch is crucial as it reflects the crop growth rate and the total DM available for ear development, especially kernel set, and is reflected in the number of kernels set per plant (Table 4-11).

After achieving the maximum leaf area phase, the crop maintains its leaf canopy and this maximum surface area is utilised for photosynthesis of DM for kernel growth and development. Grain-filling depends on remobilisation of DM when the assimilates available from this maximum green area are inadequate to meet the demand. This was the case for the rainfed crops, where the rate of ear DM partitioning to grain was 1.65 ear DM/total DM (Table 4-18) which indicated the highest dependency on remobilisation of DM for grain-filling. This is reflected in the exceptionally short period of maximum green area especially in the mid and upper canopy which averaged 87 °Cd and 56 °Cd, respectively (Table 5-6). In the irrigated crop, the addition of N, doubled the duration of maximum green area period at the lower cohort from 231 to 476 °Cd. This may have slowed down the leaf area in the mid cohort which saw the duration of maximum green area drop from 648 °Cd to 557 °Cd with the application of N. The upper cohort was more stable and was probably providing the bulk of the photosynthate used in grain-filling during this period. Therefore, the differences in the duration of the maximum green area in the mid-cohort was the most likely factor that caused differences in light interception during the linear phase.

The decline in leaf area (Table 5-7) shows that when maximum GAI was short there was a slower rate of decline in leaf area (senescence). This was observed in the lower cohort where the rate of leaf senescence coincided with the maximum green area. The rate of leaf senescence in the rainfed crop was faster at 3.85 cm<sup>2</sup>/°Cd because of the demand for remobilisation when compared with the irrigated crop which maintained its green area till the last harvest date. A similar temporal pattern was seen in the mid and upper cohort. In the mid cohort, the rate of senescence in the irrigated crops did not differ with N application, even though the duration of maximum green area was different. This was because of the difference in the value of maximum leaf area. This resulted in the senescence rate of rainfed crop at 1.45 cm<sup>2</sup>/°Cd being four times slower than the irrigated crop. In the upper cohort, the rate of leaf senescence for the rainfed crop averaged 0.82 cm<sup>2</sup>/°Cd but the rate almost tripled to 2.7 cm<sup>2</sup>/°Cd with irrigation. The short duration of the maximum green area and the slower rate of linear decline in leaf area in the rainfed crops resulted in the crop being more dependent on remobilised DM from reserves for grain-filling (Table 4-17).

### **Leaf appearance**

Leaf appearance and their subsequent expansion affect canopy development as indicated by GAI build up. Leaf appearance was only monitored in detail in Experiment 2. Figure 5-10 and Figure 5-11 show leaf appearance was complete before silking stage ended (6<sup>th</sup> February 2017, 781 °Cd).

Phyllochron for the leaf tips (initiation) during Stage 1 and 2 were affected by N (Table 5-8 & Table 5-9). In Stage 1, leaf development was slower in the lower canopy at 43.8 °Cd/leaf without N and became faster at 39.2 °Cd/leaf when N was applied. The slow leaf initiation in the crop without N may be attributed less to temperature and more towards assimilate influence as demonstrated by (Birch et al., 1998 ) and (Bos et al., 2000). The low assimilate supply associated with extreme N stress caused delay in primordial extension rather than a delay in initiation of successive primordia. Once the lower leaves are established, growth progresses quickly to catch up other crops. Thus, the outcome is a difference of five leaf tip appearance at point of inflection, where N increases leaf tips from 4.7 to 9.7. This was compensated for in Phyllochron stage 2, where leaf tip appearance becomes faster at 67.8 °Cd/leaf compared with 101 °Cd/leaf when N was applied. In the end, there was only one leaf difference with overall leaf tips per plant going from 14.8 to 15.7 with application of N.

The phyllochron for expanded leaf was associated with leaf growth more than development. Leaf growth was slower for the crop without N at phyllochron stage 1 at 65.4 °Cd/leaf with N improving the rate to 62 °Cd/leaf. This suggests connections to the delaying primordial extension associated with extreme N stress in the phyllochron of the leaf tips. Phyllochron for expanded leaf at Stage 2 showed no difference in rate of leaf growth averaging at 49.8 °Cd/leaf suggesting that overall crop phenological development was not affected. Water affected the number of expanded leaves per plant at the point of inflection by decreasing the number of leaves from 9.5 to 8 which indicate more leaves in the lower than upper canopy. Total number of expanded leaves per plant across all crops was 15.3 per plant and not affected by water and N. Generally, the overall crop phenological development was not affected. It was observed that the crops adjusted their canopy mainly through leaf area expansion.

## 5.5 Conclusion

The changes in GAI over the crop growing season is an important determinant that explains vital aspects of the canopy that further justifies the differences in the canopy capacity to intercept light.

In Experiment 1, there was no grain yield difference, at silking as displayed in the canopy capacity at around ear development and grain-filling. These crops reached critical GAI and maintained canopy cover at critical levels for a similar duration. The maximum GAI and the rate of GAI increase were also not different. This consistency in the pattern of canopy development explains the lack of differences in yield response. It was the post-silking canopy activities that caused differences in total DM, but not grain yield.

In Experiment 2, the critical GAI was reached in the irrigated crop with N at a GAI of 4.0. The rainfed crops intercepted less light because the maximum GAI was lower. This was caused by the slow rate of leaf area build-up in GAI. This indicated that resource availability was exhausted by then, which consequently impeded ear development especially kernel setting. Once the canopy was established, it briefly held the GAI at the maximum level before going into a slow progressive decline of GAI. The difference due to N application in the rainfed crop was caused by a large leaf area in the mid and upper cohorts of the crop. The combined effects of 1) low maximum GAI, 2) the short duration of leaf green area holding duration and 3) the slow senescence of low GAI, all translated to low post-silking DM from photosynthesis for grain-filling.

The irrigated crop on the other hand, increased maximum GAI to around 3.5 but regardless did not reach the critical GAI level. Water and N improved kernel set but most of the resources at the ear development stage were rather invested into canopy development and maintenance. Thereafter, the irrigated crops prolonged the maximum GAI to benefit kernel sink demand at grain-filling stage and replenish all reserve DM pool. After all this priority activity was complete, the crops made a sharp decline into senescence to mark the end of the cropping season.

The important aspects of the canopy that affect the yield are rate and duration of GAI increase which determine the maximum GAI and affect ear development activities especially kernel setting and the rapid linear phase of grain-filling. Past this stage, is the gradual grain-filling phase which coincides with the green area holding phase and influenced by the movement DM withdrawn through remobilisation from reserves and re-deposited DM as replenishment. The extent of this replenishment process is governed by the green area longevity and senescence.

## Chapter 6

# Radiation use efficiency (RUE) and nitrogen (N)

### 6.1 Introduction

This chapter deals with Objective 3 which is to examine crop N dynamics. To do this, it quantifies the N changes during vegetative development, N remobilisation at kernel development and to the end of kernel growth, with assessment of N retention and leaf senescence for crops with different yield potentials. In Chapter 5, there were two scenarios presented, the amount of light intercepted was affected by water post-silking (Experiment 1) and by water from early growth stages (Experiment 2). In this chapter, the photosynthetic capacity of the crop is examined through differences in RUE as related to N content in the leaf to assess how it was affected by water and N availability.

The rationale for this analysis is that under optimal growing conditions, total DM is determined by the amount of light intercepted and its efficiency of conversion into DM, expressed as RUE. For a given amount of available N, there is a trade-off for plants between maintaining a large leaf area, and thus maximizing radiation interception over time, versus concentrating N into a small leaf area to maintain a high leaf N concentration and thus maximize photosynthesis of existing and new leaves (shown as increased efficiency of conversion). Reducing leaf size leads to the efficient use of N for the production of DM under N-limiting conditions in the early stages of crop growth (Lemaire et al., 2008; Lemaire et al., 2007; Massignam et al., 2012). Changes in specific leaf N are used to examine how the plants trade-off the N allocation between leaves, stem and kernels. This chapter explores the crop strategies that maize used to deal with different water and N supplied in Experiments 1 and 2.

## 6.2 Materials and methods

### 6.2.1 Measurement

Measurements for the total above ground DM and iPAR were described in Section 3.3. Data were collected for sampling dates at pre and post silking through grain-filling to physiological maturity.

The leaves were separated into three cohorts depending on the location the cob bearing leaf. The leaf/leaves which had sheath(s) wrapped around the cob(s) plus the two leaves below and above are referred to as the mid cohort. The lower and upper cohorts were separated by this mid cohort.

Plant tissue N content of each cohort was measured using Near Infrared spectroscopy (NIR). Dried samples of green leaves were obtained from the dry matter described in Section 3.3.1. Plant materials were chopped by hand and passed through a Retsch knife mill (Model SM100). The sub-samples were ground through a 1 mm stainless steel sieve (Cyclotec Mill, USA). Analyses of the N content was conducted using a Foss NIR Systems 5000 Rapid Content Analyser (Welltech Scientific Inc. 14600 Flint Lee Road, Unit-A, Chantilly, VA 20151 USA).

### 6.2.2 Calculations

#### Radiation use efficiency (RUE)

The RUE was calculated from the linear regression between total biomass accumulated and cumulative iPAR (Plénet et al., 2000; Sinclair and Muchow, 1999). The measurements for light interception were described in Section 3.3.5. Linear regressions were performed for each plot after which an ANOVA on the regression coefficients was carried out to determine whether they could be pooled.

#### Tissue N content

The plant tissue N content was calculated from crude protein (CP) in Equation 6.1 (Kyriazakis and Oldham, 1993).

$$\text{Equation 6-1} \quad \text{CP} = \text{N\%} * 6.25$$

#### Crop N content

Total crop N content (kg/ha) was calculated by multiplying the dry matter (kg/ha) and the N concentration (% N) of each plant component (Subedi and Ma, 2005).

## Specific Leaf N

Specific leaf N (SLN) at silking is the ratio of leaf N ( $\text{g}/\text{m}^2$ ) to GAI ( $\text{m}^2/\text{m}^2$ ) at silking and post-silking (Equation 6.5).

$$\text{Equation 6-2} \quad \text{SLN (g/m}^2\text{)} = \text{Leaf N uptake at silking (g/m}^2\text{)} / \text{GAI at silking (m}^2/\text{m}^2\text{)} * 10^{-1}$$

## 6.3 Results

### 6.3.1 Experiment 1

#### Radiation use efficiency (RUE)

The efficiency of light conversion into DM is shown in Figure 6-1. The linear regression was taken through the sample points and not forced through zero. The treatments separated towards the later growing stage indicated by the dispersed data points at the reproductive stages. The coefficient of determination and regression equations are presented in Appendix B.

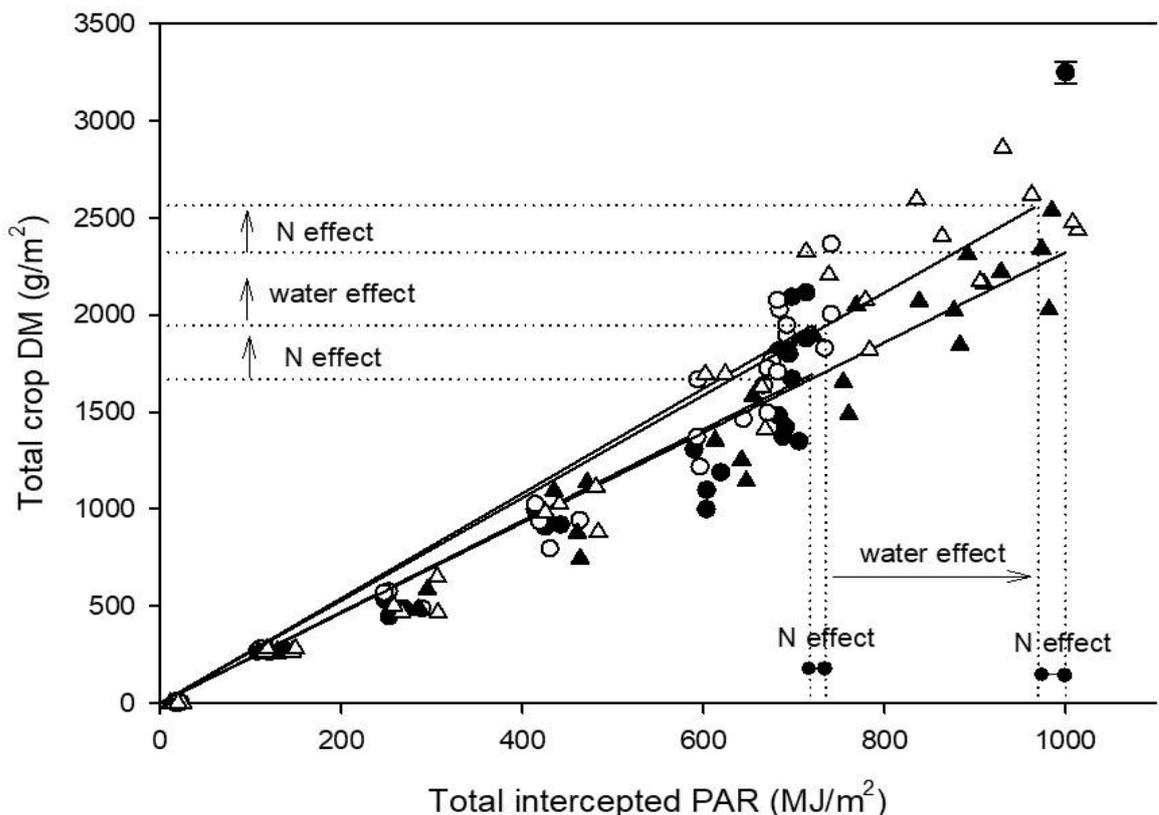


Figure 6-1 Total crop dry matter ( $\text{g}/\text{m}^2$ ) against intercepted PAR ( $\text{MJ}/\text{m}^2$ ) for maize in response to nil N (●) and 300 kg N/ha (○) under rainfed (Irr1) and nil N (▲) and 300 kg N/ha (△) under irrigation (Irr4) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bar indicates the standard error.

The RUE calculated from the linear regressions indicated an increase with N ( $P=0.019$ ) but not water ( $P=0.787$ ) (Table 6-1). Specifically, RUE increased from 2.21 to 2.49 g/MJ with N.

**Table 6-1 Radiation use efficiency (g/MJ iPAR) for maize in response to nil N and 300 kg N/ha under rainfed (Irr1) and irrigation (Irr4) for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

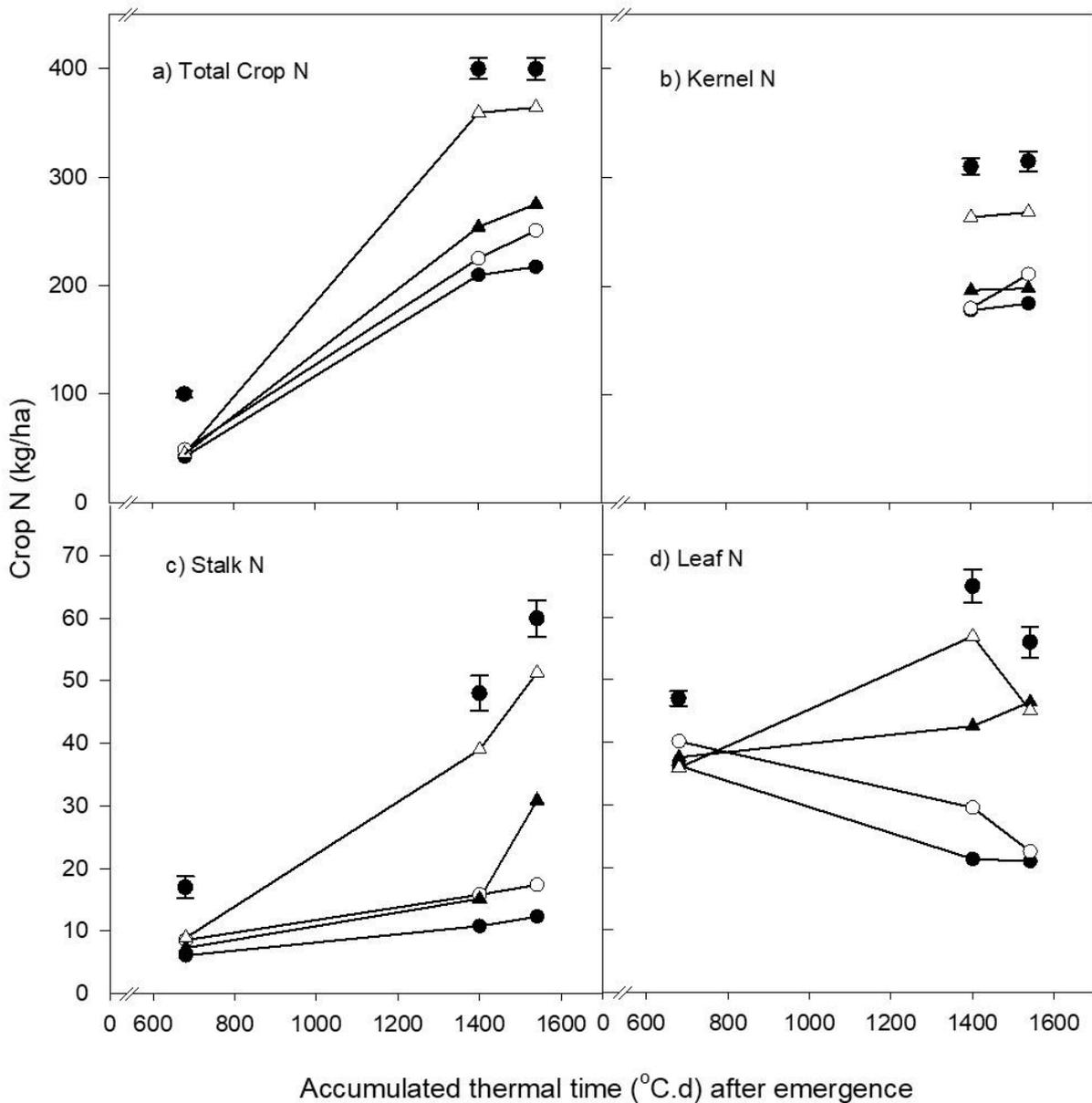
N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
0	2.21	2.21	2.21 <sub>b</sub>
300	2.45	2.53	2.49 <sub>a</sub>
Mean	2.33	2.37	2.35

$SED_N=0.089$ ,  $SED_W=0.121$ ,  $SED_{N*W}=0.150$ ,  $P_N=0.019$ ,  $P_W=0.787$ ,  $P_{N*W}=0.602$

Means with no letters are not significantly different at  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### Crop nitrogen dynamics

Crop N content at silking/post-silking was measured to quantify the changes in N content within and among organs during kernel filling. Figure 6-2 shows the general increase in total crop N content from N uptake and remobilisation of N within the crop. The three sampling points indicated the total crop N and the amount of N partitioned to respective organs.



**Figure 6-2** Crop N content against thermal time for the total crop (a), kernel (b), stalk (c) and leaf (d) for maize in response to nil N (●) and 300 kg N/ha (○) under rainfed (Irr1) and nil N (▲) and 300 kg N/ha (△) under irrigation (Irr4) for three silking/post-silking sampling dates of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bars represent standard error of the means at each harvest date.

From the sampling at 679 °Cd (early silking), which was around early silking, the crop N content increased only in the stalk (Table 6-2). Total crop N at 679 °Cd was not affected by water ( $P=0.924$ ) or N ( $P=0.158$ ) and averaged 45.2 kg N/ha for all the crops. The N content averaged 37.5 kg N/ha for leaves across all the crops. Stalk N responded positively to N ( $P=0.048$ ) but not water ( $P=0.702$ ) shown by the increase from 6.71 to 8.73 kg N/ha when fertilised. Leaf N content also showed no effect of water ( $P=0.797$ ) or N ( $P=0.586$ ). At this point in time kernels were being initiated.

**Table 6-2 Total crop, leaf, kernel and stalk N (kg/ha) at early silking (679 °Cd) for maize in response to nil N and 300 kg N/ha under rainfed (Irr1) and under irrigation (Irr4) in 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
<u>Total crop N (kg N/ha)</u>			
0	42.3	44.9	43.6
300	48.7	44.8	46.7
Mean	45.5	44.9	45.2
SED <sub>N</sub> =1.994, SED <sub>W</sub> =6.309, SED <sub>N*W</sub> =6.617, P <sub>N</sub> =0.168 P <sub>W</sub> =0.924, P <sub>N*W</sub> =0.158			
<u>Leaf N (kg N/ha)</u>			
0	36.2	37.6	36.9
300	40.1	35.9	38.0
Mean	38.2	36.7	37.5
SED <sub>N</sub> =1.911, SED <sub>W</sub> =5.114, SED <sub>N*W</sub> =5.459, P <sub>N</sub> =0.586, P <sub>W</sub> =0.797, P <sub>N*W</sub> =0.195			
<u>Stalk N (kg N/ha)</u>			
0	6.10	7.31	6.71 <sub>b</sub>
300	8.55	8.91	8.73 <sub>a</sub>
Mean	7.33	8.11	7.72
SED <sub>N</sub> = 0.814, SED <sub>W</sub> =1.857, SED <sub>N*W</sub> =2.028, P <sub>N</sub> =0.048, P <sub>W</sub> =0.702, P <sub>N*W</sub> =0.616			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

Figure 6-2 shows a general N increase in total crop N from ~45.2 kg N/ha at 679 °Cd to at least 200 kg N/ha at 1400 °Cd (during grain-filling). The amount of N at 1400 °Cd differed amongst treatments being highest with N (P=0.046), when it increased from 230 to 289 kg N/ha (Table 6-3). Kernel N content averaged 204 kg N/ha with no effect of water (P=0.157) or N (P=0.135). In the stalk, there was an interaction (P=0.037) with water and N. The N content in the stalk did not increase under rainfed conditions (Irr1) and averaged 13.3 kg N/h but increased from 15.2 to 39.0 kg N/ha with irrigation and N. Leaf N content showed a trend of an increase (P=0.052) from an average of 25.4 to 49.7 kg N/ha with water.

**Table 6-3 Total crop, leaf, kernel and stalk N content (kg/ha) during grain-filling (1400 °Cd) for maize in response to nil N and 300 kg N/ha at Irr1 and Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
<u>Total crop N (kg N/ha)</u>			
0	208	252	230 <sub>b</sub>
300	220	357	289 <sub>a</sub>
Mean	214	305	260
SED <sub>N</sub> =22.1, SED <sub>W</sub> =40.2, SED <sub>N*W</sub> =45.8, P <sub>N</sub> =0.046, P <sub>W</sub> =0.109, P <sub>N*W</sub> =0.088			
<u>Leaf N (kg N/ha)</u>			
0	21.3	42.6	31.9
300	29.5	56.9	43.2
Mean	25.4 <sub>b</sub>	49.7 <sub>a</sub>	37.6
SED <sub>N</sub> =5.04, SED <sub>W</sub> =7.75, SED <sub>N*W</sub> =9.25, P <sub>N</sub> =0.066, P <sub>W</sub> =0.052, P <sub>N*W</sub> =0.563			
<u>Kernel N (kg N/ha)</u>			
0	178	196	187
300	178	264	220
Mean	178	230	204
SED <sub>N</sub> =18.8, SED <sub>W</sub> =27.7, SED <sub>N*W</sub> =33.5, P <sub>N</sub> =0.132, P <sub>W</sub> =0.157, P <sub>N*W</sub> =0.135			
<u>Stalk N (kg N/ha)</u>			
0	10.8 <sub>b</sub>	15.2 <sub>b</sub>	13.0
300	15.8 <sub>b</sub>	39.0 <sub>a</sub>	27.4
Mean	13.3	27.1	25.8
SED <sub>N</sub> =7.12, SED <sub>W</sub> =7.90, SED <sub>N*W</sub> =10.64, P <sub>N</sub> =0.006, P <sub>W</sub> =0.082, P <sub>N*W</sub> =0.037			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

At crop maturity (1541 °Cd), total crop N responded to the main effects of N ( $P=0.007$ ) and water ( $P=0.037$ ) (Table 6-4). Crop N increased from 240 to 306 kg N/ha with N and from 228 to 317 kg N/ha with water. Leaf N content was only affected by water ( $P<0.001$ ) and increased from 21.7 to 45.7 kg N/ha, but not N ( $P=0.984$ ). Kernel N content was affected by N ( $P=0.018$ ) and increased from 182 to 234 kg N/ha. Stalk N content showed a main effect of N ( $P=0.018$ ) with an increase from 20.0 to 34.3 kg N/ha and a trend ( $P=0.063$ ) to increase with water.

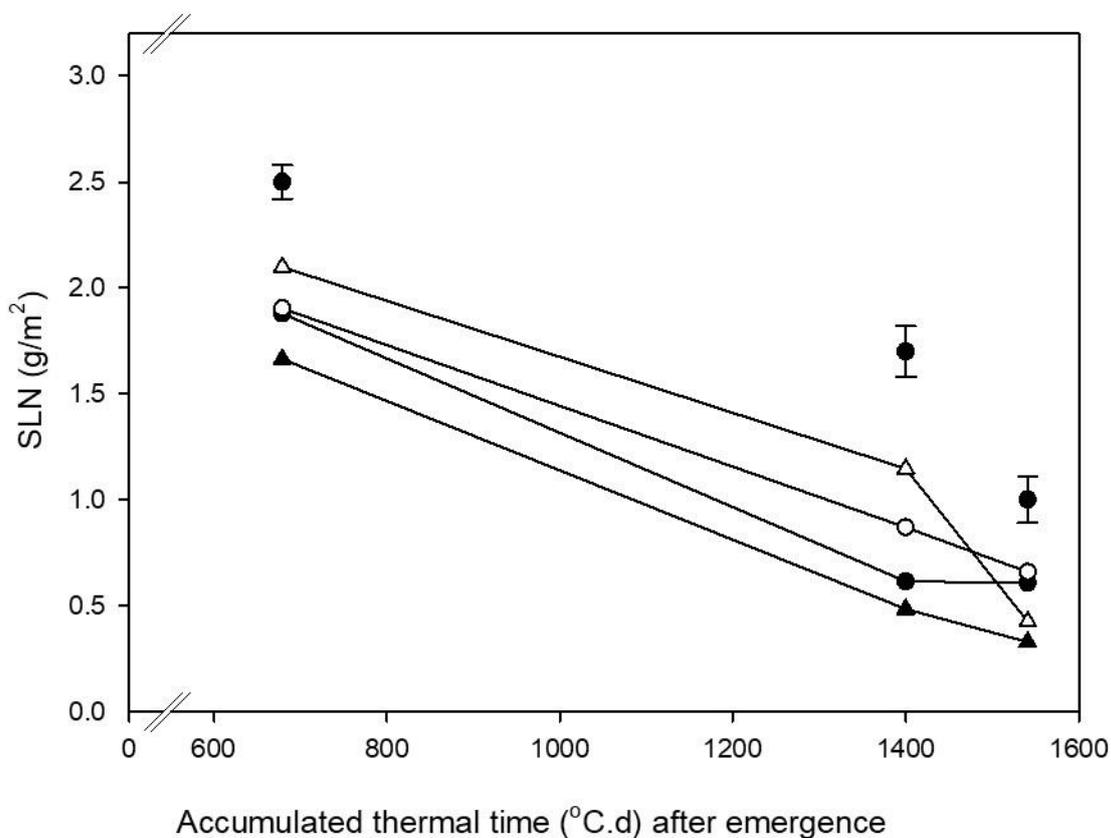
**Table 6-4 Total crop, leaf, kernel and stalk N content (kg/ha) at crop maturity (1541 °Cd) for maize in response to nil N and 300 kg N/ha at Irr1 and Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
<u>Total crop N (kg N/ha)</u>			
0	205	275	240 <sub>b</sub>
300	251	360	306 <sub>a</sub>
Mean	228 <sub>b</sub>	317 <sub>a</sub>	273
SED <sub>N</sub> =14.90, SED <sub>W</sub> =24.71, SED <sub>N*W</sub> =28.86, P <sub>N</sub> =0.007, P <sub>W</sub> =0.037, P <sub>N*W</sub> =0.239			
<u>Leaf N (kg N/ha)</u>			
0	21.0	46.4	33.7
300	22.5	45.1	33.8
Mean	21.7 <sub>b</sub>	45.7 <sub>a</sub>	33.7
SED <sub>N</sub> =4.91, SED <sub>W</sub> =1.17, SED <sub>N*W</sub> =5.05, P <sub>N</sub> =0.984, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.776			
<u>Kernel N (kg N/ha)</u>			
0	189	198	182 <sub>b</sub>
300	211	264	234 <sub>a</sub>
Mean	189	231	210
SED <sub>N</sub> =12.57, SED <sub>W</sub> =15.60, SED <sub>N*W</sub> =20.03, P <sub>N</sub> =0.004, P <sub>W</sub> =0.075, P <sub>N*W</sub> =0.426			
<u>Stalk N (kg N/ha)</u>			
0	9.1	30.9	20.0 <sub>b</sub>
300	17.4	51.3	34.3 <sub>a</sub>
Mean	13.3	41.1	27.2
SED <sub>N</sub> =4.13, SED <sub>W</sub> =9.66, SED <sub>N*W</sub> =10.51, P <sub>N</sub> =0.018, P <sub>W</sub> =0.063, P <sub>N*W</sub> =0.201			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### Specific leaf nitrogen

Specific leaf N (SLN) at silking/post-silking was also calculated (Figure 6-3). There was a linear decline in SLN as the crop matured.



**Figure 6-3** Specific leaf nitrogen against thermal time for silking/post-silking sampling dates for maize in response to nil N (●) and 300 kg N/ha (○) under rainfed (Irr1) and nil N (▲) and 300 kg N/ha (△) under irrigation (Irr4) for three silking/post-silking sampling dates of 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand. Error bars represent standard error of the means of the SLN at each harvest date.

SLN at silking/post-silking was affected by the interaction between water and N ( $P=0.031$ ) at 679 °Cd (Table 6-3). SLN averaged 1.89 g/m<sup>2</sup> when rainfed but was lower at 1.66 g/m<sup>2</sup> with irrigation only and 2.10 g/m<sup>2</sup> with irrigated and N. This same response pattern (water and N interaction  $P=0.053$ ) was observed at 1400 °Cd. The SLN was highest at 1.15 g/m<sup>2</sup> with irrigation and N but dropped to 0.49 g/m<sup>2</sup> when irrigated without N with the rainfed treatments intermediate. The SLN at 1541 °Cd was only affected by water ( $P=0.007$ ), being 0.63 g/m<sup>2</sup> when rainfed but dropping to 0.38 g/m<sup>2</sup> when only irrigated.

**Table 6-5 Specific leaf nitrogen (SLN) (g/m<sup>2</sup>) for post-silking samples at 679, 1400, 1541 °Cd for maize in response to nil N and 300 kg N/ha at Irr1 and Irr4 for 2015/16 (Experiment 1) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
<u>SLN (g N/m<sup>2</sup>) @679 °Cd</u>			
0	1.88 <sub>ab</sub>	1.66 <sub>b</sub>	1.77
300	1.90 <sub>ab</sub>	2.10 <sub>a</sub>	2.00
Mean	1.89	1.88	1.89
SED <sub>N</sub> =0.0732, SED <sub>W</sub> =0.1670, SED <sub>N*W</sub> =0.1823, P <sub>N</sub> =0.020, P <sub>W</sub> =0.957, P <sub>N*W</sub> =0.031			
<u>SLN (g N/m<sup>2</sup>) @1400 °Cd</u>			
0	0.62 <sub>ab</sub>	0.49 <sub>b</sub>	0.55
300	0.87 <sub>ab</sub>	1.15 <sub>a</sub>	1.01
Mean	0.74	0.82	0.78
SED <sub>N</sub> =0.0848, SED <sub>W</sub> =0.1817, SED <sub>N*W</sub> =0.2005, P <sub>N</sub> =0.002, P <sub>W</sub> =0.716, P <sub>N*W</sub> =0.053			
<u>SLN (g N/m<sup>2</sup>) @1541 °Cd</u>			
0	0.61	0.33	0.47
300	0.66	0.43	0.54
Mean	0.63 <sub>a</sub>	0.38 <sub>b</sub>	0.51
SED <sub>N</sub> = 0.069, SED <sub>W</sub> =0.039, SED <sub>N*W</sub> =0.079, P <sub>N</sub> =0.325, P <sub>W</sub> =0.007, P <sub>N*W</sub> =0.755			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### 6.3.2 Experiment 2

#### Radiation use efficiency

There was a linear relationship between total dry matter and intercepted PAR for all treatments (Figure 6-4) in Experiment 2. A table of co-efficients of the linear regression is presented in Appendix B.

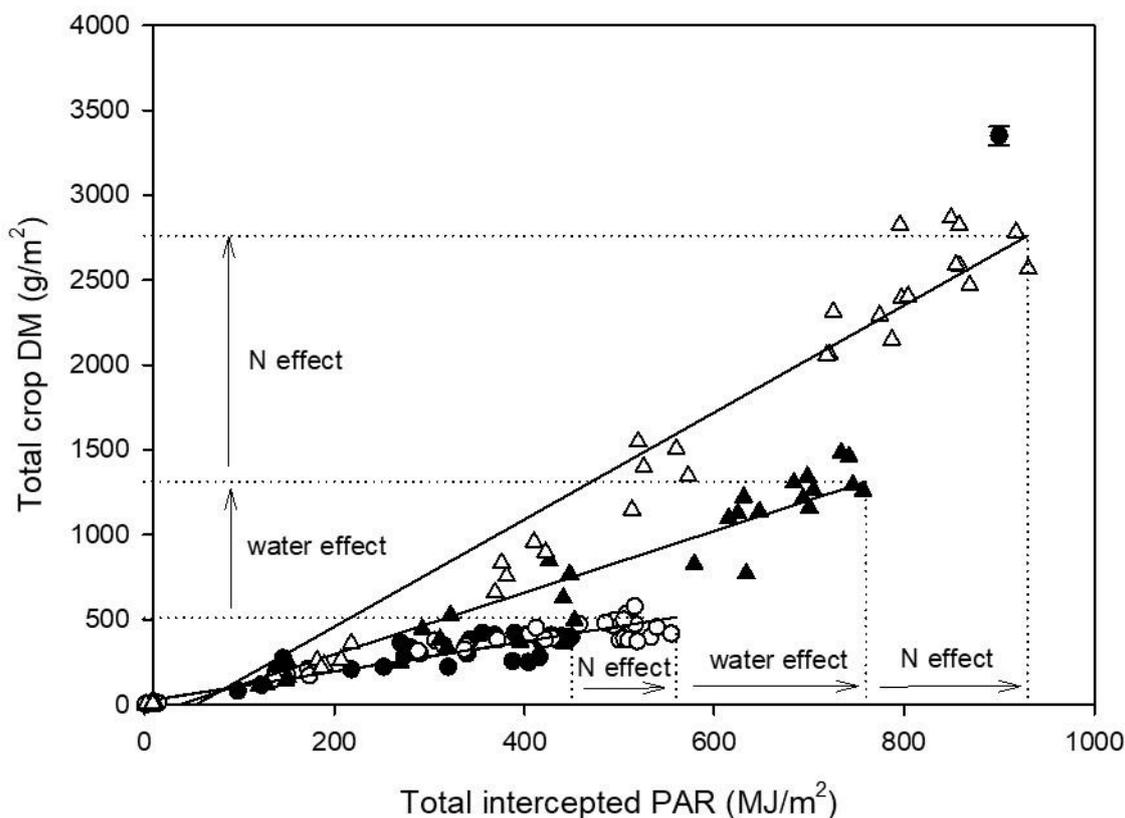


Figure 6-4 Total crop dry matter against ( $\text{g}/\text{m}^2$ ) against total PAR intercepted ( $\text{MJ}/\text{m}^2$ ) for maize in response to nil N ( $\bullet$ ) and 500 kg N/ha ( $\circ$ ) under rainfed and nil N ( $\blacktriangle$ ) and 500 kg N/ha ( $\triangle$ ) with irrigation for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bar indicates the standard error.

The RUE was affected by the interaction ( $P < 0.001$ ) between water and N (Table 6-6). RUE was 0.88 g DM/MJ under rainfed conditions, regardless of N level, but increased to 1.82 g DM/MJ with irrigation and further to 3.15 g DM/MJ with N and irrigation.

**Table 6-6 Radiation use efficiency (g/MJ iPAR) for maize in response to two N levels (nil and 500 kg N/ha) for each of two water levels (rain fed and irrigated) when grown in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

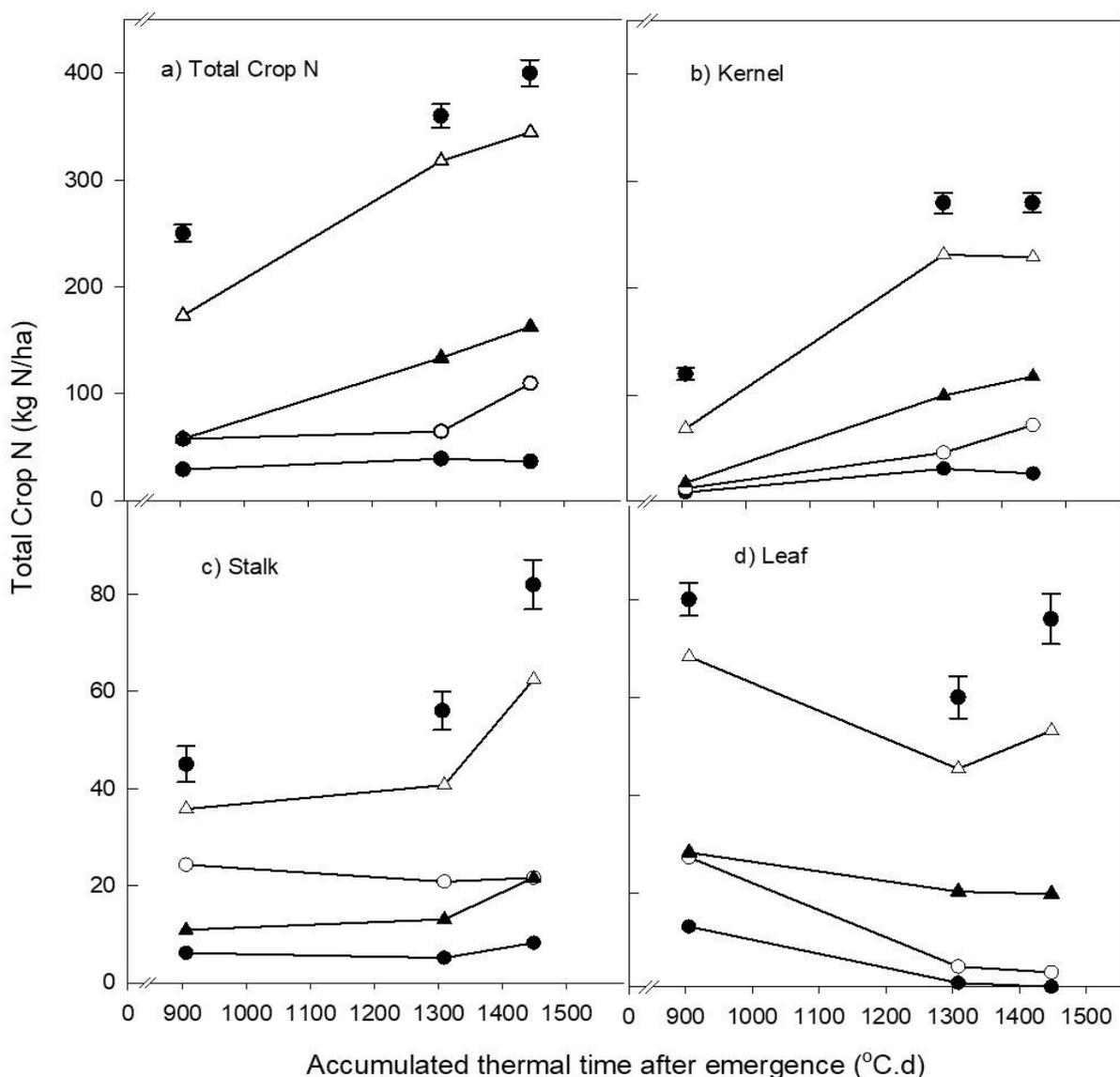
N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
0	0.87 <sub>c</sub>	1.82 <sub>b</sub>	1.34
500	0.89 <sub>c</sub>	3.15 <sub>a</sub>	2.02
Mean	0.88	2.49	1.68

SED<sub>N and W</sub>=0.0819, SED<sub>N\*W</sub>=0.1158, P<sub>N</sub><0.001, P<sub>W</sub><0.001, P<sub>N\*W</sub><0.001

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### Crop nitrogen dynamics

Crop N dynamics at three post-silking sampling dates showed a response to water and N (Figure 6-5).



**Figure 6-5 Crop N against thermal time for the total crop (a), kernel (b), stalk (c) and leaf (d) for maize in response to nil N (●) and 500 kg N/ha (○) under rainfed and nil N (▲) and 500 kg (△) with irrigation for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard error of the means.**

At 905 °Cd around late silking stages, there was an interaction between water and N for total crop N ( $P=0.003$ ), leaf N ( $P=0.002$ ) and kernel N ( $P=0.003$ ) with main effects of water ( $P=0.030$ ) and N ( $P<0.001$ ) for stalk N (Table 6-7). Total crop N averaged 40.7 kg N/ha when rainfed and only increased to 173 kg N/ha with irrigation and N. Leaf N increased from 20.3 kg N/ha under rainfed conditions to 68.3 kg N/ha with irrigation and N. Kernel N averaged 10.3 kg N/ha when rainfed but increased to 69.0 kg N/ha with irrigation and N. Stalk N was 15.2 kg N/ha when rainfed and increased to 23.3 kg N/ha with irrigation, and from 8.50 to 30.0 kg N/ha with N.

**Table 6-7 Total crop, leaf, kernel and stalk N (kg/ha) at late silking (905 °Cd) for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops in 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
<u>Total crop N (kg N/ha)</u>			
0	28.3 <sub>b</sub>	57.7 <sub>b</sub>	43.0
500	53.2 <sub>b</sub>	173 <sub>a</sub>	113
Mean	40.7	115.3	78.0
SED <sub>N and W</sub> =10.42, SED <sub>N*W</sub> =14.73, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.003			
<u>Leaf N (kg N/ha)</u>			
0	13.3 <sub>b</sub>	28.4 <sub>b</sub>	20.8
500	27.4 <sub>b</sub>	68.3 <sub>a</sub>	47.9
Mean	20.3	48.3	34.3
SED <sub>N and W</sub> =3.35, SED <sub>N*W</sub> =4.74 P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.002			
<u>Kernel N (kg N/ha)</u>			
0	9.61 <sub>b</sub>	18.4 <sub>b</sub>	14.0
500	11.0 <sub>b</sub>	69.0 <sub>a</sub>	40.0
Mean	10.3	43.7	27.0
SED <sub>N and W</sub> =5.70, SED <sub>N*W</sub> =8.06, P <sub>N</sub> =0.003, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.003			
<u>Stalk N (kg N/ha)</u>			
0	6.10	10.9	8.50 <sub>b</sub>
500	24.3	35.8	30.0 <sub>a</sub>
Mean	15.2 <sub>b</sub>	23.3 <sub>a</sub>	27.9
SED <sub>N and W</sub> =3.29, SED <sub>N*W</sub> =4.65, P <sub>N</sub> <0.001, P <sub>W</sub> =0.030, P <sub>N*W</sub> =0.327			

Means with subscript letters in common are not significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

At 1308 °Cd (grain-filling) there was also an interaction between water and N for total crop N ( $P=0.033$ ), leaf N ( $P<0.001$ ) and kernel N ( $P=0.044$ ) but a main effect of water ( $P=0.003$ ) and N ( $P<0.001$ ) for stalk N (Table 6-8). Total crop N averaged 24.0 kg N/ha when rainfed without N and increased with irrigation from 133 to 318 kg N/ha with N. Leaf N was 3.44 kg N/ha when rainfed and increased to 20.4 kg N/ha with irrigation and further to 45.5 kg N/ha with irrigation and N. Kernel N averaged 14.6 kg N/ha when rainfed without N and increased from 100 kg N/ha with irrigation to 231

kg N/ha with irrigation and N. For stalk, the N content increased from 13.0 to 37.6 kg N/ha with irrigation and from 9.15 to 30.8 kg N/ha with N.

**Table 6-8 Total crop, leaf, kernel and stalk N (kg/ha) during grain-filling (1308 °Cd) for maize grown at two N levels (nil and 500 kg N/ha) either rainfed or irrigated in 2016/17 (Experiment 2) at Lincoln University, Canterbury New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
<u>Total crop N (kg N/ha)</u>			
0	10.8 <sub>c</sub>	133 <sub>b</sub>	72.8
500	36.3 <sub>cb</sub>	318 <sub>a</sub>	177
Mean	24.0	225	125
SED <sub>N and W</sub> =24.9, SED <sub>N*W</sub> =35.2, P <sub>N</sub> =0.014, P <sub>W</sub> =0.001, P <sub>N*W</sub> =0.033			
<u>Leaf N (kg N/ha)</u>			
0	1.79 <sub>c</sub>	20.4 <sub>b</sub>	11.1
500	5.10 <sub>c</sub>	45.4 <sub>a</sub>	25.3
Mean	3.44	32.9	18.2
SED <sub>N and W</sub> =2.22, SED <sub>N*W</sub> =3.14, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> <0.001			
<u>Kernel N (kg N/ha)</u>			
0	7.08 <sub>c</sub>	100 <sub>b</sub>	53.5
500	22.1 <sub>bc</sub>	231 <sub>a</sub>	127
Mean	14.6	166	90.1
SED <sub>N and W</sub> =20.1, SED <sub>N*W</sub> =28.5, P <sub>N</sub> =0.022, P <sub>W</sub> =0.002, P <sub>N*W</sub> =0.044			
<u>Stalk N (kg N/ha)</u>			
0	5.18	13.1	9.15 <sub>b</sub>
500	20.8	40.7	30.8 <sub>a</sub>
Mean	13.0 <sub>b</sub>	37.6 <sub>a</sub>	19.9
SED <sub>N and W</sub> =3.79, SED <sub>N*W</sub> =5.36, P <sub>N</sub> <0.001, P <sub>W</sub> =0.003, P <sub>N*W</sub> =0.142			

Means with subscripts in common are not different at  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

At physiological maturity at 1448 °Cd, there were main effects of water for total crop N ( $P=0.048$ ) and kernel N ( $P=0.037$ ) but an interaction between water and N for leaf N ( $P<0.001$ ) and stalk N ( $P<0.001$ ) (Table 6-9). Total crop N increased from 63.4 kg N/ha when rainfed to 272 kg N/ha with irrigation. Leaf N averaged 2.50 kg N/ha under rainfed conditions compared with 19.9 kg N/ha when irrigated and 53.1 kg N/ha when irrigated and fertilised with N. Kernel N increased ( $P<0.037$ ) from a mean of 49.2 kg N/ha when rainfed to 184 kg N/ha with irrigation. Stalk N was lowest at 8.18 kg N/ha when rainfed without N and increased to 21.6 kg N/ha for rainfed crops with N. For irrigated crops without N, there was 21.6 kg N/ha of stalk N and this increased to 62.4 kg N/ha under irrigation and N.

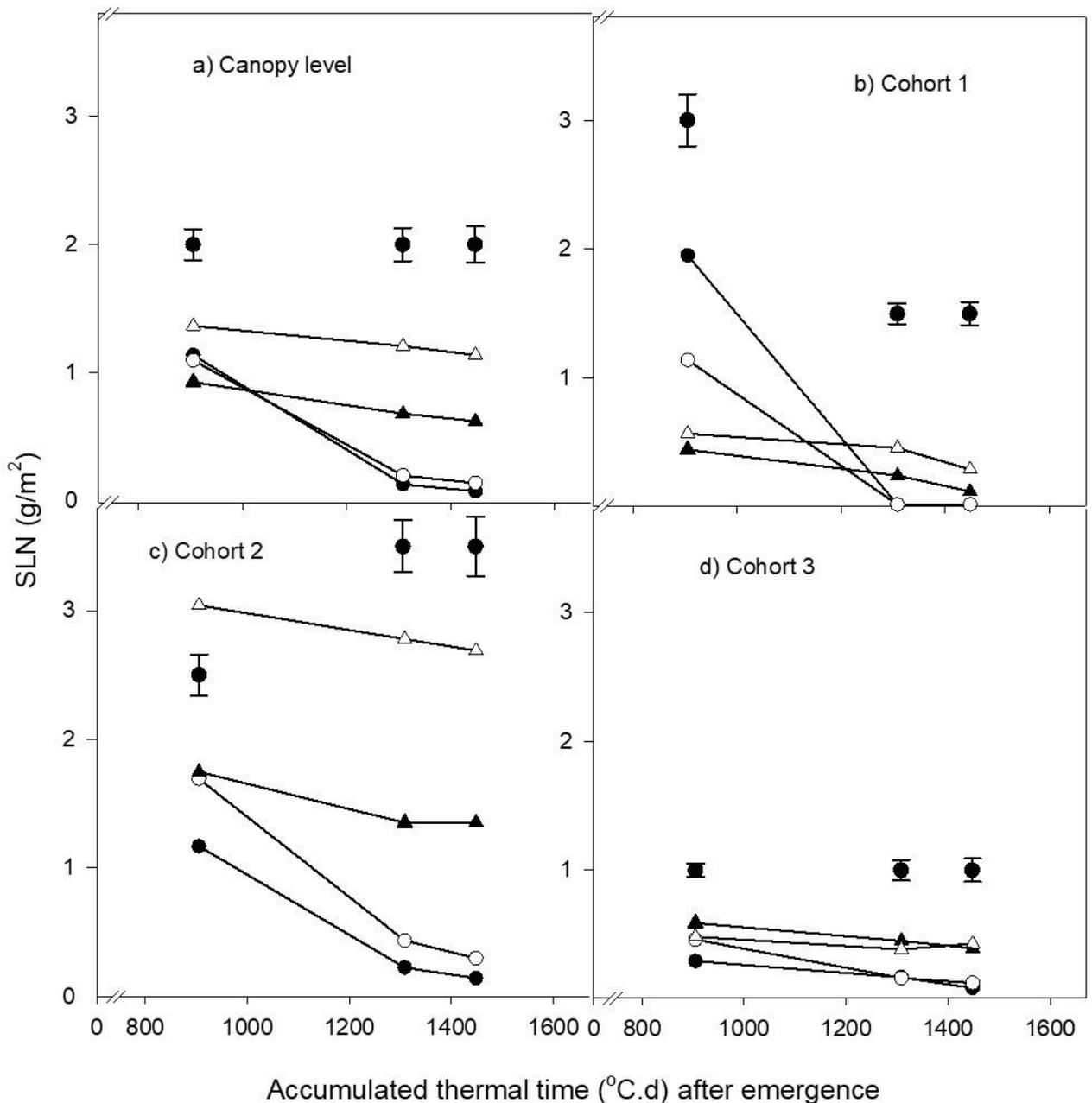
**Table 6-9 Total crop, leaf, kernel and stalk N (kg/ha) at physiological maturity (1448 °Cd) for maize grown at two N levels (nil and 500 kg N/ha) and either rainfed or irrigated in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
	<u>Total crop N (kg N/ha)</u>		
0	25.6	182	104
500	101	363	232
Mean	63.4 <sub>a</sub>	272 <sub>b</sub>	168
SED <sub>N and W</sub> =15.76, SED <sub>N*W</sub> =22.29, P <sub>N</sub> =0.078, P <sub>W</sub> =0.048, P <sub>N*W</sub> =0.186			
	<u>Leaf N (kg N/ha)</u>		
0	0.96 <sub>c</sub>	19.9 <sub>b</sub>	10.4
500	3.94 <sub>c</sub>	53.1 <sub>a</sub>	28.5
Mean	2.50	36.5	19.5
SED <sub>N and W</sub> =4.20, SED <sub>N*W</sub> =5.94, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> <0.001			
	<u>Kernel N (kg N/ha)</u>		
0	16.5	140	78.1
500	81.8	229	155
Mean	49.2 <sub>b</sub>	184 <sub>a</sub>	117
SED <sub>N and W</sub> =7.94, SED <sub>N*W</sub> =11.23, P <sub>N</sub> =0.065, P <sub>W</sub> =0.037, P <sub>N*W</sub> =0.372			
	<u>Stalk N (kg N/ha)</u>		
0	8.18 <sub>c</sub>	21.6 <sub>b</sub>	14.9
500	21.6 <sub>b</sub>	62.4 <sub>a</sub>	47.0
Mean	14.9	47.0	31.0
SED <sub>N and W</sub> =2.33, SED <sub>N*W</sub> =3.30, P <sub>N</sub> <0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> <0.001			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

## Specific leaf nitrogen

There was a decrease in SLN with leaf senescence throughout the post-silking period as the crops matured (Figure 6-6). However, the decline was accelerated when resources were limited. The pattern of decrease in SLN in overall canopy was predominantly related to changes in Cohort 2, which is the mid-cohort positioned around the ear. Cohorts 2 and 3 showed irrigated crops had a high SLN and were able to maintain this through kernel-filling. At silking, the lower cohort (1) had low SLN levels in the irrigated crop but retained N under rainfed conditions.



**Figure 6-6** SLN against thermal time for post-silking sampling points for maize in response to nil N (●) and 500 kg N/ha (○) under rainfed and nil N (▲) and 500 (△) kg N/ha with irrigation for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard error of the means.

Total leaf SLN for the canopy at late silking stage (905 °Cd) was not affected by water ( $P=0.832$ ) or N ( $P=0.155$ ) (Table 6-10). There were different responses in the three cohorts: Cohort 1 was affected by water ( $P=0.014$ ), Cohort 2 showed main effects of water ( $P<0.001$ ) and N ( $P=0.001$ ) with a trend to an interaction ( $P=0.059$ ). Cohort 3 was unaffected by water ( $P=0.337$ ) or N ( $P=0.853$ ) and averaged 0.46 g N/m<sup>2</sup>. Total SLN averaged 1.23 g N/m<sup>2</sup> at the total canopy level. In Cohort 1, SLN was 1.55 g N/m<sup>2</sup> when rainfed but only 0.51 g N/m<sup>2</sup> when irrigated. SLN in Cohort 2 increased from 1.43 to 2.39 g N/m<sup>2</sup> with irrigation and from 1.46 to 2.37 g N/m<sup>2</sup> with N.

**Table 6-10 Specific leaf nitrogen (g N/m<sup>2</sup>) around late silking stage (905 °Cd) for maize grown at two N levels (nil and 500 kg N/ha) and either rainfed or irrigated in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
<u>Total SLN</u>			
0	1.14	0.93	1.03
500	1.10	1.37	1.79
Mean	1.12	1.15	1.23
SED <sub>N and W</sub> =0.1310, SED <sub>N*W</sub> =0.1852, P <sub>N</sub> =0.155, P <sub>W</sub> =0.832, P <sub>N*W</sub> =0.093			
<u>Cohort 1 SLN</u>			
0	1.95	0.45	1.20
500	1.14	0.57	0.85
Mean	1.55 <sub>a</sub>	0.51 <sub>b</sub>	1.03
SED <sub>N and W</sub> =0.359, SED <sub>N*W</sub> =0.508 P <sub>N</sub> =0.358, P <sub>W</sub> =0.014, P <sub>N*W</sub> =0.218			
<u>Cohort 2 SLN</u>			
0	1.17	1.75	1.46 <sub>b</sub>
500	1.70	3.04	2.37 <sub>a</sub>
Mean	1.43 <sub>b</sub>	2.39 <sub>a</sub>	1.91
SED <sub>N and W</sub> =0.1847, SED <sub>N*W</sub> =0.2613 P <sub>N</sub> =0.001, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.059			
<u>Cohort 3 SLN</u>			
0	0.30	0.59	0.44
500	0.46	0.48	0.47
Mean	0.38	0.54	0.46
SED <sub>N and W</sub> =0.1586, SED <sub>N*W</sub> =0.2243, P <sub>N</sub> =0.853, P <sub>W</sub> =0.337, P <sub>N*W</sub> =0.404			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

The SLN during grain-filling (1308 °Cd) showed an interaction between N and water ( $P= 0.029$ ) at the canopy level, a main effect of water ( $P<0.001$ ) in Cohort 1, an interaction between N and water ( $P=0.019$ ) in Cohort 2 and a main effect of water ( $P=0.002$ ) in Cohort 3 (Table 6-11). The overall canopy SLN averaged 0.17 g N/m<sup>2</sup> when rainfed and increased from 0.68 g N/m<sup>2</sup> when irrigated to 1.21 g N/m<sup>2</sup> with irrigation and N. The SLN in Cohort 1 was negligible for the fully senesced leaves when rainfed and 0.35 g N/m<sup>2</sup> with irrigation. In Cohort 2, the SLN averaged 0.33 g N/m<sup>2</sup> when

rained and increased from 1.35 g N/m<sup>2</sup> when irrigated to 2.78 g N/m<sup>2</sup> with irrigation and N. Cohort 3 had SLN of 0.17 g N/m<sup>2</sup> when rained and 0.42 g N/m<sup>2</sup> with irrigation.

**Table 6-11 Specific leaf nitrogen (g N/m<sup>2</sup>) during grain-filling (1308 °Cd) for maize grown at two N levels (nil and 500 kg N/ha) either rained or irrigated in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rained	Irrigation	
	<u>Total SLN</u>		
0	0.13 <sub>c</sub>	0.68 <sub>b</sub>	0.41
500	0.20 <sub>c</sub>	1.21 <sub>a</sub>	0.70
Mean	0.17	0.95	0.56
SED <sub>N and W</sub> =0.0925, SED <sub>N*W</sub> =0.1308, P <sub>N</sub> =0.007, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.029			
	<u>Cohort 1 SLN</u>		
0	0.00	0.25	0.12
500	0.00	0.46	0.23
Mean	0.00 <sub>b</sub>	0.35 <sub>a</sub>	0.18
SED <sub>N and W</sub> =0.0531, SED <sub>N*W</sub> =0.0751, P <sub>N</sub> =0.067, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.067			
	<u>Cohort 2 SLN</u>		
0	0.22 <sub>c</sub>	1.35 <sub>b</sub>	0.79
500	0.43 <sub>c</sub>	2.78 <sub>a</sub>	1.61
Mean	0.33	2.06	1.20
SED <sub>N and W</sub> =0.224, SED <sub>N*W</sub> =0.317, P <sub>N</sub> =0.003, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.019			
	<u>Cohort 3 SLN</u>		
0	0.17	0.45	0.31
500	0.17	0.39	0.28
Mean	0.17 <sub>b</sub>	0.42 <sub>a</sub>	0.29
SED <sub>N and W</sub> =0.0658, SED <sub>N*W</sub> =0.0930, P <sub>N</sub> =0.604, P <sub>W</sub> =0.002, P <sub>N*W</sub> =0.654			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

The response in SLN around physiological maturity (1448 °Cd) (Table 6-12) was consistent with the earlier measurement. There was an interaction between N and water (P= 0.025) at the canopy level, a main effect of water in Cohort 1 (P=0.006), an interaction between N and water in Cohort 2 (P=0.008) and a main effect of water in Cohort 3 (P<0.001). Overall SLN at the canopy level was 0.11 g N/m<sup>2</sup> when rained and increased from 0.62 g N/m<sup>2</sup> when irrigated to 1.14 g N/m<sup>2</sup> with irrigation plus N. Cohort 1 had no measurable SLN when rained, because all leaves were dead but 0.21 g N/m<sup>2</sup> with irrigation. In Cohort 2, the SLN averaged 0.22 g N/m<sup>2</sup> when rained and increased from 1.35 g N/m<sup>2</sup> when irrigated to 2.70 g N/m<sup>2</sup> with irrigation and then N. The SLN in Cohort 3 was 0.11 g N/m<sup>2</sup> when rained and 0.41 g N/m<sup>2</sup> with irrigation.

**Table 6-12 Specific leaf nitrogen (g N/m<sup>2</sup>) around physiological maturity (1448 °Cd) for maize grown at two N levels (nil and 500 kg N/ha) either rainfed or irrigated in 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigation	
<u>Total SLN</u>			
0	0.08 <sub>c</sub>	0.62 <sub>b</sub>	0.35
500	0.14 <sub>c</sub>	1.14 <sub>a</sub>	0.64
Mean	0.11	0.88	
SED <sub>N and W</sub> =0.0878, SED <sub>N*W</sub> =0.1241, P <sub>N</sub> =0.006, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.025			
<u>Cohort 1 SLN</u>			
0	0.00	0.12	0.06
500	0.00	0.29	0.15
Mean	0.00 <sub>b</sub>	0.21 <sub>a</sub>	0.10
SED <sub>N and W</sub> =0.0616, SED <sub>N*W</sub> =0.0871, P <sub>N</sub> =0.192, P <sub>W</sub> =0.006 P <sub>N*W</sub> =0.192			
<u>Cohort 2 SLN</u>			
0	0.14 <sub>c</sub>	1.35 <sub>b</sub>	0.75
500	0.30 <sub>c</sub>	2.70 <sub>a</sub>	1.49
Mean	0.22	2.02	1.21
SED <sub>N and W</sub> =0.1875, SED <sub>N*W</sub> =0.2651, P <sub>N</sub> =0.002, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.008			
<u>Cohort 3 SLN</u>			
0	0.09	0.40	0.24
500	0.13	0.43	0.28
Mean	0.11 <sub>b</sub>	0.41 <sub>a</sub>	0.26
SED <sub>N and W</sub> =0.0583, SED <sub>N*W</sub> =0.0824, P <sub>N</sub> =0.549, P <sub>W</sub> <0.001, P <sub>N*W</sub> =0.974			

Means with different letters are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### Individual leaf area

The leaf surface area of individual leaves was affected by water and nitrogen (Figure 6-7). In both rainfed and irrigated crops, the lower canopy (first 6 leaves) were not affected by water or nitrogen. However, from leaf 7 upwards irrigated leaves were larger than rainfed and the effect of nitrogen was evident for both rainfed and irrigated crops.

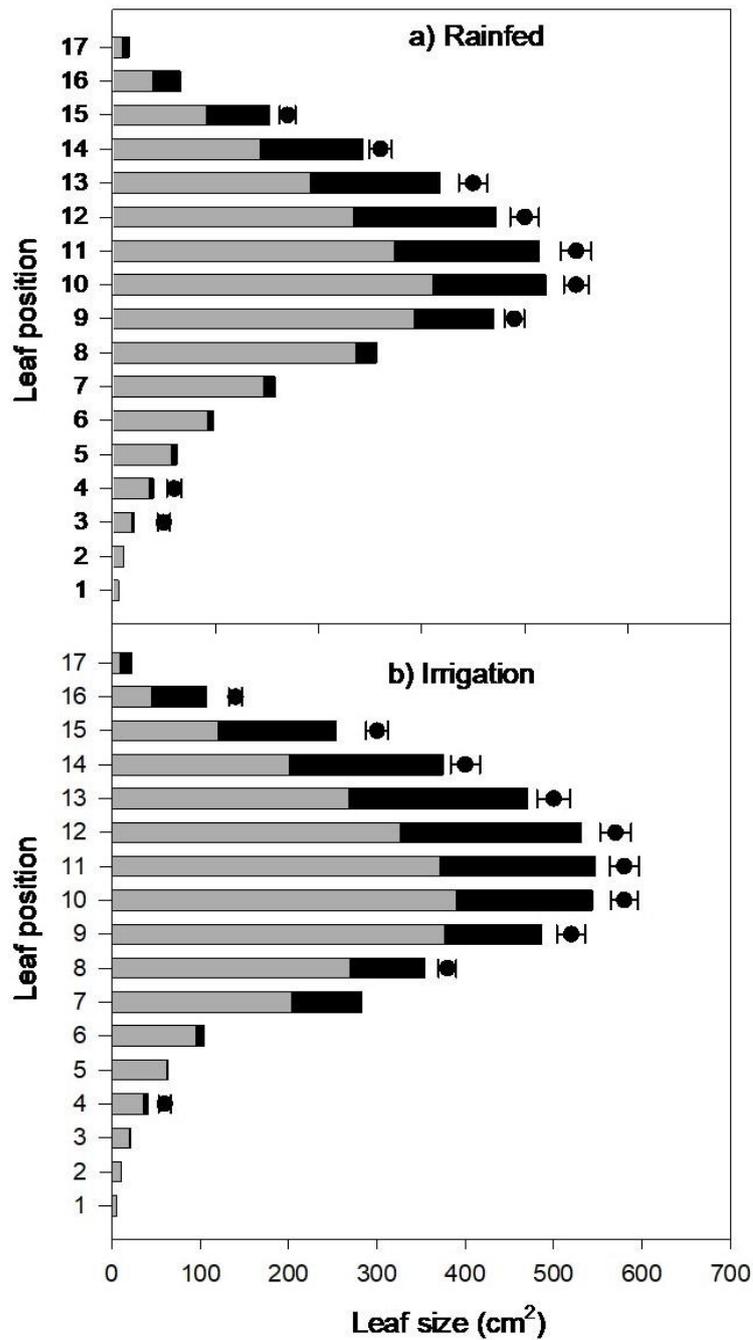


Figure 6-7 Leaf number/position versus size for different maize canopy structure in response to nil N (unshaded bar) and 500 kg N/ha (shaded bar) under rainfed (a) and nil N (unshaded) and 500 (shaded) kg N/ha with irrigation (b) for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Error bars indicate the standard error of the means.

## 6.4 Discussion

Objective 3 of the thesis was to examine the N dynamics at the switch from vegetative to reproductive development. Nitrogen remobilisation for kernel development at the start and during the linear phase of growth and N retention through leaf senescence were examined for crops with different yield potential. The contribution of RUE as a determinant of the total DM accumulated was also examined in terms of N as a key constituent to RUE that drives DM production. The results focus on the leaf as the main photosynthetic organ which acquires and utilises N to increase RUE.

### Experiment 1

There were no differences in grain yield in Experiment 1 as reported in Chapter 4, but there were differences in the total DM which indicated a main effect from water and N. Field observations indicate there was post-silking senescence caused by wilting in rainfed crops. These differences in total DM were examined in Chapter 5, and indicated differences in the amount of light intercepted were caused by water supply. This chapter focusses on the differences in total DM yield as a result of differences in RUE and how this was affected by N.

### RUE

The differences in RUE corresponded to N availability with soil moisture (uptake) and the distribution of N (utilisation) which is affected by the competing demands for photosynthesis function and leaf expansion for light capture. This was consistent with previous reports that show SLN differs with soil N supply (Muchow and Sinclair, 1994). The application of urea increased soil N availability and crop uptake and consequently RUE increased from 2.21 to 2.49 g/MJ (Table 6-1). However, water did not affect RUE which averaged 2.33 g/MJ under rainfed and 2.37 g/MJ under irrigation. The implication is that rainfall (Figure 3-2) during the vegetative phase provided sufficient soil moisture to allow no difference in the amounts of N uptake from the soil as the irrigated crops and thus the imposed water limitation did not inhibit N uptake in that year.

The increase in total crop DM as a result of an N effect on RUE (Figure 6-1), was mainly due to the increase in leaf N partitioning into SLN. The allocation of N between photosynthesis and leaf expansion is apparent in Figure 6.1. The impact of nitrogen on RUE is shown by the difference in slopes between the N treatments within rainfed and irrigated conditions. In contrast, the extension of the lines between irrigated and rain-fed crops shows the water effect on light interception. This is consistent with a priority for canopy expansion which averaged 3.71 m<sup>2</sup>/m<sup>2</sup> for all the crops (Table 5-2).

The water effect on intercepted PAR was due to post-silking senescence associated with water stress which caused severe wilting in rainfed crops rather than any difference in SLN.

## Crop nitrogen dynamics

In this section, the effect of N on the RUE is explained in relation to crop N dynamics. The crop N dynamics are quantified based on the dimension of plant volume on a DM basis and involves N uptake which depends on shoot demand and its growth potential and the availability of N in the soil (Gastal and Lemaire, 2002). Different N uptake is an indication of the capacity of the leaf to demand N. In Experiment 1, the effect of water was prominent on leaf N showing that the irrigated crops acquired higher N levels than rainfed crops (Figure 6-2). Under irrigation, the application of N increased leaf N during grain-filling but these dropped at late grain-filling. When irrigated but without N, the leaf maintained a steady N content. For the rainfed crops, the leaf N content decreased regardless of the N applied. This decline appears to have affected the amount of N available to the kernel and stalk. The effect of water and N indicate the capacity of a leaf to acquire N through improved leaf area.

The highlighted pattern of N partitioning in the crop was quantified according to post-silking events. At early silking (679 °Cd) (Table 6-2), there was no difference in leaf N that averaged 37.5 kg N/ha. This contributed most of the total crop N of 45.2 kg N/ha and implies a similarity in crop growth to this point, as reported in Section 4.4.1. Differences amongst treatments were more apparent in the stalk N content which increased from 6.71 to 8.73 kg N/ha with application of N. However, this did not affect total crop N which suggests the stalk N was an indication of the storage of N in preparation for ear development. Nitrogen uptake was the same and indicated N availability at that time.

During the grain-filling phase at 1400 °Cd, kernel N was not different and averaged 204 kg N/ha among all the crops. This suggests that the kernel N demand was met from each of the crops. However, this was achieved in different ways as indicated by changes in the total crop and stalk N. The total crop N increased from 230 to 289 kg N/ha with N application (Table 6-3). This crop response is explained by the amount of N in the leaf and then how much of this was accumulated in the stalk sinks after kernel demand was met. Leaf N increased with irrigation from 25.4 to 49.7 kg N/ha, however, it was the response to applied N that triggered different N uptake and partitioning scenarios. Under irrigation, the application of N increased leaf N to 56.9 kg N/ha and this treatment also accumulated the highest amount of stalk N at 39 kg/ha, after kernel demand was met. This suggests the stem had become a stronger sink for N than the kernel or leaves. Moreover, in the crop under irrigation and without N application, the leaf N was consistent at 42.6 kg N/ha. This resulted in lower N partitioned to the stalk because all N uptake in that period was assigned to the kernel. This stalk N was equivalent to the 13.3 kg N/ha of stalk N under rainfed conditions. The leaf N content of the crop when rainfed consequently dropped to 25.4 kg N/ha as N was remobilised to meet kernel N demand. Stalk N remained constant as there was no surplus N available. Thus, it was the low stalk N

content of the rainfed and the irrigated crops without N application that explains the total crop N decrease, shown by the significant main effect of N.

By crop maturity stage at 1541 °Cd, the total crop N increased from 228 to 317 kg N/ha with water and from 240 to 306 kg N/ha with N and this corresponded to the changes in leaf N (Table 6-4). Leaf N was still affected by water, decreasing from 45.7 to 21.7 kg N/ha when irrigated. However, the physiological response of the crop was sensitive to N. Under irrigation, the crop with N lost about 10 kg N/ha of leaf N as shown by the decline to 45.1 kg N/ha. This decrease was consistent with N being remobilised from the leaf and partitioned into the stalk, which increased by about the same amount to 51.3 kg N/ha. During this period there was no evidence of N being partitioned to the kernel which had reached its maximum N level and was stable at 230 kg N/ha. The crop without N application continued to maintain a steady leaf N content of 45.1 kg N/ha and therefore there were no differences between the N treatments. However, the crop without N application maintained leaf N, but there may have been continued N uptake after kernel N was met, because total crop N increased by 25 kg N/ha which would account for the increase in stalk N to 30.9 kg N/ha.

Under rainfed conditions, the crop with N applied decreased the leaf N content to 22.5 kg N/ha which was remobilised into the kernel. This contributed to the increased kernel N content to 211 kg N/ha. In contrast, the rainfed crop without N maintained its leaf N content at 21 kg N/ha. This suggests that the increase in kernel N of 11 kg N/ha in between 1400 and 1541 °Cd came from uptake rather than translocation from leaves or the stalk.

From these findings, it is observed that the application of water and N increased the leaf weight, in terms of structural and storage N capacity which enabled greater N uptake. The leaf N content reflects photosynthetic and non-photosynthetic capacity per unit leaf area on DM basis as such, it is associated with changes in the anatomy of the leaf. A higher leaf N content indicates a higher number of layers of cells in the palisade and parenchyma layers, suggesting that leaf thickness, and the number of cells and chloroplasts per unit leaf area all tend to increase in direct proportion with N (Klein et al., 1991). The uptake of water into the vacuole increases cell volume (Mizukami, 2001) and allows for more storage N. Leaf N content can therefore be expected to have modified both leaf volume per unit leaf area and the amount of photosynthetic enzyme (rubisco) per unit leaf volume. Therefore it appears that the irrigated crops increased non-photosynthetic N, while photosynthetic components remained steady and/or gradually depleted with leaf age (post-silking). This is consistent with the increased RUE with N but not water.

### **Specific leaf nitrogen**

SLN is a leaf surface area based measurement. It assumes light interception and the compounds located in the chloroplast thylakoid membranes associated with the light reactions are surface based and associated with, rubisco, the enzyme that catalyses initial CO<sub>2</sub> fixation (Field and Mooney, 1986). In contrast leaf N content is a weight based measurement. The general decline in silking/post-silking SLN indicated the remobilisation of N from leaf to grain-filling and then to other vegetative sinks. This was demonstrated by the parallel decline in SLN between 679 and 1400 °Cd before completing senescence at 1541 °Cd (Figure 6-3). The SLN differences among crops show that the applied N resulted in a higher SLN which is consistent with the higher RUE (Figure 6-1).

At silking there was adequate N available to meet shoot growth potential so additional N was used to increase SLN. There was also an interaction between N and water. The leaf appears to have promoted the use of N to build leaf volume in terms of leaf thickness (Mizukami, 2001) at the expense of SLN. This was evident both at 679 and 1400 °Cd (Table 6-5). Under irrigation leaf volume increased, but the application of N increased SLN content. However, for the crops without N, the available N was used for non-photosynthetic structures. The rainfed crops did not increase leaf volume therefore the applied N increased the SLN. This was evident at the silking stage at 679 °Cd when irrigated crops had a SLN of 2.1 g N/m<sup>2</sup> but without N this was lower at 1.66 g N/m<sup>2</sup> while under rainfed, there was no difference (Figure 6.3). Less water available, meant a higher SLN. The same effect was observed at 1400 °Cd, where SLN was lower when irrigated with or without N.

At crop maturity (1541 °Cd), there was a shift in the SLN response where rainfed crops had a higher SLN of 0.63 g N/m<sup>2</sup>. In contrast, both irrigated crops finished with a SLN of only 0.38 g N/m<sup>2</sup>. This suggests the photosynthetic nitrogenous apparatus of the leaf N was depleted for all crops. The remobilised N in the irrigated crops was observable as organic N for non-photosynthetic functions, as seen in the increase in stalk N (Figure 6-2).

At the silking phase when canopy development was completed, marked at 679 °Cd, the application of water and N did not affect light interception (Figure 5-1), and the leaf N volume was unaffected. However, the SLN differed with addition of water and N. This suggests that the crops prioritized leaf area for light interception and leaf structural development more than investing the N into its photosynthetic apparatus. This explains the differences in RUE. As such, the maize crop strategy when N availability cannot meet crop N demand, was to reduce SLN while maintaining leaf area which is consistent with previous reports (Massignam et al., 2012).

### 6.4.2 Experiment 2

In Experiment 2, there were significant differences in grain yield and the total DM as reported in Chapter 4. Chapter 5 explained these differences were due differences in the total iPAR. There was an interaction for which each crop progressively increased the light intercepted in response to water and N regimes. In this section, the contribution of RUE to yield differences is examined and differentiated from the contribution of light interception in the previous chapter. In contrast to Experiment 1, where light interception was not different through the vegetative to silking phase, in Experiment 2, water and N limitations were evident on light intercepted in the early growth stages (Table 5-3 and Figure 6-2).

#### Radiation use efficiency

Experiment 2 provided contrasting soil conditions that resulted in different N uptake with distinct RUE responses. This is demonstrated by the interaction in the RUE response to water and N (Figure 6-4). The trade-off for N between SLN and leaf expansion was more obvious as crop growth was affected from early stages (Figure 4-6). Rainfed crops with or without N had the lowest RUE of 0.87 g/MJ (Table 6-6). The implication is that water stress severely restricted N uptake even when it was applied. Thus, adding N did not increase RUE but did increase light interception probably because N promoted shoot meristem tissue growth. This is support by Volenec and Nelson (1983) in their work on tall fescue, which found that addition of N fertilizer triggered modifications in the number of cells matured per day per cell column but the length of fully elongated epidermal cells was unaffected in the leaf intercalary meristem. The water limitations appeared to suppress CO<sub>2</sub> fixation as shown by the difference in RUE between the rainfed and irrigated but no N crops (y-axis change). In addition the decreased cell turgor reduced leaf elongation due to the low water potential (Van Volkenburgh and Boyer, 1985) which reduced total light interception as shown by the differences in the x-axis of Figure 6.6

Thus, irrigation without N increased RUE to 1.82 g/MJ and suggests that irrigation improved the availability of the N available from soil mineralisation, promoted cell turgor and leaf elongation and increased photosynthetic capacity. Irrigation with N resulted in the highest RUE to 3.15 g/MJ. In this situation, the crop N demand was met and there was also a balance between N demand for photosynthesis and the ability to maximize light interception.

#### Crop nitrogen dynamics

The relationship between N uptake and the influence of N on RUE is explained in the crop N dynamics. Results from Experiment 2, followed those of Experiment 1, where irrigation promoted cellular expansion resulting in an increased plant volume or leaf area (Mizukami, 2001). Irrigation with N application resulted in higher N uptake resulting in high leaf N content and the faster build-up

of kernel N. However, the kernel N in the irrigated crop without N lagged behind the fertilised crop because it was solely reliant on soil N availability (Figure 6-5). Under rainfed conditions leaf N content decreased significantly as N was remobilised to support kernel N. There was nil to limited N deposited into the stalk as shown by the consistent stalk N content.

At late silking at 905°C.d, full canopy expansion was reached, and grain-filling initiated. The differences in leaf N suggest different shoot growth potential dependent on the availability of N from the soil and N uptake. Irrigation and N application resulted in a leaf N content of 68.3 kg N/ha as N uptake was not restricted (Table 6-7). However, irrigation without N had a lower leaf N content at 28.4 kg N/ha as N uptake depended on available and mineralised N (Table 3-1). This amounted to similar leaf N content of the rainfed crops which averaged 20.3 kg N/ha. This suggests they mainly relied on availability of mineral N under the water deficit conditions. The implication is that even though N supply differed with 500 kg N/ha added, the rainfed crop did not have access to all of this and depended on the water flux and the N concentration of the soil solution (Kovács, 2005). The lack of differences in the irrigated crop without N and the rainfed crops is reflected in the potential organ and plant size. It seems likely that was achieved through increased cell numbers and their size. The consistency in organ volume was chiefly from larger cells in the irrigated crops but in the rainfed crops it was through increased cell numbers (Sylvester and Smith, 2009).

The changes in N level in the leaf indicate N uptake and partitioning into the kernel. After leaf expansion was complete, the utilization of N shifted from its emphasis on leaf expansion to kernel growth. This creates a trade-off for N between storage in kernels and photosynthesis. Kernel N was highest at 69.0 kg N/ha with irrigation and the N application, indicating high N availability to maintain high leaf and kernel N. This corresponding effect of leaf and kernel N is also seen in all the other crops where kernel N dropped to 18.4 kg N/ha under irrigation and without N application and was not different to the rainfed crops which had a kernel N of 10.3 kg N/ha. Kernel N reflected leaf N content and indicated crop dependence on the continued N supply from the soil and not from remobilised N.

Stalk N only reflected the structural composition because at this stage it appears to be a weak N sink. Thus, the total crop N was mainly influenced by the leaf and kernel N and amounted to 173 kg N/ha with irrigation but dropped to 57.7 kg N/ha without N and 40.7 kg N/ha when rainfed.

Following into grain-filling as kernel N sink demand became stronger, leaf N was compromised to meet these N needs. Midway through grain-filling at 1308 °Cd, there was a reduction in leaf N content to near zero under rainfed conditions (Table 6-8), indicating nearly all N had been remobilised from the leaves and these had senesced. Leaf N was 45.5 kg N/ha for irrigation with N after remobilisation of N into the kernel while irrigation without N application, maintained leaf N at

20.4 kg N/ha. The high N supply from uptake and remobilised N from the leaf enabled kernel N levels to reach the maximum at 231 kg N/ha for the crop under irrigation and N, whilst the crop without N relied entirely on N uptake and showed a slower rate of increase in kernel N reaching only 100 kg N/ha. When rainfed without N, the kernel N content was unchanged at 7.08 kg N/ha with the application of N only producing an intermediate response. Once again, the stalk N was unchanged despite leaf senescence and kernel filling, demonstrating its structural N composition and also suggesting it was a weak N sink. The combined leaf and kernel activity resulted in the highest total crop N under irrigation and N application at 318 kg N/ha and 133 kg N/ha without N (which reflects the plant available soil N across the season). Under rainfed conditions crop N attained an intermediate N level of 36.2 kg N/ha when N was applied but was only 10.8 kg N/ha without N application which shows a low level of uptake of plant available soil N. Together these results highlight a continued N supply from soil and fertiliser in the irrigated crops but an N limitation under rainfed conditions due to low soil water status.

At physiological maturity (1448 °Cd), the continued supply of N as affected by soil water was evident in kernel N sink demand and vegetative sinks (stalk and leaf sink N). As leaf senescence continued to progress, the leaf N content under irrigation remained constant at 53.1 kg N/ha with N and lower at 19.9 kg N/ha without N application (Table 6-9). When rainfed, the leaf N content remained depleted at a minimum of 2.5 kg N/ha. The kernel N responded to the N supplied from the leaf as kernel N requirements for irrigated crops were met. This was shown by the increase in kernel N from 49.2 to 184 kg N/ha in response to irrigation. The indication is that once the irrigated crops had met kernel N demand, excess N was diverted to stalk which became the main N sink. In contrast, the rainfed crops had low N uptake which did not satisfy kernel N requirement and thus no possibility of restoring vegetative N levels. The excess N diverted into the stalk increased its N content in the irrigated crop from 21.6 to 62.4 kg N/ha with N application.

As observed in Experiment 1, Experiment 2 also showed that the application of water and N increased the leaf volume by increasing its structure and storage capacity to accommodate increased N uptake. Thus, the increased N uptake at post-silking supported non-photosynthetic N production (kernel filling) while maintaining photosynthetic components, which explains why N and not water was responsible for the increased RUE. It was the availability of N from N application and mineralisation in the soil, its efficiency in N uptake as affected by soil water, and N utilisation in the crop that all affected N allocated to photosynthesis which had an overall impact on RUE.

## Specific leaf nitrogen

Nitrogen status at the whole crop level changes with crop N demand and is controlled by N components associated with photosynthesis (Kull, 2002). As such the response of RUE to nitrogen supply is explained by the changes in SLN. At silking the SLN reached a peak before the N was saturated from N rich source organ, the leaf into the main N storage organ, the kernel. The decline in SLN post-silking was caused by increased kernel N demand (Figure 6-6). The mid-canopy (Cohort 2) was found to have a higher SLN which is consistent with it being the most productive section of the canopy and also the most important unit of the canopy that directly supplies assimilates into the ear (Teixeira et al., 2011). The canopy N dilution is more prominent in the mid canopy as leaves in this cohort are exposed directly to solar radiation and have high N concentration (Hikosaka et al., 1994) before being diluted into the plant volume (Greenwood et al., 1990). The overall canopy SLN corresponds to that of the mid cohort as it has the highest SLN compared with the other cohorts. Senescence is programmed in such a way that the lower and upper cohorts remobilise N into the mid canopy to maintain its N levels for as long as possible, which also supports N supply to the growing kernel.

The partitioning of N into leaf growth and photosynthesis is clearly illustrated in this period. At late silking (905 °Cd), the SLN in the overall canopy averaged 1.23 g N/m<sup>2</sup> for all the crops (Table 6-10). This consistency in SLN under different water and N conditions demonstrates the effect of water in prioritising leaf expansion and how the N is used for sustaining SLN. The allocation of N to leaf expansion is shown in Figure 6-7 and is also supported by the measurements of total and maximum leaf area per plant at each cohort in Table 5-5. Water affected the increased leaf area in all the cohorts from a total area 2978 to 3568 cm<sup>2</sup> but the effect of N increased leaf area from 934 to 1481 cm<sup>2</sup> in the mid and from 428 to 873 cm<sup>2</sup> in the upper canopy. This indicates N promoted growth to support the apical meristem localised in this area of the plant where the ear growth occurs. The effect of N application on SLN was also evident in this part of the canopy, where N and also water increased both SLN and leaf area simultaneously. The lower and upper cohorts responded differently. The changing responses of SLN at the different cohorts, collectively showed no response to water and N at the canopy level.

Focusing on the mid-cohort (Cohort 2), the effect of leaf size and PPFd also influences the distribution of SLN within the canopy and was obvious at 905 °C.d. In the mid cohort SLN increased from 1.43 to 2.39 g N/m<sup>2</sup> with irrigation and from 1.46 to 2.37 g N/m<sup>2</sup> with N. The increase in SLN with water was also associated with large leaf area per plant in this cohort because of the actively growing ear. In all crops, the SLN in this cohort was responsive to the high PPFd levels as most light is captured in this portion of the canopy. This meant more light was saturated in this section of the canopy which maintained the high N leaf response to the high PPFd. The rainfed crops, on the other

hand, had smaller leaf size in both Cohorts 1 and 2 which meant light was uniformly saturated, resulting in the higher SLN of 1.55 g N/m<sup>2</sup> in the lower cohort. Unlike the rainfed crop, in the irrigated crop, most of N in the lower cohort was translocated into the mid canopy probably due to the shading effect from the bigger leaves in upper canopy and this explains the low SLN of 0.51 g N/m<sup>2</sup>. The increase in SLN in Cohort 2 with N application was due to the increased N availability and uptake. High PPFD in this cohort, triggered an increase in SLN and was attributed to leaf thickness, which indicates the number of cells and chloroplasts per unit leaf area all increased in line with N uptake (Grindlay, 1997).

It is Cohort 3 that receives unlimited PPFD as the leaves are at the top of the canopy. However, the SLN was the same for all the crops and averaged 0.46 g N/m<sup>2</sup>. This reflected the N distribution in the canopy and N was translocated from older leaves to the younger leaves to sustain potential growth (Koch et al., 1988) during the vegetative phase. This was the upper portion of the canopy where overall leaf area was lowest at 650 cm<sup>2</sup> associated with the relatively low SLN. Thus, it appears the utilization of N for leaf actively was exhausted so it was unable to access N to maximize photosynthesis.

During grain-filling at 1308 °Cd, the overall SLN in all the crops had dropped (Figure 6-6). Under irrigation, the SLN was 1.21 N/m<sup>2</sup> with urea and 0.68 g N/m<sup>2</sup> without urea, and under rainfed conditions, the SLN was 0.35 g N/m<sup>2</sup> (Table 6-10). The overall canopy SLN corresponded to that of the mid cohort as it had the highest SLN. As observed in Cohort 2, under irrigation, the SLN was 2.78 g N/m<sup>2</sup> with urea and 1.35 g N/m<sup>2</sup> without urea, and under rainfed conditions, the SLN 0.33 was g N/m<sup>2</sup>. The trade-off between N to maintain SLN and remobilisation of N into kernel sinks was more evident at this stage. The irrigated crops showed a small decrease in SLN and managed to retain SLN at high levels because of greater N uptake, shown by the highest total crop N. In contrast the rainfed crops, had limited N supply and restricted N uptake which meant they quickly remobilised leaf N to meet demand from the kernel N sink. There was also a significant decrease in SLN under rainfed conditions in Cohort 1 which meant there was no reserve to sustain photosynthesis. All its leaf N was remobilised into the kernel.

The end of grain-filling (physiological maturity) at 1448 °Cd showed a pattern consistent with results at 1308 °Cd, where SLN continued to decline as N was diverted into N sinks. The overall canopy SLN showed the rainfed crops had a low SLN of 0.11 g N/m<sup>2</sup> and this increased from 0.62 to 1.14 g N/m<sup>2</sup> with irrigation and urea (Table 6-12). In the rainfed crop, leaf SLN was completely depleted in all the cohorts. In contrast, the irrigated crops were able to retain SLN in the mid cohort but still meet kernel N demand. By the end of grain-filling, the irrigated crops had effectively utilized N to restore all vegetative N sinks.

The differences in RUE are consistent with the changes in SLN over the period of grain-filling. At the start of grain-filling when the canopy was at its maximum potential, SLN was uniform for all the crops. However, SLN dropped for the rainfed crops by mid grain-filling while the irrigated crops retained their SLN in the mid cohort. This suggests higher SLN levels contributed to higher RUE in maize and maintained high levels of SLN throughout the growing season and through grain-filling (Goron et al., 2017). The intermediate response of irrigation and N application was because of the leaf area and structural volume, and N uptake which maintained SLN in the mid-cohort. Soil water and N uptake played an important part in maintaining the SLN in the leaf while meeting kernel N demand.

## 6.5 Conclusion

In Experiment 1, the intensity of water and N limitations were mild. Under these conditions, the maize crop strategy was demonstrated when N availability could not meet N kernel demand. This was shown as a reduction in SLN at the cost of maintaining leaf area for light interception, thus resulting in reduced RUE.

In Experiment 2, when the canopy had reached its maximum potential, the amount of light interception differed for each crop. Irrigation and N application increased light interception and leaf structural volume, but the SLN was consistent with all other crops. Irrigation without N application only increased light interception, and the leaf structural volume but not the SLN. When rainfed, N was unable to be utilised for leaf area production and therefore SLN increased. However, the crop could not retain N as SLN due to the limited N uptake. The consequence was remobilised N being required to meet growing kernel N demands. The amount of SLN and its ability to be maintained during the entire cropping phase determined the RUE response.

When water was not a limiting factor, leaf N was prioritised for light interception to maximise leaf area and weight at the cost of maintaining minimum levels of SLN necessary for unrestricted growth. However, under water stress conditions, leaf expansion was restricted, and N was diverted to increasing SLN levels. This phenomenon has a direct effect on both RUE and light interception. The availability of N in the soil, soil water and N uptake are important factors that determine N utilisation in the plant and ultimately the RUE.

## Chapter 7

### Plant water use and dry matter production

#### 7.1 Introduction

Objective 4 of this research was to explain the impact of crop water use on canopy development for the different yield scenarios. The contribution of N to RUE and DM yield was accounted for in Chapter 5. This chapter quantifies the available soil water and crop water use to account for the effects of water on canopy development and its contribution toward yield. Only Experiment 2 was analysed as soil moisture content measurements for Experiment 1 had stopped at silking.

The main functions that water and N affects simultaneously are photosynthesis and canopy expansion. Water affects the leaf and canopy photosynthetic capacity through stomatal activities. Evapotranspiration drives water from the soil for plant utilization and transpiration occurs through the stomata. The stomata control both the entry of carbon dioxide and the exit of water from the leaves of plants (Chaves et al., 2002). When there is a lack of water, the stomata closes to prevent significant water loss. As a result, photosynthesis will slow down because there will be less carbon dioxide entering the plant (Pinheiro and Chaves, 2011). This affects the water dynamics between the soil water supply and plant water use. The other main process affected by a lack of water is canopy expansion. A reduction in cell expansion occurs at lower water levels of water stress than photosynthesis so this is usually the first sign of water stress in a crop. The level of water stress a crop is experiencing is determined by the amount of water in the soil. The timing of water stress then affects the yield potential and the supply of assimilate by affecting the ability of crops to capture and utilise available energy.

## 7.2 Materials and methods

### 7.2.1 Drained upper limits (DUL) and lower limits (LL)

For the rainfed treatments, the DUL and LL were determined from field measurements. Under irrigation, attaining the LL is impractical because it requires soil to be completely dried down which is contradictory to the irrigation treatment. For irrigated crops percolating water movement through the soil continuously recharged soil water in each layer, hence making it impractical to obtain LL (Appendix C). The amount of water that will move through the soil column depends on the volume of soil that will supply water, and its moisture content (Read, 1959). The irrigated treatment demonstrates a “wetting front movement” of soil water where water moves down through the soil as progressive layers exceed field capacity. Light irrigation or rainfall only re-wets the top part of the root zone, leaving patches of un-watered zone below (Witelski, 2005). Therefore, estimates of LL were used instead of the actual field measurements. The estimates of LL were taken from the corresponding adjacent rainfed plots.

Refer to Section 3.5.3 for all information regarding the material and methods of this chapter.

## 7.3 Calculations

### 7.3.1 The critical limiting deficit ( $D_L$ )

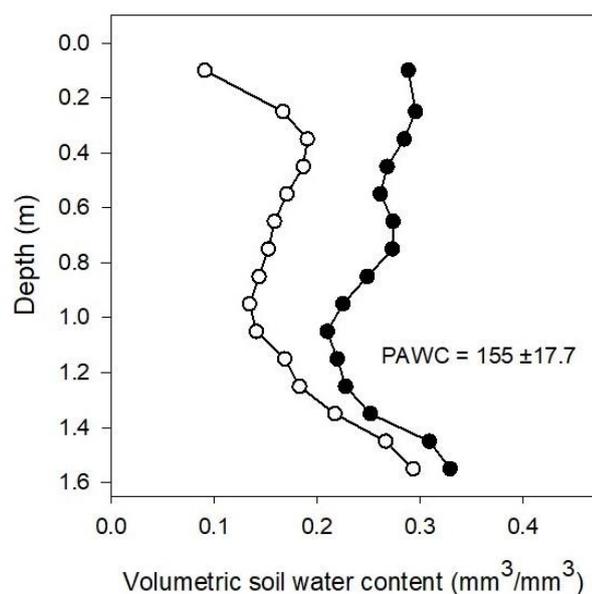
The effect of water stress on GAI and DM yield was quantified in terms of how much actual soil moisture deficit (ASMD) the maize crops were able to withstand before yield loss was evident. The  $D_L$  was determined using a broken stick approach to identify the point where crop yields of the unirrigated crops show a reduction relative to the irrigated crops. The first line segment constrained to have a y-intercept of one and a slope of zero. There were two parameters tested, the  $D_L$  and the slope of decline. The relative GAI and DM yield were attained as the ratio of irrigated to rainfed for each of the two N treatments. Calculations for the ASMD are given in Section 3.5.3. The slope of the N treatments in the plots were analysed using one-way ANOVA to assess the differences.

For all other calculation on soil moisture and plant water use, refer to Section 3.5.3

## 7.4 Results

### 7.4.1 Plant available water content (PAWC)

The mean DUL and LL of the soil water content within the soil profile are shown in Figure 7-1. The soil measurements were taken from 18/11/2016 to 28/04/2017, which represents the entire growing season. The roots were extracting soil water to 1.2 to 1.3 m depths. In these depths, the DUL ranged between 0.18 to 0.32 mm<sup>3</sup>/mm<sup>3</sup> and the LL ranged from 0.08 to 0.19 mm<sup>3</sup>/mm<sup>3</sup>.



**Figure 7-1 The LL (○) and DUL (●) of the available soil water content (mean of plots) for rainfed maize in response to nil N and 500 kg N/ha for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

The PAWC which contributed to growth averaged 177 mm for this soil (Table 7-1).

**Table 7-1 Mean of the plant available water content (mm) to 1.5 m soil depth for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops in 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
0	156	181	169
500	154	218	186
Mean	155	200	177

SED<sub>N and W</sub>=17.68, SED<sub>N\*W</sub>=25.01, P<sub>N</sub>=0.350, P<sub>W</sub>=0.085, P<sub>N\*W</sub>=0.302

Means with different letter are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### 7.4.2 Actual soil moisture deficit (ASMD)

The starting ASMD deficit before water treatments were applied indicated for the irrigated crops was between 43 and 53 mm and the rainfed which was around 8 to 10 mm (Figure 7-2). The application of irrigation and rainfall maintained the ASMD level to below 70 mm. Under rainfed conditions the ASMD continued to drop to a maximum of 146 mm before rainfall increased soil water content after 1000 °Cd (Figure 3-3). As expected, the maximum soil moisture deficit (MSMD) was affected by irrigation ( $P < 0.001$ ) (Table 7-2). The MSMD was higher for the rainfed crops was 143 and 76.2 mm under irrigation.

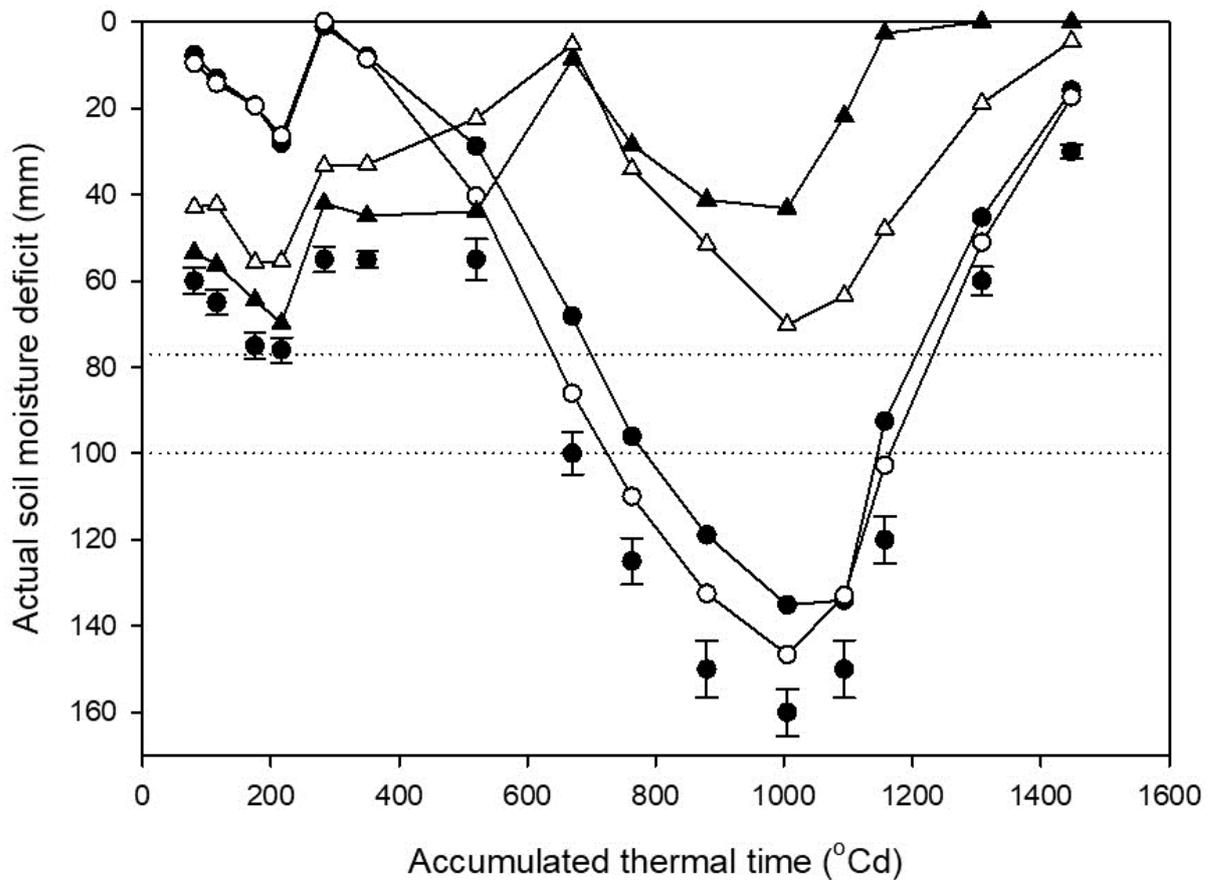


Figure 7-2 Actual soil moisture deficit (ASMD) (mm) from 0.0 - 1.5 m soil depth against accumulated thermal time for maize in response to nil N (●) and 500 kg N/ha (○) under rainfed and nil N (▲) and 500 (△) kg N/ha with irrigation for 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Dotted lines indicate the  $D_L$  for yield at 100 mm without N and 77 mm with 500 kg N/ha. Error bars indicate the standard error of the means.

**Table 7-2 The maximum soil moisture deficit (mm) measured during the growing season for maize in response to two N levels (0 and 500 kg N/ha) for rainfed and irrigated crops in 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand.**

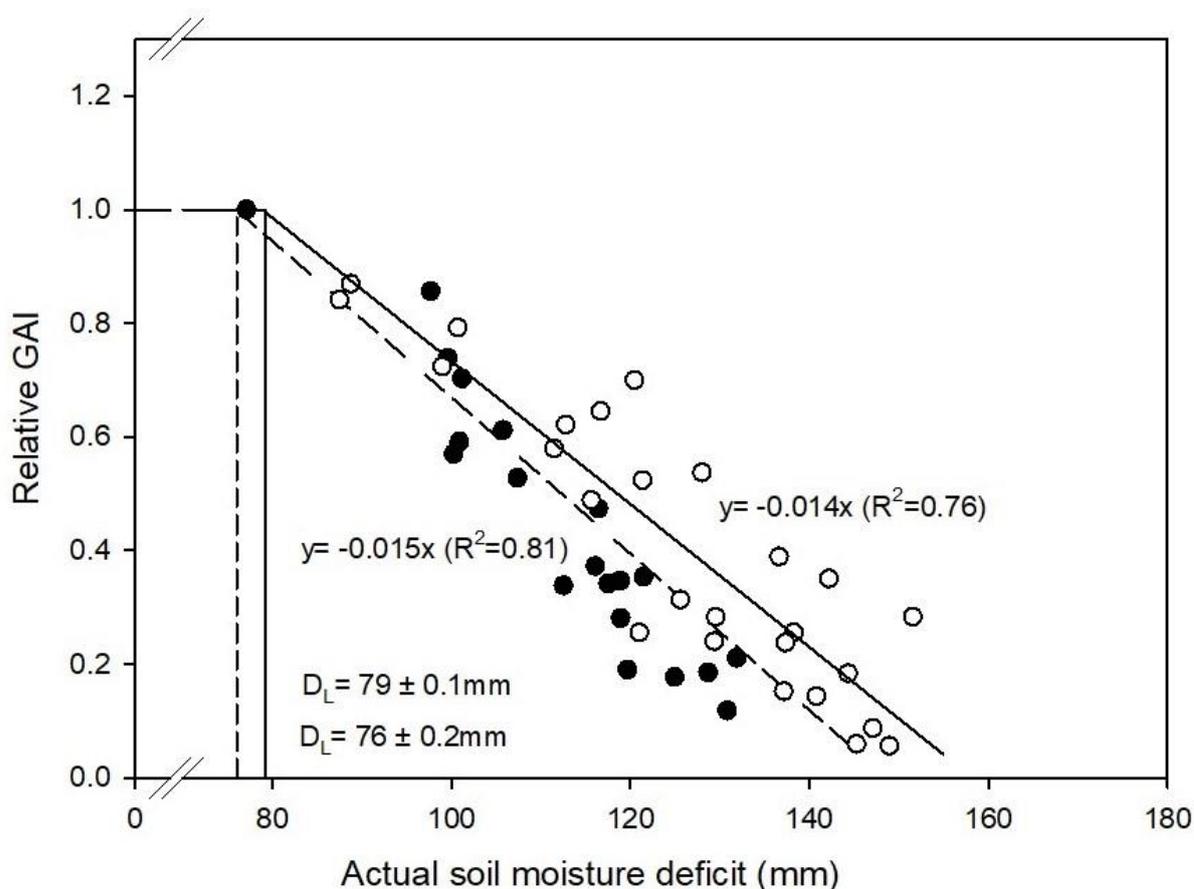
N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
0	140	70.6	105
500	146	81.8	114
Mean	143 <sub>a</sub>	76.2 <sub>b</sub>	110

SED<sub>N and W</sub>=7.43, SED<sub>N\*W</sub>=10.51, P<sub>N</sub>=0.287, P<sub>W</sub><0.001, P<sub>N\*W</sub>=0.721

Means with different letter are significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

### 7.4.3 Critical limiting deficit ( $D_L$ )

Analyses showed the  $D_L$  for the GAI was 79 mm with N ( $P=0.05$ ) and without N application was 76 mm (Figure 7-3). The rate of reduction in GAI due to water stress was 1.4% GAI/mm with N ( $P=0.06$ ) and 1.5% GAI/mm without N application.



**Figure 7-3 Decrease in relative GAI of (a) irrigation without N ( $\blacktriangle$ ) relative to rainfed without N ( $\bullet$ ) and (b) irrigation with 500 kg N/ha ( $\triangle$ ) relative to rainfed with 500 kg N/ha ( $\circ$ ) for maize during 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand.**

For total dry matter yield, the  $D_L$  was different for the two N conditions ( $P=0.003$ ). Without N application, the  $D_L$  was 77 and 100 mm with N (Figure 7-4). However, the rate of reduction was faster at 1.89% DM/mm ( $P=0.003$ ) for the crops with N when the ASMD was higher than  $D_L$ . Without N application, the rate of DM reduction was 1.24 % DM/mm when ASMD increased past the given  $D_L$ .

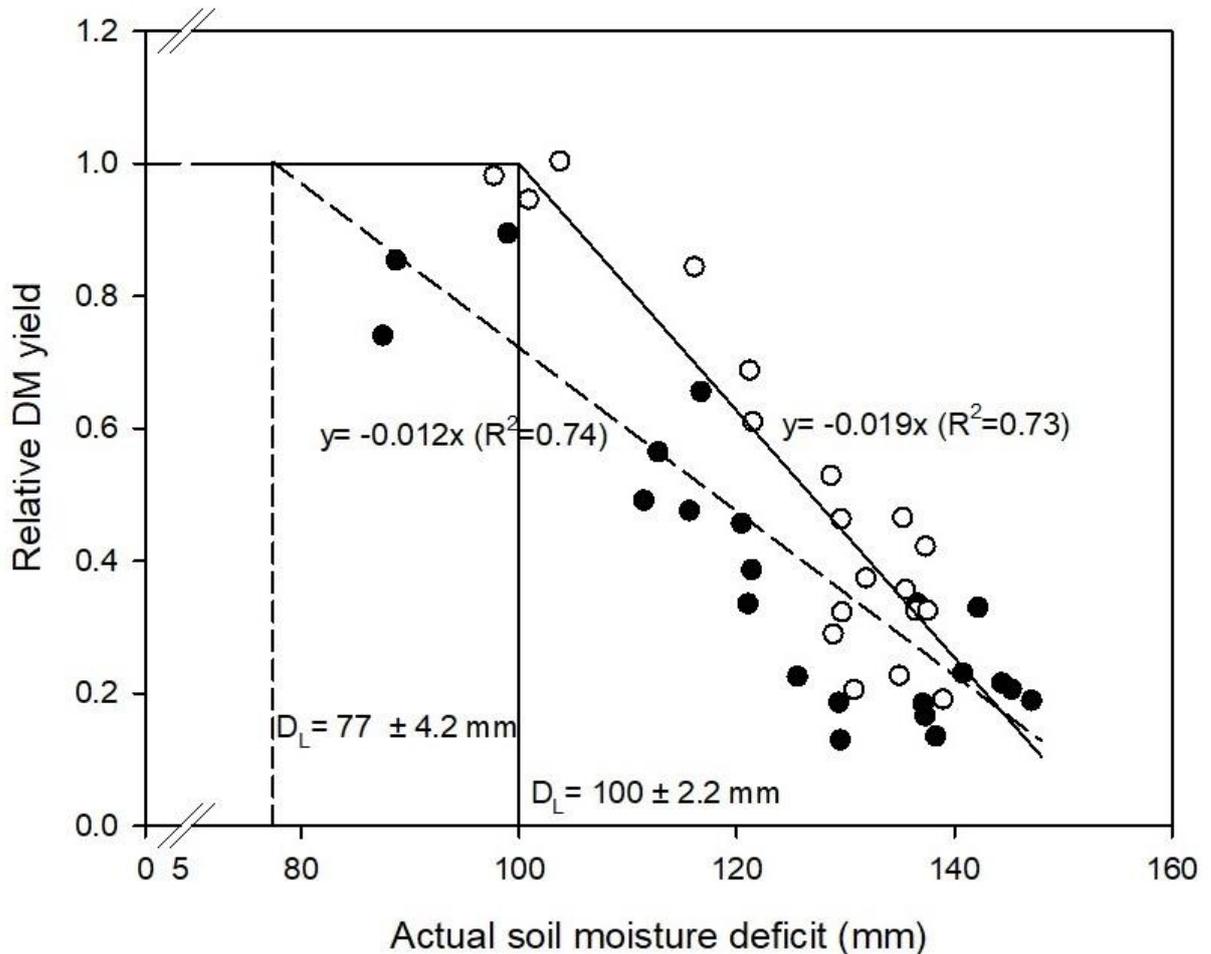


Figure 7-4 Decrease in relative yield of (a) irrigation without N ( $\blacktriangle$ ) relative to rainfed without N ( $\bullet$ ) and (b) irrigation with 500 kg N/ha ( $\triangle$ ) relative to rainfed with 500 kg N/ha ( $\circ$ ) for maize during 2016/17 (Experiment 2) at Lincoln University, Canterbury, New Zealand. Dotted lines indicate slope and  $D_L$  for under rainfed and solid lines are under irrigated conditions.

#### 7.4.4 Crop water use and water use efficiency (WUE)

The total water use for the crops showed an interaction ( $P=0.036$ ) between water and N (Table 7-4). Water used by the rainfed crops was 368 mm and increased from 462 to 525 mm when irrigated with N.

**Table 7-3 Total water use (mm) for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops in 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand.**

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
0	364 <sub>c</sub>	462 <sub>b</sub>	413
500	371 <sub>c</sub>	525 <sub>a</sub>	448
Mean	368	494	431

SED<sub>N and W</sub>=11.26, SED<sub>N\*W</sub>=15.93, P<sub>N</sub>=0.015, P<sub>W</sub><0.001, P<sub>N\*W</sub>=0.036

Means with common subscript letters are not significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

The WUE showed an interaction between water and N ( $P=0.003$ ) (Figure 7-5) (Table 7-4). There was 17.9 kg DM/mm conversion rate when rainfed and this did not differ from the crop under irrigation without N at 25.7 kg DM/mm but improved with the application of N to 47.2 kg DM/mm of water used.

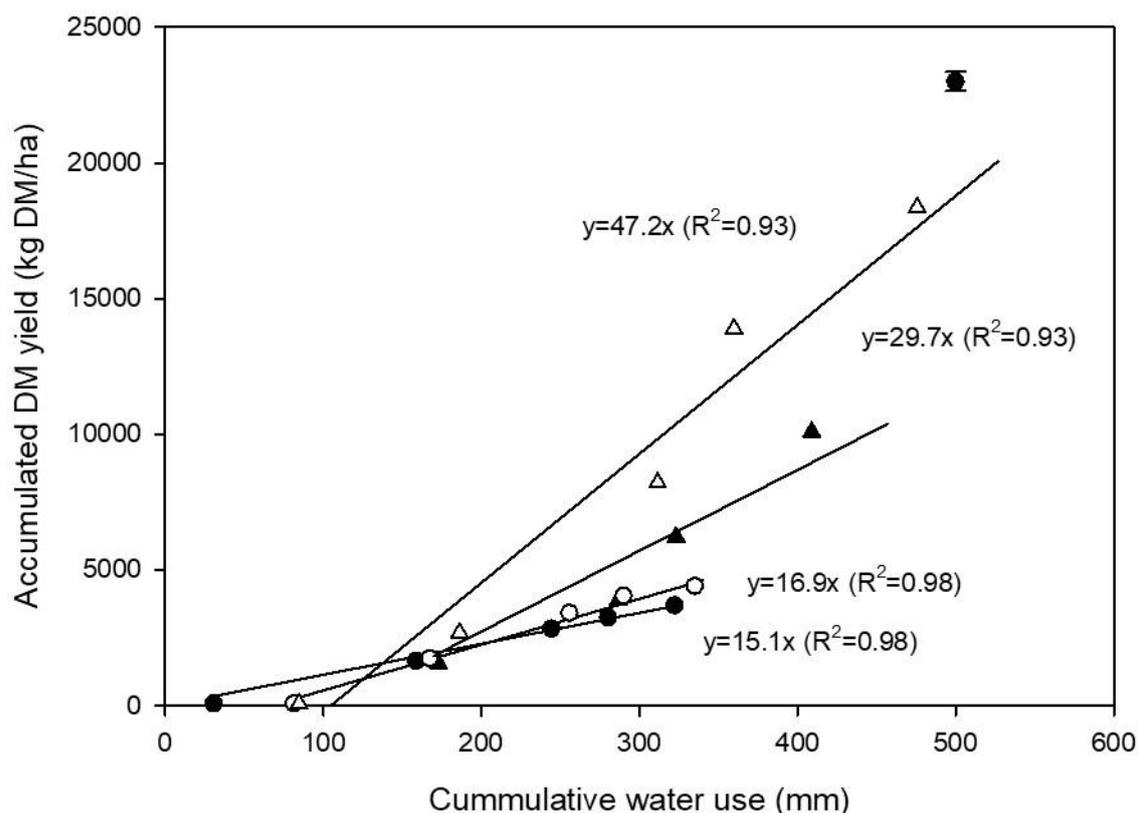


Figure 7-5 Accumulated DM yield (kg DM/ha) against cumulative annual water use (mm) for maize in response to nil N (●) and 500 kg N/ha (○) under rainfed and nil N (▲) and 500 (△) kg N/ha with irrigation for 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand. Error bar indicates the standard error.

Table 7-4 Water use efficiency (DM/mm) for maize in response to two N levels (nil and 500 kg N/ha) for rainfed and irrigated crops in 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand.

N (kg/ha)	Water		Mean
	Rainfed	Irrigated	
0	15.3 <sub>a</sub>	25.7 <sub>a</sub>	20.5
500	20.6 <sub>a</sub>	47.0 <sub>b</sub>	33.8
Mean	17.9	36.4	26.1

SED<sub>N and W</sub>=2.38, SED<sub>N\*W</sub>=3.37, P<sub>N</sub><0.001, P<sub>W</sub><0.001, P<sub>N\*W</sub>=0.003

Means with common subscript letters are not significantly different  $\alpha=0.05$ . SED is the standard error of differences and P is the probability level.

## 7.5 Discussion

This discussion is focused on Objective 4 which was to explain the impact of crop water use on canopy expansion under the different yield scenarios. In Chapter 6, the allocation of N within the leaf for photosynthetic functions was mainly affected by water and N requirement for leaf expansion. In this discussion the contribution of water to GAI and DM is identified in association to N effects. Thus two areas are addressed, to indicate whether the irrigated crops were stressed and whether the non-irrigated crop with N used more soil water than when N limited.

### 7.5.1 Plant available water content (PAWC)

The capacity of a crop to extract water is determined by the available soil water. The distribution of soil pore sizes, which is influenced by soil texture, plays a crucial role in determining the soil's capacity to retain moisture (Jamieson and Ewert, 1999). The extent to which the LL and DUL were reached at each layer under rainfed conditions, showed that roots extracted water to depths between 1.2 m and 1.3 m before LL closed in towards the DUL (Figure 7-1). This was used to suggest the point of maximum extraction depth. The difference in PAWC between layers was because of the infiltration in the top unsaturated layers and percolation in the subsequent layers (Fu et al., 2019) and likely because of the soil texture.

### 7.5.2 Actual soil moisture deficit (ASMD) and Critical limiting deficit (D<sub>L</sub>)

Accumulated thermal time was used to show how the ASMD progressed among the different treatments over the growing season (Figure 7-2). The ASMD in the rainfed crop increased from nil deficit at 283 °Cd to 135 mm without N and 147 mm with N at 1005 °Cd. This indicated that the canopy development and kernel formation were deprived of water at these critical growth phases. This was because there was only 4.6 mm of rain in this period (between 25/01/17 to 13/03/2017) and points out that the rainfed crop was at the LL of the soil water content during this period.

A comparison of the MSMD in this experiment with studies done by Jamieson et al. (1995b) in the Lincoln, Canterbury area indicated a MSMD of 205 mm under mobile rainshelter for their mid-season drought treatment imposed. Their mid-season drought treatment was deprived of 192 mm in an 18 m<sup>2</sup> plot size. However, their grain yield averaged 11 t/ha for this treatment. In comparison, the rainfed crop in this experiment only yielded 0.9 t/ha of grain and reached a maximum ASMD of 143 mm. The main reason for this very low yield was because the rainfed crops in this experiment was exposed to both an early and mid-season drought stress therefore severely affecting growth. The duration of stress below 50% of PAWC, was about 600 °Cd.

The  $D_L$  for GAI was affected by N, indicating that water was a dominant factor in leaf expansion. The leaf developmental phase, from 0 – 600 °Cd, was the period when phyllochron for appearance of leaf tips and fully expanded leaves occurs and this was only affected by N and not water (Table 5-8 and Table 5-9) (Section 5.4.2). As indicated in Figure 7-2, this phase occurred when the  $D_L$  was less than 76 mm when crops were not under water stress. After leaf initiation, leaf expansion was affected by water. The rainfed crops experienced a maximum ASMD of 143 mm (Table 7-2) during the period between 600 -1000 °Cd. Their GAI decreased (in comparison to irrigated crop) at a rate of 1.5% DM/mm without N and 1.4 % DM/mm with N when ASMD exceeded ~ 76 mm. The irrigated crop with N had a maximum deficit of 81.8 mm during the late phase of leaf expansion growth at around 900°Cd and this suggests that GAI may have been reduced by ~3%.

The DM yield  $D_L$  was an indication of total water uptake from the soil (Figure 7-4). In this scenario, the root capacity for water uptake was increased by the addition of N. The plasticity in plant root systems is apparent in the plant's ability to adapt its root system design to efficiently acquire resources under different environmental conditions. This adaptation is influenced by factors such as the type, abundance, and spatial distribution of soil resources (Fitter et al., 1994; Hodge, 2004). Under non-limiting N conditions, maize increases both the length and density of lateral roots (Yu et al., 2014). Because of the greater soil coverage area, especially in the top nutrient rich layer of the soil, the crop improved efficiency of water extracted from the soil by 0.7% resulting in the 23 mm gap in  $D_L$ .

### **7.5.3 Crop water use and water use efficiency (WUE)**

Crop water use is directly associated with transpiration and is affected by stomatal activities and leaf properties. The transpiration rate is directly proportional to the ability of the plant to absorb water by the roots from the soil to meet demand. When there is a soil water deficit, the stomata close to prevent transpiration. This will cause the leaf surface temperature to rise since there will be less transpiration to cool the leaf (Bridge et al., 2013). This was observed in the rainfed crops where the water use was the lowest at 368 mm (Table 7-3). In the irrigated crop, water was not a limitation to growth, so the difference was caused by N. It has been shown that N slows the elongation of epidermal cells in tall fescue, allowing for a greater number of mesophyll cells in the division phase (MacAdam et al., 1989). Therefore, it is apparent that the irrigated crop without N, promoted epidermal cell elongation and decreased the number of mesophyll cell hence altering leaf thickness and causing a decrease in evapotranspiration rate. Water use in the irrigated crop with N had larger leaves enabling the crop to transpire 63 mm more water.

The relationship between the water use efficiency and the increase of radiation interception resulting from the application of N is inherently interconnected through photosynthesis (Zhou et al.,

2021). The rainfed crops had a low WUE averaging 17.9 kg DM/ha/mm because of the low evapotranspiration rate and an ASMD which fell below the  $D_L$  for the GAI and DM yield (Table 7-4 and Figure 7-5).

A higher leaf N content indicates a greater number of layers of cells in the palisade and parenchyma layers, suggesting thicker leaves and consequently more intercellular surface area for leaf gas exchange (Klein et al., 1991). This was the case in the irrigated crop with N, the WUE was the highest at 47 kg DM/mm/ha because of the increased RUE. However, when irrigated without N, the RUE would be lower because the leaf thickness was reduced, resulting in a lower WUE of 25.7 kg DM/ha/mm.

## 7.6 Conclusion

Establishing the DUL and the LL is required to determining other variables which affect water limitation in plant use. The PAWC under this soil for this maize crop was 177 mm. The MSMD reached by the crops and its timeliness affected crop growth and the ability of the crop to recover from water stress. The  $D_L$  for canopy leaf expansion was dependent on water. The  $D_L$  for DM yield was dependent on root capacity and N uptake. Water use and WUE are dependent on evapotranspiration and are an important leaf parameter that affects RUE in the photosynthesis process. The non-irrigated crop with N did not use more soil water, instead had a higher  $D_L$  for DM yield because of greater root capacity.

## Chapter 8

### General discussions

#### 8.1 Introduction

The overall aim of this thesis was to examine the influence of N and water on canopy and phenological development that influence crop growth through dry matter production and the mechanisms involved in yield formation. This study investigated the allocation strategy of N in maize crops, with particular emphasis on its effect on light interception in relation to canopy expansion and photosynthesis through RUE.

The experiments examined the effects of N limitation caused by different water conditions. There were two experiments conducted with a common objective to create crops with different yield potentials. These were carried out under consecutive growing seasons. Experiment 1 was in growing season of 2015/16 and Experiment 2 in 2016/17. Experiment 1 used a split plot design with four rates of N (N1-N4) applied as nil, 75, 150 and 300 kg N/ha under four water regimes; Irr1 - Irr4 defined by the accumulated potential soil moisture deficit 443, 367, 301 and 226 mm respectively (Figure 3-2). Experiment 2 only used two levels of water: under rainfed conditions and irrigation (accumulated potential soil moisture deficit at 536 and 296 mm, respectively) and N at rates 0 and 500 kg N/ha in a completely randomised block design (Figure 3-3). Both experiments were conducted within the vicinity of Lincoln University research fields.

Key physiological findings from the results chapter are discussed in this chapter. These findings are subsequently used to provide recommendations for the management and utilisation of N and water resources to achieve optimal yield responses. Additionally, this research offers suggestions for a potential modelling approach to assess canopy expansion and RUE at the crop-level.

#### 8.2 Rationale

During the early stages of leaf growth, there is a large demand for N due to the simultaneous processes of development of the photosynthetic machinery and leaf expansion (Evans, 1989; Johnson et al., 2010), causing cell division and chloroplast formation to compete for N (Kusumi et al., 2010; Miyazawa et al., 2003). A deficiency in N impedes cell division and consequently leaf growth, which impacts the final leaf area (Roggatz et al., 1999). The strategy maize crop uses in response to N deficiency is to expand leaf size at the cost of leaf N concentration and photosynthetic capacity (Vos et al., 2005), given water is not limiting. Moreover, after the leaf has fully expanded, the duration of the high photosynthetic rate is the key to increasing photosynthetic output (Makino et al., 1984;

Richards, 2000). An increase in N availability, promotes the maintenance of photosynthetic protein (Rubisco) in leaves, delaying and slowing down senescence (Osaki, 1995). In mature leaves, the influx of N decreases in equilibrium with the N diluted out from the leaves (Imai et al., 2005; Makino et al., 1984), indicating the capacity of the leaf to acquire and store N whilst meeting kernel N demand. The leaf structure is also affected by water, which alters N partitioning in the leaf. Water promotes both expansion rate and cell division in young leaf tissues and also affects the cell size of epidermis and mesophyll in mature parts of the leaf (Tardieu et al., 2000). The production of DM is determined by the combination of the light captured by a crop and the efficiency with which this energy is utilised. This discussion focuses on the relationship between leaf expansion and photosynthetic capacity and their association with LI and RUE and their contribution to yield.

### 8.3 Comparison between cropping seasons

The maximum yield achieved under high N and water conditions between the two cropping seasons differed due to the established plant population. The total DM yield achieved in Experiment 1 was 25.1 t/ha (Table 4-2) and in Experiment 2 was 28.9 t/ha (Table 4-10). In Experiment 1 the plant population was 8.7 plant/m<sup>2</sup> (Section 3.2.1) whilst Experiment 2 was 11.5 plant/ m<sup>2</sup> (Section 3.2.2). The differences in total DM were because crops in Experiment 1 were unable to compensate for the loss of in captured iPAR at pre-silking stage.

From emergence to silking (Table 8-1), crops in Experiment 1 accumulated a total of 472 g/m<sup>2</sup> but this doubled to 925 g/m<sup>2</sup> in Experiment 2. This was not due to the number of days to reach silking or differences in thermal time, but rather because of the differences in iPAR which was 292 MJ/m<sup>2</sup> for crops in Experiment 1 and 426 MJ/m<sup>2</sup> for Experiment 2.

**Table 8-1 The accumulated number of days, degree day (°Cd), total intercepted photosynthetic active radiation (iPAR) and dry matter (DM) from emergence to silking for cropping season 2015/16 (Experiment 1) and 2016/17 (Experiment 2).**

Parameter	Experiment 1	Experiment 2
Total DM (g/m <sup>2</sup> )	472	925
Number of days from emergence to silking	87±3	90±2
Thermal time accumulated (°Cd)	781±4	790±3
iPAR (MJ/m <sup>2</sup> )	292	426

From silking to emergence (Table 8-2) there was only a difference of 245 g/m<sup>2</sup> between crops in Experiment 1 and 2. The crops in Experiment 1 were able to accumulate comparable DM at post-silking. This was again due to the iPAR, however, in this phase the iPAR was 588 MJ/m<sup>2</sup> in that period in Experiment 1 and 98 MJ/m<sup>2</sup> less than crops in Experiment 2. The number of days from emergence to silking was 115 days for crops in Experiment 2 but was 26 days more than that in Experiment 1, however. Despite this there was no differences in thermal time between the two seasons which averaged 819±3 °Cd for Experiment 1 and 810±3 °Cd in Experiment 2. The difference in the numbers of days was mainly because of the cooler temperatures towards the end of the season in Experiment 2 (Appendix D). However, the consistency in thermal time shows, that this was the main driver of phenological development.

**Table 8-2 Accumulated number of days, degree day (°Cd), total intercepted photosynthetic active radiation (iPAR), dry matter (DM), and from silking to crop maturity for cropping season 2015/16 (Experiment 1) and 2016/17 (Experiment 2).**

Parameter	Experiment 1	Experiment 2
Total DM (g/m <sup>2</sup> )	2148	1903
Number of days from emergence to silking	89±2	115±4
Thermal time accumulated (°Cd)	819±3	810±3
iPAR (MJ/m <sup>2</sup> )	588	490

Apart from the differences in plant population, there was a notable difference in accumulated potential soil moisture deficit. Experiment 1 had an accumulated potential soil moisture deficit of 443 mm for the rainfed crop compared to 536 mm in the rainfed crop in Experiment 2. This indicated that Experiment 2 had higher evapotranspiration rates than Experiment 1 and its effect was evident on the growth of the rainfed crops.

#### **8.4 Dry matter accumulation and yield formation.**

The grain yield potentials illustrated in Experiments 1 and 2 is indicated by the CHI and partitioning of DM into grain yield. This was captured in the rate and duration of ear development. In Experiment 1, there were no differences in grain yield which averaged 12.4 t/ha for all the crops. However, the differences in total DM increased from 19.1 to 22.1 t/ha with irrigated crops under Irr3 and Irr4 and increased from 19.9 – 22.2 t/ha with N (Table 4-1). The pattern of growth showed total DM accumulation rate was 27.8 kg/ha/°Cd and lasted for a duration of 785 °Cd. This pattern of growth did not differ among crops (Figure 4-2). Ear growth also responded similarly with no changes in the temporal pattern of growth. Ear growth averaged 34.3 kg/ha/°Cd with duration of 409 °Cd (Table 4-4) across all the crops. The total DM at the start of ear development indicated an average of 10.1 t/ha with no difference among the crops (Table 4-9). The main result was the rate of DM partitioning into kernel growth, but this did not affect grain yield because there was a kernel sink limitation. This

indicated the supply of assimilate was adequate to fulfil canopy development and kernel growth, thereby explaining the consistent grain yield. There were differences in leaf rate and duration, but these were trivial and GAI development was unaffected (Table 5-2). Remobilised DM from the leaf and stalk compensated for 4.04 t/ha of the kernel DM requirement for Irr1 crops (Table 4-7) towards kernel growth. The post-silking DM from photosynthesis averaged 11.5 t/ha in crops under Irr2-Irr4 and 11.3 t/ha for crops under N2-N4 (Table 4-8). This assimilate went into increasing total DM once kernel sink limits were met. Throughout the other results chapters only the highest and lowest Irrigation and N treatments were examined due to the lack of differences in grain yield and the results mainly explained the differences in total DM in the upper and lower treatments.

Experiment 2 was designed to ensure differences in grain yield. There was an interaction between water and N under rainfed conditions, and there were extremely low grain yields of 0.98 t/ha (Table 4-10). Under irrigation there was 9.0 t/ha which almost doubled to 16.3 t/ha with N application. Total DM followed with a similar response with rainfed accumulating only 4.10 t/ha and 14.3 t/ha under irrigation with a doubling effect with N, creating a total DM of 28.9 t/ha. The yield differences were explained by the growth patterns. The increase in duration of total DM accumulation was affected by water and was 618 °Cd under rainfed and 1487 °Cd when fully irrigated (Table 4-12). The rate of total DM increase was unaffected, indicating the duration of photosynthesis was most important for the production of assimilates. The rate of ear DM increase was affected by an interaction between water and N (Table 4-13). The rate of ear DM increased from 0.004 kg/ha/°Cd under rainfed to 0.015 kg/ha/°Cd under irrigation and further to 0.027 kg/ha/°Cd with N application. Duration of ear DM accumulation averaged 661 °Cd across all the crops. This indicated that the phenological development was the same among the crops but only kernel growth differed with the different amounts of assimilates supplied. This is reiterated in the DM available at the start of ear development (Table 4-18). When rainfed the available DM at the start of ear development was 3.02 t/ha without N. The crop under rainfed and N had an intermediate response. Dry matter was 4.12 t/ha when irrigated without N and further increased to 8.95 t/ha with N application. It was the different rate of DM increase as affected by water which resulted in the final grain yield differences. Post-silking DM production and DM remobilisation into kernel growth reflected this continued pattern of assimilate supply.

## 8.5 Light interception and canopy development

The main variable in light interception that caused changes in intercepted light was the GAI. In Experiment 1, intercepted light accumulated to 570 MJ/m<sup>2</sup> for Irr1 and was higher at 1082 MJ/m<sup>2</sup> for Irr2 (Table 5-1). All crops reached a maximum GAI at 3.7 m<sup>2</sup>/m<sup>2</sup> at a rate of 0.01 m<sup>2</sup>/m<sup>2</sup>/°Cd with a

duration of 677 °Cd (Table 5-2). This indicated that the build-up of GAI up till silking was uniform across all the crops. The main difference in GAI was observed after 1000 °Cd when the crops under Irr1 were wilting because of severe water stress which induced a pre-senescence effect.

Experiment 2, light interception was different across all the crops. Intercepted light progressively increased with water and N. Under rainfed conditions the total light intercepted was 448 MJ/m<sup>2</sup> and increased to 551 MJ/m<sup>2</sup> with N, and when irrigated was 816 MJ/m<sup>2</sup> and further increased to 1005 MJ/m<sup>2</sup> with N (Table 5-3). The rate and duration change quantify the capacity of the crop to capture light and depend on the changes in pigment protein complexes. Directly linked to development of the GAI are the processes of leaf development and expansion. The maximum GAI was affected by the main effects of water and N where GAI increased from 2.14 to 3.49 m<sup>2</sup>/m<sup>2</sup> with water and from 2.48 to 3.14 m<sup>2</sup>/m<sup>2</sup> with N application (Table 5-4). This was due to the linear rate of increase in GAI which averaged 0.004 m<sup>2</sup>/m<sup>2</sup>/°Cd but there was a more rapid growth at 0.024 m<sup>2</sup>/m<sup>2</sup>/°Cd when irrigated with N applied. This rapid rate of increase resulted in a shorter period of 166 °Cd to reach maximum GAI while on the other hand, without N had a longer duration of 958 °Cd. The duration for the rainfed crops fell in between at 558 °Cd. The main treatment effect on the maximum GAI at early leaf development stage was affected by leaf tip appearance (Table 5-8) and how fast leaves expanded as counted from the appearance of the ligule (Table 5-9). Nitrogen increased the phyllochron for the leaf tips by 4.1 °Cd and expanded leaves by 3.4 °Cd at the first stage, allowing more time and area for the leaves to intercept light at the early vegetative growth stages. As water usually affects leaf expansion after the developmental phase, under rainfed conditions with N, this phase was reduced dramatically with the D<sub>L</sub> for GAI exceeding 76 mm ASMD at around 600 °Cd (Figure 7-2). This explains the interaction of water and N in the differences in leaf area at the whole canopy and cohort level (Table 5-5 and Table 5-6), and the increase in intercepted light between the rainfed crops with N applied. These interactions reflect the interconnection of leaf growth and development in their ability to provide assimilates from photosynthesis and the effect of N distribution in the plant.

## 8.6 Radiation use efficiency and nitrogen

RUE incorporates a measure of the complete photosynthesis process that includes light reactions and carbon reduction reactions (Blankenship, 2021). Both at crop level-RUE and leaf photosynthesis level SLN is a key factor connecting leaf N concentration to DM production. For Experiment 1, the SLN was affected by an interaction between water and N at around silking at canopy level (Table 5-6). The SLN was highest at 2.1 g N/m<sup>2</sup> for the irrigated crop with N and lower at 1.66 g N/m<sup>2</sup> without N. The rainfed crops produced an intermediate response averaging to 1.89 g N/m<sup>2</sup>. Throughout grain-filling (kernel growth) the SLN declined progressively into crop maturity as N was diluted into the grains and stem as a storage organ.

In Experiment 2, the SLN averaged 1.23 g N/m<sup>2</sup> in all crops (Table 6-10). This was further dissected at cohort levels. The changes in SLN at the lower cohort was affected by water, where SLN was 1.55 g N/m<sup>2</sup> under rainfed and 0.51 g N/m<sup>2</sup> under irrigation. The mid cohort was affected by both water and N, increasing SLN from 1.43 to 2.39 g N/m<sup>2</sup> with water and from 1.46 to 2.37 g N/m<sup>2</sup> with N. The upper cohort, which is responsible for most of the assimilate supply during grain-filling, was unaffected by water or N and averaged 0.46 g N/m<sup>2</sup>. Specific leaf N is a result of plant growth and development dynamics (Hammer et al., 2010). Nitrogen uptake is closely related to leaf area growth (Lemaire et al., 2007) especially during the canopy development phase, before stem elongation (Van Oosterom et al., 2010). Pre-anthesis N is distributed among organs in a hierarchical manner, with the structural stem N and growing leaf N demands being satisfied first (Hammer et al., 2010). This demand is indicated in the leaves as a critical SLN level. Once the leaf N requirements have been fulfilled, any surplus N is subsequently assigned to these organs as either luxury or storage N. A canopy with a large GAI is expected to decrease SLN levels due to the process of N dilution. The SLN of a crop is a result of the intricate interplay between the overall N uptake of the crop, the relative size of its organs (which affects crop N requirements), and the hierarchical allocation of N (Van Oosterom et al., 2010). The hierarchical allocation of N explains the exhaustion of N once the N is allocated to the last leaves at the top of the canopy, resulting consistent SLN levels.

Apart from the growth and development requirement for N, the hierarchical allocation of N with regard to SLN is also influenced by leaf shading and how light is diminished as it proceeds into a canopy and is intercepted by leaves. The intensity of solar radiation reaching each fraction is calculated using the Beer-Lambert equation (Equation 2-1) where the extinction co-efficient, the  $k$  values plays an important role in allocation of light process proteins and chloroplasts. This affects the partitioning of SLN in the mid-cohort which is strategically located crucially for photosynthesis and assimilate supply to kernel development and grain-filling demand.

## 8.7 Water use and dry matter production

The changes in total DM as a result of water use is the measure of SLN capacity in the CO<sub>2</sub> fixation process. The different growth rates are explained by WUE and mainly reflected in the rate of leaf DM increase. In Experiment 2, there were differences in grain yield and total DM caused by differences in growth. The WU was an important factor that directly contributed to crop growth. Crop requirement for growth and development was derived from the PAWC which was based on the DUL and LL and indicated the root capacity to extract water and the soil capacity for water infiltration and percolation through the layers (Table 7-1). From the ASMD, the  $D_L$  was established for GAI and was 76 mm without N and 79 mm for crops with N, and for total DM the  $D_L$  was defined at 77 mm without

N application and 100 mm when N was applied (Figure 7-3 and Figure 7-4). These parameters linked SLN and water requirements to crop growth and development needs.

For the crops their water requirement is derived from evapotranspiration. Water use was measured based on stomatal and mesophyll conductance of leaf water dynamics which involves the potential and not the actual soil moisture deficit. Crop WU showed an interaction between water and N, averaging 368 mm under rainfed conditions and increased from 462 to 525 mm when irrigated with N (Table 7-3). When converted to WUE only the crop under irrigation and N was efficiently converting water to DM at 47 kg DM/mm of water (Table 7-4). The WUE for the rainfed crops was 17.9 kg DM/mm and did not differ from the irrigated crop without N which had a WUE of 25.7 kg DM/mm. This indicated that the photosynthetic capacity of the crop varied with SLN and crop water use to produce the end result which is indicated as the total DM.

## 8.8 Recommendations

In depth understanding into elements of SLN is essential for estimation of the SLN throughout the crop growing season. As identified from the discussion, the main elements of SLN are GAI, light interception, and plant water use. The development of crop models allows advanced understanding of the relationship between GAI and SLN. However, there is a need for clear approaches to establish the relationship between SLN, light interception and water use. N associated with the photosynthetic apparatus exists in two major pools: the thylakoid membrane bound proteins involved in light reaction and soluble proteins involved in CO<sub>2</sub> assimilation. Experimental approaches to enhancing Crop-based growth and development models towards cross-scale approach in cooperating photosynthetic models, underlines the importance of establishing relationship between SLN and vertical profile of canopy chlorophyll, and determining critical level of SLN in association with water use. A recommendation for more experimentation is for work into vertical profiling of the canopy for LI, GAI, SLN and DM partitioning.

In this research, there was a limitation on the in-depth studies into the root/water response to water and N due to the limited number of treatments in Experiment 2. In arable soils in New Zealand, N mobility in soils might be limited by water shortage. In this case, longer roots a wider dispersion of roots in the soil is important for utilization of heterogeneous distribution of N in the soil. Identifying suitable hybrids with longer root depth and greater spatial distribution of later roots and their density in the soil in terms of assessing PAWC will benefit farmers looking for stabilised and consistent yields between seasons.

The practical application of results from this research suggests farmers to target input of water and N fertilizer towards maximising canopy efficiency in the mid-cohort. The canopy architecture of the

maize crop is widest at this position in the canopy and N concentration in the leaves higher due to more sunlight penetrating this portion of the canopy. The application of water at silking was also an important factor in maintaining canopy greenness which contributed to DM regained in the stalk which is suitable for silage. Attaining a crop that targets more grain yield than silage requires, a crop that translocate DM away from stalk elongation and structural build-up that is at leaf 6 and 7 and reserve resources, especially water and N for leaves that carry the ear or for nodes that carry the ear primordia. This will address the kernel sink limitation noted in this study.

## **8.9 Conclusion**

In understanding the yield formation process of maize, this study discovered that in the grain-filling process stalk and leaf DM reserves remobilized to meet grain demand. When grain demand was met, DM from post-silking photosynthesis was diverted to regain stalk DM and this occurred late in the crop cycle. The completely irrigated crop with N produced the largest yield, as expected; nevertheless, this crop was able to meet grain-filling demand mostly from current photosynthate. It did not exhaust all of the reserves in the stalk and stem. Grain-filling is sink limited, which means that reduced N and water rates can produce the same grain yield, according to the results of the yield potential shown in the two experiments. There were adequate DM reserves to match the grain demand if the grain sink capacity was to be increased. This mechanism of DM remobilisation and grain sink limitation was influenced by the timeliness and availability of total DM at different stages of the crop. The availability of total DM was influenced by RI due to changes in GAI in the season and affected by RUE as SLN changed.

## Appendix A

### Information on Urea fertilizer application

#### A.1 Experiment 1

Fertilizer was applied as Urea; containing 46 % N. The rates used for the four treatments were as follows: Nil fertilizer applied, 75, 150 and 300 kg N ha<sup>-1</sup>. First fertilizer application was at one month after planting (dating date 5/11/2015) and four other application followed every three weeks.

Fertilizer was applied by hand and evenly spread across the plot. For each plot size of 26.8 m<sup>2</sup> (5.0m \*5.3m, excluding guard rows). The actual application on plot basis was as follows:

- 300 kg N/ha – 0.350 kg/plot
- 150 kg N/ha – 0.175 kg/plot
- 75 kg N/ha – 0.087 kg/plot

#### A.2 Experiment 2

Nitrogen treatments received nil and 500 kg N/ha using Urea fertilizer (46% N). The fertilizer was applied at the following dates: 6th and 20th of December 2016. Fertiliser was applied manually by hand. Planting date was 1/11/2016.

## Appendix B

### Table of co-efficients for radiation use efficiency (RUE) regression

#### B.1 Experiment 1

Table B 1 The co-efficient for RUE from linear regression for Experiment 1

	N (kg/ha)	a	A (SE)	b	b (SE)	R <sup>2</sup>
Rainfed	0	2.458	0.127	-76.2	64.9	0.9157
	300	2.769	0.128	-121.4	65.3	0.9497
Irrigation	0	2.419	0.101	-95.1	61.5	0.9612
	300	2.777	0.1	-132.8	61.6	0.9535

#### B.2 Experiment 2

Table B 2 The co-efficients for RUE from linear regression for Experiment 2

	N (kg/ha)	a	A (SE)	b	b (SE)	R <sup>2</sup>
Rainfed	0	0.8692	0.115	21.14	34.5	0.9924
	500	0.8852	0.0945	18.5	34.6	0.9812
Irrigation	0	1.815	0.0697	-66.7	32.1	0.9964
	500	3.1544	0.0584	-171.5	32.7	0.9912

## Appendix C Plant available water content

The increase in PAWC is explained by the “wetting front movement” principle. Only the top 0.5 m layer was subjected to drying as the irrigation continuously passes through the profile draining all excess water into the progressive layers and keeping each layer at DUL. The soil measurements were taken from 18/11/2016 to 28/04/2017, which represents the entire growing season.

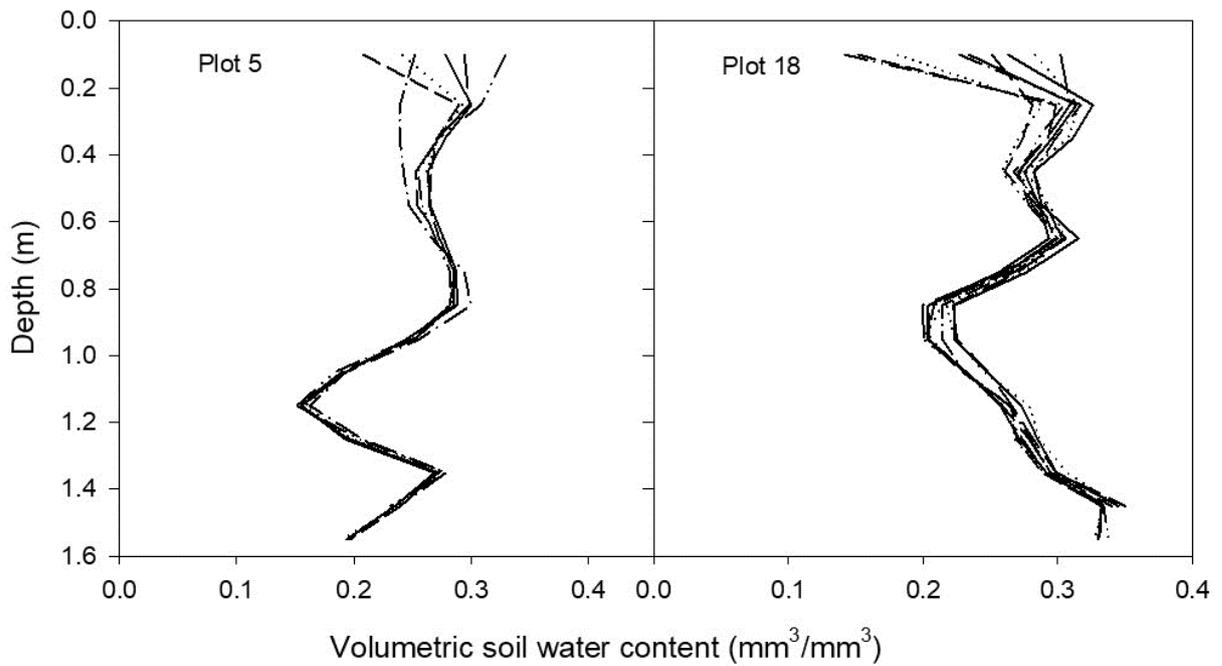


Figure C-1 The irrigation treatments showing a “wetting front movement” as water passes through in the lower layers, maintaining the soil profile continuously at DUL. Plot 5 and plot 18 of the irrigation with N fertilizer application at dates from planting into silking stages for maize crops in 2016/17 (Experiment 2) when grown at Lincoln University, Canterbury, New Zealand.

## Appendix D Temperature in the growing seasons

Weekly average, maximum and minimum temperatures from emergence to crop maturity for maize cropping seasons 2015/16 and 2016/17.

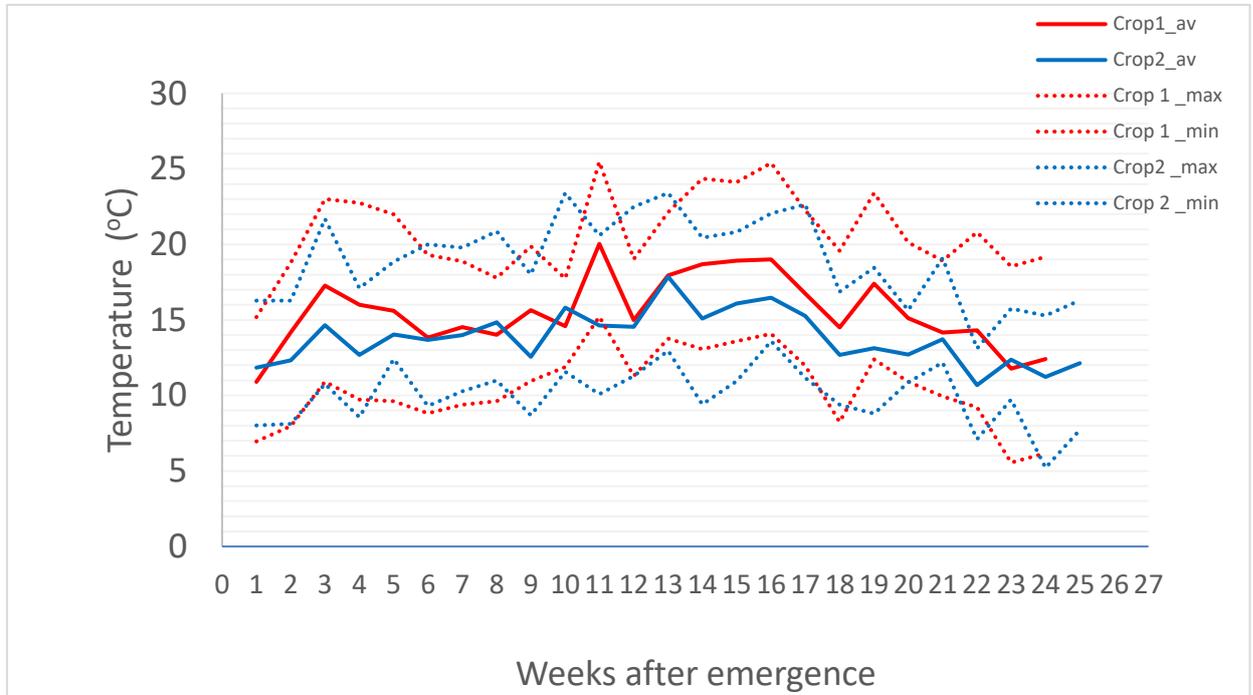


Figure D-1 Weekly changes in average (solid line), maximum (dotted line above solid line) and minimum (dotted line below solid line) temperatures (°C) from emergence to crop maturity for maize in Experiment 1 (red line) and 2 (blue line).

## References

- 2018 Genetic Technology Ltd (2018). Pioneer Brand products. New Zealand.
- Abendroth, L., Elmore, R., Boyer, M., and Marlay, S. (2011). Corn growth and development (PMR 1009). Ames: Iowa State University.
- Adhikari, N. R., Ghimire, S. K., Sah, S. K., and Koirala, K. B. (2015). "Frequency distribution and mean comparisons of red light absorbance-transmittance of the e1 leaf sectors of five pipeline maize hybrids during early grain filling in subtropical winter," Rep. No. 2167-9843. PeerJ PrePrints.
- Aitken, Y. (1980). The early maturing character in maize (*Zea mays* L.) in relation to temperature and photoperiod. *Zeitschrift fur Acker-und Pflanzenbau* **149**, 89-106.
- Ali, A. S., and Elozeiri, A. A. (2017). Metabolic processes during seed germination. *Advances in seed biology* **2017**, 141-166.
- Aluko, G., and Fischer, K. (1988). The effect of changes of assimilate supply around flowering on grain sink size and yield of maize (*Zea mays* L.) cultivars of tropical and temperate adaptation. *Australian Journal of Agricultural Research* **39**, 153-161.
- Andrade, F. H. (1995). Analysis of growth and yield of maize, sunflower and soybean grown at Balcarce, Argentina. *Field Crops Research* **41**, 1-12.
- Angus, J., Cunningham, R., Moncur, M., and Mackenzie, D. (1980). Phasic development in field crops I. Thermal response in the seedling phase. *Field crops research* **3**, 365-378.
- Arable Industry Marketing Initiative (2018). New Zealand survey of maize areas and volumes: June 1 2018. FAR and Saville stat, New Zealand.
- Arkebauer, T. J., Norman, J. M., and Sullivan, C. Y. (1995). From cell growth to leaf growth: III. Kinetics of leaf expansion. *Agronomy Journal* **87**, 112-121.
- Baker, C., Horrocks, R., and Goering, C. (1975). Use of the Gompertz function for predicting corn leaf area. *Transactions of the ASAE* **18**, 323-0326.
- Bange, M., Hammer, G., and Rickert, K. (1997). Environmental control of potential yield of sunflower in the subtropics. *Australian journal of agricultural research* **48**, 231-240.
- Bassetti, P., and Westgate, M. E. (1993). Water deficit affects receptivity of maize silks. *Crop Science* **33**, 279-282.
- Bassi, D., Menossi, M., and Mattiello, L. (2018). Nitrogen supply influences photosynthesis establishment along the sugarcane leaf. *Scientific reports* **8**, 2327.
- Baumont, M., Parent, B., Manceau, L., Brown, H. E., Driever, S. M., Muller, B., and Martre, P. (2019). Experimental and modeling evidence of carbon limitation of leaf appearance rate for spring and winter wheat. *Journal of Experimental Botany* **70**, 2449-2462.
- Bewley, J. D. (2001). Seed germination and reserve mobilization. *e LS*.
- Birch, C., Hammer, G., and Rickert, K. (1998a). Improved methods for predicting individual leaf area and leaf senescence in maize (*Zea mays*). *Australian Journal of Agricultural Research* **49**, 249-262.
- Birch, C., Hammer, G., and Rickert, K. (1998b). Temperature and photoperiod sensitivity of development in five cultivars of maize (*Zea mays* L.) from emergence to tassel initiation. *Field Crops Research* **55**, 93-107.
- Birch, C., Vos, J., Kiniry, J., Bos, H., and Elings, A. (1998c). Phyllochron responds to acclimation to temperature and irradiance in maize. *Field Crops Research* **59**, 187-200.
- Birch, C., Vos, J., Kiniry, J., Bos, H., and Elings, A. (1998). Phyllochron responds to acclimation to temperature and irradiance in maize. *Field Crops Research* **59**, 187-200.
- Birch, C., Vos, J., and Van der Putten, P. (2003). Plant development and leaf area production in contrasting cultivars of maize grown in a cool temperate environment in the field. *European Journal of Agronomy* **19**, 173-188.
- Blankenship, R. E. (2021). "Molecular mechanisms of photosynthesis," John Wiley & Sons.
- Bonhomme, R. (2000). Bases and limits to using 'degree. day' units. *European journal of agronomy* **13**, 1-10.

- Bonhomme, R., Ruget, F., Derieux, M., and Vincourt, P. (1982). Relationship between aerial dry matter production and intercepted solar radiation for various maize genotypes.
- Booker, J. W. (2009). Production, distribution and utilisation of maize in New Zealand, Lincoln University.
- Borrás, L., Westgate, M. E., and Otegui, M. E. (2003). Control of kernel weight and kernel water relations by post-flowering source-sink ratio in maize. *Annals of botany* **91**, 857-867.
- Bos, H., Tijani-Eniola, H., and Struik, P. (2000). Morphological analysis of leaf growth of maize: responses to temperature and light intensity. *NJAS: Wageningen Journal of Life Sciences* **48**, 181-198.
- Bradford, K., and Hsiao, T. (1982). Physiological responses to moderate water stress. *Physiological plant ecology II: water relations and carbon assimilation*, 263-324.
- Bridge, L., Franklin, K. A., and Homer, M. E. (2013). Impact of plant shoot architecture on leaf cooling: a coupled heat and mass transfer model. *Journal of The Royal Society Interface* **10**, 20130326.
- Brito, C. D. d., Loureiro, M. B., Teles, C. A. S., Schuck, M. R., Fernandez, L. G., and Castro, R. D. d. (2015). Behavior of *Jatropha curcas* L. seeds under osmotic stress: germination and cell cycle activity. *Acta Scientiarum. Agronomy* **37**, 279-287.
- Brown, H. E., Moot, D. J., Fletcher, A. L., and Jamieson, P. D. (2009). A framework for quantifying water extraction and water stress responses of perennial lucerne. *Crop and Pasture Science* **60**, 785-794.
- Brown, P. W., and Tanner, C. (1983). Alfalfa stem and leaf growth during water stress 1. *Agronomy Journal* **75**, 799-805.
- Carberry, P., Muchow, R., and McCown, R. (1989). Testing the CERES-Maize simulation model in a semi-arid tropical environment. *Field Crops Research* **20**, 297-315.
- Cassman, K. G., Peng, S., Olk, D., Ladha, J., Reichardt, W., Dobermann, A., and Singh, U. (1998). Opportunities for increased nitrogen-use efficiency from improved resource management in irrigated rice systems. *Field crops research* **56**, 7-39.
- Ceulemans, R., Impens, I., Laker, M., ASSCHE, F. V., and Mottram, R. (1988). Net CO<sub>2</sub> exchange rate as a sensitive indicator of plant water status in corn (*Zea mays* L.). *Canadian Journal of Plant Science* **68**, 597-606.
- Chapman, S. C., and Edmeades, G. O. (1999). Selection Improves Drought Tolerance in Tropical Maize Populations: II. Direct and Correlated Responses among Secondary Traits. *Crop Science* **39**, 1315-1324.
- Chapman, S. C., Hammer, G. L., and Meinke, H. (1993). A sunflower simulation model: I. Model development. *Agronomy Journal* **85**, 725-735.
- Chaves, M. M., Pereira, J. S., Maroco, J., Rodrigues, M. L., Ricardo, C. P. P., Osório, M. L., Carvalho, I., Faria, T., and Pinheiro, C. (2002). How plants cope with water stress in the field? Photosynthesis and growth. *Annals of botany* **89**, 907-916.
- Ciampitti, I. A., and Vyn, T. J. (2012). Physiological perspectives of changes over time in maize yield dependency on nitrogen uptake and associated nitrogen efficiencies: A review. *Field Crops Research* **133**, 48-67.
- Cirilo, A. G., and Andrade, F. H. (1994). Sowing date and maize productivity: I. Crop growth and dry matter partitioning. *Crop science* **34**, 1039-1043.
- Clewer, A. G., and Scarisbrick, D. H. (2001). "Practical Statistics and Experimental Design for Plant and Crop Science," John Wiley & Sons Ltd., . 332 pp., Chichester, England.
- Coelho, D. T., and Dale, R. F. (1980). An Energy-Crop Growth Variable and Temperature Function for Predicting Corn Growth and Development: Planting to Silking 1. *Agronomy Journal* **72**, 503-510.
- Cutforth, H., and Shaykewich, C. (1990). A temperature response function for corn development. *Agricultural and Forest Meteorology* **50**, 159-171.
- Dale, R. F., Coelho, D. T., and Gallo, K. P. (1980). Prediction of Daily Green Leaf Area Index for Corn 1. *Agronomy Journal* **72**, 999-1005.
- Dangl, J. L. (2000). Senescence and programmed cell death. *Biochemistry and molecular biology of plants*, 1044-1100.

- De Haan, K., Khomik, M., Green, A., Helgason, W., Macrae, M. L., Kompanizare, M., and Petrone, R. M. (2021). Assessment of different water use efficiency calculations for dominant forage crops in the Great Lakes Basin. *Agriculture* **11**, 739.
- De Vries, F. P. (1989). "Simulation of ecophysiological processes of growth in several annual crops," *Int. Rice Res. Inst.*
- DeBruin, J. L., Hemphill, B., and Schussler, J. R. (2018). Silk development and kernel set in maize as related to nitrogen stress. *Crop Science* **58**, 2581–259.
- Dos Santos, C. L., Abendroth, L. J., Coulter, J. A., Nafziger, E. D., Suyker, A., Yu, J., Schnable, P. S., and Archontoulis, S. V. (2022). Maize leaf appearance rates: A synthesis from the united states corn belt. *Frontiers in Plant Science* **13**, 872738.
- Drake, B. G., González-Meler, M. A., and Long, S. P. (1997). More efficient plants: a consequence of rising atmospheric CO<sub>2</sub>? *Annual review of plant biology* **48**, 609-639.
- Dwyer, L., and Stewart, D. (1986). Leaf Area Development in Field-Grown Maize 1. *Agronomy Journal* **78**, 334-343.
- Dwyer, L., Stewart, D., Hamilton, R., and Houwing, L. (1992a). Ear position and vertical distribution of leaf area in corn. *Agronomy Journal* **84**, 430-438.
- Dwyer, L., Stewart, D., and Tollenaar, M. (1992b). Analysis of maize leaf photosynthesis under drought stress. *Canadian Journal of Plant Science* **72**, 477-481.
- Earl, H., and Tollenaar, M. (1999). Using chlorophyll fluorometry to compare photosynthetic performance of commercial maize (*Zea mays* L.) hybrids in the field. *Field Crops Research* **61**, 201-210.
- Earl, H. J., and Davis, R. F. (2003). Effect of drought stress on leaf and whole canopy radiation use efficiency and yield of maize. *Agronomy journal* **95**, 688-696.
- Edmeades, G., and Lafitte, H. (1993). Defoliation and plant density effects on maize selected for reduced plant height. *Agronomy Journal* **85**, 850-857.
- Edwards, G. E., and Baker, N. R. (1993). Can CO<sub>2</sub> assimilation in maize leaves be predicted accurately from chlorophyll fluorescence analysis? *Photosynthesis research* **37**, 89-102.
- Edwards, J. (2009). Maize growth and development. *Maize growth and development*.
- Eghball, B., and Maranville, J. W. (1991). Interactive effects of water and nitrogen stresses on nitrogen utilization efficiency, leaf water status and yield of corn genotypes. *Communications in Soil Science and Plant Analysis* **22**, 1367-1382.
- El Hallof, N., and Sárvári, M. (2006). Effect of different fertilizer doses on yield, LAI and photosynthetic activity of maize hybrids. *Cereal Research Communications*, 441-444.
- Evans, J. R. (1983). Nitrogen and photosynthesis in the flag leaf of wheat (*Triticum aestivum* L.). *Plant physiology* **72**, 297-302.
- Evans, J. R. (1989). Photosynthesis and nitrogen relationships in leaves of C<sub>3</sub> plants. *Oecologia* **78**, 9-19.
- Evans, R. G., and Sadler, E. J. (2008). Methods and technologies to improve efficiency of water use. *Water resources research* **44**.
- Evanylo, G. K., and Alley, M. M. (1997). Presidedress soil nitrogen test for corn in Virginia. *Communications in soil science and plant analysis* **28**, 1285-1301.
- Fairey, N., and Daynard, T. (1978). Quantitative distribution of assimilates in component organs of maize during reproductive growth. *Canadian Journal of Plant Science* **58**, 709-717.
- Field, C. (1986). The photosynthesis-nitrogen relationship in wild plants. *On the economy of plant form and function*, 25-55.
- Field, C., and Mooney, H. A. (1986). The photosynthesis-nitrogen relationship in wild plants. *On the economy of form and function*.
- Fischer, R. A., and Hagan, R. M. (1965). Plant water relations, irrigation management and crop yield. *Experimental Agriculture* **1**, 161-177.
- Fitter, A., Caldwell, M., and Pearcy, R. (1994). Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. *Exploitation of environmental heterogeneity by plants: ecophysiological processes above-and belowground*, 305-323.
- Fletcher, A., L, Maley, S., Wilson, D. R., and Ruiters, J. M. (2008). Using plastic mulch to increase maize silage production in cool climate with a short growing season. *In "Global issues, Paddock*

- action. Proceedings of the 14th Australian Agronomy Conference" (M. Unkovich, ed.), Vol. 2008. Australian society of agronomy, Adelaide, South Australia.
- Fletcher, A. L. (2004). Understanding'Challenger'sweet corn yield, quality and phenology responses to phosphorus, Lincoln University.
- Fu, Q., Hou, R., Li, T., Li, Y., Liu, D., and Li, M. (2019). A new infiltration model for simulating soil water movement in canal irrigation under laboratory conditions. *Agricultural Water Management* **213**, 433-444.
- Gallo, K. P., Daughtry, C. S., and Wiegand, C. L. (1993). Errors in measuring absorbed radiation and computing crop radiation use efficiency. *Agronomy Journal* **85**, 1222-1228.
- Gastal, F., and Lemaire, G. (2002). N uptake and distribution in crops: an agronomical and ecophysiological perspective. *Journal of Experimental Botany* **53**, 789-799.
- Ge, S., Smith, R. G., Jacovides, C. P., Kramer, M. G., and Carruthers, R. I. (2011). Dynamics of photosynthetic photon flux density (PPFD) and estimates in coastal northern California. *Theoretical and Applied Climatology* **105**, 107-118.
- Giauffret, C., Bonhomme, R., and Derieux, M. (1995). Genotypic differences for temperature response of leaf appearance rate and leaf elongation rate in field-grown maize. *Agronomie* **15**, 123-137.
- Giauffret, C., Bonhomme, R., Derieux, M., and Dorvillez, D. (1991). Conversion of intercepted radiation into aerial dry biomass for three maize genotypes. Influence of plant density. *Maydica (Italy)*.
- Gonzalez-Dugo, V., Durand, J.-L., and Gastal, F. (2010). Water deficit and nitrogen nutrition of crops. A review. *Agronomy for sustainable development* **30**, 529-544.
- Goron, T. L., Nederend, J., Stewart, G. L., Deen, B., and Raizada, M. N. (2017). Mid-Season Leaf Glutamine Predicts End-Season Maize Grain Yield and Nitrogen Content in Response to Nitrogen Fertilization Under Field Conditions. *Agronomy*.
- Gowik, U., and Westhoff, P. (2011). The path from C3 to C4 photosynthesis. *Plant Physiology* **155**, 56-63.
- Grant, R., Jackson, B., Kiniry, J., and Arkin, G. (1989). Water deficit timing effects on yield components in maize. *Agronomy journal* **81**, 61-65.
- Greenwood, D., Lemaire, G., Gosse, G., Cruz, P., Draycott, A., and Neeteson, J. (1990). Decline in percentage N of C3 and C4 crops with increasing plant mass. *Annals of botany* **66**, 425-436.
- Grindlay, D. (1997). REVIEW Towards an explanation of crop nitrogen demand based on the optimization of leaf nitrogen per unit leaf area. *The Journal of Agricultural Science* **128**, 377-396.
- Hammer, G., and Muchow, R. C. (1994). Assessing climatic risk to sorghum production in water-limited subtropical environments I. Development and testing of a simulation model. *Field Crops Research* **36**, 221-234.
- Hammer, G. L., van Oosterom, E., McLean, G., Chapman, S. C., Broad, I., Harland, P., and Muchow, R. C. (2010). Adapting APSIM to model the physiology and genetics of complex adaptive traits in field crops. *J. Exp. Bot.* **61**, 2185 - 2202. .
- Han, C., Yin, X., He, D., and Yang, P. (2013). Analysis of proteome profile in germinating soybean seed, and its comparison with rice showing the styles of reserves mobilization in different crops. *PLoS one* **8**, e56947.
- Hardwick, R. (1987). The nitrogen content of plants and the self-thinning rule of plant ecology: a test of the core-skin hypothesis. *Annals of Botany* **60**, 439-446.
- Hay, R. K. M., and Porter, J. R. (2006). "The physiology of crop yield," 2nd ed../Ed. Oxford, UK, Ames, Iowa: Blackwell Pub., Oxford, UK.
- Hayhoe, H., Dwyer, L., Stewart, D., White, R., and Culley, J. (1996). Tillage, hybrid and thermal factors in corn establishment in cool soils. *Soil and Tillage Research* **40**, 39-54.
- Hesketh, J., and Warrington, I. (1989). Corn growth response to temperature: rate and duration of leaf emergence. *Agronomy Journal* **81**, 696-701.
- Hikosaka, K., Terashima, I., and Katoh, S. (1994). Effects of leaf age, nitrogen nutrition and photon flux density on the distribution of nitrogen among leaves of a vine (*Ipomoea tricolor* Cav.) grown horizontally to avoid mutual shading of leaves. *Oecologia* **97**, 451-457.

- Hipps, L. (1983). Assessing the interception of photosynthetically active radiation in winter wheat. *Agricultural Meteorology* **28**.
- Hochman, Z., Dalgliesh, N., and Bell, K. (2001). Contributions of soil and crop factors to plant available soil water capacity of annual crops on Black and Grey Vertosols. *Australian Journal of Agricultural Research* **52**, 955-961.
- Hodge, A. (2004). The plastic plant: root responses to heterogeneous supplies of nutrients. *New phytologist* **162**, 9-24.
- Hunt, R. (1982). "Plant growth curves. The functional approach to plant growth analysis," Edward Arnold Ltd.
- Hunt, R., and Parsons, I. T. (1974). A computer program for deriving growth-functions in plant growth-analysis. *Journal of Applied Ecology*, 297-307.
- Hunter, R., Tollenaar, M., and Breuer, C. (1977). Effects of photoperiod and temperature on vegetative and reproductive growth of a maize (*Zea mays*) hybrid. *Canadian Journal of Plant Science* **57**, 1127-1133.
- Imai, K., Suzuki, Y., Makino, A., and Mae, T. (2005). Effects of nitrogen nutrition on the relationships between the levels of *rbcS* and *rbcL* mRNAs and the amount of ribulose 1· 5-bisphosphate carboxylase/oxygenase synthesized in the eighth leaves of rice from emergence through senescence. *Plant, Cell & Environment* **28**, 1589-1600.
- Jamieson, P., and Ewert, F. (1999). The role of roots in controlling soil water extraction during drought: an analysis by simulation. *Field Crops Research* **60**, 267-280.
- Jamieson, P., Francis, G., Wilson, D., and Martin, R. (1995a). Effects of water deficits on evapotranspiration from barley. *Agricultural and Forest Meteorology* **76**, 41-58.
- Jamieson, P., Martin, R., and Francis, G. (1995b). Drought influences on grain yield of barley, wheat, and maize. *New Zealand journal of crop and horticultural science* **23**, 55-66.
- Johnson, I. R., Thornley, J. H., Frantz, J. M., and Bugbee, B. (2010). A model of canopy photosynthesis incorporating protein distribution through the canopy and its acclimation to light, temperature and CO<sub>2</sub>. *Annals of Botany* **106**, 735-749.
- Jones, C. A., Kiniry, J. R., and Dyke, P. (1986). CERES-Maize: A simulation model of maize growth and development.
- Keating, B., and Wafula, B. (1992). Modelling the fully expanded area of maize leaves. *Field Crops Research* **29**, 163-176.
- Kiniry, J., Landivar, J., Witt, M., Gerik, T., Cavero, J., and Wade, L. (1998). Radiation-use efficiency response to vapor pressure deficit for maize and sorghum. *Field Crops Research* **56**, 265-270.
- Kiniry, J. R., Bean, B., Xie, Y., and Chen, P.-y. (2004). Maize yield potential: critical processes and simulation modeling in a high-yielding environment. *Agricultural Systems* **82**, 45-56.
- Kiniry, J. R., Wood, C. A., Spanel, D. A., and Bockholt, A. J. (1990). Seed Weight Response to Decreased Seed Number in Maize. *Agronomy Journal* **82**, 98-102.
- Klein, I., DeJong, T., Weinbaum, S., and Muraoka, T. (1991). Specific leaf weight and nitrogen allocation responses to light exposure within walnut trees. *HortScience* **26**, 183-185.
- Koch, G. W., Schulze, E. D., Percival, F., Mooney, H., and Chu, C. (1988). The nitrogen balance of *Raphanus sativus* x *raphanistrum* plants. II. Growth, nitrogen redistribution and photosynthesis under NO<sub>3</sub><sup>-</sup> deprivation. *Plant, Cell & Environment* **11**, 755-767.
- Kosgey, J. R. (2011). Elucidating the physiological mechanism of 'stay green' in maize hybrids – crop growth processes and nitrogen economy., Lincoln University, New Zealand
- Kovács, G. J. (2005). Modelling of adaptation processes of crops to water and nitrogen stress. *Physics and Chemistry of the Earth, Parts A/B/C* **30**, 209-216.
- Kuhlmann, A., Neuweiler, I., Van Der Zee, S., and Helmig, R. (2012). Influence of soil structure and root water uptake strategy on unsaturated flow in heterogeneous media. *Water Resources Research* **48**.
- Kull, O. (2002). Acclimation of photosynthesis in canopies: models and limitations. *Oecologia* **133**, 267-279.
- Kusumi, K., Hirotsuka, S., Shimada, H., Chono, Y., Matsuda, O., and Iba, K. (2010). Contribution of chloroplast biogenesis to carbon–nitrogen balance during early leaf development in rice. *Journal of Plant Research* **123**, 617-622.

- Kyriazakis, I., and Oldham, J. (1993). Diet selection in sheep: the ability of growing lambs to select a diet that meets their crude protein (nitrogen $\times$  6.25) requirements. *British journal of Nutrition* **69**, 617-629.
- Leegood, R. C. (2002). C4 photosynthesis: principles of CO<sub>2</sub> concentration and prospects for its introduction into C3 plants. *Journal of experimental botany* **53**, 581-590.
- Lemaire, G., and Gastal, F. (1997). N uptake and distribution in plant canopies. *Diagnosis of the nitrogen status in crops*, 3-43.
- Lemaire, G., van Oosterom, E., Jeuffroy, M.-H., Gastal, F., and Massignam, A. (2008). Crop species present different qualitative types of response to N deficiency during their vegetative growth. *Field Crops Research* **105**, 253-265.
- Lemaire, G., van Oosterom, E., Sheehy, J., Jeuffroy, M. H., Massignam, A., and Rossato, L. (2007). Is crop N demand more closely related to dry matter accumulation or leaf area expansion during vegetative growth? *Field Crops Research* **100**, 91-106.
- Li, H., Kuang, N., Gou, Q., Ma, Y., and Li, Q. (2021). Effects of different film mulches on photosynthetic characteristics and yield of summer maize (*Zea mays* L.) in the North China Plain. *Archives of Agronomy and Soil Science* **67**, 179-190.
- Li, Y., Tao, H., Zhang, B., Huang, S., and Wang, P. (2018). Timing of Water Deficit Limits Maize Kernel Setting in Association With Changes in the Source-Flow-Sink Relationship. *Front. Plant Sci.* **9**.
- Liu, W.-Y., Chang, Y.-M., Chen, S. C.-C., Lu, C.-H., Wu, Y.-H., Lu, M.-Y. J., Chen, D.-R., Shih, A. C.-C., Sheue, C.-R., and Huang, H.-C. (2013). Anatomical and transcriptional dynamics of maize embryonic leaves during seed germination. *Proceedings of the National Academy of Sciences* **110**, 3979-3984.
- Lizaso, J., Batchelor, W., and Westgate, M. (2003). A leaf area model to simulate cultivar-specific expansion and senescence of maize leaves. *Field crops research* **80**, 1-17.
- Loomis, R., Williams, W., Duncan, W., Dovrat, A., and Nunez, F. (1968). Quantitative descriptions of foliage display and light absorption in field communities of corn plants 1. *Crop Science* **8**, 352-356.
- Loss, S., Kirby, E., Siddique, K., and Perry, M. (1989). Grain growth and development of old and modern Australian wheats. *Field Crops Research* **21**, 131-146.
- Ma, W., Bicknell, K., and Renwick, A. (2019). Feed use intensification and technical efficiency of dairy farms in New Zealand. *Australian Journal of Agricultural and Resource Economics* **63**, 20-38.
- MacAdam, J. W., Volenec, J. J., and Nelson, C. J. (1989). Effects of nitrogen on mesophyll cell division and epidermal cell elongation in tall fescue leaf blades. *Plant Physiology* **89**, 549-556.
- Maddonni, G., and Otegui, M. (1996). Leaf area, light interception, and crop development in maize. *Field Crops Research* **48**, 81-87.
- Major, D. J., Beasley, B. W., and Hamilton, R. I. (1991). Effect of maize maturity on radiation-use efficiency. *Agronomy Journal* **83**, 895-903.
- Makino, A., Mae, T., and Ohira, K. (1984). Relation between nitrogen and ribulose-1, 5-bisphosphate carboxylase in rice leaves from emergence through senescence. *Plant and Cell Physiology* **25**, 429-437.
- Massignam, A., Chapman, S., Hammer, G., and Fukai, S. (2012). Effects of nitrogen supply on canopy development of maize and sunflower. *Crop and Pasture Science* **62**, 1045-1055.
- Matthews, R., Harris, D., Williams, J., and Rao, R. N. (1988). The physiological basis for yield differences between four genotypes of groundnut (*Arachis hypogaea*) in response to drought. II. Solar radiation interception and leaf movement. *Experimental Agriculture* **24**, 203-213.
- Millner, J. P., Villaver, R., and Hardacre, A. (2005). The yield and nutritive value of maize hybrids grown for silage *New Zealand Journal of Agriculture Research* **48**, 101-108.
- Miyazawa, S. I., Makino, A., and Terashima, I. (2003). Changes in mesophyll anatomy and sink-source relationships during leaf development in *Quercus glauca*, an evergreen tree showing delayed leaf greening. *Plant, Cell & Environment* **26**, 745-755.
- Mizukami, Y. (2001). A matter of size: Developmental control of organ size in plants. *Curr. Opin. Plant Biol.* **4**.

- Monsi M, and T., S. (1953). Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Japanese Journal of Botany* **14**, 22-52.
- Monteith, J. (1977). Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London* **281**, 277-294.
- Moot, D., Brown, H. E., Teixeira, E., and Pollock, K. (2003). Crop growth and development affect seasonal priorities for lucerne management. *NZGA: Research and Practice Series* **11**, 201-208.
- Moot, D. J., Matthew, C., Kemp, P. D., and Scott, W. R. (2007). Husbandary and role of pastures and forage crops in grazing systems *New Zealand Society of Animal Production* **14**, 23 -33.
- Morris, N. J., Hurley, T. D., and Densley, R. J. (2016). National and regional maize grain and silage strip trial yields. In "Journal of New Zealand Grasslands", Vol. 78, Timaru.
- Muchow, R. (1989a). Comparative productivity of maize, sorghum and pearl millet in a semi-arid tropical environment I. Yield potential. *Field Crops Research* **20**, 191-205.
- Muchow, R. (1989b). Comparative productivity of maize, sorghum and pearl millet in a semi-arid tropical environment II. Effect of water deficits. *Field Crops Research* **20**, 207-219.
- Muchow, R. (1990). Effect of nitrogen on partitioning and yield in grain sorghum under differing environmental conditions in the semi-arid tropics. *Field crops research* **25**, 265-278.
- Muchow, R. (1994). Effect of nitrogen on yield determination in irrigated maize in tropical and subtropical environments. *Field Crops Research* **38**, 1-13.
- Muchow, R., and Carberry, P. (1989). Environmental control of phenology and leaf growth in a tropically adapted maize. *Field Crops Research* **20**, 221-236.
- Muchow, R., and Carberry, P. (1990). Phenology and leaf-area development in a tropical grain sorghum. *Field Crops Research* **23**, 221-237.
- Muchow, R., and Davis, R. (1988). Effect of nitrogen supply on the comparative productivity of maize and sorghum in a semi-arid tropical environment II. Radiation interception and biomass accumulation. *Field Crops Research* **18**, 17-30.
- Muchow, R. C., and Sinclair, T. R. (1994). Nitrogen Response of Leaf Photosynthesis and Canopy Radiation Use Efficiency in Field-Grown Maize and Sorghum. *Crop Science*.
- Muchow, R. C., Sinclair, T. R., and Bennett, J. M. (1990). Temperature and solar radiation effects on potential maize yield across locations. *Agronomy journal* **82**, 338-343.
- Nleya, T., Chungu, C., and Kleinjan, J. (2016). Corn growth and development. *Grow Corn Best Manag. Pract.*
- Nonogaki, H. (2008). Seed germination and reserve mobilization. *eLS*.
- Novoa, R., and Loomis, R. (1981). Nitrogen and plant production. *Plant and soil* **58**, 177-204.
- Osaki, M. (1995). Comparison of productivity between tropical and temperate maize: I. Leaf senescence and productivity in relation to nitrogen nutrition. *Soil Science and Plant Nutrition* **41**, 439-450.
- Otegui, M. E., and Melón, S. (1997). Kernel set and flower synchrony within the ear of maize: I. Sowing date effects. *Crop Science* **37**, 441-447.
- Otegui, M. E., Nicolini, M. G., Ruiz, R. A., and Dodds, P. A. (1995). Sowing date effects on grain yield components for different maize genotypes. *Agronomy Journal* **87**, 29-33.
- Ouattar, S., Jones, R. J., and Crookston, R. K. (1987). Effect of water deficit during grainfilling on the pattern of maize kernel growth and development. *Crop Sci.*, 726-730.
- Padilla, J., and Otegui, M. (2005). Co-ordination between leaf initiation and leaf appearance in field-grown maize (*Zea mays*): genotypic differences in response of rates to temperature. *Annals of Botany* **96**, 997-1007.
- Pepper, G., Pearce, R., and Mock, J. (1977). Leaf orientation and yield of maize 1. *Crop Science* **17**, 883-886.
- Pinheiro, C., and Chaves, M. (2011). Photosynthesis and drought: can we make metabolic connections from available data? *Journal of experimental botany* **62**, 869-882.
- Pioneer Brand Products (2016). Maize for silage 2015/2016. (P. Brand, ed.). Pioneer, New Zealand.
- Plénet, D., Mollier, A., and Pellerin, S. (2000). Growth analysis of maize field crops under phosphorus deficiency. II. Radiation-use efficiency, biomass accumulation and yield components. *Plant and Soil* **224**, 259-272.

- Porter, J. R., and Gawith, M. (1999). Temperatures and the growth and development of wheat: a review. *European journal of agronomy* **10**, 23-36.
- Pugnaire, F. I., Serrano, L., and Pardos, J. (1999). Constraints by water stress on plant growth. *Handbook of plant and crop stress* **2**, 271-283.
- Read, D. (1959). Horizontal movement of water in soil. *Canadian Journal of Soil Science* **39**, 27-31.
- Reddy, V. M., and Daynard, T. B. (1983). Endosperm characteristics associated with rate of grain filling and kernel size in corn. **v. 28**.
- Richards, F. (1969). The quantitative analysis of growth. In 'Plant Physiology: a Treatise'. (Ed. FC Steward.) Vol. 5A. Academic Press: New York and London.
- Richards, R. (2000). Selectable traits to increase crop photosynthesis and yield of grain crops. *Journal of experimental botany* **51**, 447-458.
- Ritchie, J. (1981). Soil water availability. *Plant and soil*, 327-338.
- Ritchie, J. T., and Nesmith, D. S. (1991). Temperature and crop development. *Modeling plant and soil systems* **31**, 5-29.
- Ritchie, S., Hanway, J., and Benson, G. (1986). How a corn plant develops. Iowa State University Extension, Special Report No. 48. Iowa State University Ames.
- Robert, N., Huet, S., Hennequet, C., and Bouvier, A. (1999). Methodology for choosing a model for wheat kernel growth. *Agronomie* **19**, 405-417.
- Robertson, M. (1994). Relationships between internode elongation, plant height and leaf appearance in maize. *Field Crops Research* **38**, 135-145.
- Robertson, M., Silim, S., Chauhan, Y., and Ranganathan, R. (2001). Predicting growth and development of pigeonpea: biomass accumulation and partitioning. *Field Crops Research* **70**, 89-100.
- Rochette, P., Desjardins, R. L., Pattey, E., and Lessard, R. (1996). Instantaneous measurement of radiation and water use efficiencies of a maize crop. *Agronomy Journal* **88**, 627-635.
- Roggatz, U., McDonald, A., Stadenberg, I., and Schurr, U. (1999). Effects of nitrogen deprivation on cell division and expansion in leaves of *Ricinus communis* L. *Plant, Cell & Environment* **22**, 81-89.
- Salette, J., and Lemaire, G. (1981). The variation of nitrogen content during growth of forage grasses: a dilution equation.
- Schussler, J., and Westgate, M. (1991). Maize kernel set at low water potential: I. Sensitivity to reduced assimilates during early kernel growth. *Crop science* **31**, 1189-1195.
- Scotter, D. (1977). Field capacity and available soil water. *Inf Ser NZ Dep Sci Ind Res*.
- Severini, A. D., Borrás, L., Westgate, M. E., and Cirilo, A. G. (2011). Kernel number and kernel weight determination in dent and popcorn maize. *Field Crops Research* **120**, 360-369.
- Shaykewich, C. (1995). An appraisal of cereal crop phenology modelling. *Canadian Journal of Plant Science* **75**, 329-341.
- Sims, D. A., and Gamon, J. A. (2002). Relationships between leaf pigment content and spectral reflectance across a wide range of species, leaf structures and developmental stages. *Remote sensing of environment* **81**, 337-354.
- Sinclair, T. R., and Horie, T. (1989). Leaf nitrogen, photosynthesis, and crop radiation use efficiency: a review. *Crop science* **29**, 90-98.
- Sinclair, T. R., and Muchow, R. C. (1999). Radiation use efficiency. *Advances in agronomy* **65**, 215-265.
- Stevens, W., Hoefft, R., and Mulvaney, R. (2005). Fate of nitrogen-15 in a long-term nitrogen rate study: I. Interactions with soil nitrogen. *Agronomy Journal* **97**, 1037-1045.
- Stevenson, B., Laubscher N, Kannemeyer R, Drewry J, Harmsworth G, and N, S. (2022). What is soil health? Soil Health Factsheet. (M. W. L. Research., ed.).
- Stewart, D., and Dwyer, L. M. (1994). A model of expansion and senescence of individual leaves of field-grown maize (*Zea mays* L.). *Canadian journal of plant science* **74**, 37-42.
- Stockle, C. O., and Kemanian, R. (2009). Crop radiation capture and use efficiency: A framework for crop growth analysis. In "Crop physiology: Applications for genetic improvement and agronomy." (V. O. C. Sadras, D.F. Elsevier,, ed.), pp. 145-170, Burlington, USA.

- Stone, P., Sorensen, I., and Jamieson, P. (1999). Effect of soil temperature on phenology, canopy development, biomass and yield of maize in a cool-temperate climate. *Field crops research* **63**, 169-178.
- Stone, P. J., Wilson, D. R., and Gillespie, R. N. (1997). Water deficit effects on growth, water use and yield of sweet corn *Proceedings Agronomy Society of N.Z* **27**, 45-50.
- Stone, P. J., Wilson, D. R., Reid, J. B., and Gillespie, R. N. (2001). Water deficit effects on sweet corn. I. Wateruse, radiation use efficiency, growth, and yield. *Aust. J. Agric. Res.* **52**, 103-13.
- Subedi, K., and Ma, B. (2005). Nitrogen uptake and partitioning in stay-green and leafy maize hybrids. *Crop Science* **45**, 740-747.
- Sylvester, A. W., and Smith, L. G. (2009). Cell Biology of Maize Leaf Development. In "Handbook of Maize: Its Biology" (J. L. Bennetzen and S. C. Hake, eds.), pp. 179-203. Springer New York, New York, NY.
- Tanner, C., and Sinclair, T. (1983). Efficient water use in crop production: Research or re-search? *Limitations to efficient water use in crop production*, 1-27.
- Tardieu, F., Reymond, M., Hamard, P., Granier, C., and Muller, B. (2000). Spatial distributions of expansion rate, cell division rate and cell size in maize leaves: a synthesis of the effects of soil water status, evaporative demand and temperature. *Journal of Experimental Botany* **51**, 1505-1514.
- Teixeira, E., George, M., Brown, H., and Fletcher, A. (2011). A framework for quantifying maize leaf expansion and senescence at the individual leaf level. *Agronomy New Zealand* **41**, 59-65.
- Tewes, A., and Schellberg, J. (2018). Towards remote estimation of radiation use efficiency in maize using UAV-based low-cost camera imagery. *Agronomy* **8**, 16.
- Thornley, J. H., and France, J. (2007). "Mathematical models in agriculture: quantitative methods for the plant, animal and ecological sciences," Cabi.
- Tollenaar, M. (1977). Sink source relationships during reproductive development in maize. a review.
- Tollenaar, M. (1989). Genetic improvement in grain yield of commercial maize hybrids grown in Ontario from 1959 to 1988. *Crop. Sci.* **29**, 1365–1371.
- Tollenaar, M., and Aguilera, A. (1992). Radiation use efficiency of an old and a new maize hybrid. *Agronomy journal* **84**, 536-541.
- Tollenaar, M., and Bruulsema, T. (1988). Efficiency of maize dry matter production during periods of complete leaf area expansion. *Agronomy Journal* **80**, 580-585.
- Trápani, N., Hall, A. J., Sadras, V. O., and Vilella, F. (1992). Ontogenetic changes in radiation use efficiency of sunflower (*Helianthus annuus* L.) crops. *Field Crops Research* **29**, 301-316.
- Tsimba, R., Gunn, T., Densley, R., Millar, J., Williams, I., and Clausen, C. (2020). Quantification of nitrogen leaching losses under a typical maize silage cropping system. *Nutrient Management in Farmed Landscapes*. <http://flrc.massey.ac.nz/publications.html>. Occasional Report.
- Urban, A., Rogowski, P., Wasilewska-Dębowska, W., and Romanowska, E. (2021). Understanding Maize Response to Nitrogen Limitation in Different Light Conditions for the Improvement of Photosynthesis. *Plants* **10**, 1932.
- Uribelarrea, M., Crafts-Brandner, S. J., and Below, F. E. (2009). Physiological N response of field-grown maize hybrids (*Zea mays* L.) with divergent yield potential and grain protein concentration. *Plant and soil* **316**, 151-160.
- Valentine, I., and Kemp, P. D. (2007). Pasture and supplements for grazing animals. *New Zealand Society of Animal Production* **14**, 3-11.
- Van Esbroeck, G., Ruiz Corral, J., Sanchez Gonzalez, J., and Holland, J. (2008). A comparison of leaf appearance rates among teosinte, maize landraces and modern maize. *Maydica* **53**, 117.
- Van Oosterom, E., Borrell, A., Chapman, S., Broad, I. J., and Hammer, G. (2010). Functional dynamics of the nitrogen balance of sorghum: I. N demand of vegetative plant parts. *Field Crops Research* **115**, 19-28.
- Van Volkenburgh, E., and Boyer, J. S. (1985). Inhibitory effects of water deficit on maize leaf elongation. *Plant Physiology* **77**, 190-194.
- Verheul, M., Picatto, C., and Stamp, P. (1996). Growth and development of maize (*Zea mays* L.) seedlings under chilling conditions in the field. *European Journal of Agronomy* **5**, 31-43.

- Vinocur, M. G., and Ritchie, J. T. (2001). Maize leaf development biases caused by air–apex temperature differences. *Agronomy Journal* **93**, 767-772.
- Volenc, J., and Nelson, C. (1983). Responses of tall fescue leaf meristems to N fertilization and harvest frequency 1. *Crop Science* **23**, 720-724.
- Vos, J., Van Der Putten, P., and Birch, C. (2005). Effect of nitrogen supply on leaf appearance, leaf growth, leaf nitrogen economy and photosynthetic capacity in maize (*Zea mays* L.). *Field Crops Research* **93**, 64-73.
- Wang, Y., Janz, B., Engedal, T., and de Neergaard, A. (2017). Effect of irrigation regime on water use efficiency and nitrogen uptake in maize. *Agriculture Water Management* **179**, 271-276.
- Watt, J. P. C., and Brugham, S. (1991). "Physical properties of eight soils of the Lincoln area, Canterbury, Christchurch, New Zealand.," New Zealand
- Weaich, K., Bristow, K. L., and Cass, A. (1996). Modeling preemergent maize shoot growth: I. physiological temperature conditions. *Agronomy Journal* **88**, 391-397.
- Webb, T., Claydon, J., and Harris, S. (2000). Quantifying variability of soil physical properties within soil series to address modern land-use issues on the Canterbury Plains, New Zealand. *Soil Research* **38**, 1115-1129.
- Westgate, M., Forcella, F., Reicosky, D., and Somsen, J. (1997). Rapid canopy closure for maize production in the northern US corn belt: radiation-use efficiency and grain yield. *Field Crops Research* **49**, 249-258.
- Westgate, M. E. (1994). Water status and development of the maize endosperm and embryo during drought. *Crop science* **34**, 76-83.
- White, J., Millner, J., and Moot, D. (1999). Cereals. *New Zealand pasture and crop science (eds., White, JGH and Hodgson, J.)*, 213-234.
- Wilson, D., Muchow, R., and Murgatroyd, C. (1995). Model analysis of temperature and solar radiation limitations to maize potential productivity in a cool climate. *Field crops research* **43**, 1-18.
- Wilson, D. R., Johnstone, J. V., and Salinger, M. J. (1994 ). Maize production potential and climatic risk in the South Island of New Zealand. *New Zealand Journal of Crop and Horticultural Science* **22** 321-334.
- Witelski, T. P. (2005). Motion of wetting fronts moving into partially pre-wet soil. *Advances in Water Resources* **28**, 1133-1141.
- Wu, Y.-w., Zhao, B., Li, X.-l., Liu, Q.-l., Feng, D.-j., Lan, T.-q., Kong, F.-l., Li, Q., and Yuan, J.-c. (2022). Nitrogen application affects maize grain filling by regulating grain water relations. *Journal of Integrative Agriculture* **21**, 977-994.
- Xianshi, G., Sinclair, T., and Ray, J. (1998). Effect of drought history on recovery of transpiration , photosynthesis and leaf area development in maize. In "Soil and Crop Science Society of Florida Proceedings".
- Yin, X., Schapendonk, A. H., Kropff, M. J., van Oijen, M., and Bindraban, P. S. (2000). A generic equation for nitrogen-limited leaf area index and its application in crop growth models for predicting leaf senescence. *Annals of Botany* **85**, 579-585.
- Yu, P., White, P. J., Hochholdinger, F., and Li, C. (2014). Phenotypic plasticity of the maize root system in response to heterogeneous nitrogen availability. *Planta* **240**, 667-678.
- Zhang, Z., Zhang, Y., Shi, Y., and Yu, Z. (2020). Optimized split nitrogen fertilizer increase photosynthesis, grain yield, nitrogen use efficiency and water use efficiency under water-saving irrigation. *Scientific Reports* **10**, 20310.
- Zhao, Q., Chen, S., and Dai, S. (2013). C4 photosynthetic machinery: insights from maize chloroplast proteomics. *Frontiers in plant science* **4**, 85.
- Zhou, H., Zhou, G., Zhou, L., Lv, X., Ji, Y., and Zhou, M. (2021). The interrelationship between water use efficiency and radiation use efficiency under progressive soil drying in maize. *Frontiers in Plant Science* **12**, 794409.