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**Elucidating the physiological mechanism of ‘stay
green’ in maize hybrids – crop growth processes
and nitrogen economy**

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

at
Lincoln University
New Zealand

by
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Lincoln University
Canterbury, New Zealand

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Abstract of a thesis submitted in partial fulfilment of the requirements for the
degree of Doctor of Philosophy

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maize hybrids – crop growth processes and nitrogen
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The study reported in this thesis was established during 2008/09 and 2009/10 at Lincoln University, New Zealand, to investigate the physiological mechanisms of the 'stay-green' trait in maize hybrids. In 2008/09, the response of ‘P39K38’ (sgr 6), ‘P38V12’ (sgr 7), ‘P38F70’ (sgr 8), and ‘P38G43’ (sgr 9) to 0 or 270 kg nitrogen (N) ha⁻¹ and nil or full irrigation was quantified. Only the response of ‘P39K38’ (sgr 6) and ‘P38G43’ (sgr 9) to four rates of N (0; 0 (V6) and 50 (V12); 150 (V6) and 0 (V12) and 150 (V6) and 50 (V12) kg N ha⁻¹) applied at six (V6) and 12 (V12) fully expanded leaves was examined in 2009/10, when crops were fully irrigated.

Increased ‘stay-green’ rating either had no influence or led to a decline in dry matter accumulation and grain yield because of the reduction in total intercepted photosynthetically active radiation (iPAR). Total dry matter and grain yield were similar amongst the hybrids in 2008/09. However, ‘P39K38’ (sgr 6), yielded 2.0 and 1.8 t ha⁻¹ more dry matter and grain yield, respectively, than ‘P38G43’ (sgr 9) in 2009/10. Total iPAR was 5% higher among the low ‘stay-green’ (sgr 6 and 7) hybrids because for ‘P39K38’ (sgr 6), leaves in positions 8-14 were 10% larger. Thus, the critical green area index (GAI) was reached 70-110 °C.d earlier in these hybrids than in the high ‘stay-green’ hybrids. Consequently, mean maximum GAI in the low ‘stay-green’ hybrids was 4-13% higher and better synchronised with the peak of solar radiation.

GAI decline during grain filling was consistent and influenced by the nitrogen x hybrid interaction. The ‘stay-green’ trait was only exhibited in the presence of adequate N. When

additional N was not provided, the 'stay-green' trait had no effect on leaf senescence. However, when N was available, 'P38G43' (sgr 9), senesced 1-2 fewer ($P < 0.046$) leaves at physiological maturity compared with the other hybrids. The decline in GAI was also affected by the interaction of water and N, with the least ($P < 0.001$) number of leaves senesced when both were provided, suggesting that both acted synergistically to delay leaf senescence.

The stay green hybrids did not show any preferential sequestration of N, but its remobilisation within the crop differed during grain filling. For example, 'P39K38' (sgr 6) had 25 kg N ha^{-1} more in its kernels from the remobilization of stalk and leaf N than 'P38G43' (sgr 9) at physiological maturity. As a consequence of the smaller leaf size and slower decline in leaf N content during grain filling, the high 'stay-green' hybrids, maintained a high specific leaf N (SLN) concentration (g m^{-2}) for longer than the other hybrids. The decline in SLN was consistent with the increase in the number of leaves senesced, suggesting that leaf senescence was associated with the decline in SLN. Total dry matter converged between the hybrids in 2008/09 because the radiation use efficiency (RUE) provided a compensatory influence. RUE was therefore 8% ($2.68 \text{ vs. } 2.48 \text{ g dry matter MJ}^{-1} \text{ PAR absorbed}$) higher in the high 'stay-green' (sgr 8 and 9) hybrids compared with the low 'stay-green' (sgr 6 and 7) hybrids.

Overall, the selection for high 'stay-green' rating may have led to a decline in the partitioning of N to the kernels and consequently contributed to lower grain N levels. Thus, the hybrid 'stay-green' trait may only provide an opportunity for a prolonged harvest window before crops are ensiled. Otherwise it had a negative effect on dry matter yield and grain protein content in these environmental conditions.

Table of Contents

Abstract	i
Table of Contents	iii
List of Tables	x
List of Figures	xv
Appendices	xxii
Abbreviations	xxiv
Chapter 1. General Introduction	1
1.1 Forage maize in New Zealand farming systems	1
1.2 ‘Stay-green’ trait	1
1.3 Dry matter accumulation and grain yield.....	2
1.3.1 Environmental variables.....	2
1.3.2 Physiological response to N and water	4
1.4 Aims and objectives	4
1.4.1 Thesis structure	5
Chapter 2. Review of the Literature	7
2.1 Introduction	7
2.2 Thermal time (Tt).....	7
2.2.1 Theoretical framework	8
2.3 Vegetative growth and development.....	9
2.3.1 Germination and emergence.....	10
2.3.2 Leaf initiation and appearance rate	11
2.3.3 Canopy development.....	13
2.3.3.1 Green area	13
2.3.3.2 Nitrogen.....	14
2.3.3.3 Water deficits	15
2.3.4 Dry matter accumulation.....	18
2.3.4.1 Solar radiation interception.....	19
2.3.4.2 Extinction coefficient.....	20
2.3.4.3 Photosynthetic rate	20
2.3.4.4 Radiation use efficiency.....	25
2.3.4.5 Water use efficiency.....	26
2.3.4.6 Potential soil moisture deficit.....	27
2.3.4.7 Partitioning of dry matter	27

2.4	Reproductive growth.....	28
2.4.1	Photoperiod	28
2.4.2	Silking	28
2.4.3	Ear growth.....	29
2.4.4	Kernel growth.....	29
2.4.5	Physiological maturity.....	30
2.4.6	Senescence	30
2.5	Yield and yield components.....	31
2.5.1	Grain yield.....	31
2.5.1.1	Number of kernels per ear.....	32
2.5.1.2	Seed weight	32
2.5.2	Crop harvest index	32
2.6	What is the ‘stay-green’ trait?	33
2.7	Conclusions	36
	Chapter 3. Materials and Methods	37
3.1	Introduction.....	37
3.2	Experiment 1	37
3.2.1	Soil type and fertility.....	37
3.2.2	Experimental design.....	38
3.2.3	Cultural practices.....	38
3.2.3.1	Seed bed preparation.....	38
3.2.3.2	Crop establishment.....	39
3.2.4	Treatments	39
3.2.4.1	Nitrogen.....	39
3.2.4.2	Irrigation.....	39
3.2.4.3	Maize Hybrids.....	40
3.2.5	Weed control	41
3.3	Experiment 2	41
3.3.1	Soil type and fertility.....	41
3.3.2	Experimental design	41
3.3.3	Cultural practices.....	42
3.3.3.1	Crop establishment.....	42
3.3.3.2	Irrigation.....	42
3.3.3.3	N application	42

3.3.3.4	Weed control	42
3.4	Measurements	43
3.4.1	Crop establishment.....	43
3.4.2	Green area index and dry matter accumulation.....	43
3.4.3	Chlorophyll content.....	44
3.4.4	Photosynthetic activity and leaf senescence.....	44
3.4.5	Final harvest	45
3.4.6	N content	45
3.5	Climatic and seasonal weather conditions	46
3.6	Calculations and data analyses for Experiments 1 and 2	48
3.6.1	Thermal time	48
3.6.2	Leaf appearance rate.....	49
3.6.3	Green area	49
3.6.4	Light interception	50
3.6.5	Water budget	50
3.6.6	Dry matter	54
3.6.7	Statistical analyses.....	55
 Chapter 4. Dry matter accumulation and yield formation in maize hybrids differing in 'stay-green' rating		56
4.1	Introduction	56
4.2	Materials and Methods.....	56
4.3	Measurements	57
4.4	Calculations and data analyses.....	57
4.5	Results.....	57
4.5.1	Final yield.....	57
4.5.2	Crop harvest index (HI).....	57
4.5.3	Yield components.....	58
4.5.3.1	Kernel weight per ear (g)	58
4.5.3.2	Number of kernels per ear.....	59
4.5.3.3	Seed weight	59
4.5.4	Non kernel ear dry matter.....	60
4.5.5	Dry matter accumulation.....	61
4.5.5.1	Duration to silking and physiological maturity.....	61
4.5.5.2	Total dry matter.....	61

4.5.5.3	Leaf dry matter	63
4.5.5.4	Stalk dry matter	64
4.5.5.5	Ear DM.....	66
4.5.5.6	Grain growth	66
4.6	Discussion	68
4.6.1	Total crop DM and grain yield (t ha ⁻¹)	68
4.6.2	Crop harvest index	69
4.6.3	Number of kernels per ear and the seed weight (mg)	69
4.6.4	Non kernel ear dry matter (t ha ⁻¹).....	70
4.6.5	Crop growth and DM partitioning.....	70
4.6.5.1	Total dry matter.....	70
4.6.5.2	Leaf dry matter.....	70
4.6.5.3	Stalk dry matter	71
4.6.5.4	Kernel growth.....	71
4.7	Conclusions	73
Chapter 5. Light interception and the development of green area in hybrid maize of different ‘stay-green’ rating		74
5.1	Introduction	74
5.2	Materials and methods	75
5.2.1	Measurements.....	75
5.2.2	Calculations and data analysis.....	75
5.3	Results.....	76
5.3.1	Total intercepted PAR.....	76
5.3.2	Canopy extinction coefficient (kpar).....	79
5.3.3	Green area development.....	79
5.3.3.1	Green area index	79
5.3.3.2	Green area duration (days).....	84
5.3.4	Leaf appearance rate.....	84
5.3.4.1	Leaf tips.....	84
5.3.4.2	Fully expanded leaves	88
5.4	Discussion	92
5.4.1	Canopy light interception	92
5.4.1.1	Total intercepted PAR.....	92
5.4.1.2	Extinction coefficient (kpar)	93
5.4.2	Leaf area development	93

5.4.2.1	Canopy establishment	93
5.4.2.2	Canopy development.....	94
5.4.2.3	Green area index decline.....	95
5.4.3	Leaf appearance.....	95
5.4.3.1	Leaf tips.....	95
5.4.3.2	Fully expanded leaves	96
5.5	Conclusions	98
Chapter 6. Radiation use efficiency and crop N content		99
6.1	Introduction	99
6.2	Materials and methods	99
6.3	Measurements	99
6.4	Calculations and data analysis	100
6.5	Results.....	101
6.5.1	RUE.....	101
6.5.2	Chlorophyll content.....	102
6.5.3	Leaf senescence.....	104
6.5.3.1	Number of senesced leaves	104
6.5.4	Crop N dynamics.....	107
6.5.4.1	Total crop N (kg ha ⁻¹).....	107
6.5.4.2	Kernel N	109
6.5.4.3	Stalk N.....	111
6.5.4.4	Leaf N content.....	113
6.6	Discussion	124
6.6.1	RUE.....	124
6.6.2	Chlorophyll content and leaf senescence	125
6.6.3	N uptake and partitioning during grain filling	125
6.6.4	Specific leaf N concentration (g m ⁻²)	126
6.6.4.1	Lower leaves	126
6.6.4.2	Middle leaves	127
6.6.4.3	Top leaves	127
6.7	Conclusions	129
Chapter 7. Experiment 2: DM accumulation, light interception, RUE and N content..		130
7.1	Introduction.....	130
7.2	Materials and methods	130

7.2.1	Experimental design and treatments	130
7.2.2	Crop establishment	131
7.3	Measurements	131
7.4	Calculations and data analyses	132
7.5	Results	132
7.5.1	Dry matter accumulation	132
7.5.1.1	Final harvest	132
7.5.1.2	Non kernel ear dry matter	133
7.5.2	Dry matter accumulation	133
7.5.2.1	Duration to silking and physiological maturity.....	133
7.5.2.2	Total dry matter.....	134
7.5.2.3	Leaf dry matter.....	134
7.5.2.4	Stalk dry matter	136
7.5.2.5	Ear dry matter.....	137
7.5.2.6	Kernel growth.....	137
7.5.3	Light interception	139
7.5.3.1	Total intercepted PAR.....	139
7.5.3.2	Canopy extinction coefficient (kpar)	139
7.5.4	Green area development.....	140
7.5.4.1	Green area index increase	140
7.5.4.2	Green area index decline	142
7.5.4.3	Leaf appearance	144
7.5.5	RUE.....	147
7.5.6	Gross photosynthesis.....	148
7.5.7	Chlorophyll content.....	148
7.5.8	Leaf senescence.....	149
7.5.9	Crop N content	150
7.5.9.1	Final harvest.....	150
7.5.9.2	Silking to physiological maturity.....	151
7.5.9.3	Specific leaf N concentration (g m ⁻²).....	153
7.6	Discussion	155
7.6.1	Dry matter accumulation.....	155
7.6.2	Crop N content	156
7.6.3	Radiation use efficiency	157

7.6.4	Non kernel ear dry matter.....	158
7.7	Conclusions.....	159
	Chapter 8. General discussion and conclusions.....	160
8.1	Influence of the hybrid ‘stay-green’ trait.....	160
8.1.1	Dry matter and grain yield.....	160
8.1.2	Dry matter accumulation.....	161
8.1.2.1	Canopy development.....	162
8.1.2.2	Post-silking dry matter accumulation.....	163
8.1.3	Light interception and RUE.....	164
8.1.3.1	Light interception.....	164
8.1.3.2	RUE.....	165
8.1.4	Nitrogen dynamics.....	165
8.1.4.1	N uptake.....	166
8.1.4.2	N remobilisation.....	166
8.2	N partitioning strategy for cool temperate climates.....	167
8.3	Whither ‘stay-green’?.....	169
8.4	Maize ideotype.....	170
8.5	Scope for further research.....	171
8.5.1	Exploring the productivity of extremely low rated ‘stay-green’ hybrids.....	171
8.5.2	Increased plant population and remobilization of leaf N.....	171
8.5.3	Reduction of the non kernel ear dry matter.....	171
8.6	Conclusions.....	172
	References.....	173
	Appendices.....	193
	Acknowledgements.....	200

List of Tables

Table 3.1: Soil test results from 2 nd October 2008 (Experiment 1) and 7 th November 2009 (Experiment 2) for the experimental site at the Horticultural Research Area, Lincoln University, New Zealand. Recommended soil nutrient levels for maize are included for comparison (Steele 1984).....	38
Table 3.2: Performance characteristics of the four Pioneer [®] brand maize hybrids grown at Lincoln University, New Zealand, during 2008.....	40
Table 3.3: Mean, minimum and maximum temperature (°C) and the long term mean (LTM, 1975-2007) for Experiment 1 (08/09) and Experiment 2 (09/10) at Lincoln University, Canterbury, New Zealand.....	46
Table 3.4: Total amount of water (mm) applied to the irrigated maize crops grown in Experiment 1 at Lincoln University, New Zealand, during 2008.	52
Table 3.5: Total amount of water (mm) applied to all maize crops grown in Experiment 2 at Lincoln University, New Zealand, during 2009.....	53
Table 4.1: Mean total crop dry matter (t ha ⁻¹) and grain yield (t ha ⁻¹) at final harvest of four maize hybrids grown with 0 or 270 kg N ha ⁻¹ when rain fed or irrigated at Lincoln University, New Zealand, during 2008.	58
Table 4.2: Crop harvest index of four maize hybrids grown with 0 or 270 kg N ha ⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.....	58
Table 4.3: Number of kernels per ear of four maize hybrids grown with 0 or 270 kg N ha ⁻¹ and either rainfed or irrigated at Lincoln University, New Zealand, during 2008.....	59
Table 4.4: Individual grain weight (mg) of four maize hybrids grown with 0 or 270 kg N ha ⁻¹ and either rain fed or fully irrigated at Lincoln University, New Zealand, during 2008.....	60
Table 4.5: The non kernel ear dry matter (t ha ⁻¹) of maize hybrids grown with 0 or 270 kg N ha ⁻¹ and either rainfed or irrigated at Lincoln University, New Zealand, during 2008.....	60
Table 4.6: The DUR (°C.d) of linear accumulation of leaf dry matter (5-95% of maximum) in four maize hybrids grown at Lincoln University, New Zealand, during 2008.	64
Table 4.7: The mean maximum leaf dry matter (t ha ⁻¹) of maize hybrids grown with 0 or 270 kg N ha ⁻¹ at Lincoln University, New Zealand, during 2008.	64
Table 4.8: Maximum accumulated stalk dry matter (t ha ⁻¹) in four maize hybrids grown with 0 or 270 kg N ha ⁻¹ at Lincoln University, New Zealand, during 2008.....	65

Table 4.9: Stalk dry matter ($t\ ha^{-1}$) at physiological maturity (1470 °C.d) in four maize hybrids grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.....	65
Table 5.1: Total intercepted photosynthetically active radiation ($MJ\ m^{-2}$) of four maize hybrids grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.....	77
Table 5.2: The linear rate of increase of total intercepted PAR ($MJ\ m^{-2}\ day^{-1}$) between 40 and 150 days after sowing in hybrid maize grown with 0 or 270 kg N ha^{-1} and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.....	77
Table 5.3: The duration of the lag phase (days) for accumulation of PAR ($MJ\ m^{-2}$) for hybrid maize either rain fed or irrigated at Lincoln University, New Zealand, during 2008.....	79
Table 5.4: The duration (°C.d) to critical green area index in hybrid maize grown with 270 kg N ha^{-1} and either rain fed or fertilised at Lincoln University, New Zealand, during 2008.....	81
Table 5.5: Mean green area index ($m^2\ m^{-2}$) at 800 °C.d of four maize hybrids grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand during 2008.....	82
Table 5.6: Total and the cohort leaf area (cm^2 per plant) at 800 °C.d of four hybrids grown at Lincoln University, New Zealand, during 2008.....	83
Table 5.7: The rate of decline ($m^2\ m^{-2}$) (°C.d ⁻¹) in GAI after silking for hybrid maize crops grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008. ...	83
Table 5.8: Green area duration (days) in hybrid maize grown with 0 or 270 kg N ha^{-1} and either irrigated or rain fed at Lincoln University, New Zealand, during 2008.....	84
Table 5.9: The phyllochron _(tip) (°C.d) during Stage 1 (up to 465 °C.d after emergence) for maize hybrids grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.....	85
Table 5.10: The phyllochron _(tip) (°C.d) during Stage 2 (465 -700 °C.d after emergence) for maize hybrids grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.....	85
Table 5.11 Number of visible leaf tips per plant at the point of inflection (up to 465 °C.d after emergence) in maize hybrids grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.	87
Table 5.12: The phyllochron _(ligule) (°C.d) during Stage 1 in hybrid maize grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.	88

Table 5.13: The point of inflection ($^{\circ}\text{C.d}$) in the rate of appearance of ligules of hybrid maize grown with 0 or 270 kg N ha $^{-1}$ at Lincoln University, New Zealand, during 2008.....	89
Table 5.14: The number of leaves per plant at the point of inflection in the rate of appearance of fully expanded leaves of hybrid maize either rainfed or irrigated at Lincoln University, New Zealand, during 2008.....	91
Table 5.15: Number of fully expanded leaves per plant of four maize hybrids grown at Lincoln University, New Zealand, during 2008.....	91
Table 6.1: Radiation use efficiency (g dry matter MJ $^{-1}$ PAR absorbed) in maize grown with 0 or 270 kg N ha $^{-1}$ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.....	101
Table 6.2: Average SPAD readings (SPAD units) per leaf at 800 $^{\circ}\text{C.d}$ after emergence in hybrid maize grown with 0 or 270 kg N ha $^{-1}$ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.....	104
Table 6.3: Average SPAD readings (SPAD units) per leaf at 1470 $^{\circ}\text{C.d}$ after emergence in hybrid maize grown with 0 or 270 kg N ha $^{-1}$ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.....	104
Table 6.4: Number of senesced leaves per plant at silking (710 $^{\circ}\text{C.d}$) and physiological maturity (1470 $^{\circ}\text{C.d}$) in hybrid maize grown with either 0 or 270 kg N ha $^{-1}$ at Lincoln University, New Zealand, during 2008.....	105
Table 6.5: Number of senesced leaves per plant at silking (710 $^{\circ}\text{C.d}$) and physiological maturity (1470 $^{\circ}\text{C.d}$) in hybrid maize grown with either 0 or 270 kg N ha $^{-1}$ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.....	107
Table 6.6: Total kernel N (kg ha $^{-1}$) at final harvest in hybrid maize grown with 0 or 270 kg N ha $^{-1}$ at Lincoln University, New Zealand, during 2008.....	110
Table 6.7: Rate of increase of kernel N (kg ha $^{-1}$ day $^{-1}$) from silking to physiological maturity in hybrid maize grown with 0 or 270 kg N ha $^{-1}$ and either irrigated or rain fed at Lincoln University, New Zealand, during 2008.....	110
Table 6.8: Nitrogen harvest index (%) in hybrid maize either rain fed or irrigated at Lincoln University, New Zealand, during 2008.....	111
Table 6.9: Stalk N (kg ha $^{-1}$) at 800 $^{\circ}\text{C.d}$ and physiological maturity (1470 $^{\circ}\text{C.d}$) for hybrid maize grown with 0 or 270 kg N ha $^{-1}$ at Lincoln University, New Zealand, during 2008.....	112

Table 6.10: Stalk N (kg ha^{-1}) translocation and its efficiency (%) during grain filling in hybrid maize grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.....	113
Table 6.11: Total leaf N (kg ha^{-1}) 7 days after silking (800 $^{\circ}\text{C.d}$) in hybrid maize grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.....	114
Table 6.12: Total leaf N (kg ha^{-1}) at physiological maturity (1470 $^{\circ}\text{C.d}$) in hybrid maize grown with 0 or 270 kg N ha^{-1} and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.	114
Table 6.13: Total leaf N (kg ha^{-1}) translocated from silking to physiological maturity (grain filling) in hybrid maize grown with 0 or 270 kg N ha^{-1} and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.	115
Table 6.14: Leaf N (kg ha^{-1}) translocated from silking to physiological maturity (grain filling) in hybrid maize grown with 0 or 270 kg N ha^{-1} and its efficiency (%) of translocation in rain fed or irrigated crops grown at Lincoln University, New Zealand, during 2008.....	115
Table 6.15: Specific leaf N concentration (g m^{-2}) of the lower leaves at 800 $^{\circ}\text{C.d}$ for hybrid maize grown with 0 or 270 kg N ha^{-1} and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.	116
Table 6.16: Specific leaf N concentration (g m^{-2}) of the lower leaves at 1360 $^{\circ}\text{C.d}$ for hybrid maize grown with 0 or 270 kg N ha^{-1} and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.....	118
Table 6.17: Specific leaf N concentration (g m^{-2}) of the lower leaves at 1360 $^{\circ}\text{C.d}$ for hybrid maize grown with 0 or 270 kg N ha^{-1} and either irrigated or rain fed at Lincoln University, New Zealand, during 2008.....	118
Table 6.18: Specific leaf N concentration (g m^{-2}) of the middle leaves at 800 $^{\circ}\text{C.d}$ for hybrid maize grown with 0 or 270 kg N ha^{-1} and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.....	119
Table 6.19: Specific leaf N concentration (g m^{-2}) across irrigation treatments of the middle leaves at 1360 $^{\circ}\text{C.d}$ for hybrid maize grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.	121
Table 6.20: Specific leaf N concentration (g m^{-2}) of the top leaves at 800 $^{\circ}\text{C.d}$ for hybrid maize grown with 0 or 270 kg N ha^{-1} and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.	122

Table 6.21: Specific leaf N concentration (g m^{-2}) of the top leaves at 1360 °C.d for hybrid maize grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.....	122
Table 7.1: Non kernel ear dry matter (t ha^{-1}) at 250, 370, 620, and 800 °C.d after silking in maize hybrids grown at Lincoln University, New Zealand, during 2009.	133
Table 7.2: Total dry weight (t ha^{-1}) of the bottom, middle and top leaves at silking of maize hybrids grown at Lincoln University, New Zealand, during 2009.....	135
Table 7.3: Maximum green area index in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.....	141
Table 7.4: Total leaf area per plant in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.	143
Table 7.5: Green area index at physiological maturity (1450 °C.d) in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.....	143
Table 7.6: Green area index decline (per °C.d) during grain filling in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.....	144
Table 7.7: Final number of leaves per plant in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.....	146
Table 7.8: Gross photosynthesis rate ($\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in maize hybrids grown at Lincoln University, New Zealand, during 2009.....	148
Table 7.9: Stalk N content (kg N ha^{-1}) at silking (790 °C.d) and physiological maturity (1450 °C.d) in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.	152
Table 7.10: Specific leaf N concentration (g m^{-2}) in the lower, middle and top leaves at silking (790 °C.d) in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.	153
Table 7.11: Specific leaf N concentration (g m^{-2}) in the lower, middle and top leaves at physiological maturity (1450 °C.d) in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.....	154

List of Figures

Figure 1.1: Mean monthly solar radiation (MJ m^{-2}) (\circ), maximum (\blacksquare) and mean (\square) temperature ($^{\circ}\text{C}$) recorded at Broadfields meteorological station, Canterbury, New Zealand, during the 2000-2010 maize growing seasons.....	3
Figure 1.2: Outline of thesis structure.	6
Figure 2.1: The modified thermal time response to temperature showing the linear response between 0 and 18 $^{\circ}\text{C}$ (dotted line). Reproduced with permission from Wilson <i>et al.</i> 1995.....	13
Figure 2.2: Effects of water stress on net photosynthesis (\square) and leaf expansion rate (\blacksquare) of the sixth leaf blade of a 4-5 week old maize plant grown under controlled environment conditions. Adapted with permission from Boyer, 1970.	17
Figure 2.3: Typical temperature response curve for photosynthesis in C_3 (\square) and C_4 (\blacksquare) plants. Reproduced with permission from Edwards and Walker, 1983.....	22
Figure 2.4: Type A and B ‘stay-greens’ in a hypothetical leaf. Chlorophyll content (\square), photosynthetic capacity (\blacksquare) and the normal pattern of chlorophyll decline (\circ) are indicated on an arbitrary scale. The arrows indicate the start of senescence in a non ‘stay-green’ phenotype. Adapted with permission from Thomas and Howarth, 2000.....	34
Figure 3.1: Incident solar radiation for November-May 2008/09 (\blacksquare) and 2009/10 (\square) recorded at Broadfields’ meteorological station, Canterbury, New Zealand. The dotted line represents the long term mean (1975-2007).....	47
Figure 3.2: Penman potential evapotranspiration for November-May 2008/09 (\blacksquare) and 2009/2010 (\square) recorded at Broadfields’ meteorological station, Canterbury, New Zealand. The dotted line represents the long term mean (1975-2007).....	48
Figure 3.3: The weekly water budget for the maize crops grown in Experiment 1 at Lincoln University, New Zealand, during 2008 and either rain fed (dashed line) or fully irrigated (solid line). Rainfall (\blacksquare), irrigation (▒), D_p at emergence (arrow) and the critical deficit (D_c) (dotted line) are also indicated.....	52
Figure 3.4: The weekly water budget for the maize crops grown in Experiment 2 at Lincoln University, New Zealand, during 2009 fully irrigated (solid line). Rainfall (\blacksquare), irrigation (▒), D_p at emergence (solid arrow) and the critical deficit (D_c) (dotted line) are also indicated. The dashed line indicates the maximum deficit ($D_{p_{\text{max}}}$) and the arrow physiological maturity.....	53

- Figure 4.1: Accumulated dry matter ($t\ ha^{-1}$) for total crop (black), ears (red), kernels (dark green), stalks (dark blue) and leaves (pink) in fully irrigated crops of ‘P39K38’ (sgr 6) (a and b) and ‘P38G43’ (sgr 9) (c and d), grown at Lincoln University, New Zealand, during 2008. The crops either received 270 (closed symbols) or 0 $kg\ N\ ha^{-1}$ (open symbols). The solid arrow represents silking and the dotted physiological maturity ($1470\ ^\circ C.d$). 62
- Figure 4.2: Mean accumulated dry matter ($t\ ha^{-1}$) of both levels of N for total crop (black), ears (red), kernels (dark green), stalks (dark blue) and leaves (pink) in fully irrigated (closed symbols) and rain fed (open symbols) crops grown at Lincoln University, New Zealand, during 2008. The dashed arrow shows the start of irrigation, the solid silking and the dotted physiological maturity ($1470\ ^\circ C.d$). 63
- Figure 4.3: Ear dry matter ($t\ ha^{-1}$) versus total crop dry matter ($t\ ha^{-1}$) for ‘P39K38’ (sgr 6) (\triangle), ‘P38V12’ (sgr 7) (\square), ‘P38F70’ (sgr 8) (∇) and ‘P38G43’ (sgr 9) (\circ) maize hybrids grown with (a) 0 (open symbols) or with 270 $kg\ N\ ha^{-1}$ (closed symbols) and (b) irrigated (closed symbols) or rain fed (open symbols) at Lincoln University, New Zealand, during 2008. 67
- Figure 4.4: Kernel dry matter ($t\ ha^{-1}$) versus (a) total dry matter ($t\ ha^{-1}$) and (b) total ear dry matter ($t\ ha^{-1}$) for ‘P39K38’ (sgr 6) (\triangle), ‘P38V12’ (sgr 7) (\square), ‘P38F70’ (sgr 8) (∇) and ‘P38G43’ (sgr 9) (\circ) maize hybrids grown with 0 (open symbols) or 270 $kg\ N\ ha^{-1}$ (closed symbols) at Lincoln University, New Zealand, during 2008.. 67
- Figure 5.1: Total intercepted photosynthetically active radiation ($MJ\ m^{-2}$) versus days after emergence for (a) ‘P39K38’ (sgr 6), (b) ‘P38V12’ (sgr 7), (c) ‘P38F70’ (sgr 8) and (d) ‘P38G43’ (sgr 9) maize hybrids grown at Lincoln University, New Zealand, during 2008. The solid line represents the fitted regression while the dotted the extrapolation to the x-axis. 78
- Figure 5.2: Proportion of intercepted photosynthetically active radiation versus the green area index for ‘P39K38’ (sgr 6, \triangle), ‘P38V12’ (sgr 7, \square), ‘P38F70’ (sgr 8, ∇) and ‘P38G43’ (sgr 9, \circ) maize hybrids grown with 0 (open symbols) or 270 $kg\ N\ ha^{-1}$ (closed symbols) at Lincoln University, New Zealand, during 2008. The solid line represents the fitted regression $y = 0.98(1 - e^{-0.77x})$; $R^2 = 0.93$ and the dotted 95% PAR absorptance and critical green area index, respectively. 80
- Figure 5.3: Green area index against accumulated thermal time ($^\circ C.d$) after emergence for ‘P39K38’ (sgr 6, \triangle), ‘P38V12’ (sgr 7, \square), ‘P38F70’ (sgr 8, ∇) and ‘P38G43’ (sgr 9, \circ) maize hybrids grown with 270 (closed symbols) or 0 (open symbols)

kg N ha⁻¹ at Lincoln University, New Zealand, during 2008. The dotted line represents the critical green area index, the arrows silking date and the error bars the standard error of the means at each harvest date..... 81

Figure 5.4: Number of visible leaf tips per plant versus accumulated thermal time (°C.d) in hybrid maize grown with 0 (open symbols) or 270 (closed symbols) kg N ha⁻¹ at Lincoln University, New Zealand, during 2008. The error bars represent the standard error of the means at each harvest date (leaf tips). Stage 1 equations were: $y = 0.0275x + 1$ and $y = 0.0292x + 1$, $R^2 = 0.99$ for the unfertilised and N fertilised crops, respectively..... 86

Figure 5.5: Number of visible leaf tips per plant versus accumulated thermal time (°C.d) after emergence in maize hybrids ‘P39K38’ (sgr 6, △), ‘P38V12’ (sgr 7, □), ‘P38F70’ (sgr 8, ▽) and ‘P38G43’ (sgr 9, ○) grown at Lincoln University, New Zealand, during 2008. The error bars represent the standard error of the means at each harvest date (leaf tips). Stage 1 equations were as follows: $y = 0.0286x + 1$ (sgr 6), $y = 0.0276x + 1$ (sgr 7), $y = 0.0294x + 1$ (sgr 8) and $y = 0.0277x + 1$ (sgr 9); $R^2 = 0.99$ 87

Figure 5.6: Number (n) of fully expanded leaves versus accumulated thermal time (°C.d) in hybrid maize grown with 0 (open symbols) or 270 (closed symbols) kg N ha⁻¹ at Lincoln University, New Zealand, during 2008. The error bars represent the standard error of the means at each harvest date (leaves). Stage 1 equations were: $y = 0.0174x$ and $y = 0.0185x$; $R^2 = 0.99$ for the unfertilised and N fertilised crops, respectively..... 89

Figure 5.7: Number (n) of fully expanded leaves versus accumulated thermal time (°C.d) after emergence in maize hybrids ‘P39K38’ (sgr 6, △), ‘P38V12’ (sgr 7, □), ‘P38F70’ (sgr 8, ▽) and ‘P38G43’ (sgr 9, ○) grown at Lincoln University, New Zealand, during 2008. The arrow indicates silking and the error bars the standard error of the means (leaves). Stage 1 equations were as follows: $y = 0.0179x$ (sgr 6), $y = 0.0175x$ (sgr 7), $y = 0.0189x$ (sgr 8) and $y = 0.0176x$ (sgr 9); $R^2 = 0.99$ 90

Figure 6.1: Radiation use efficiency (g dry matter MJ⁻¹ PAR absorbed) in ‘P39K38’ (sgr 6, △), ‘P38V12’ (sgr 7, □), ‘P38F70’ (sgr 8, ▽) and ‘P38G43’ (sgr 9, ○) maize hybrids grown with 0 (open symbols) or 270 (closed symbols) kg N ha⁻¹ at Lincoln University, New Zealand, during 2008. The error bars represent the standard error of the hybrid means (g m⁻²) at each sample date..... 102

- Figure 6.2: SPAD readings (SPAD units) per leaf versus specific leaf N concentration (g m^{-2}) for ‘P39K38’ (sgr 6, \triangle), ‘P38V12’ (sgr 7, \square), ‘P38F70’ (sgr 8, ∇) and ‘P38G43’ (sgr 9, \circ) maize hybrids grown with 0 (open symbols) or 270 (closed symbols) kg N ha^{-1} at Lincoln University, New Zealand, during 2008. 103
- Figure 6.3: Number of senesced leaves per plant versus accumulated thermal time ($^{\circ}\text{C.d}$) in ‘P39K38’ (sgr 6, \triangle), ‘P38V12’ (sgr 7, \square), ‘P38F70’ (sgr 8, ∇) and ‘P38G43’ (sgr 9, \circ) maize hybrids grown with 0 (open symbols) or 270 (closed symbols) kg N ha^{-1} at Lincoln University, New Zealand, during 2008. For the fertilised crops, the respective equations for the hybrids were; $y = 0.95e^{0.0016Tt}$; $y = 1.15e^{0.0015Tt}$; $y = 1.08e^{0.0015Tt}$ and $y = 0.64e^{0.0018Tt}$; $R^2 = 0.98$. The arrow indicates silking and the error bars represent the standard error of the hybrid means (leaves per plant) at each sample date. 106
- Figure 6.4: Mean N content (kg ha^{-1}) for total crop (black), kernels (red), stalk (dark green), and leaves (pink) against accumulated thermal time ($^{\circ}\text{C.d}$) after emergence in irrigated crops of ‘P39K38’ (sgr 6) (a and b) and ‘P38G43’ (sgr 9) (c and d), grown with 270 (solid symbols) or 0 kg N ha^{-1} (open symbols) at Lincoln University, New Zealand, during 2008. The solid arrow represents 7 days after silking (800 $^{\circ}\text{C.d}$) and the dotted physiological maturity (1470 $^{\circ}\text{C.d}$). 108
- Figure 6.5: Mean N content (kg ha^{-1}) for total crop (black), kernels (red), stalk (dark green), and leaves (pink) against accumulated thermal time ($^{\circ}\text{C.d}$) after emergence in irrigated (solid symbols) or rain fed (open symbols) crops grown at Lincoln University, New Zealand, during 2008. The solid arrow represents 7 days after silking (800 $^{\circ}\text{C.d}$) and the dotted physiological maturity (1470 $^{\circ}\text{C.d}$). 109
- Figure 6.6: Mean (across N and irrigation levels) specific leaf N concentration (g m^{-2}) during grain filling of the lower leaves of (a) ‘P39K38’ (sgr 6), (b) ‘P38V12’ (sgr 7), (c) ‘P38F70’ (sgr 8) and (d) ‘P38G43’ (sgr 9) grown at Lincoln University, New Zealand, during 2008. The solid arrow indicates 7 days after silking (800 $^{\circ}\text{C.d}$) and the dashed late grain filling (1360 $^{\circ}\text{C.d}$). 117
- Figure 6.7: Mean (across N and irrigation levels) specific leaf N concentration (g m^{-2}) during grain filling of the middle leaves of (a) ‘P39K38’ (sgr 6), (b) ‘P38V12’ (sgr 7), (c) ‘P38F70’ (sgr 8) and (d) ‘P38G43’ (sgr 9) grown at Lincoln University, New Zealand, during 2008. The solid line represents 7 days after silking (800 $^{\circ}\text{C.d}$) and the dashed late grain filling (1360 $^{\circ}\text{C.d}$). 120
- Figure 6.8: Mean (across N and irrigation levels) specific leaf N concentration (g m^{-2}) during grain filling of the top leaves of (a) ‘P39K38’ (sgr 6), (b) ‘P38V12’ (sgr 7),

(c) ‘P38F70’ (sgr 8) and (d) ‘P38G43’ (sgr 9) grown at Lincoln University, New Zealand, during 2008. The respective equations were: (a) $y = 2.71 - 0.0012x$; $R^2 = 0.99$, (b) $y = 2.31 - 0.0007x$; $R^2 = 0.99$, (c) $y = 2.24 - 0.0006x$; $R^2 = 0.98$ and (d) $y = 2.64 - 0.0008x$; $R^2 = 0.97$. The solid line represents 7 days after silking (800 °C.d) and the dashed late grain filling (1360 °C.d). 123

Figure 7.1: Total dry matter ($t\ ha^{-1}$) versus accumulated thermal time (°C.d) for ‘P39K38’ (sgr 6, ◇) and ‘P38G43’ (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009. The solid and dotted arrows indicate silking and physiological maturity, respectively. The error bars represent the standard error of the means ($t\ ha^{-1}$) at each sample date. 134

Figure 7.2: Total leaf dry matter ($t\ ha^{-1}$) accumulation versus thermal time (°C.d) for ‘P39K38’ (sgr 6, ◇) and ‘P38G43’ (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009. The arrow indicates silking while the error bar represents the standard error of the means ($t\ ha^{-1}$). 135

Figure 7.3: Stalk dry matter ($t\ ha^{-1}$) accumulation against thermal time (°C.d) for ‘P39K38’ (sgr 6, ◇) and ‘P38G43’ (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009. The solid and dotted arrows indicate silking and physiological maturity, respectively. The dotted line represents the decline in stalk dry matter ($y = 10.61 - 0.0032x$, $R^2 = 0.96$). 136

Figure 7.4: Ear dry matter ($t\ ha^{-1}$) versus accumulated thermal time (°C.d) after silking (a) and against total crop dry matter (b) for ‘P39K38’ (sgr 6, ◇) and ‘P38G43’ (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009. The dotted line indicates physiological maturity while the error bars represent the standard error of the means ($t\ ha^{-1}$). 137

Figure 7.5: Total kernel dry matter ($t\ ha^{-1}$) versus (a) accumulated thermal time (°C.d) after silking and (b) total ear dry matter ($t\ ha^{-1}$) for ‘P39K38’ (sgr 6, ◇) and ‘P38G43’ (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009. The dotted line indicates physiological maturity while the error bar represents the standard error of the means ($t\ ha^{-1}$) at physiological maturity. 138

Figure 7.6: Total accumulated intercepted photosynthetically active radiation ($MJ\ m^{-2}$) versus time in ‘P39K38’ (sgr 6, ◇) and ‘P38G43’ (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009. The respective equations for the solid lines were $y = 1040.0/(1+e^{(-0.0373(x-90.3)})}$ and $y = 988.6/(1+e^{(-0.0367(x-92.0)})}$, $R^2 = 0.99$. The dotted lines represent the extrapolated pattern of increase

- before the start of measurements. The error bars represent the standard error (MJ m^{-2}) at each sample date. 139
- Figure 7.7: Proportion of intercepted photosynthetically active radiation versus the green area index for ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The solid line represents the fitted regression $y = 0.98(1 - e^{-0.74x})$, $R^2 = 0.99$, and the dotted 95% PAR absorptance and critical green area index, respectively. 140
- Figure 7.8: Green area index versus thermal time ($^{\circ}\text{C.d}$) after emergence in ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The solid arrow indicates silking while the dotted line represents the critical green area index. The dotted arrow indicates physiological maturity and the error bars represent the standard error of the means ($\text{m}^2 \text{m}^{-2}$) at each sample date. 141
- Figure 7.9: Leaf area (cm^2) versus leaf position in ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The arrow indicates the position of the ear leaf and the error bars represent the standard error of the means (cm^2) for each leaf position. 142
- Figure 7.10: Number of visible leaf tips per plant versus accumulated thermal time ($^{\circ}\text{C.d}$) in ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The dashed and dotted lines represent the duration ($^{\circ}\text{C.d}$) to the point of inflection in ‘P39K38’ (sgr 6) and ‘P38G43’ (sgr 9), respectively. The graph was constrained to intercept the y axis at (0, 1). 145
- Figure 7.11: Number of fully expanded leaves per plant versus accumulated thermal time ($^{\circ}\text{C.d}$) in ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The dashed and dotted lines represent the duration ($^{\circ}\text{C.d}$) to the point of inflection in ‘P39K38’ (sgr 6) and ‘P38G43’ (sgr 9), respectively. The graph was constrained to intercept the axis at the origin. 146
- Figure 7.12: Radiation use efficiency (g dry matter per MJ absorbed PAR) in ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand during 2009. The equation for the regression of total crop dry matter (g m^{-2}) on total absorbed PAR (MJ m^{-2}) was $y = 3.03x - 309.2$ (>8 fully expanded leaves), $R^2 = 0.99$. The dashed line represents the extrapolated RUE before 8 fully expanded leaves (shown by arrow) and the dotted the bilinear response. 147

- Figure 7.13: Ear leaf SPAD readings (SPAD units) versus time (DAE) for ‘P39K38’ (sgr 6, ◇) and ‘P38G43’ (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009. The arrow indicates silking while the error bars represent the standard error of the means (SPAD units) at each sample date. 149
- Figure 7.14: Number of senesced leaves per plant versus thermal time (°C.d) in ‘P39K38’ (sgr 6, △) and ‘P38G43’ (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009. The respective equations were $y = 0.0068x - 2.20$; $R^2 = 0.95$ and $y = 0.0073x - 2.92$; $R^2 = 0.99$. The solid arrow indicates silking and the dotted physiological maturity. The error bars represent the standard error of the means (leaves per plant) at each sample date. 150
- Figure 7.15: Mean N content (kg ha^{-1}) for total crop (a), kernel (b), leaves (c) and stalk (d) against accumulated thermal time (°C.d) after silking in ‘P39K38’ (sgr 6, △) and ‘P38G43’ (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009. The dotted arrows indicate physiological maturity and the error bars the standard error of the means (kg ha^{-1}) at each sample date. 151

Appendices

- Appendix 1: Accumulated dry matter for total crop (black), ear (red), kernel (dark green), stalk (dark blue) and leaves (pink) in fully irrigated crops of ‘P38V12’ (sgr 7) (a and b) and ‘P38F70’ (sgr 8) (c and d), grown at Lincoln University, New Zealand, during 2008. The crops either received 270 (solid symbols) or 0 (open symbols) kg N ha⁻¹. The solid arrow represents silking and the dotted physiological maturity (1470 °C.d).....193
- Appendix 2: Measurements of green area index obtained using the SunScan (open symbols) and leaf area meter (closed symbols) for maize hybrids grown at Lincoln University, New Zealand, during 2008. The solid line indicates the fitted regression $y = 0.97(1 - e^{-0.76x})$; $R^2 = 0.96$194
- Appendix 3: Regression of the calculated against the measured leaf area (cm²) for ‘P39K38’ (sgr 6, △), ‘P38V12’ (sgr 7, □), ‘P38F70’ (sgr 8, ▽) and ‘P38G43’ (sgr 9, ○) maize hybrids grown with 0 (open symbols) or 270 (closed symbols) kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.....195
- Appendix 4: Total leaf area (cm²) per plant at 800 °C.d of hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.....195
- Appendix 5: Mean N content (kg ha⁻¹) for total crop (black), kernels (red), stalk (dark green), and leaves (pink) against accumulated thermal time (°C.d) after emergence in irrigated crops of ‘P38V12’ (sgr 7) (a and b) and ‘P38F70’ (sgr 8) (c and d), grown with 270 (solid symbols) or 0 kg N ha⁻¹ (open symbols) at Lincoln University, New Zealand, during 2008. The solid arrow represents 7 days after silking (800 °C.d) and the dotted physiological maturity (1470 °C.d).....196
- Appendix 6: SPAD readings (SPAD units per leaf) of the lower leaves at 800 °C.d after emergence in hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008..197
- Appendix 7: Total crop N (kg ha⁻¹) 7 days after silking (800 °C.d) in hybrid maize grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.....197

Appendix 8: Proportion of intercepted photosynthetically active radiation versus green area index measurements obtained from the SunScan (open symbols) and leaf area meter (closed symbols) in maize hybrids grown at Lincoln University, New Zealand, during 2009. The solid line represents the fitted regression $y = 0.98(1 - e^{-0.74x})$, $R^2 = 0.99$198

Appendix 9: Calculated versus measured leaf area (cm²) in ‘P39K38’ (sgr 6, ◇) and ‘P38G43’ (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009.....199

Abbreviations

Abbreviation	Description	Units
a.s.l	Altitude (above sea level)	m
b_0	Intercept used to calculate the base temperature	-
b_1	Slope used to calculate the thermal time requirement	-
CRM	Silage comparative maturity	-
Dc	Critical deficit	mm
DUR	Duration of linear growth	°C.d
E_T	Transpiration	mm
E_S	Soil evaporation	mm
GAI	Green area index	$m^2 m^{-2}$
iPAR	Intercepted photosynthetically active radiation	$MJ m^{-2}$
iPAR _d	Daily iPAR	$MJ m^{-2}$
HI	Harvest index	-
I	Irradiance at a point in the canopy	-
I_0	Irradiance above the canopy	-
IRGA	Infra red gas analyzer	-
k	Extinction coefficient	-
kpar	Extinction coefficient for PAR	-
ks	Extinction coefficient for total solar radiation	-
LHCII	Light harvesting complex II	-
LAI	Leaf area index	$m^2 m^{-2}$
LTM	Long term mean	-
N_{oa}	Organic nitrogen concentration	$g N m^{-2}$
NIR	Near infra red spectroscopy	-
NHI	Nitrogen harvest index	%
PAR	Photosynthetically active radiation	$MJ m^{-2}$

Phyllochron _(tip)	Interval between the appearance of successive leaf tips	°C.d
Phyllochron _(ligule)	Interval between the appearance of successive fully expanded leaves	°C.d
P _{max}	Maximum gross photosynthesis	μmol CO ₂ m ⁻² s ⁻¹
PPFD	Photosynthetic photon flux density	μmol m ⁻² s ⁻¹
PSII	Photosystem II	-
PSMD _{max}	Maximum potential soil moisture deficit	mm
Q	Quantity of solar radiation received	MJ m ⁻²
RUE	Radiation use efficiency	g dry matter MJ ⁻¹
<i>See2β</i>	Senescence retarding associated gene	-
sgr	Stay-green rating	-
SLN	Specific leaf nitrogen concentration	g N m ⁻²
SPAD	Soil and Plant Analyzer Development	-
T _b	Base temperature	°C
TDR	Time Domain Reflectometry	-
T _{max}	Maximum temperature	°C
T _{opt}	Optimum temperature	°C
Tt	Thermal time	°C.d
Y	Total dry matter yield	kg or t ha ⁻¹
φ	Volumetric extensibility of the cell wall	-
γ	Yield threshold pressure	-
τ	Fraction of PAR intercepted	-
β	Fraction of PAR transmitted	-
φ	Daily incident PAR	MJ m ⁻²
Θ	Proportion of ground cover	-
α	Soil diffusivity constant	mms ^{-1/2}

Chapter 1

General Introduction

1.1 Forage maize in New Zealand farming systems

The dairy industry is New Zealand's major export earner with total revenue projected to be NZ\$ 11.9 billion in 2012 (DairyNZ 2010). It has experienced phenomenal growth over the last 10 years, particularly in Canterbury (Moot *et al.* 2010), where the average herd number has increased from 450 to 730 animals, with the stocking rate at an all time high of 3.3 animals per hectare (DairyNZ 2010). This has exerted pressure on stock feed with an increased demand for high quality feed to supplement the intake of ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) pasture (Valentine & Kemp 2007). Maize (*Zea mays* L.) silage has been identified as a suitable rotational crop because of its high dry matter yield (Moot *et al.* 2007) associated with a high radiation use efficiency (RUE) (Sinclair & Muchow 1999) and metabolisable energy (ME) content of 10.3-11.3 MJ per kg of dry matter (Millner *et al.* 2005). Maize silage may also help to mitigate some of the environmental issues associated with dairy farming and dilute the high protein content of pasture (Densley *et al.* 2010).

In the cool temperate climate of New Zealand, maize production is constrained by the growth duration which is limited by cool spring soil temperatures and early frost in autumn (Wilson *et al.* 1994). Further, the high evapotranspiration in mid to late summer can result in moisture stress which hastens leaf senescence, and reduces seasonal accumulated dry matter (Stone *et al.* 2001a; Stone *et al.* 2001b) in many regions. The decline in its RUE during grain filling as a result of N remobilization also lowers its potential productivity (Sinclair & Muchow 1999). Consequently, alternative options to increase maize productivity have been explored. The 'stay-green' trait has proved attractive because of its potential to mitigate some of the above constraints (Borrell & Hammer 2000; Rajcan & Tollenaar 1999a).

1.2 'Stay-green' trait

'Stay-green' is a characteristic exhibited in certain plant species where the plant's normal process of senescence is delayed (Thomas & Howarth 2000). Although the physiological mechanism(s) that underlie the trait are unclear (Donnison *et al.* 2007; Hortensteiner 2009),

the recent identification of a ‘stay-green’ gene will advance the understanding of this phenomenon (Barry 2009). It is associated with late season stalk health, and characterised by increased lodging resistance (Wilkinson & Hill 2003) and delayed leaf senescence (Thomas & Smart 1993). The ability of ‘stay-green’ crops to delay senescence of their leaves has elicited interest because of the potential to intercept more solar radiation and increase plant productivity (Hortensteiner 2009). Furthermore, this ability also provides a prolonged harvest window for silage preparation (Havilah & Kaiser 1994).

In both maize and sorghum, the ‘stay-green’ trait has also been linked with increased dry matter productivity under water stress (Borrell *et al.* 2000b; Rivero *et al.* 2007). With global trends indicating a drier future environment (Salinger *et al.* 2005), this trait warrants further investigation. Studies have also shown a close relationship between N remobilization and leaf senescence (Borrell *et al.* 2001; Thomas *et al.* 2002). Elucidation of the mechanism behind this trait will provide an understanding of the link between leaf senescence and N remobilisation. Furthermore, ‘stay-green’ hybrids may offer the opportunity to intercept more solar radiation during grain filling and increase dry matter production (Rajcan & Tollenaar 1999a). However, to date the yield benefits remain unclear in New Zealand.

1.3 Dry matter accumulation and grain yield

1.3.1 Environmental variables

The influence of environmental variables on crop productivity has been examined extensively because the environment exerts the greatest effect on dry matter accumulation (Monteith 1977). It is difficult to assess independently the impact of a particular environmental factor on crop performance because under field conditions the variables are confounded (e.g. temperature and solar radiation) (Muchow *et al.* 1990). Hay and Porter (2006) presented a quantitative framework which encapsulates the fundamental role of the environment on crop growth and development (Equation 1.1). In agreement with both Tollenaar and Dwyer (1999) and Stockle and Kemanian (2009), this framework shows that the total quantity of solar radiation received (Q), the fraction intercepted by the canopy (I) and its efficiency of conversion into dry matter (RUE) are the predominant influences on total dry matter (Y) accumulation.

$$Y = Q * I * RUE$$

Equation 1.1

Figure 1.1 shows the mean monthly solar radiation (MJ m^{-2}), maximum and mean temperature ($^{\circ}\text{C}$) recorded at Broadfields meteorological station, Canterbury, New Zealand during a typical maize growing season (September-April). As maximum solar radiation is received between November and January, this period should be synchronized with maximum GAI (green area index) for maximum dry matter accumulation (Stone *et al.* 1999).

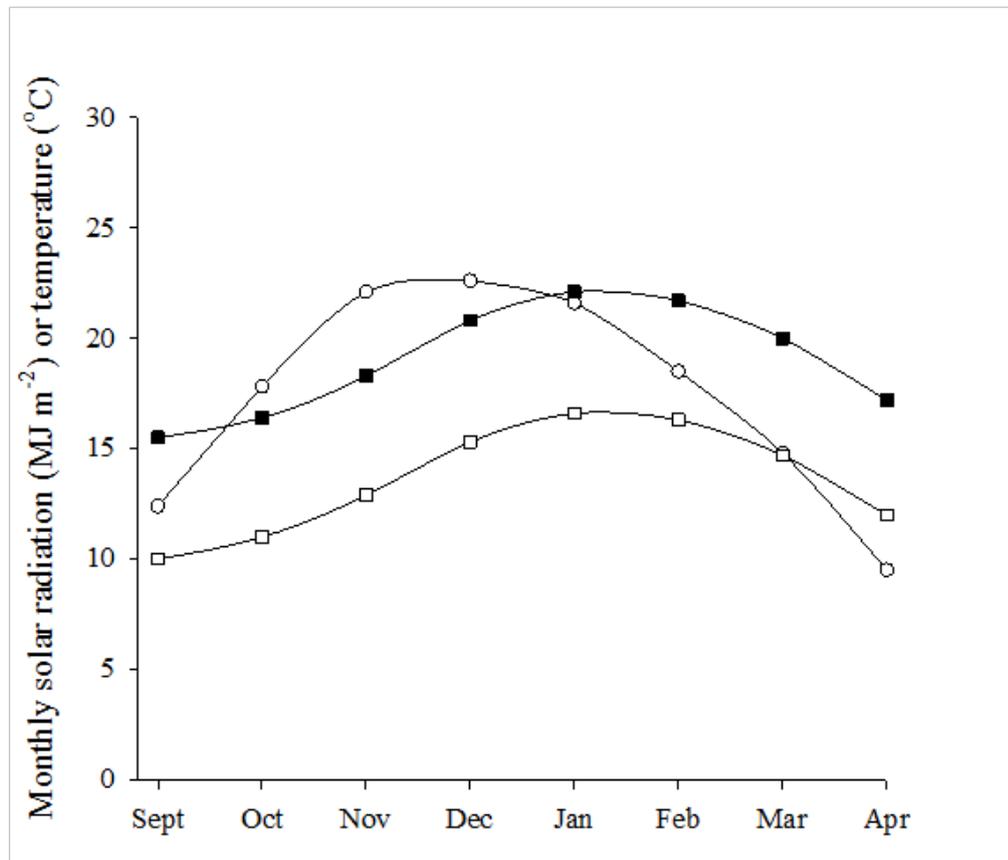


Figure 1.1: Mean monthly solar radiation (MJ m^{-2}) (○), maximum (■) and mean (□) temperature ($^{\circ}\text{C}$) recorded at Broadfields meteorological station, Canterbury, New Zealand, during the 2000-2010 maize growing seasons.

Temperature strongly influences crop development and several authors have reported a linear relationship between the rate of development and temperature above a critical threshold (base temperature) (Angus *et al.* 1981; Moot *et al.* 2000; Warrington & Kanemasu 1983a). In maize, a base temperature of 8°C is commonly used (Birch *et al.* 1998a; Birch *et al.* 1999). However, in the cool temperate environment of Canterbury, New Zealand, where the mean temperature during the maize growing season is $\sim 15^{\circ}\text{C}$ (Wilson & Salinger 1994), maize development responds to temperatures below those often reported (Wilson *et al.* 1995).

1.3.2 Physiological response to N and water

Both N and water influence crop growth (Lawlor 2002; Stone *et al.* 2001b). It is only under severe N deficiency that crop development is affected (Muchow 1988). Effects of N deficiency on growth are manifest through a reduction in the rate of cell division and expansion, and consequently reduced leaf area (Vos *et al.* 2005). Apart from canopy development, N also influences the rate of canopy photosynthesis by directly affecting the quantity of catalytic enzymes (e.g. Rubisco) (Lawlor 2002) and indirectly through a reduced leaf area for solar radiation interception (Muchow & Davies 1988).

Because of its C₄ photosynthetic pathway, typical RUE for maize ranges between 1.6-1.7 g of dry matter per MJ iPAR (Sinclair & Horie 1989). However, these relatively high RUEs are not sustained throughout the growing season. RUE eventually declines to 1.2 g dry matter per MJ iPAR after silking, due to a reduction in SLN concentration (g m⁻²), as a result of increased N remobilization to the grain (Muchow 1988; Muchow *et al.* 1990).

Due to the high mid to late summer temperatures and low rainfall experienced in the Canterbury region (Figure 1.1), maize crops are irrigated to avoid water stress. Water stress can limit N uptake (Dale 1982; Li *et al.* 2006), hastens leaf senescence and reduces the duration of grain filling (Muchow & Carberry 1989; Stone *et al.* 2001b). Earlier, during vegetative growth, water deficits reduce the rate of leaf expansion, and potential leaf area is not attained (Muchow & Carberry 1989). Consequently solar radiation interception and dry matter accumulation are lowered (Jamieson *et al.* 1995b).

1.4 Aims and objectives

Based on this overview, this study aims to understand the physiological basis of the 'stay-green' trait in maize, at the plant-whole crop level, and quantify any resultant contributions to yield. The specific objectives are:

- Quantify any contributions to dry matter and grain yield accruing from the 'stay-green' trait.
- Examine how different N and moisture levels influence the response of maize hybrids of different 'stay-green' rating (sgr) (6-9).

- Investigate the crop physiological mechanisms of variation in the 'stay-green' rating among these hybrids.

1.4.1 Thesis structure

This thesis consists of 8 chapters as illustrated in Figure 1.2. These are the General Introduction (Chapter 1), Review of Literature (Chapter 2), Materials and Methods (Chapter 3), Experiment 1 (Chapters 4-6) and Experiment 2 (Chapter 7) results, and a General Discussion (Chapter 8).

Chapter 1 provides an overview of the role of maize silage in New Zealand farming systems and the impact of environmental conditions on its growth and development. In Chapter 2, literature on maize growth and development is reviewed in the context of the potential mechanisms for increased dry matter and yield with the incorporation of the 'stay-green' trait. Here, growth processes with a direct impact on dry matter accumulation and yield in a maize crop are considered. Chapter 3 outlines the two experiments whose data are presented in Chapters 4-7.

Chapter 4 presents data on dry matter accumulation and partitioning as influenced by the hybrid 'stay-green' rating, fertiliser N and moisture availability. In Chapter 5, the factors which determine the quantity of solar radiation intercepted are examined with specific reference to the role of the hybrid 'stay-green' trait. Consequently the absorbed solar radiation is utilised to describe dry matter accumulation. Chapter 6 presents data on the efficiency of utilization of this absorbed solar radiation together with its major determinants. In addition to data on gross photosynthesis, Chapter 7 presents data similar to those found in Chapters 4-6 from Experiment 2 measurements. Chapter 8 discusses the general implications of the 'stay-green' trait on maize growth and development with reference to the outlined objectives, and highlights the scope for further research.

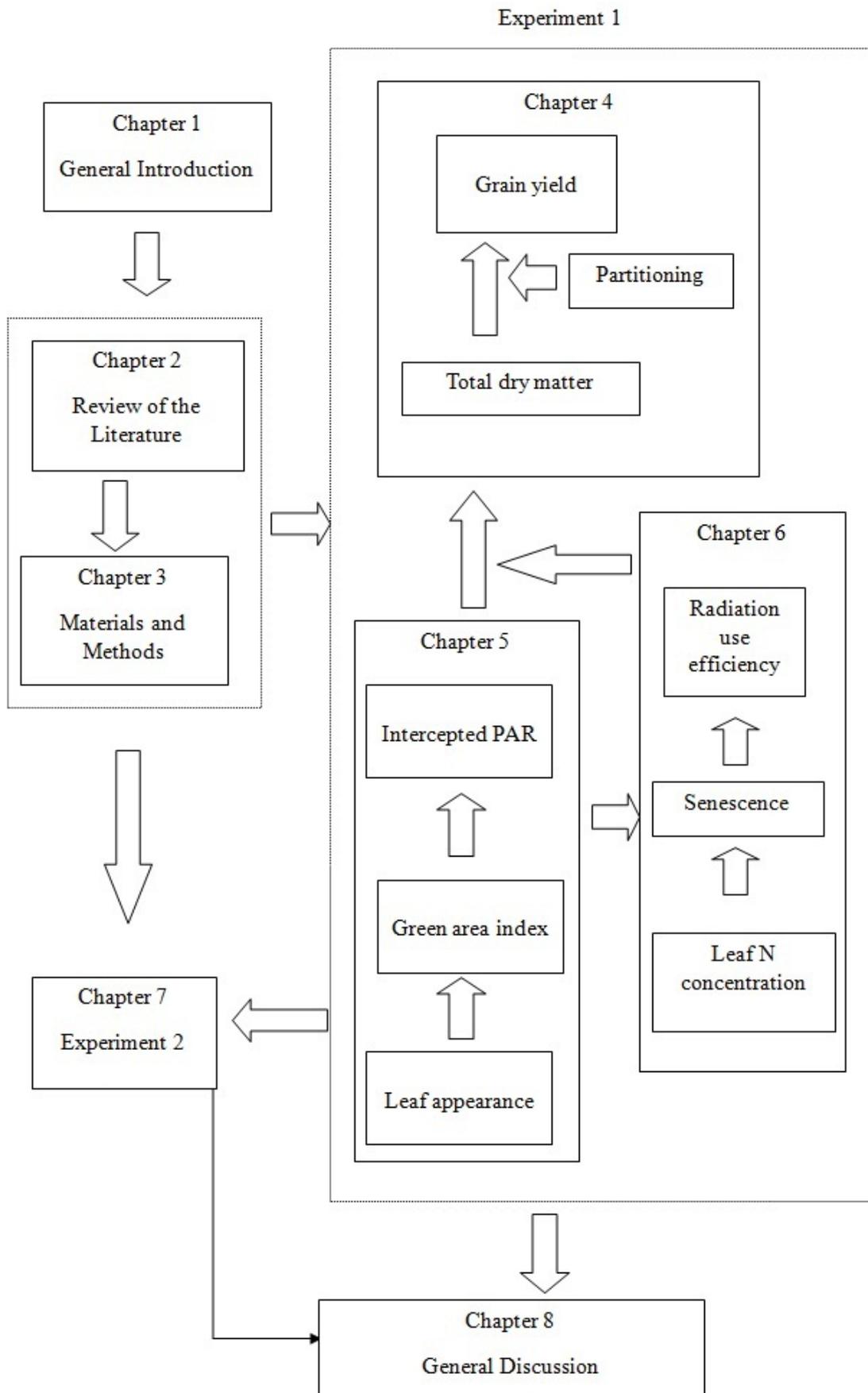


Figure 1.2: Outline of thesis structure.

Chapter 2

Review of the Literature

2.1 Introduction

This literature review is structured to reflect the growth and development of a maize crop. It covers the key stages in the development of the crop, from germination and emergence through to senescence and physiological maturity. Key biophysical factors that influence growth and development are considered with emphasis on the 'stay-green' trait and its potential to influence growth and development especially under conditions of limited soil moisture and nitrogen (N) availability.

The review initially outlines thermal time as the central basis used to quantify development in this study. Vegetative growth is then discussed in relation to temperature, availability of N and moisture which are considered critical because of their role in the development of leaf area and canopy expansion. Canopy development is considered in the context of determining the rate of biomass increase through its influence on the amount of iPAR. Intercepted PAR then drives photosynthetic activity to synthesize dry matter which is partitioned for maintenance, growth and yield. Finally, during the reproductive growth phase, a proportion of the dry matter and N are recycled for grain growth, and plant structures senesce. In this review, leaf senescence is given particular consideration because of the inherent potential influence of the 'stay-green' trait which may also influence canopy development, iPAR and its efficiency of utilization, and hence dry matter accumulation and grain yield.

2.2 Thermal time (Tt)

Temperature influences biomass accumulation through its integral role in crop development processes (Bonhomme 2000a; Coelho & Dale 1980). Based on this, Russelle *et al.* (1984) suggested the use of a temperature index in growth functions. They argued this would minimise the effect of temperature variation and permit a more meaningful treatment comparison among experiments than that based on time. Moreover, the duration between two phenological stages tends to be more stable when thermal time is used as compared to days (Hay & Porter 2006).

The time based concept of thermal time (Tt) is therefore commonly used to derive quantitative descriptions for the relationship between plant development rate and temperature (Bonhomme 2000a). The validity of these descriptions is based on three assumptions. First, that all processes involved in development are temperature dependant with one process limiting growth (Whisler *et al.* 1986). Secondly, the temperature response of the limiting process is indicative of the temperature response of overall crop development (Whisler *et al.* 1986). Lastly, the rate of the limiting process is proportional to mean temperature within given temperature limits (Muchow *et al.* 1990; Warrington & Kanemasu 1983b). Therefore, assuming a linear approximation of a sigmoidal response (Tollenaar *et al.* 1979), development rate increases linearly above a base temperature (T_b) to an optimum temperature (T_{opt}) before declining linearly to zero when the maximum temperature (T_{max}) is attained (Kiniry *et al.* 1991).

2.2.1 Theoretical framework

A clear understanding of the theoretical basis of the thermal time concept is necessary to justify its use to calculate or predict the duration of development. The rate of development is directly proportional to mean temperature (Ritchie & NeSmith 1991) as given in Equation 2.1.

$$\frac{\delta R}{\delta t} \propto T \quad \text{Equation 2.1}$$

Where, $\frac{\delta R}{\delta t}$ is the rate of the process under consideration, R the morphological state e.g. leaf appearance and T is the mean daily temperature. Since the rate of development is reduced by a threshold temperature (T_b), then Equation 2.1 can be modified to yield Equation 2.2.

$$\frac{\delta R}{\delta t} = a(T - T_b) \quad \text{Equation 2.2}$$

Where a is a developmental rate constant and T_b is the base temperature. Generally, when $T_b > T$, $a = 0$ and no development occurs (Thornley & France 2007).

The reciprocal of the duration of development is also linearly related to temperature (Tardieu *et al.* 1999), hence,

$$\frac{1}{d} = a(T - T_b) \quad \text{Equation 2.3}$$

Where d is the duration in days.

Since the duration of a developmental phase is the product of the rate of development and time (Bonhomme 2000a), Equation 2.2 can be modified as follows:

$$\frac{\delta R}{\delta t} \delta t = a(T - T_b) \delta t \quad \text{Equation 2.4}$$

Summing up the individual time steps to derive the duration of development for the phase yields the following equation:

$$R = a \int_0^d (T - T_b) \delta t \quad \text{Equation 2.5}$$

Thus, on a daily time scale the degree.day ($^{\circ}\text{C}\cdot\text{d}$) sum is a constant equal to $\frac{1}{a}$ (Bonhomme 2000a).

2.3 Vegetative growth and development

Phenological development is defined as the initiation, differentiation, expansion and loss of plant structures (Bonhomme 2000a; Hay & Porter 2006). It is under both genotypic and environmental influence (Birch *et al.* 2003), and consists of a sequence of discrete phases each lasting a definite period of time (Thornley & France 2007). Germination, vegetative growth, reproductive growth, physiological maturity (Angus *et al.* 1981) and senescence (Thomas & Stoddart 1980) are the five stages of development of an annual crop. Temperature exerts the greatest influence on these processes (Warrington & Kanemasu 1983a, 1983b), but soil moisture (Forcella *et al.* 2000) and severe nitrogen deficiency (Muchow 1988) can also affect plant development. The effect of photoperiod on plant development is variable across species and cultivars (Warrington & Kanemasu 1983a; Wilson *et al.* 1995).

Growth is an irreversible increase in plant dry weight (Hunt 1982; Richards 1969), which is closely linked with development. However, while plant development can occur with or without growth (Angus *et al.* 1981; Hay & Porter 2006), growth is maximized when the largest quantity of radiation is intercepted by the plant in each development phase provided temperatures are above T_b (Angus *et al.* 1981; Stone *et al.* 1999).

2.3.1 Germination and emergence

At physiological maturity five embryonic leaves already exist within the maize seed (Duncan 1975) and metabolic activity commences when the seed imbibes sufficient water to fully hydrate the cells (Hanway 1963). The end of the germination phase is marked by the emergence of the radicle, while the extension of the mesocotyl and the coleoptile above ground indicates emergence (Blacklow 1973). Because emergence is a continuous process dependent on a number of soil environmental factors (Miedema 1982), it cannot effectively be represented by a simple function such as the linear function of time suggested by Blacklow (1972). Temperature has been shown to exert its greatest influence on the duration of the pre-emergence period (Angus *et al.* 1981) and model analysis has shown a linear relationship between temperature and pre-emergent growth rates in maize (Weaich *et al.* 1996), peanut (Awal & Ikeda 2002), legume cover crops (Qi *et al.* 1999) and several temperate pasture species (Moot *et al.* 2000).

Although germination is not evenly distributed around 50% emergence (Forcella *et al.* 2000), the duration to 50% emergence is often used to denote the emergence date in temperature dependent growth models (Angus *et al.* 1981). Within the suboptimal temperature range (8°C-34°C) for maize development (Muchow *et al.* 1990), the inverse of the duration to 50% emergence ($1/t_{50\%}$) has been found to be a linear function of temperature (Warrington & Kanemasu 1983a). Linear regression models fitted to describe this relationship are usually of the form suggested by Angus *et al.* (1981) as given in Equation 2.6. From this linear relationship, the intercept (b_0) and slope (b_1) are used to calculate the base temperature (T_b) and the thermal time requirement for this physiological phase as shown by Equation 2.7 (Qi *et al.* 1999). For maize, a base temperature of 8 °C is commonly used (Muchow *et al.* 1990). Under controlled environment conditions, Warrington and Kanemasu (1983a), report a requirement of 62.5 °C.d for the germination and emergence phase in maize with a base temperature of 9 °C.

$$R = b_o + b_1 t \quad \text{Equation 2.6}$$

Where R is the rate of emergence and t is the temperature.

$$T_b = \frac{-b_o}{b_1}, Tt = \frac{1}{b_1} \quad \text{Equation 2.7}$$

2.3.2 Leaf initiation and appearance rate

Leaf initiation occurs on the leaf primordia at the top dome of vegetative shoots (Dale 1982). As leaf initials appear at a constant thermal rate from emergence until the onset of reproductive growth (Warrington & Kanemasu 1983b), the rate of leaf appearance can be considered as the visible representation of the average relative growth rate (Gmelig Meyling 1973), and a linear expression for the rate of leaf appearance against mean temperature can be derived (Carberry *et al.* 1993; Muchow & Carberry 1989).

A leaf tip is considered to have appeared when it is clearly visible in the whorl of the plant (Fletcher *et al.* 2008a). The slope of the linear regression between the numbers of emerged leaf tips against thermal time when constrained to intercept the y-axis at 1 is taken as the rate of leaf appearance (Fletcher 2005). Usually the slope of the relationship between leaf appearance rates and accumulated thermal time does not intercept the axes at the origin because the first leaf is generally well developed at germination due to its reliance on seed reserves (Gmelig Meyling 1973). A leaf is considered fully expanded when its ligule is visible above the whorl of the preceding leaf (Muchow & Carberry 1989). Westgate *et al.* (2004) have reported that in maize, ~20 °C.d was required for the differentiation of one new leaf while ~40 °C.d was necessary for the appearance of a new leaf tip. These are close to the 45.7 °C.d per leaf observed by Vos *et al.* (2005) in a maize crop grown under controlled environment conditions and 45 °C.d recorded by Hesketh and Warrington (1989). The variation in thermal time requirements reported here can be attributed to genetic differences amongst the hybrids used (Wilson *et al.* 1995).

Due to the shorter duration required for the differentiation of leaf initials in maize, most have appeared by 5-6 weeks after sowing and accumulate in the shoot apex (Fletcher *et al.* 2004). Warrington and Kanemasu (1983b) have reported a constant rate of leaf appearance of the

first 12 leaves in two maize cultivars grown in a controlled environment under a variety of temperature regimes. However, the last three leaves emerged at a faster rate because they were smaller in size (Tardieu *et al.* 1999). This distorts the linear relationship between number of emerged leaf tips or fully expanded leaves and thermal time. Differential N treatments have shown no effect on the rates of appearance of the leaf tips and ligules in maize (Vos *et al.* 2005). In contrast, under conditions of severe N limitation, the rate of leaf appearance in both maize and sorghum has been shown to respond to N availability (Muchow 1988).

Conventionally, the rate of development increases linearly above a base temperature (T_b) to an optimum temperature (T_{opt}) before declining linearly to zero when the maximum temperature (T_{max}) is attained (Section 2.2). However, there is a need to re-examine this relationship in light of the reported limited range of temperature in which the linearity between development rate and temperature holds (Bonhomme 2000a). Indeed, at low temperature the observed linearity between thermal time and leaf appearance rate does not hold (Tollenaar *et al.* 1979) and a more curvilinear response is often observed (Hesketh & Warrington 1989). Further, Bollero *et al.* (1996) have reported that under exceptionally warm or cool conditions, growing degree days accumulation using a base temperature of 10 °C was inadequate to predict maize development. These observations have led to modification of the approach in the accumulation of thermal time between 0 °C and 18 °C in temperate cool environments during the emergence to silking interval in maize (Figure 2.1).

In most models that simulate radiation receipts and biomass production from leaf area, accurate prediction of the appearance of leaf tips and fully expanded leaves is crucial (Stone *et al.* 1999) to the accurate simulation of biomass. To model leaf initiation, frequent dissections of the top dome are necessary (Warrington & Kanemasu 1983b). This is both laborious and time consuming and the frequency of leaf tip appearance is often used to represent development during this phenological phase (Thiagarajah & Hunt 1982).

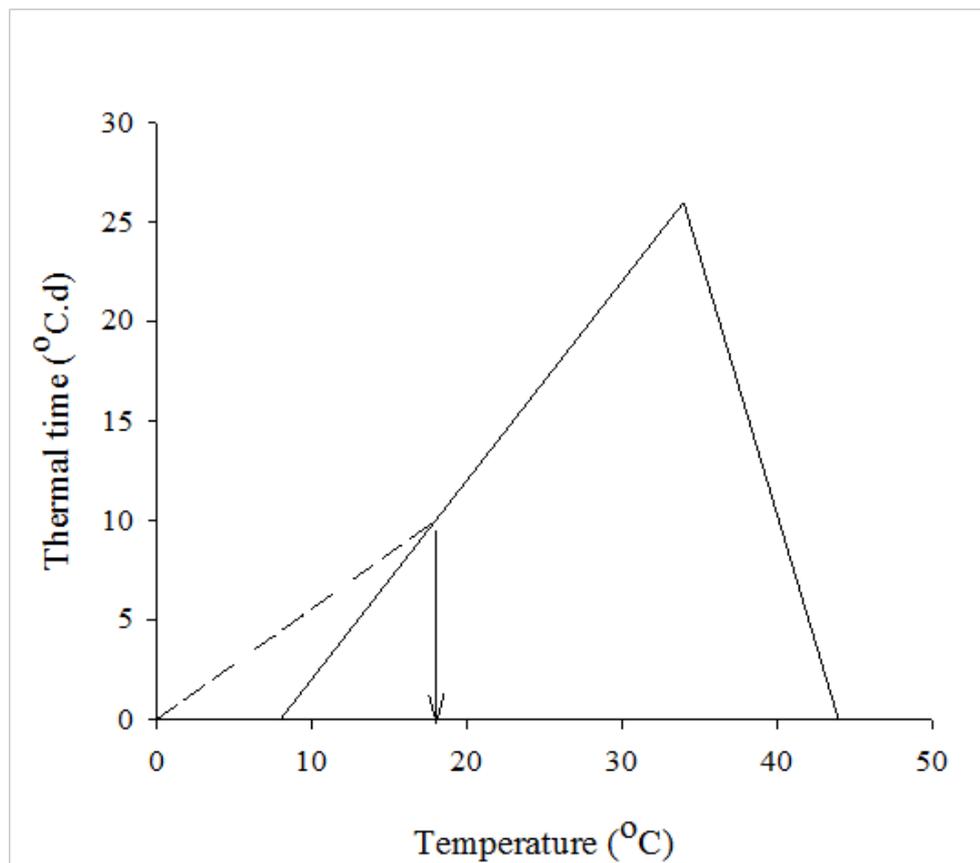


Figure 2.1: The modified thermal time response to temperature showing the linear response between 0 and 18 °C (dotted line). Reproduced with permission from Wilson *et al.* 1995.

2.3.3 Canopy development

2.3.3.1 Green area

Exchanges between the biophysical environment and the plant occur mostly via the leaf surface, hence the leaf area index (LAI) is an important variable that determines canopy structure and productivity (Dwyer & Stewart 1986b; Eriksson *et al.* 2005). The development and maintenance of green area influences the amount of solar radiation intercepted (Muchow & Carberry 1989) and therefore biomass accumulation (Muchow & Davies 1988). The proportion of total iPAR (intercepted photosynthetically active radiation) is a function of the LAI and the canopy extinction coefficient (k) (Tollenaar & Dwyer 1999).

When conditions for growth are non-limiting, temperature exerts the greatest influence on canopy development in maize (Wilson *et al.* 1995), because leaf expansion results from a number of biochemical reactions usually controlled by temperature (Bonhomme 2000a). It influences the rate of leaf tip appearance and the duration of leaf expansion (Warrington &

Kanemasu 1983b). Stone *et al.* (1999), reported a 21% reduction in dry matter in maize when grown at a mean soil temperature of 18.3 °C compared with 25.2 °C. They attributed this difference to an enhanced rate of leaf tip appearance and full expansion, leading to earlier canopy closure. In cool temperate environments, low temperature will therefore prolong the growth duration (Wilson *et al.* 1995) and distort the synchrony between the time of peak radiation interception and peak radiation occurrence (Stone *et al.* 1999). However, Muchow *et al.* (1990) showed that cooler temperatures would delay maturity thereby maximising radiation receipts and yield.

Apart from temperature which controls the rate of leaf appearance, the light environment plays an important role in the regulation of morphogenesis and the retention of chlorophyll in plants (Canfield *et al.* 1995). Due to the spectral properties of chlorophyll, the quality of light received by shaded leaves is often deprived of the red (660 nm) and blue (400-450 nm) photons (Causin *et al.* 2009), and thus contains less PAR and a lower red: far red ratio (Gan & Amasino 1997). Shaded leaves therefore lose chlorophyll and senesce faster when compared with those fully illuminated (Causin *et al.* 2006; Causin *et al.* 2009). However, in the soybean 'stay-green' mutants *cytG* and *Gd1d2*, Canfield *et al.* (1995) observed a preservation of the light harvesting complex II (LHCII) components during seedling germination in the dark. Further, some limited photosynthetic activity was also recorded (Canfield *et al.* 1995). Similarly, in 'stay-green' sorghum, the retention of chloroplast proteins late in senescence has been linked with photosynthetic activity (Borrell *et al.* 2001). Based on these observations, it can be postulated that crops with the 'stay-green' trait may retain chlorophyll and some photosynthetic activity in their lower leaves when shaded as a consequence of canopy closure.

2.3.3.2 Nitrogen

Nitrogen (N) supply presents a major restriction to crop productivity with most growth parameters being limited by its deficiency (Godwin & Jones 1991). As an essential constituent of the enzymes that regulate photosynthesis, nucleic acid and chlorophyll (Hopkins & Huner 2004), its influence is mainly on leaf area expansion and leaf senescence (Li *et al.* 2006). Nitrogen for plant growth can be derived directly from the soil through absorption of nitrate or ammonium or remobilised from older plant parts (Ta & Weiland 1992). N export from the leaf may commence shortly after the completion of leaf expansion

(Vos *et al.* 2005). However, SLN concentration (g m^{-2}) declines markedly during reproductive growth as a result of N remobilisation (Wolfe *et al.* 1988a).

Environmental conditions and/ or the genotype determines the proportion of grain N derived from remobilisation (Ta & Weiland 1992). In maize, between 60-85% of pre-anthesis N is remobilized, with 45% derived from the leaves (Ta & Weiland 1992). The export of N from the leaves reduces leaf photosynthetic rates and RUE (Sinclair & Horie 1989), and eventually leads to senescence (Nooden *et al.* 1997). To alleviate the impact of N remobilisation on photosynthetic capacity, plants need to sustain N uptake during grain filling. However, root growth declines at the onset of reproductive growth as resources are directed towards grain development (Rajcan & Tollenaar 1999b; Weiner 2004).

Rajcan and Tollenaar (1999a) report that leaf longevity in a recent 'stay-green' maize hybrid was enhanced by an increase in soil N uptake during grain filling. They attributed this observation to the preferential allocation of carbohydrates to the lower stem during grain filling which aided soil N sequestration (Rajcan & Tollenaar 1999a). Subsequently, higher rates of dry matter accumulation were achieved and more carbohydrates were allocated for further soil N uptake (Rajcan & Tollenaar 1999b). Similar observations have been reported in 'stay-green' sorghum (Borrell *et al.* 2001; Borrell & Hammer 2000) and a non-yellowing mutant of the pasture grass *Festuca pratensis* (Hauck *et al.* 1997). It therefore seems possible to delay leaf senescence and enhance dry matter accumulation concurrently as demonstrated in these 'stay-green' plants.

2.3.3.3 Water deficits

The availability of water constitutes a major challenge to agricultural productivity as soil moisture deficits affect growth directly through its effects on cellular biochemical reactions (Wolfe *et al.* 1988a) and reduction in leaf expansion through loss of turgor pressure (Taiz & Zeiger 2002). It will also indirectly influence soil N dynamics (Li *et al.* 2006). Water deficits will therefore affect leaf expansion, photosynthesis and the translocation of metabolites (Hodges 1991). Subsequently, it will also influence protein synthesis as N uptake declines with increasing water stress (Dale 1982). This close relationship between water uptake and cell expansion occurs because cell growth is a function of the gross extensibility of a cell and

the turgor pressure above a minimum threshold (Tardieu *et al.* 1999). The dependence of leaf growth on water availability can be illustrated using the Lockhart equation (Equation 2.8) (Fitter & Hay 2002).

$$\frac{1}{V} \cdot \frac{dV}{dt} = \phi(P - \gamma) \quad \text{Equation 2.8}$$

Where V is the cell volume, ϕ is the volumetric extensibility of the cell wall, P is the cell turgor pressure and γ is the yield threshold pressure.

From the above relationship, cell expansion which leads to leaf expansion occurs only when $\gamma < P$ and ceases when P falls below γ , which usually occurs when the leaf water potential is in the range of -0.2 to -0.3 MPa (Hay & Porter 2006). Photosynthesis is less sensitive to decreases in turgor pressure than leaf expansion (Taiz & Zeiger 2002). This is consistent with the data illustrated in Figure 2.2 for the sixth leaf blade of a 4-5 week old maize plant experiencing increasing water stress under constant environmental conditions. Relative leaf expansion rate per 24 h period declined from 0.20 to about 0.02 as the leaf water potential dropped from -0.2 to -0.4 MPa. However, a leaf water potential of -0.4 MPa had relatively no effect on the rate of photosynthesis (Boyer 1970).

The exact mechanism through which water stress affects photosynthesis is unclear (Lawlor 2001). However, reductions in the transpirational water loss and carbon dioxide (CO₂) exchange have been suggested as the probable causes (Keenan *et al.* 2010). The rate of transpiration is governed by the evaporative demand of the atmosphere which is modulated by the solar radiation flux population (Fitter & Hay 2002). As transpiration rate increases, leaf water potential and turgor pressure decrease (Whisler *et al.* 1986). This decrease in turgor pressure influences CO₂ exchange rate through increased stomatal resistance to water vapour exchange (Edwards & Walker 1983). Low to moderate water stress levels have also been reported to reduce the activity of Rubisco, resulting in a decline in both net and gross photosynthesis (Lawlor 2001).

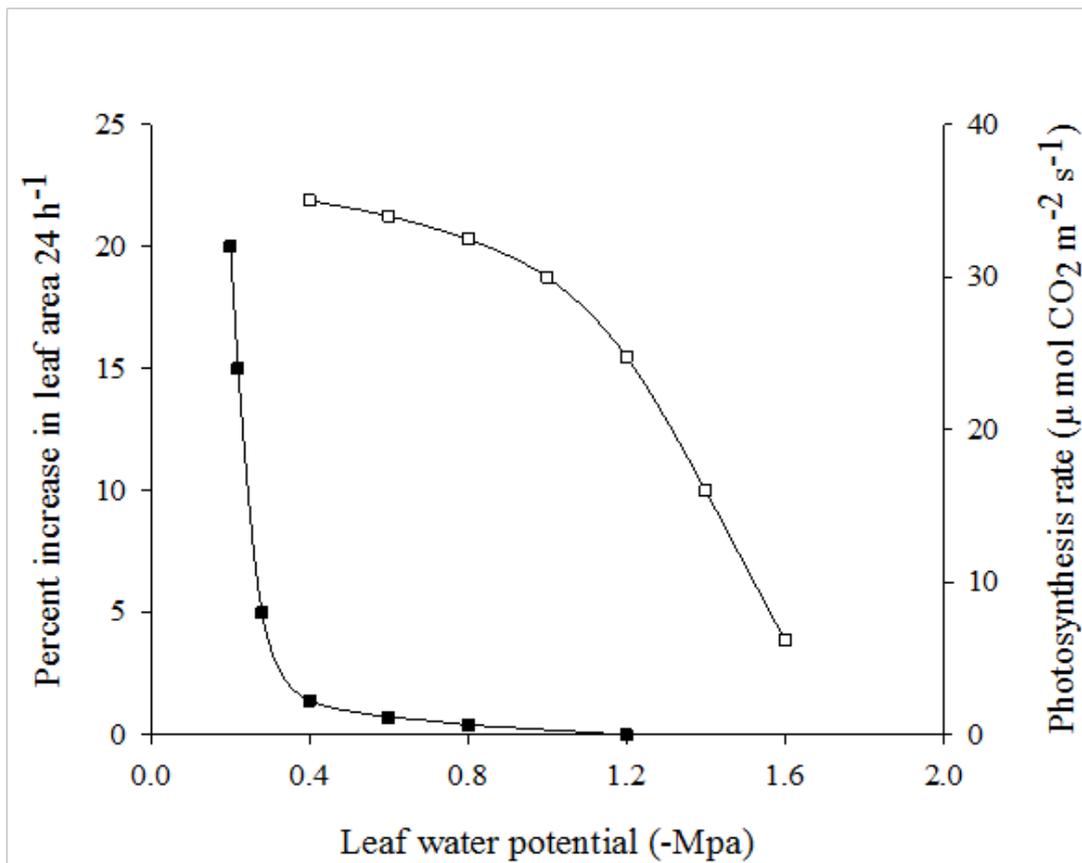


Figure 2.2: Effects of water stress on net photosynthesis (□) and leaf expansion rate (■) of the sixth leaf blade of a 4-5 week old maize plant grown under controlled environment conditions. Adapted with permission from Boyer, 1970.

Leaf area development is therefore affected by water stress mainly through its effects on cell enlargement (Begg & Turner 1976). Muchow and Carberry (1989) have reported that water stress during the vegetative growth phase mainly affected leaf appearance rate and leaf size. Consequently, mild to severe water stress will result in the development of smaller leaves and less extensive canopies, which intercept lesser amounts of PAR, leading to reduced potential for dry matter accumulation (Hay & Porter 2006). In contrast, terminal water stress mainly hastens leaf senescence, and reduces the period of effective solar radiation interception (Wolfe *et al.* 1988b).

Modelled global weather scenarios predict occurrence of more frequent droughts in the future (Salinger *et al.* 2005), which will necessitate the enhancement of drought tolerance traits. Drought avoidance strategies such as stomatal closure, allocation of more resources into the roots and reduction in canopy size reduce dry matter production (Fitter & Hay 2002). An

alternative approach is to minimize drought induced leaf senescence and increase solar radiation interception. Recent work in transgenic tobacco (*Nicotiana tabaccum cv. SR1*) plants showed that suppression of the drought induced leaf senescence conferred remarkable drought tolerance (Rivero *et al.* 2007). These transgenic plants increased cytokinin production and maintained leaf water potential during drought with minor reductions in yield when 30% of the water available to the control plants was provided (Rivero *et al.* 2007). Cytokinin is a known senescence inhibitor (Hopkins & Huner 2004). With more research, this approach may provide an opportunity to increase yield in environments with limited water supply.

The maintenance of a high SLN concentration (g m^{-2}) under water stress by sorghum with the K19 source of 'stay-green' is also reported to delay senescence and maintain photosynthetic activity (Borrell *et al.* 2001). As a consequence both RUE and transpiration efficiency were enhanced (Borrell *et al.* 2000a), and post anthesis dry matter production was 47% more in the 'stay-green' hybrids compared with the senescent hybrids (Borrell *et al.* 2000b).

Over all, the effects of water deficits on canopy development through reduced leaf expansion and early senescence are more important determinants of dry matter accumulation than the effects on photosynthetic rate as a result of CO_2 exchange (Hay & Porter 2006). However, crops may mitigate the effects of water stress on grain yield through the translocation of a greater proportion of its dry matter reserves. In a glasshouse trial of wheat grown on a limited water supply, Passioura (1976), observed that plant reserves accounted for up to two thirds of the grain dry matter at final harvest. This observation was consistent with the work of Sadras *et al.* (1993) in sunflower (*Helianthus annuus* L.) and Westgate (1994) in maize who have also reported a strong dependence of seed filling on stem assimilate in water stressed plants.

Most of the work on drought tolerance in 'stay-green' hybrids has been reported for sorghum, but there is a need to examine the drought tolerance mechanisms in other C_4 genotypes that exhibit the trait, especially those grown in environments prone to water limitations.

2.3.4 Dry matter accumulation

Close to 80% of the carbon generated through the photosynthetic process in higher plants is utilized in the synthesis of carbohydrates (Huber *et al.* 1992). These photosynthetic products

are either utilized within the leaf, immediately translocated for use in other plant parts or stored (Gordon 1985). Seasonal dry matter accumulation is therefore the integral of the net gain in C (carbon) per unit area (Monteith 1977). It is influenced by the capture and utilization of environmental resources e.g. water, nutrients, CO₂ and light (Tollenaar & Dwyer 1999).

2.3.4.1 Solar radiation interception

The relationship between dry matter accumulation and the solar radiation intercepted has received extensive review (Gallagher & Biscoe 1978; Monteith 1972; Monteith 1977; Sinclair & Muchow 1999) because solar radiation accounts for the greatest proportion of the total energy transfer between plants and the environment (Hanan 1984). Several attempts have established a link between total dry matter accumulation and the amount of PAR (photosynthetically active radiation) intercepted (Monteith 1972; Monteith 1977; Shibles & Weber 1965; Williams *et al.* 1965). PAR is the flux in the 0.4-0.7 μ m wave band of the solar spectrum that initiates the flow of energy required in photosynthesis (Hippes *et al.* 1983; Howell *et al.* 1983). It is almost independent of atmospheric conditions and nearly a constant fraction (~0.5) of solar radiation (Monteith 1972; Szeicz 1974).

Available evidence indicates that the rate of conversion of PAR into dry matter is a conservative quantity and the amount of iPAR is the variable that determines crop growth (Williams *et al.* 1965). During their vegetative growth therefore, crops will accumulate dry matter at rates which are proportional to intercepted radiation (Monteith 1977). Because the rate of conversion of intercepted radiation into dry matter is fairly constant (Gallagher & Biscoe 1978), differences in total dry matter accumulation result from differences in the amount of intercepted radiation (Stone *et al.* 1999).

As indicated in Sections 2.3.3.1-2.3.3.3, under conditions of limited N and water supply, plants with the 'stay-green' trait are anticipated to maintain their leaf area for a longer duration and hence intercept more solar radiation.

2.3.4.2 Extinction coefficient

The distribution of irradiance incident on a leaf surface is not directly proportional to leaf area index because of the mutual shading of leaves (Whisler *et al.* 1986). The extinction coefficient (k), therefore quantifies the modulation by leaf architecture of the attenuation of irradiance (Tollenaar & Dwyer 1999). The rate of attenuation of solar radiation down the canopy is related to leaf area index by the Monsi and Saeki equation (Hay & Porter 2006):

$$I = I_0 e^{-kL} \quad \text{Equation 2.9}$$

Where, I is the irradiance at a point in the canopy above which there is a LAI of L , I_0 is the irradiance above the canopy and k is the extinction coefficient.

From Equation 2.9, the extinction coefficient (k) is given by Equation 2.10.

$$-k = \ln (I/I_0)/L \quad \text{Equation 2.10}$$

In a maize crop, several factors affect canopy architecture (Maddonni *et al.* 2001) and a wide range of values for k is often reported in the literature (Fletcher 2005). However, Tollenaar and Dwyer (1999), report k is relatively stable around midday and values obtained under such conditions range between 0.35 and 0.65 (Stockle & Kemanian 2009). Even then, a small change in k can have a large impact on calculated radiation interception when LAI is small (<3). This is particularly important in Canterbury, where most maize crops typically have low maximum LAI (<4) and the establishment of LAI is very slow and therefore LAI is often less than this. For example, when LAI is 2, then calculated radiation interception would be 0.55 for k of 0.4 but 0.73 for k of 0.65.

2.3.4.3 Photosynthetic rate

Dry matter accumulation is functionally dependent on the capacity of the crop to assimilate CO_2 through photosynthesis (Muchow & Sinclair 1994). This process requires radiant energy for the generation of NADPH (nicotinamide adenine dinucleotide phosphate) and ATP (adenosine triphosphate) necessary for the assimilation of CO_2 into simple carbohydrates. Because radiant energy is particulate and discretely packed into photons (Fitter & Hay 2002), the photosynthetic photon flux population ($\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF) is a more appropriate quantity of irradiance in the description of net CO_2 assimilation rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Maximum

photosynthetic rates (P_{\max}) are usually recorded immediately after final leaf expansion (Andre *et al.* 1978) and in maize ranges between 45-52 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Muchow & Sinclair 1994; Sinclair & Horie 1989; Vos *et al.* 2005). Availability of Rubisco (Grindlay 1997), the regeneration of RuBP (ribulose 1, 5 bis-phosphate) and the CO_2 partial pressure within the leaf may limit photosynthetic capacity (Hay & Porter 2006). To counter the limitations imposed by a low CO_2 concentration level on photosynthetic capacity, C_4 (the four carbon oxaloacetate is the initial product of carboxylation) plants have evolved a mechanism to deliver CO_2 into the Calvin cycle at a higher concentration compared with the C_3 (the three carbon phosphoglyceric acid is the initial product of carboxylation) plants (Lawlor 2001). Consequently C_4 plants are able to maintain smaller stomatal apertures and thus achieve higher water use efficiency (WUE) (Nobel 1999). Similarly, Greenwood *et al.* (1990) have reported higher nitrogen use efficiency (NUE) among C_4 plants because of their higher growth rates.

Under optimum conditions, gross photosynthetic rate increases linearly from zero at a crop specific temperature between 0 and 10 °C to a maximum in the range between 25-35 °C (Whisler *et al.* 1986). Temperature has both immediate and long term effects on photosynthesis. Cellular membranes are known to respond to temperature by altering their fluidity and permeability resulting in their malfunction at low and high temperatures (Hay & Porter 2006). Enzymatic activity is also closely related to temperature as shown by the reduction in catalytic capacity of the enzyme Pyruvate, Pi dikinase at low temperature in C_4 plants (Edwards & Walker 1983) and maize in particular (Long 1983). Low temperatures will therefore directly reduce the photosynthetic rate while damage to the photosynthetic system could result from photo-inhibition (light induced damage of PSII) and photo-oxidation (oxidation reactions induced by light) (Wilson *et al.* 1995). At temperatures between 15-20 °C, the energy costs associated with the C_4 photosynthetic pathway are higher than the gain in dry matter and C_3 plants are more efficient within this temperature range (Figure 2.3) (Hay & Porter 2006). In maize, temperatures below 16 °C reduce dry matter accumulation due to the inefficient utilization of intercepted PAR (Wilson *et al.* 1995).

Thus, when growth conditions are limited by N, 'stay-green' plants will be expected to maintain higher photosynthetic rates because of their ability to extract soil N more efficiently (Section 2.3.3.2). Further, as a consequence of a higher SLN concentration (g m^{-2}),

photosynthetic rates will decline more gradually during senescence. Moderate moisture deficits are also unlikely to severely reduce their photosynthetic rates (Section 2.3.3.3).

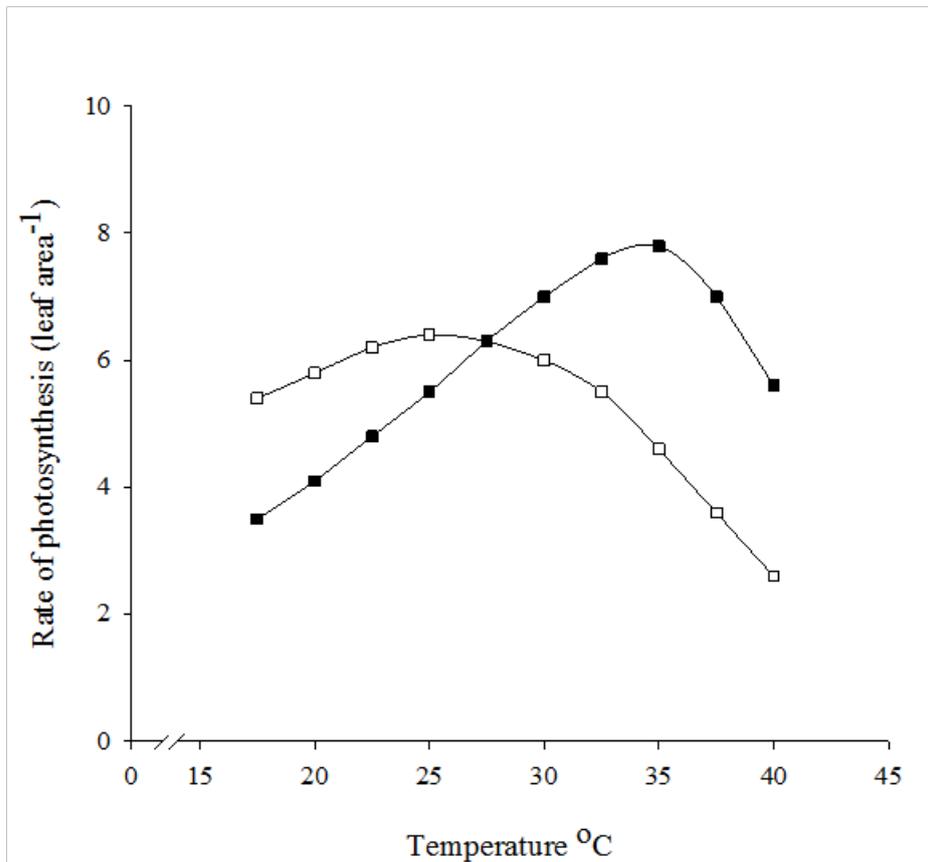


Figure 2.3: Typical temperature response curve for photosynthesis in C₃ (□) and C₄ (■) plants. Reproduced with permission from Edwards and Walker, 1983.

(a) Specific leaf N concentration (g m⁻²)

Approximately 75% of all nitrogenous compounds in the leaves of C₃ plants are associated with photosynthesis (Lawlor 2001). Of this, a large proportion constitute the broad range of enzymes which catalyse CO₂ fixation in leaves (Hopkins & Huner 2004). In C₃ plants for example, Rubisco may constitute up to 30% of the total leaf protein (Hay & Porter 2006) while 20-25% is within the thylakoids (Hortensteiner 2006; Lawlor 2001). This would suggest a relationship between photosynthesis and leaf N content (Grindlay 1997; Sinclair & Horie 1989). A close examination of the net photosynthetic rate at light saturation has shown a near linear increase in light saturated net photosynthesis with an increase in SLN concentration (g m⁻²) in sorghum (*Sorghum bicolor* L. Moench) and rice (*Oryza sativa* L.) (Anten *et al.* 1995). Further, experimental data from work done in maize supports the existence of a strong association between specific leaf N concentration (g m⁻²) and photosynthetic capacity (Muchow & Davies 1988; Muchow & Sinclair 1994).

Sinclair and Horie (1989) have described this relationship using a logistic equation that relates organic nitrogen concentration per unit leaf area and net photosynthesis:

$$P_{\max} = A_m \left| \frac{2}{1 + \exp(-\alpha(N_{oa} - N_o))} - 1 \right| \quad \text{Equation 2.11}$$

Where:

N_{oa} is the organic nitrogen concentration (g N m^{-2}),

A_m is the asymptote of P_{\max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for infinite value of N_{oa} ,

N_o (g N m^{-2}) is the value of N_{oa} for $P_{\max} = 0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and α determines the steepness of the slope ($\mu\text{mol CO}_2 \mu\text{mol PPF D}^{-1}$).

Such logistic functions can be considered to provide a general indication of the relationship between the SLN concentration (g m^{-2}) and photosynthetic capacity because nitrate-N has been found to account for at most 6% of the total leaf nitrogen (Vos *et al.* 2005). Leaves with a greater SLN concentration (g m^{-2}) will therefore have higher photosynthetic rates with increased PPF D (Grindlay 1997), while N deficient leaves will saturate at lower PPF D levels (Lawlor 2001). The net effect of N deficiency on photosynthesis is the reduced carboxylation efficiency and P_{\max} as a result of reduced leaf protein and chlorophyll per unit area of leaf (Lawlor 2001). Because of the CO_2 concentration mechanism in C_4 plants, net photosynthetic rates saturate at high PPF D and at lower SLN concentration (g m^{-2}) resulting in higher quantum yields compared with C_3 plants (Anten *et al.* 1995).

Plants partition available N in favour of either structural development or maintenance of its SLN concentration (g m^{-2}) (Sinclair & Horie 1989; Vos *et al.* 2005). ‘Stay-green’ hybrids are envisaged to partition proportionately more of their N into the leaf organic pools and also remobilise less N towards grain filling (Borrell *et al.* 2003). Thus, the SLN concentration (g m^{-2}) of ‘stay-green’ hybrids remains higher than that of the senescent hybrids during grain filling (Borrell *et al.* 2001). Consequently, higher photosynthetic rates are likely to be attained by these hybrids.

(b) Chlorophyll concentration

Chlorophyll is a key constituent of the photosynthetic system. Paradoxically this pigment is a potential cell phototoxin, and is therefore bound as a chlorophyll-protein complex (Hortensteiner 2009). This complex constitutes approximately 20% of the total cellular N, which is remobilised when N demand exceeds supply (Hortensteiner 2006). Chlorophyll degradation is therefore a prerequisite for N remobilisation (Thomas *et al.* 2002), and its concentration declines with a decline in leaf N (Hay & Porter 2006). However, in a number of species, genetic variants and mutants that retain chlorophyll during senescence exist (Barry 2009; Subedi & Ma 2005; Thomas *et al.* 2002). Chlorophyll concentration therefore declines steadily during senescence in these ‘stay-green’ plants (Thomas & Smart 1993). Where this steady decline in chlorophyll concentration is coupled with photosynthetic activity (functional ‘stay-greens’), there is potential to increase plant productivity (Barry 2009).

It is often necessary to estimate the N concentration of a crop to predict its N fertiliser requirements. Under field conditions, instantaneous non destructive measurements are more attractive compared with the more costly and time consuming laboratory analyses (Monje & Bugbee 1992). Wood *et al.* (1992) have suggested the use of the leaf chlorophyll as an N indicator because of its close correlation with tissue N concentration and photosynthetic capacity (Evans 1983). The portable chlorophyll meter, (SPAD-502 Chlorophyll Meter, Konica Minolta Sensing, Inc., Japan), has been shown to provide an accurate estimate of leaf chlorophyll content under both controlled (Smart *et al.* 1995) and field conditions (Markwell *et al.* 1995). This instrument measures the spectral absorbance of the leaf in the red (650 nm) and infra-red (940 nm) regions (Hoel & Solhaug 1998; Monje & Bugbee 1992) and calculates a numerical SPAD (Soil and Plant Analyzer Development) value in the range 0 to 80 proportional to the leaf chlorophyll content (Wood *et al.* 1992).

Chapman and Barreto (1997), reported a direct correlation between the leaf chlorophyll concentration and the SLN concentration (g m^{-2}) during the vegetative growth stage of a tropical maize crop. Rajcan and Tollenaar (1999b) have also found agreement between leaf chlorophyll content estimates from a SPAD meter and the rate of leaf senescence in maize after silking. Further, Markwell *et al.* (1995), obtained a strong correlation ($R^2 = 0.94$) between chlorophyll concentration ($\mu\text{mol m}^{-2}$) and the SPAD-502 meter readings of soybean

(*Glycine max*) and maize. From this work, they developed an exponential relationship between the two parameters (Equation 2.12).

$$\text{Chlorophyll } (\mu\text{mol m}^{-2}) = 10^{(\text{SPAD}^{0.265})} \quad \text{Equation 2.12}$$

Where, SPAD represents the SPAD-502 value.

Other researchers have reported systematic errors in the use of the SPAD-502 as an indirect indicator of crop N status due to the non homogeneity in the distribution of chlorophyll within the leaves (Lin *et al.* 2010; Monje & Bugbee 1992). SPAD values were also observed to differ with the level of irradiance received (Hoel & Solhaug 1998), due to the changes in chlorophyll orientation (Brugnoli & Bjorkman 1992). However, both Markwell *et al.* (1995) and Monje and Bugbee (1992) argue that if suitably calibrated, the SPAD meter can be a useful diagnostic tool and suitable for studies in photosynthesis and crop physiology.

2.3.4.4 Radiation use efficiency

At the canopy level, the relationship between biomass accumulation and solar radiation intercepted provides an indication of the crop's efficiency in its use of radiant energy (Gallagher & Biscoe 1978), and summarises its potential to accumulate biomass (Sinclair & Horie 1989). Initially thought to be a constant quantity (Gallagher & Biscoe 1978; Monteith 1977), RUE will in fact differ depending on the leaf quantum efficiency (Muchow & Sinclair 1994). It is influenced by leaf growth, N uptake and partitioning and mobilization during grain fill (Muchow & Davies 1988). In addition to SLN concentration (g m^{-2}), water deficits, temperature and the radiation environment have all been reported to influence RUE (Sinclair & Muchow 1999). RUE is low during early vegetative growth because most of the leaves are exposed to radiation levels approaching light saturation, and hence are less efficient (Sinclair & Horie 1989). Near surface soil temperatures also increase due to exposure to longer periods of direct sunlight (Wilson *et al.* 1995).

Linear increases in RUE with increasing SLN concentration (g m^{-2}) have been reported for maize (Muchow & Davies 1988). However, Muchow and Sinclair (1994) have shown that a hyperbolic function best described the relationship between RUE and SLN concentration (g m^{-2}) in maize. RUE therefore achieves an asymptotic value at high SLN concentration (g m^{-2})

of 1.8 g m^{-2} and declines curvilinearly at levels below the saturating leaf N content (Sinclair & Muchow 1999). Theoretical analyses and experimental work have confirmed that plants with the C_4 photosynthetic pathway have higher RUE values than those with the C_3 pathway (Monteith 1977; Sinclair & Horie 1989) mainly due to differences in their photosynthetic capacity (Hay & Porter 2006). For maize grown under favourable conditions, maximum RUE is fairly constant in the range $1.6\text{-}1.7 \text{ g dry matter MJ}^{-1} \text{ iPAR}$ (Muchow & Sinclair 1994; Muchow *et al.* 1990) compared with $1.2 \text{ g dry matter MJ}^{-1} \text{ iPAR}$ for soybean and $1.4 \text{ g dry matter MJ}^{-1} \text{ iPAR}$ for rice (Sinclair & Horie 1989). This is close to the $3.8 \text{ g dry matter MJ}^{-1}$ absorbed PAR reported by Lindquist *et al.* (2005) for their maize crop grown at Lincoln, Nebraska. The decline in RUE during grain filling to approximately $1.2 \text{ g dry matter MJ}^{-1} \text{ iPAR}$ has been associated with the mobilization of N into the grain (Muchow *et al.* 1990).

Studies on the comparison of RUE among crops with and without delayed leaf senescence are limited. Based on the assumption of an increase in photosynthetic activity and an extension of its duration (Section 2.3.4.3), more PAR could be intercepted or a higher RUE anticipated among the ‘stay-green’ crops especially towards the end of the season. However, this hypothesis requires quantification given the theoretical nature of the assumptions and the possible existence of negative feedback mechanisms.

2.3.4.5 Water use efficiency

Transpirational water loss is an inevitable consequence of the process of photosynthesis and most plants experience some degree of water stress. Because water has a lower molecular weight than CO_2 , its diffusion coefficient is higher and it diffuses ~ 1.6 times faster than CO_2 under normal conditions (Fitter & Hay 2002). Since the amount of water transpired is potentially greater than the CO_2 fixed, C_4 plants have evolved a mechanism to utilize water more efficiently by concentrating CO_2 within the bundle sheath cells (Hay & Porter 2006). This creates a steeper potential difference between internal and atmospheric CO_2 concentration levels, causing the stomata to partially constrict and limit the amount of water lost through transpiration (Nobel 1999). C_4 plants have a water use efficiency of $2\text{-}5 \text{ g CO}_2$ per kg of water which is approximately double the $1\text{-}3 \text{ g CO}_2$ per kg of water for C_3 species (Nobel 1999).

2.3.4.6 Potential soil moisture deficit

To explain the effect of water deficits on dry matter a quantitative measure of drought severity is necessary (Jamieson *et al.* 1995b). The potential soil moisture deficit (PSMD) is an attractive approach because of its independence of soil moisture content (Jamieson *et al.* 1995a) and its maximum (PSMD_{max}) quantifies the total amount of moisture stress experienced by the crop (French & Legg 1979). Using the PSMD approach, Stone *et al.* (2001a), calculated an average decline of 27 kg dry matter ha⁻¹ mm⁻¹ above the critical deficit (Dc) in a crop of sweet corn grown at Lincoln, New Zealand. Sweet corn and maize are the same species, hence, these values may be considered representative of maize (*Zea mays* L.), grown under similar conditions. Several authors report that dry matter accumulation under moisture stress conditions correlated well with the amount of water transpired below the PSMD_{max} (Hammer *et al.* 1997; Jamieson & Francis 1991; Mills *et al.* 2006).

2.3.4.7 Partitioning of dry matter

There is a quantitative relationship between growth and resource allocation (Weiner 2004) that gives rise to an allometric growth behaviour where resource allocation is a function of plant size (Farrar 1992). While resource allocation may be genetically predetermined, a considerable degree of plasticity exists which allows plants to respond to the prevailing growth conditions (Weiner 2004). Plants will therefore allocate their resources towards increasing the uptake of the resource that is most limiting to growth (Whisler *et al.* 1986), a concept known as optimal allocation theory (Bloom *et al.* 1985). Early resource allocation will therefore favour root growth as the plant attempts to acquire nutrients necessary for structural development (Bloom *et al.* 1985; Gedroc *et al.* 1996). With the enhancement of root growth, nutrient acquisition ceases to be a limiting factor and the allometric resource allocation trajectory shifts the equilibrium of resource partitioning in favour of above ground structures (Weiner 2004). This allometric growth behaviour is sensitive to developmental switches and programmed adjustments come into play at the appropriate time (Farrar 1992). Therefore, the transition from vegetative to reproductive development triggers a shift in assimilate partitioning in favour of the developing grain (Hay & Porter 2006).

As a consequence of the modifications on the vegetative growth and development by the 'stay-green' trait in maize, reproductive growth and development may differ between early

and late senescence crops. These changes will mainly influence the rate and quantity of dry matter accumulated with concomitant effects on ear and kernel development.

2.4 Reproductive growth

2.4.1 Photoperiod

Photoperiod influences plant development through its effects on the duration of developmental events (Ellis *et al.* 1992; Tollenaar *et al.* 1979). It most influences the time taken to induce floral primordia (Whisler *et al.* 1986). Wilson *et al.* (1995) have reported no photoperiod effect on the phenology of three maize cultivars grown in a cool temperate environment even when the photoperiod differed between 13.9-16.4 hours. Photoperiod also had no effect on the duration of grain-filling in a maize crop grown in a semi-arid tropical environment (Muchow & Carberry 1989). Thus, under Canterbury conditions, where Wilson *et al.* (1995) carried out their study, photoperiod may be considered inconsequential to maize growth and development and is not considered further in this study.

2.4.2 Silking

Floral maturity (anthesis and silking) is a critical developmental stage in maize. It signals the end of the vegetative growth stage, and determines the success of kernel set. In maize, anthesis precedes silking by a short duration and the anthesis silking interval (Boone *et al.* 1984) is crucial in determining the success of fertilisation and hence grain yield (Bolaños & Edmeades 1996). This is because fertilisation of the florets is dependent on the synchrony of anthesis and silking, both of which are sensitive to environmental stress (Abrecht & Carberry 1993; Jacobs & Pearson 1991). Water stress and nutrient deficiency have both been reported to lengthen the anthesis silking interval (Borras *et al.* 2007; Edmeades *et al.* 1993), so that pollen is shed before the silks are receptive (Duncan 1975; Jacobs & Pearson 1991).

Under Canterbury conditions, floral maturity is likely to suffer from the effects of moisture stress and benefit from irrigation because silking occurs under conditions of increased temperature and high evaporative demand (Stone *et al.* 2001a; Stone *et al.* 2001b).

2.4.3 Ear growth

Ear development commences following fertilisation and up to eight potential ears may initially develop. The number of ears that develop further will depend on the plant population and the availability of nutrients (Evans 1975). Usually only the top 1-2 ears become dominant and progress with further development (Duncan 1975).

In maize, ear dry matter accumulation follows the common sigmoid growth pattern (Otegui & Bonhomme 1998). Andrade *et al.* (2002), reported a strong correlation between ear growth rate and its N content which may suggest an influence of N on biomass partitioning to the ear (D'Andrea *et al.* 2008). Water also plays an important role in the translocation of assimilates (Zinselmeier *et al.* 1999) and the expansion of cells during kernel growth (Egli 1998). Because of this influence the maximum grain moisture content determines the maximum grain volume (Borras *et al.* 2003; Gambin *et al.* 2007), which explains the response of the ear growth rate to irrigation. Hence, 'stay-green' crops are anticipated to accumulate ear dry matter at faster rates due to their favourable N status and water regime during grain filling (Section 2.3.4.3).

2.4.4 Kernel growth

Grain growth in cereals occurs as a result of dry matter deposition in the endosperm and three distinct phases have been identified (Egli 1998). The lag phase is dominated by active cell division and water uptake which expands the kernel volume without an appreciable increase in dry matter (Fraser *et al.* 1982). This is followed by a linear growth phase of effective grain filling where carbohydrates are deposited in the kernel at a maximum rate (Melchiori & Caviglia 2008; Tollenaar 1977), before the decline in growth rate towards physiological maturity (Egli 1998). A similar pattern of growth has been observed in maize (Westgate 1994), soybean (Fraser *et al.* 1982) and wheat (Ibrahim *et al.* 1992).

The demand for assimilate to support kernel growth dominates crop resource allocation after silking (Egli 1981; Tollenaar & Dwyer 1999) and where supply is inadequate to meet growth requirements, remobilisation occurs (Passioura 1976). The plant water status plays an important role in the translocation of assimilates to the developing kernel (Zinselmeier *et al.* 1999) and controls the duration of grain filling (Gambin *et al.* 2007). Thus water deficits

shorten the duration of grain filling by increasing the rate of development (NeSmith & Ritchie 1992), and limiting its rate of dry matter accumulation (Westgate 1994).

Kernel growth may therefore progress normally if either plant reserves are remobilised into the kernel or the plant kernels are able to actively access moisture during water deficits. Enhanced remobilisation of reserves for kernel growth during water stress has been reported in wheat, sunflower and maize (Section 2.3.3.3). Westgate and Thomson Grant (1989) suggested the existence of osmotic gradients and the vascularisation of the caryopsis as possible reasons for the continued accumulation of water under moisture stress conditions. Osmotic gradients may play a part in the maintenance of a favourable water balance in 'stay-green' crops (Section 2.3.3.3) which can be expected to benefit these crops during kernel development.

2.4.5 Physiological maturity

Physiological maturity is the time when grain dry matter increase stops. In maize it is reached when the kernels attain their maximum dry weight (Brooking 1990). The development of the black layer in 90% of the grains is often used as an indication of physiological maturity (Evans 1975; Stone *et al.* 1999). However, when growth conditions during late grain filling are characterised by low temperatures, the development of the black layer is slow (Wilson *et al.* 1995) and not an accurate indicator of physiological maturity and the use of ear moisture content is recommended (Brooking 1990). However this approach can only be used retrospectively.

2.4.6 Senescence

Senescence is the terminal phase of plant growth that is normally associated with degenerative changes that culminate in the eventual death of the leaf or plant (Smart *et al.* 1995). It is an important but complex developmental process responsible for the decline in plant productivity (Thomas & Stoddart 1980). Due to the well coordinated alterations in cell structure, metabolism and gene expression, this process is considered a programmed cell death (Gan & Amasino 1997; Nooden *et al.* 1997). It is thought to be under genetic control (Hopkins & Huner 2004; Nooden *et al.* 1997), but water stress and N deficiency (Wolfe *et al.* 1988a), as well as hormonal influences (Nooden 1980; Thimann 1980) can often accelerate its onset.

However, in the absence of exogenous stress factors, leaf age is the most important influence in the initiation of senescence (Gan & Amasino 1997). The degenerative changes that precede senescence include a decline in the photosynthetic activity (Leopold 1980), decreased protein synthesis (Thimann 1980), organelle disintegration (Thomas & Stoddart 1980) and an increase in maintenance respiration rate (Gifford *et al.* 1984). While senescence may start soon after the attainment of full leaf size when N demand exceeds its supply (Leopold 1980), grain filling generally hastens the process, suggesting a link between the remobilization of resources for grain filling and senescence (Borrell *et al.* 2001).

In summary, N availability influences the rate of dry matter allocation (Sections 2.4.3 and 2.4.4), and the reported differential rates of N sequestration between the early and late senescent crops (Section 2.3.3.2) will impact on ear growth and development. The ‘stay-green’ crops are therefore anticipated to accumulate ear and kernel dry matter faster and also mitigate the effects of water stress during grain filling (Section 2.3.3.3).

2.5 Yield and yield components

2.5.1 Grain yield

Grain yield is the product of the number of kernels per unit area and the mean kernel weight (Hawkins & Cooper 1981; Melchiori & Caviglia 2008). Because kernel weight is relatively stable (Tollenaar *et al.* 1994), the number of kernels per unit area is the major determinant of grain yield in maize. N influences grain yield mainly through its effects on the number of kernels initiated (Echarte *et al.* 2004; Jacobs & Pearson 1991) and the reduction in the number of kernels aborted after fertilisation (Bänziger *et al.* 2002).

Grain yield responds to moisture availability through an increase in the number of kernels per ear and their weight (Maddonna *et al.* 1998). This may be related to one or a combination of factors. First, moisture deficits have been reported to limit the delivery of sucrose necessary for starch deposition during early kernel development leading to ovary abortion (Section 2.4.3). Secondly, water plays an important role in the expansion of cells during kernel growth (2.4.4), and the maximum grain moisture content determines the maximum grain volume (Borras *et al.* 2003; Gambin *et al.* 2007). Thirdly, moisture deficits may affect grain yield indirectly through its influence on soil N dynamics (Section 2.3.3.3). An example is the

nitrate ion which is relatively mobile in the presence of water, and wholly dependent on an aqueous medium for its uptake (Hay & Porter 2006).

2.5.1.1 Number of kernels per ear

Both kernel set and the quantity of assimilate partitioned to the kernels during the post silking growth phase determine the number of kernels per ear and hence grain yield (Cirilo & Andrade 1994; Otegui & Bonhomme 1998). While the potential number of kernels per ear in maize is established around silking (Cirilo & Andrade 1994), the pre-silking growth environment plays a major role (Otegui & Bonhomme 1998; Plenet *et al.* 2000b). Both water stress and nutrient deficiency lengthen the anthesis-silking interval, so that pollen was shed before the silks were receptive (Section 2.4.2) and kernel number per ear decreases probably through an increased number of unfertilised florets (Bänziger *et al.* 2002). Kernel growth may also be arrested soon after fertilisation if water stress increases in severity and interrupts the delivery of assimilate to the developing kernel (Zinselmeier *et al.* 1999).

2.5.1.2 Seed weight

Assimilate supply to the kernels during the post silking development phase determines the final kernel number and weight (Bänziger *et al.* 2002), through its effects on the kernel growth rate (Borras *et al.* 2003). If growth conditions deteriorate after kernel numbers have been determined, maize crops rationalise assimilate supply in favour of the earliest initiated kernels and the mean kernel weight is reduced (Tollenaar 1977). Yield plasticity therefore enables crops to realign assimilate supply with sink demand as reported in other crops (Berenguer & Faci 2001; Hay 1999; Smith *et al.* 1999).

2.5.2 Crop harvest index

Crop harvest index (HI) is the harvestable proportion of the above ground dry matter (Lecoeur & Sinclair 2001), which in most commercial maize hybrids is approximately 0.5 (Muchow *et al.* 1990). The rate of increase in crop HI is best described using a logistic growth function (Soltani *et al.* 2004) and this pattern of growth appears not to differ with water deficits (Lecoeur & Sinclair 2001). Crop HI may actually increase with moisture stress because

fertilised but unirrigated crops may develop a greater sink capacity (Jacobs & Pearson 1991), and remobilise more plant reserves towards grain filling (Husain *et al.* 1988; Wardlaw 1967).

In cereals, optimisation of harvest index has been the primary objective of most yield improvement programmes (Duncan 1975). However, some authors suggest that maximum yield potential has been achieved from harvest index and no further gains can be realised from harvest index improvements (Tollenaar & Dwyer 1999). Future yield increases would have to come from the production of higher dry matter through improved RUE or an increased amount of iPAR by the crop (Hay & Porter 2006). This has led to the evaluation of secondary traits with the potential for yield increases especially under limiting conditions e.g. ‘stay-green’ (Barry 2009; Hortensteiner 2009).

2.6 What is the ‘stay-green’ trait?

‘Stay-green’ is a characteristic exhibited in certain plant species where the normal process of senescence of a plant is delayed (Borrell & Hammer 2000). The physiological basis of the trait in maize remains largely unknown but recent studies have linked it to a variation in the genome, probably through the alteration of the genes that trigger and regulate the progression of senescence (Donnison *et al.* 2007). Based on the correlation between pigment stability and photosynthetic activity, Thomas and Smart (1993) have categorised ‘stay-greens’ into four groups (types A-D). In type A, senescence is delayed but once initiated proceeds at the normal rate, while in type B, senescence is initiated normally but proceeds at a slower rate (Figure 2.4) (Thomas & Howarth 2000; Thomas & Smart 1993). Type A and B ‘stay-greens’ are functional because chlorophyll retention is coupled with photosynthetic capacity (Thomas *et al.* 2002), and can potentially increase plant productivity (Hortensteiner 2009; Thomas & Howarth 2000). In contrast, type C and D (cosmetic) ‘stay-greens’ retain chlorophyll during senescence, however, photosynthetic capacity declines as normal (Thomas & Smart 1993) e.g. the non-yellowing mutants of *Festuca pratensis* (Hauck *et al.* 1997).

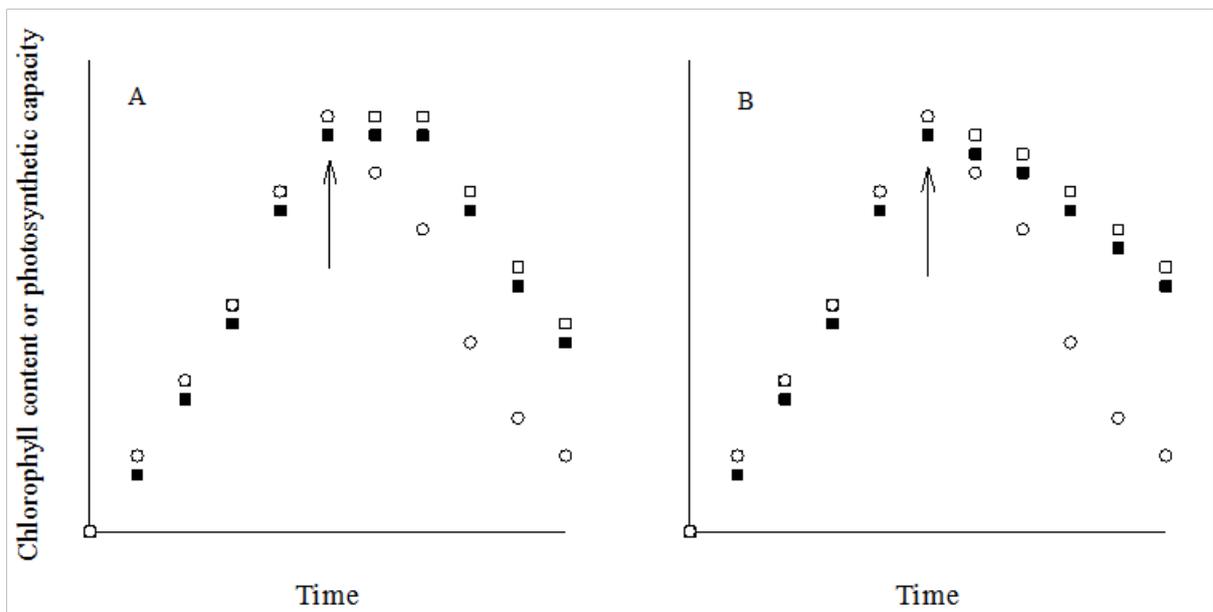


Figure 2.4: Type A and B ‘stay-greens’ in a hypothetical leaf. Chlorophyll content (□), photosynthetic capacity (■) and the normal pattern of chlorophyll decline (○) are indicated on an arbitrary scale. The arrows indicate the start of senescence in a non ‘stay-green’ phenotype. Adapted with permission from Thomas and Howarth, 2000.

In *Lolium temulentum*, for example, genotypes expressing the ‘stay-green’ trait showed a normal pattern of soluble protein degradation but more stable light harvesting and reaction centre thylakoid membrane proteins during senescence (Thomas *et al.* 2002). This suggests that light interception and some limited photosynthetic activity may continue after senescence has commenced. Indeed Donnison *et al.* (2007), reported a small extension in the photosynthetic activity in maize during the later stages of senescence in a mutant with a senescence retarding associated gene (*See2β*). This contrasted with the work of Smart *et al.* (1995) who reported a decline in photosynthetic activity despite the retention of chlorophyll during senescence in maize grown under controlled environment conditions.

The identification of a ‘stay-green’ gene (Section 1.2) supports earlier work in maize which showed the ‘stay-green’ trait to be highly heritable (Edmeades *et al.* 1997). In Iowa for example, DuVick (1997) evaluated 36 hybrids released between 1930-1991 and observed that for every decade the ‘stay-green’ score had increased 0.6 ($R^2 = 0.66$). Thus, newer hybrids yielded higher than older hybrids because of lower rates of leaf senescence (Valentinuz & Tollenaar 2004) due to increased tolerance of biotic and abiotic stresses (DuVick 2005).

Further, in wheat (Jamieson *et al.* 1998), maize (Tollenaar & Daynard 1978) and field bean (Husain *et al.* 1988), post anthesis biomass accumulation is largely dependent on GLAI, hence, its maintenance is expected to lead to more dry matter accumulation. Extensive studies in sorghum (Borrell *et al.* 2000a; Borrell *et al.* 2000b) and maize (Rajcan & Tollenaar 1999a, 1999b) varieties exhibiting the ‘stay-green’ phenotypic characteristic corroborate these findings. By delaying its senescence, ‘stay-greens’ have the opportunity to intercept more solar radiation and hence accumulate more dry matter. However, the amount of photosynthate accumulated during this period needs to be quantified to determine its contribution to overall dry matter accumulation.

Because plants partition available N into structural development or maintenance of its specific leaf N concentration (Section 2.3.4.3), ‘stay-greens’ could develop smaller leaves when N availability is not optimum (Hauck *et al.* 1997). However, to maximise dry matter yield, crops need to actively accumulate N and develop a large leaf area during their vegetative growth, then remobilise a substantial proportion of this N towards grain development (Stone *et al.* 2001b).

In summary, there is potential to increase crop productivity through the use of crops that exhibit phenotypic characteristics consistent with type A and B ‘stay-green’. First, under conditions of limited N availability, enhanced soil N uptake during grain fill can alleviate N stress and limit leaf senescence and lengthen the duration of light interception (Section 2.3.3.1). Secondly, ‘stay-green’ mutants may be able to utilise water more efficiently through reduction of water stress induced leaf senescence (Section 2.3.3.3). This reduction has been positively correlated with yield (Hortensteiner 2009). Thirdly, where chlorophyll retention during senescence is coupled with photosynthetic activity, dry matter accumulation is enhanced (Section 2.3.4.3). However, Subedi and Ma (2005) report that in maize grown under controlled environment conditions, the ‘stay-green’ trait was only exhibited when N availability did not limit growth. This requires further investigation under field conditions.

2.7 Conclusions

- The use of thermal time to describe crop growth and development offers a unique advantage over the conventional method of using time because of the physiological significance of temperature as a process driver. It also provides a repeatable prediction when the crop reaches specific development milestones in different thermal regimes.
- Genetic variants or mutants which exhibit the ‘stay-green’ trait extract more soil N during senescence than their wild counterparts and increase their productivity through delay in leaf senescence. In maize, however, the delay in senescence has yielded inconsistent results.
- By delaying their senescence, ‘stay-green’ hybrids theoretically have the opportunity to intercept more solar radiation and accumulate more dry matter.
- Because of the greater N sequestration during grain filling, ‘stay-green’ crops remobilize less N from their vegetative structures and potentially increase their SLN concentration (g m^{-2}) and photosynthetic rate.
- It is unclear if the ‘stay-green’ trait can make a significant contribution to RUE during grain filling given the relatively minor difference in photosynthetic activity reported between ‘stay and non-stay green’ crops.
- Apart from quantifying the contribution to dry matter and grain yield which may accrue from the ‘stay-green’ trait, it is also important to understand its physiological basis.

Chapter 3

Materials and Methods

3.1 Introduction

This chapter provides details for Experiment 1 in 2008/09 followed by those for Experiment 2 in 2009/10. The experimental site, experimental design, cultural practises and environmental conditions are specified for each season. Measurements carried out during both seasons were similar, hence a common section has been used for their description (Section 3.4). Additional measurements carried out during 2009/10 are described separately in that section (Section 3.4.4). Calculations and data analysis are also described (Section 3.6). More specific information on particular materials or methods relevant for each results chapter are provided within those chapters.

3.2 Experiment 1

3.2.1 Soil type and fertility

Experiment 1 was carried out at the Horticultural Research Area, block H13, Lincoln University, Canterbury (43° 38'S, 172° 28'E, 11 m a.s.l.). The soil is a Templeton silt loam soil (NewZealandSoilBureau 1968) with 0.4-1.0 m silt loam overlying gravel. It has recently been re-classified as a Typic Immature Pallic Soil (Hewitt 1998) which is the equivalent of a '*Udic Ustrochrepts*' using the USDA nomenclature (Soil-Survey-Staff 1999). It is a recent soil developed on fine greywacke alluvium with low phosphorus retention, moderate to high base saturation (>50%) and low levels of extractable sulphate (Cox 1978). The site was previously under oats (2005 & 2008) and consecutive crops of wheat (2006/07).

A soil test taken on the 2nd of October 2008, after the initial ploughing showed a pH of 6.0 (1:2 (v/v) soil: water), an Olsen P level of 14 mg/L (0.5 M NaHCO₃, pH 8.5) and 74 kg/ha available N (anaerobic incubation followed by extraction using 2 M KCl then determined using NIR) (Blackmore *et al.* 1987) to 0.15 m (Table 3.1). During land preparation, 560 kg ha⁻¹ of 20% Potash Super, containing 7.4% P, 10% K, 8.6% S and 16% Ca was applied on 22nd October 2008. A second soil test four weeks after emergence (7th November 2008)

showed that the Olsen P level had risen to 33 mg/L while the pH and available N were 6.0 and 74 kg N ha⁻¹ (0.15 m), respectively. The mineral N content measured at 0.3 m depths to 1.0 m was 44 kg N ha⁻¹.

Table 3.1: Soil test results from 2nd October 2008 (Experiment 1) and 7th November 2009 (Experiment 2) for the experimental site at the Horticultural Research Area, Lincoln University, New Zealand. Recommended soil nutrient levels for maize are included for comparison (Steele 1984).

Nutrient	pH	N ¹	N ²	P ³	K	Ca	Mg	Na
Unit	-	kg ha ⁻¹		mg/L	me/100g			
Season 1	6.0	74	44	14	0.32	6.5	0.91	0.12
MAF QT ⁴	-	-	-	-	10	10	25	6
Season 2	5.9	82	200	17	0.53	6.2	0.99	0.17
MAF QT ⁴	-	-	-	-	12	9	25	9
Recommended	5.8-6.3	-	-	14-22	>5	-	5	-

¹ Available N (0.15 m depth)

² Mineral N (1.0 m depth)

³ Olsen P

⁴ Ministry of Agriculture and Fisheries quick test results

3.2.2 Experimental design

Experiment 1 was a split plot randomised complete block design with two water regimes (dry or fully irrigated) as the main plots. Two rates of N (0 and 270 kg N ha⁻¹) and four hybrids (Section 3.2.4.3) were fully randomised in the sub-plots.

3.2.3 Cultural practices

3.2.3.1 Seed bed preparation

Land preparation commenced on the 20th of October 2008 and standard farm practice was followed to attain a suitable seedbed.

3.2.3.2 Crop establishment

The experiment was hand planted on the 24th October 2008 using a jab maize planter. Each sub-plot measured 4.9 (7 rows) x 10 m with the between row and within row plant spacing of 0.7 m and 0.15 m, respectively. Crop establishment was monitored by use of a 1.0 m length of row selected at random in each plot. Daily counts of emerged seedlings were recorded until emergence was complete. Emergence was defined as the time when at least 50% of the coleoptiles had emerged (Angus *et al.* 1981; Warrington & Kanemasu 1983a). The emergence date was then determined retrogressively. Five contiguous plants were selected for non-destructive sampling and tagged 10 days after emergence (DAE). Initially two seeds were sown per space and these were thinned to one plant per space three weeks later. A population count after hand thinning found 9.25 plants m⁻² against a target of 9.5 plants m⁻². There were three replicates of each treatment. An air temperature probe was installed at 1.4 m above ground on each replicate on the 9th of December 2008. The three probes were connected to a Hobo 4 channel external logger (Onset Computer Corporation, Bourne, MA, USA).

3.2.4 Treatments

3.2.4.1 Nitrogen

Two levels of N were used in this study (Section 3.2.2). For the fertilised plots, additional N was provided as urea (46% N) and broadcast by hand in two applications of 135 kg N ha⁻¹ on 24th November and 17th December, 2008. A light overhead sprinkler irrigation of 10 mm followed each application to dissolve the urea. The level of N applied to the fertilised crops was chosen to provide sufficient N to produce an average yield of 18-20 t ha⁻¹ of dry matter (Moot *et al.* 2007) with ~1.5% N (Reid *et al.* 2006).

3.2.4.2 Irrigation

In this study, crops were either fully irrigated or rain fed (Section 3.2.2). To monitor moisture extraction from the soil profile, Neutron (Troxler 4300 Neutron Probe) tubes and Time Domain Reflectometry (TDR) (Trase System 1 Model 6050 X1) rods were installed on the 15th of December 2008 in each plot. TDR rods were installed to a depth of 0.2 m and Neutron tubes at variable depths between 0.4 and 1.0 m depending on the depth to gravel. Irrigation water was supplied by T-tape laid parallel to each row and close to the zone of root growth. This allowed water to be applied at a uniform rate without the risk of runoff. All plots were provided with 40 mm of water on the 2nd of December 2008 to ensure maximum

establishment of plants in all treatments. Irrigation for the treatments that received additional water was provided to maintain the available soil moisture content of the top 0.2 m above 50% (Stone *et al.* 2001a). Irrigation volume was measured using a flow meter (Neptune, type Sz, size 25.4 mm) connected to the main line.

3.2.4.3 Maize Hybrids

Four Pioneer[®] brand maize hybrids of ‘stay-green’ rating (sgr) 6-9 were procured from Genetic Technologies Limited, Christchurch. The ‘stay-green’ rating is a visual rating on a scale of 1-9 of the plant’s health and vigour at silage harvest (Beavis *et al.* 1994), with a lower score corresponding to a quicker loss of green area (Genetic-Technologies-Limited 2008). A selection of the major agronomic traits of the four hybrids is presented in Table 3.2. Silage comparative relative maturity (CRM), compares Pioneer[®] brand maize hybrids on their relative rates of attainment of harvestable whole plant dry matter with low CRM’s indicative of early maturity (Genetic-Technologies-Limited 2008).

Among these hybrids, ‘P38V12’ (sgr 7) was considered drought tolerant while ‘P38F70’ (sgr 8) was quite susceptible to water stress. Both ‘P39K38’ (sgr 6) and ‘P38G43’ (sgr 9) were considered moderately drought tolerant. This is a quantitatively based score (1-9) with the larger scores indicating greater tolerance, while the ‘stay-green’ score is visually based. Prior to sowing, a germination test was performed with a sample of 50 grains randomly selected from each bag of seed. At least 95% germination rate was recorded for all hybrids.

Table 3.2: Performance characteristics of the four Pioneer[®] brand maize hybrids grown at Lincoln University, New Zealand, during 2008.

Hybrid	Stay green rating	Comparative relative maturity	Drought tolerance
‘P39K38’ [†]	6	87	6
‘P38V12’	7	87	8
‘P38F70’	8	93	4
‘P38G43’ [†]	9	87	7

Pioneer[®] brand products are provided subject to the terms and conditions of purchase, which are part of the labelling and purchase documents. † Hybrids sown in 2009.

3.2.5 Weed control

A pre-emergence application of Atrazine (2-chloro-4-ethylamino-6-isopropylamino-1,3,5-triazine) at 1.5 l ha^{-1} was used to control broad leaf weeds. A field assessment taken four weeks after emergence indicated the presence of fat hen (*Chenopodium album* L.), hairy night shade (*Solanum physalifolium* Rusby), black night shade (*Solanum nigrum* L.) and corn bind (*Convolvulus arvensis* L.). A post emergence application of Atrazine at 2 litres ha^{-1} was applied one week later. This application was effective and further, limited, weed control was achieved through hand weeding.

3.3 Experiment 2

3.3.1 Soil type and fertility

Experiment 2 was also at Lincoln University on a deep Templeton silt loam in the Horticultural Research Area, block H 10. Compared with the previous season, this site was on a well developed soil that had previously been under perennial ryegrass based pasture (2005-2008) and barley (2008 to autumn 2009). Soil tests on 7th of November 2009 showed a pH of 5.9, an Olsen P level of 17 mg/L and $82 \text{ kg available N to } 0.15 \text{ m}$ (Table 3.1). The mineral N content to 1.0 m was also measured on the same date and found to be 200 kg N ha^{-1} .

3.3.2 Experimental design

Experiment 2 was a randomised complete block with two hybrids ('P39K38' (sgr 6) and 'P38G43' (sgr 9)) and four rates of N ($0, 50, 150$ and 200 kg N ha^{-1}) split between two growth stages as follows: $0; 0$ (V6) and 50 (V12); 150 (V6) and 0 (V12) and 150 (V6) and 50 (V12) kg N ha^{-1} . The development stage V6 represents six fully expanded leaves while V12 is 12 fully expanded leaves as defined by Ritchie *et al.* (1993). The times of fertiliser application were selected to occur at developmental stages when nutrient requirements were greatest. The V6 stage usually coincides with the start of the rapid stalk elongation while the V12 stage corresponds with the period when the size of the ear and the potential number of kernels on each ear are determined (Ritchie *et al.* 1993). There were three replicates of each treatment. Each plot measured 5.6 (8 rows) $\times 10 \text{ m}$ with the between row and within row distances being 0.7 m and 0.15 m , respectively. Irrigation water was provided following the water budget depicted by Figure 3.4 in Section 3.6.5.

3.3.3 Cultural practices

3.3.3.1 Crop establishment

Land preparation commenced on the 8th of October 2009 and standard farm practice was followed to attain a suitable seedbed. A basal application of 200 kg ha⁻¹ of superphosphate was applied on the 6th of November 2009. The seed was drilled with a Stanhay precision seeder on the 12th November 2009 at a target population of 10 plants m⁻².

On the same day, three soil and one air temperature probes were installed and connected to a Hobo 4 channel external logger. A rain gauge was also installed. Crop establishment was monitored as in Experiment 1 (Section 3.2.3.2). A population count on the 10th of December 2009 found 7.0 plants m⁻², which was lower than targeted probably because of seeder precision or the low minimum temperature at emergence (Table 3.3). Plants for non destructive sampling were selected as described in Section 3.2.3.2.

3.3.3.2 Irrigation

A pair of Neutron tubes and TDR rods were installed in replicates 2 and 3 on the 19th of November 2009 to monitor moisture extraction from the soil profile. Each Neutron tube was installed to a depth of 1.0 m and the TDR rods to a depth of 0.2 m. The trigger for irrigation was set at 60% of total available soil water to cater for the variability in water levels within the experimental plots observed during Experiment 1.

3.3.3.3 N application

For the fertilised plots, additional N was provided as urea (46% N) and broadcast by hand in two applications on the 30th of December 2009 and 5th of February 2010. These dates were selected to coincide with the V6 and V12 stages of growth, respectively (Ritchie *et al.* 1993). A light overhead sprinkler irrigation of 10 mm followed each application to dissolve the urea.

3.3.3.4 Weed control

The major weeds in this experiment were also fat hen, hairy night shade and black night shade. A post-emergence application of Atrazine (2-chloro-4-ethylamino-6-isopropylamino-

1,3,5-triazine) at 1.5 litres ha⁻¹ was applied on the 15th of December 2009 to control these broad leaved weeds. Further weed control was achieved through hand weeding.

3.4 Measurements

The measurements described in this section were made in both experiments 1 and 2.

3.4.1 Crop establishment

In both experiments, at least 50% of the seedlings had emerged 2 weeks after sowing (Sections 3.2.3.2 and 3.3.3.1). Plants for non destructive sampling (Sections 3.2.3.2 and 3.3.3.1), were selected from the centre of the middle (4th) rows. Only contiguous healthy and those of uniform height were selected. Leaf appearance was monitored every 3-4 days by recording the number of fully expanded leaves and emerged leaf tips on five marked plants. A fully expanded leaf and an emerged leaf tip were recorded as defined by Muchow and Carberry (1989).

3.4.2 Green area index and dry matter accumulation

Green leaf area index was monitored destructively by harvests of three plants cut at ground level every 14 day interval using a Licor 3100 area meter (Licor Inc, Lincoln, NE, USA), starting 25 DAE. The fraction of intercepted photosynthetically active radiation (PAR) was measured at 10-14 day intervals using a SunScan Canopy Analysis System (Delta-T Devices, Cambridge-England) following the method of Gallo & Daughtry (1986). The SunScan uses a set of algorithms to compute GAI from the proportion of incident PAR that is transmitted through the canopy (Potter *et al.* 1996.).

Dry matter accumulation was also determined from these three plants. The plant components were separated into leaves and stalks before silking. After silking, each plant was stripped into three cohorts of leaves (lower, middle and top) (Rajcan & Tollenaar 1999a), stalks and ears. The middle leaves consisted of the leaf that subtends the ear and its adjacent neighbour on either side. All green leaves below and above the middle cohort were designated the lower

and top leaves, respectively. Identical components in each plot were bulked and oven dried at 65 °C in a forced draft oven to constant weight.

The approximate date for the appearance of silks was determined from the observation of leaf appearance rates. Silking has been reported to occur immediately after the end of the vegetative phase (Tollenaar & Dwyer 1999). Two weeks before silking was expected to occur, 15 contiguous (tagged and five on either side) plants in each plot were selected and the appearance of silks was monitored every 2-3 days. Silking date was recorded as the date when 50% of these plants had extruded visible silks (Ritchie *et al.* 1993).

3.4.3 Chlorophyll content

Leaf chlorophyll content was estimated using a chlorophyll meter (SPAD-502 Chlorophyll Meter, Konica Minolta Sensing, Inc., Japan) from the beginning of silking until physiological maturity (as indicated by the presence of the black layer in more than 90% of the kernels) (Duncan 1975). A single plant from the tagged set was selected and re-tagged for use to estimate the chlorophyll content in each leaf. The leaves were divided into cohorts of bottom, middle and the top leaves (Section 3.4.2). On each leaf, five SPAD meter readings were taken at points lying between about 1/3 and 2/3 from the leaf base along each leaf blade where leaf N concentration has been found to be stable (Chapman & Barreto 1997). The five readings were averaged to obtain a leaf SPAD meter reading. Individual leaf SPAD meter readings were then averaged to calculate the SPAD units in each cohort of leaves. In Experiment 2, five readings were taken on the ear leaf of each tagged plant. These were averaged to derive individual plot SPAD reading for the ear leaf.

3.4.4 Photosynthetic activity and leaf senescence

Remobilisation of N reserves from the vegetative plant parts into the grain has been linked with senescence (Gregersen *et al.* 2008). The degenerative changes that precede green area senescence include a decline in the photosynthetic activity (Leopold 1980). To examine the changes in photosynthetic activity during the grain filling period of Experiment 2, leaf photosynthesis rates were measured using the LI-6400 portable photosynthesis system (Licor Inc., Lincoln, NE, USA) on the ear leaf (Dwyer & Stewart 1986a) of a single plant in each

plot on two dates. The first measurement was taken immediately after silking (22nd February, 2010) and the second taken to coincide with late grain filling (22nd April, 2010).

Measurements were taken on all treatments but restricted to two replicates due to time constraints. The LI-6400 has two infrared gas analyzers (IRGA) that measure absolute concentrations of CO₂ and H₂O, designated as the sample and reference IRGA (Licor 1998). Net photosynthesis was derived from the difference in CO₂ concentration between the sample (leaf clamped on a 6 cm² chamber) and the reference IRGA and expressed as rates of CO₂ uptake ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Measurements commenced at solar noon on clear sunny days. The chamber CO₂ concentration was set at 400 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, temperature at 22 °C and the photosynthetic photon flux population (PPFD) maintained at 1800 $\mu\text{mol m}^{-2} \text{ s}^{-1}$.

Leaf senescence was followed through weekly counts of the number of leaves that had lost at least 50% of their chlorophyll content from silking until physiological maturity (Wolfe *et al.* 1988a). Leaf 6 and 9 were tagged on each marked plant to determine the final leaf number and also track leaf senescence.

3.4.5 Final harvest

At final harvest, the five plants per plot initially tagged for non-destructive harvests were cut at ground level. The above ground portions were separated into leaves, stalk and ears and oven dried at a temperature of 65 °C in a forced draft oven to a constant weight. The kernels were extracted from the de-husked dried ears, weighed and 250 seeds counted using a seed counter (Numerical seed counter). The grains were then weighed using a Mettler Toledo PB 1502 fine balance (Global Science and Technology Ltd, Auckland New Zealand) to determine the grain weight. Grain yield was determined from the yield per plant and the plant population.

3.4.6 N content

Samples for N analysis were ground to pass through a 1 mm screen and N concentration in each sample was determined by automated dry combustion-gas chromatography with a Vario Max CN Macro Elemental Analyser (Elementar Analysensysteme, GmbH, Germany). Nitrogen

content (kg ha^{-1}) was calculated as the product of the dry matter (kg ha^{-1}) and the N concentration (% N) in each plant part (Subedi & Ma 2005).

3.5 Climatic and seasonal weather conditions

Air temperatures were logged hourly with a set of triplicate thermistors. Penman potential evapotranspiration, incident solar radiation and the long term mean weather data were accessed from Broadfield's weather station 3 km east of the experimental site. Mean daily temperatures during Experiment 1 were within the long term means (LTM) except in January 2009 when they were 2 °C higher (Table 3.3). Minimum temperatures were also close to the LTM except in March when they were 2 °C lower. Maximum temperatures were higher than the LTM by between 1.4-4.8 °C in five of the six months of experimentation. January 2009 was exceptionally warm and the maximum daily temperature was 4.8 °C higher than the LTM. Only December recorded maximum temperatures that were within the LTM.

Table 3.3: Mean, minimum and maximum temperature (°C) and the long term mean (LTM, 1975-2007) for Experiment 1 (08/09) and Experiment 2 (09/10) at Lincoln University, Canterbury, New Zealand.

Season	Mean Temp (°C)			Minimum Temp (°C)			Maximum Temp (°C)		
	08/09	09/10	LTM	08/09	09/10	LTM	08/09	09/10	LTM
November	13.8	12.8	12.9	8.3	6.5	7.8	19.7	19.1	18.3
December	15.4	14.6	15.3	10.5	8.9	10.1	20.3	20.8	20.8
January	18.7	15.8	16.6	11.5	10.7	11.4	26.9	22.1	22.1
February	16.0	16.6	16.3	11.0	10.2	11.3	23.5	24.0	21.7
March	14.1	14.7	14.7	7.6	8.2	9.7	22.4	22.8	20.0
April	12.1	13.0	12.0	6.4	7.1	6.8	19.1	20.7	17.2
May	7.4	9.6	9.2	3.4	5.4	4.3	11.7	14.7	14.3

Mean monthly temperatures during Experiment 2 were lower than the LTM except in November, February and March when they were at the LTM. The minimum temperatures during the main maize growing period (November to March) for Experiment 2 were on average 1.2 °C lower than the LTM. Maximum temperatures were either within the LTM or

higher. April was the warmest month with the mean maximum temperature 3.5 °C higher than the LTM.

Monthly solar radiation receipts during Experiment 1 were close to the LTM during December, March and April. While November and January received about 50 MJ m⁻² more total solar radiation, there was a decline in February when a total of 440 MJ m⁻² was received compared with a LTM of 530 MJ m⁻² (Figure 3.1). Monthly solar radiation receipts during Experiment 2 were near the long term means between November and January. Only January and May had solar radiation levels below the LTM.

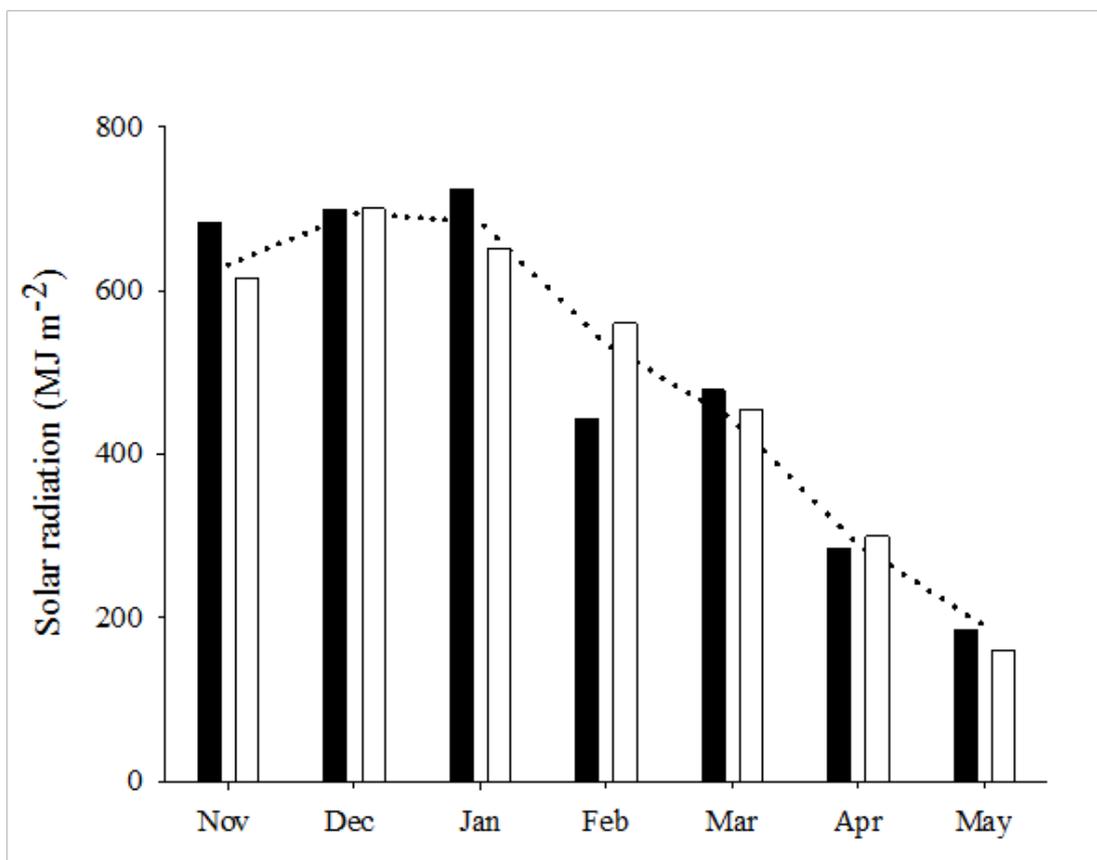


Figure 3.1: Incident solar radiation for November-May 2008/09 (■) and 2009/10 (□) recorded at Broadfields' meteorological station, Canterbury, New Zealand. The dotted line represents the long term mean (1975-2007).

The monthly Penman potential evapotranspiration (ET) (Penman 1948) during Experiment 1 was higher than the LTM in November and January because of the high temperatures recorded during that period (Figure 3.2). Penman potential ET was, however, near the LTM in

December, March, April and May but 24% lower than the LTM in February because of the high rainfall received and the reduced solar radiation. During Experiment 2, Penman potential ET in January and May was lower than the LTM but higher in March and April.

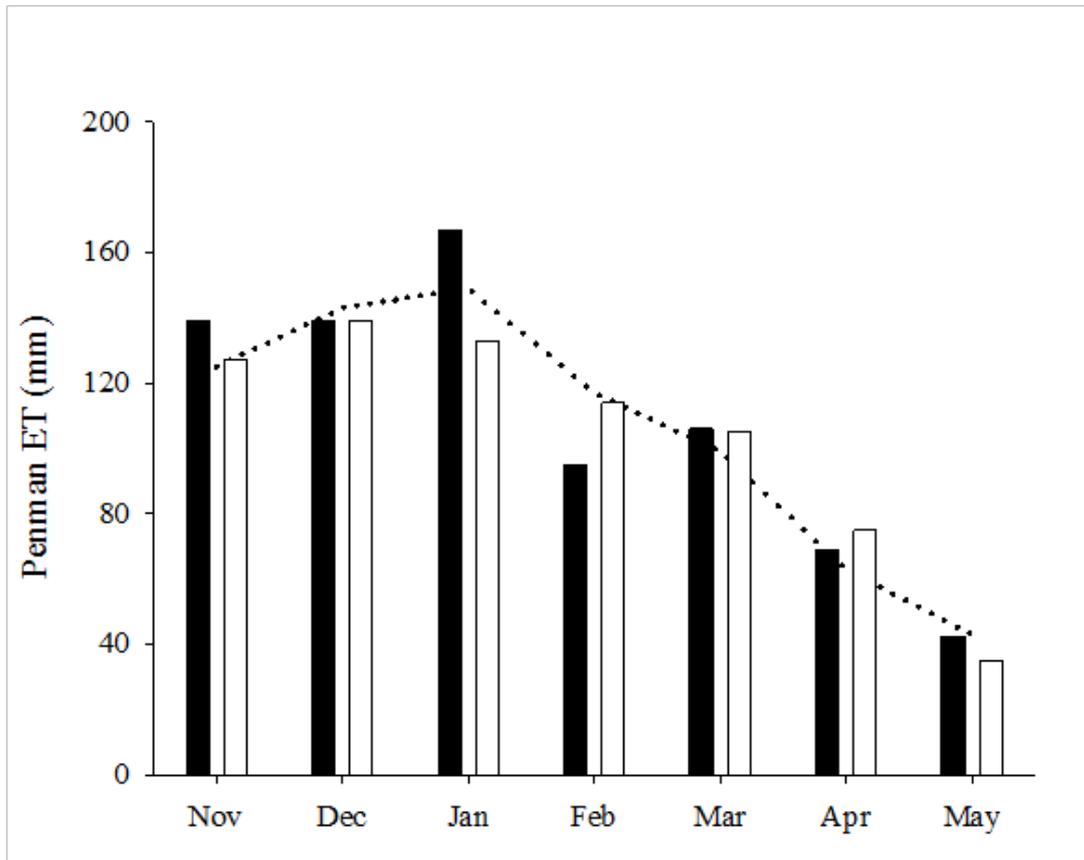


Figure 3.2: Penman potential evapotranspiration for November-May 2008/09 (■) and 2009/2010 (□) recorded at Broadfields' meteorological station, Canterbury, New Zealand. The dotted line represents the long term mean (1975-2007).

3.6 Calculations and data analyses for Experiments 1 and 2

3.6.1 Thermal time

Thermal time was calculated from air temperatures using the modified sine curve method (Jones & Kiniry 1986). This method uses the maximum and minimum daily temperatures to estimate interpolated temperatures at 3-h intervals throughout a 24 h period. This approach was justified because actual temperatures tend to vary around the daily mean according to an approximately sinusoidal curve (Bonhomme 2000a). Daily thermal units were accumulated from emergence (Section 3.23.2). Initially, a base temperature of 8 °C and a maximum of 34 °C (Jones & Kiniry 1986; Muchow & Carberry 1989) were used to accumulate thermal time (°C.d) from emergence up to silking. This however, yielded a faster leaf appearance rate per

unit of thermal time ($^{\circ}\text{C}\cdot\text{d}$) than observed because leaf appearance rate was not linearly related to thermal time ($^{\circ}\text{C}\cdot\text{d}$) at low temperature (Tollenaar *et al.* 1979; Warrington & Kanemasu 1983b). In addition, under exceptionally warm or cool soils, maize development was inadequately predicted when thermal time was calculated using a base temperature of 10°C (Section 2.3.2). Thermal time accumulation was therefore linearised between $0\text{-}18^{\circ}\text{C}$ as suggested by Wilson *et al.* (1995) for maize crops grown at this location.

3.6.2 Leaf appearance rate

The relationship between leaf appearance rates and thermal time was examined through linear regression. The slope of this relationship does not usually intercept the axes at the origin because the first leaf is well developed at germination due to its reliance on seed reserves (Gmelig Meyling 1973). Leaf tip appearance rates are therefore calculated as the slope of the linear regression between the numbers of emerged leaf tips against thermal time when constrained to intercept the y-axis at 1 (Warrington & Kanemasu 1983b). However, the last three leaves emerge at a faster rate and distort the linear relationship between number of leaf tips emerged or fully expanded leaves against thermal time (Section 2.3.2).

In this study a bilinear regression was fitted to the relationship between leaf appearance and thermal time using a series of dummy variables (Draper & Smith 1998). The maximum coefficient of determination (R^2) was used as the criterion to partition data points to the two line segments (Fletcher *et al.* 2008a).

3.6.3 Green area

Green area index (GAI) data were plotted against thermal time ($^{\circ}\text{C}\cdot\text{d}$) and a logistic function was fitted to the relationship until silking. To examine the possibility of differences in leaf size among the hybrids, one of the three plants harvested from each plot immediately after silking (when all leaves were fully expanded) was isolated. A plot of the measured area against calculated area was used to derive a constant that was used to estimate leaf area from length and maximum width measurements (McKee 1964). Using the derived constant, the green leaf area per plant (Experiment 1) or per leaf position (Experiment 2) was determined for all tagged plants.

3.6.4 Light interception

The fraction of intercepted PAR (τ) was derived following the method of Gallagher and Biscoe (1978) and shown by Equation 3.1.

$$\tau = 1.0 - \beta \quad \text{Equation 3.1}$$

Where, β is the fraction of PAR transmitted.

Incident PAR ($\text{MJ m}^{-2}\text{d}^{-1}$) was assumed to equal 0.5 of total incident short wave radiation (Monteith 1977). Total iPAR was estimated following the procedure of O'Connell *et al.* (2004). Briefly, daily estimates of τ between emergence and physiological maturity were made by linear interpolation of the instantaneous measures of τ with respect to time. Then, daily intercepted PAR (iPAR_d) was calculated using Equation 3.2.

$$\text{iPAR}_d = \tau * \varphi \quad \text{Equation 3.2}$$

Where, φ is the daily incident PAR.

Daily iPAR was then summed from emergence to physiological maturity to obtain the total iPAR.

3.6.5 Water budget

The potential soil moisture deficit (PSMD) approach was used to calculate the severity of moisture stress experienced by the crop during the growing season (Section 2.3.4.6). Potential deficits were calculated on a daily time step using the method of Stone *et al.* (2001a) as shown in Equation 3.3.

$$Dp = \Sigma PET - (\Sigma R + \Sigma I) + Ds \quad \text{Equation 3.3}$$

Where, Dp = potential soil moisture deficit, ΣPET = total Penman potential evapotranspiration, ΣR = total rain fall from emergence, ΣI = total irrigation from emergence and Ds = potential deficit at emergence.

In this approach, *PET* was adjusted for ground cover following the method of French and Legg (1979). Briefly, when ground cover was less than 50%, *PET* was equal to the mean of the evapotranspiration rate (ET) and evaporation rate (*E_s*). For ground cover more than 50%, *PET* was assumed to equal ET. Ground cover was estimated using Equation 3.4 (Jamieson *et al.* 1995b).

$$\Theta = e^{-kGAI} \quad \text{Equation 3.4}$$

Where Θ is the proportion of ground cover and *k* the extinction coefficient for total solar radiation which was assumed to equal 0.4 (Muchow *et al.* 1990).

The evaporation rate was calculated following the two step process of Ritchie (1972). In this method, rain or irrigation of more than 3 mm (Jamieson *et al.* 1984) was assumed to be freely available in the two days following the event, hence, evaporation occurred at the potential Penman rate (Fletcher 2005; Jamieson *et al.* 1984). Subsequently, evaporation was controlled by the soil hydraulic properties and was calculated as the minimum of either the potential rate or that derived using Equation 3.5 (Ritchie 1972).

$$E_s = \alpha \sqrt{t} - \alpha \sqrt{(t - 1)} \quad \text{Equation 3.5}$$

Where, *E_s* is the evaporation rate, *t* is the time (days) after soil wetting and α is the soil diffusivity constant which was assumed to equal 4.2 mm/ \sqrt{t} (Stone *et al.* 2001a).

In this study, irrigation water was supplied to avoid the critical deficit (*D_c*) which was assumed to equal 60% of total available water content (Carcova *et al.* 1998). This proportion was considered an average value between 50% (Stone *et al.* 2001a) and 70% (Muchow & Sinclair 1991). Total available water was assumed to be 250 mm/ m of soil (McKenzie 1987). All irrigated treatments received the same amount of water based on the requirements of the most depleted plot. The slight water stress experienced during early vegetative growth (<400 °C.d) was occasioned by the delay in the installation of Neutron access tubes and having to rely on TDR measurements (0–0.2 m). It was, however, considered not to have affected growth since Muchow and Sinclair (1991), reported no effect on leaf area development until 70% of transpirable water had been exhausted.

It was assumed that drainage did not occur because water applied through T-tape was at a rate below the infiltration capacity of the soil (Anwar *et al.* 2000). In Experiment 1, Dp at emergence was assumed to be zero due to soil moisture recharge during spring. The maximum Dp (Dp_{max}) experienced by the rain fed crops was 110 mm above Dc (Figure 3.3). The irrigated plots received a total of 300 mm (Table 3.4).

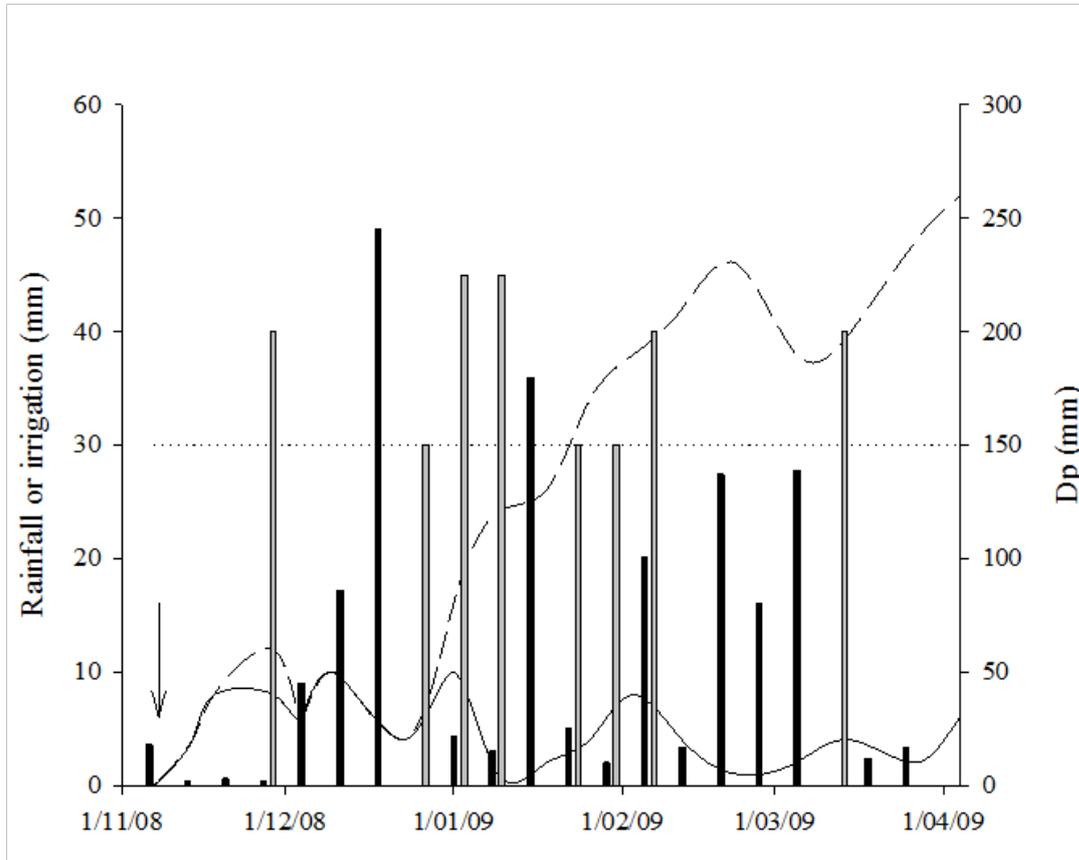


Figure 3.3: The weekly water budget for the maize crops grown in Experiment 1 at Lincoln University, New Zealand, during 2008 and either rain fed (dashed line) or fully irrigated (solid line). Rainfall (■), irrigation (▨), Dp at emergence (arrow) and the critical deficit (Dc) (dotted line) are also indicated.

Table 3.4: Total amount of water (mm) applied to the irrigated maize crops grown in Experiment 1 at Lincoln University, New Zealand, during 2008.

Year	2008		2009					Total	
Date	28/11	28/12	1/1	7/1	25/1	3/2	11/2	17/3	(mm)
Amount (mm)	40	30	45	45	30	30	40	40	300

Experiment 2 was grown under a drier environment, however as in Experiment 1 Dp was assumed to be zero at emergence (Figure 3.4). A total of 290 mm of irrigation water was supplied during this season (Table 3.5) and the Dp_{max} was 100 mm above Dc .

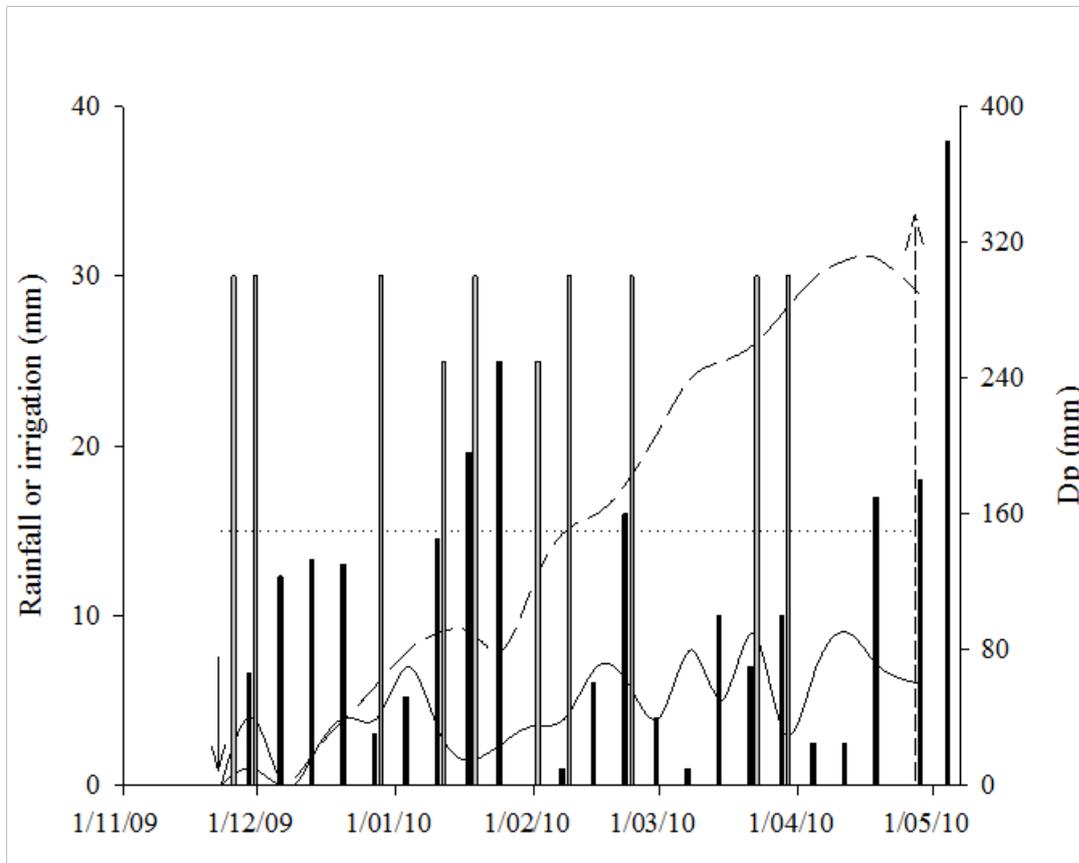


Figure 3.4: The weekly water budget for the maize crops grown in Experiment 2 at Lincoln University, New Zealand, during 2009 fully irrigated (solid line). Rainfall (■), irrigation (▨), Dp at emergence (solid arrow) and the critical deficit (Dc) (dotted line) are also indicated. The dashed line indicates the maximum deficit (Dp_{max}) and the arrow physiological maturity.

Table 3.5: Total amount of water (mm) applied to all maize crops grown in Experiment 2 at Lincoln University, New Zealand, during 2009.

Year	2009			2010							Total
Date	27/11	1/12	30/12	8/1	18/1	5/2	12/2	25/2	20/3	30/3	(mm)
Amount (mm)	30	30	30	25	30	25	30	30	30	30	290

3.6.6 Dry matter

Dry matter accumulation during the growing season was described using a logistic growth function. The logistic growth function described the pattern of observed growth with a higher R^2 and lower SE compared with the generalised logistic function (Clewer & Scarisbrick 2001). The logistic curve is also frequently used to describe growth (Weaich *et al.* 1996), with distinct phases (Egli 1998) that characterize the pattern of observed growth. Specifically, a lag phase of establishment (Wilson *et al.* 1995), was followed by a period of rapid growth commonly referred to as the exponential growth phase. During this period growth is dependent on the availability of resources (e.g. nutrients), and the efficiency (e.g. RUE) of the growth machinery (Muchow *et al.* 1990). There is then a limited asymptotic phase (Thornley & France 2007) which is consistent with the continuous smooth sigmoid growth behaviour associated with logistic growth function.

The logistic curve used to describe the relationship between dry matter and thermal time was of the form shown in Equation 3.6 (Loss *et al.* 1989).

$$Y = A + \frac{C}{(1 + e^{(-B(X-M))})} \quad \text{Equation 3.6}$$

Where:

A = starting point of the curve (0 kg biomass ha⁻¹) at time 0.

C = maximum biomass (Y) value (kg biomass ha⁻¹)

B = rate of increase of dry matter

M = point of maximum growth rate (kg ha⁻¹ °C.d).

X = thermal time (°C.d).

The DUR (°C.d) of linear growth represents the period over which the crop accumulated 5-95% of its dry matter. It was derived as shown by Equation 3.7 (Loss *et al.* 1989):

$$\text{DUR} = 6/B \quad \text{Equation 3.7}$$

3.6.7 Statistical analyses

Statistical analyses used Genstat 12, release 12.1 (Lawes Agricultural Trust, Rothamsted experimental station, UK, 2009). All variates were analysed using ANOVA procedures in a split plot (2008/09) and randomised complete block (2009/10) design structure. Fisher's protected least significant difference ($p < 0.05$) was used to separate means. Where mean data are reported, the pooled standard error of the mean is used. However, for significant two way interactions, the most conservative standard error of the mean was used. Error bars were indicated only where treatments differed.

Chapter 4

Dry matter accumulation and yield formation in maize hybrids differing in 'stay-green' rating

4.1 Introduction

Dry matter accumulation and its distribution into the harvestable part of the crop are the major drivers of yield (Tollenaar *et al.* 1994). In this study the influence of hybrid 'stay-green' rating on dry matter accumulation and yield was examined and quantified, because differences in chlorophyll retention among the hybrids (Table 3.2) could influence dry matter accumulation. In theory, the hybrids that retain more leaves during the post-silking development stage should intercept more PAR and hence, accumulate more dry matter (Muchow *et al.* 1990). With a stable crop harvest index (Bänziger *et al.* 2002; Echarte & Andrade 2003), these hybrids are anticipated to yield more.

Grain yield and crop biomass from Experiment 1 are reported in this chapter. The amount of dry matter (DM) accumulated by four maize hybrids of different 'stay-green' rating during the 2008/09 growing season is quantified in response to nitrogen and water treatments. Accumulated dry matter is partitioned into the leaves, stalk, non kernel ear components (husks, rachis and ear shank) and kernels. Logistic growth functions were fitted to within season accumulated dry matter of each component to derive a mathematical summary of the growth rates for comparison of maize hybrid, nitrogen fertiliser and irrigation effects.

4.2 Materials and Methods

The materials and methods for this section were described in Section 3.2. Split applications of N at V3 and V6 were used for the N fertilised treatments. For moisture, a total of 300 mm of water was applied to the irrigated crops with at least 50% of the total available soil moisture content maintained in the top 0.2 m of the profile.

4.3 Measurements

Dry matter accumulation was monitored by harvesting all above ground dry matter at 10-14 day intervals from 3 randomly selected contiguous plants. The total dry matter yield for each sample date was derived from these measurements multiplied by the plant population (Section 3.4). Accumulated dry matter and yield components at the last harvest were determined as described in Section 3.4.5.

4.4 Calculations and data analyses

Calculations and data analyses for this chapter were described in Section 3.6.

4.5 Results

There were no significant three way (N x water x hybrid) interactions between the treatments for grain and biomass yield.

4.5.1 Final yield

Total crop dry matter increased ($P < 0.001$) from 14.0 to 24.2 t ha⁻¹ with the addition of N (Table 4.1). Total crop dry matter (t ha⁻¹) also increased ($P < 0.012$) from 16.5 to 21.7 t ha⁻¹ with applied irrigation. Grain yield (t ha⁻¹) increased ($P < 0.05$) from 6.9 to 12.2 t ha⁻¹ with added N and from ($P < 0.050$) 8.2 to 11.0 t ha⁻¹ when irrigation water was provided. Total crop dry matter (t ha⁻¹) did not differ ($P < 0.535$) among the hybrids at final harvest and varied between 19.7 and 18.5 (± 0.99) t ha⁻¹ across treatments. Grain yield was also unaffected ($P < 0.361$) by hybrid 'stay-green' rating and averaged 9.6 (± 0.22) t ha⁻¹.

4.5.2 Crop harvest index (HI)

The crop harvest index (HI) was influenced by a water x N interaction (Table 4.2). Irrigation increased ($P < 0.001$) the crop HI from 0.44 to 0.48 without added N but with N applied irrigation had no effect (~ 0.50). The crop HI was also influenced by the hybrid x N interaction. The harvest index increased ($P < 0.027$) from 0.46 to at least 0.50 by additional N in all hybrids except 'P38G43' (sgr 9).

Table 4.1: Mean total crop dry matter (t ha⁻¹) and grain yield (t ha⁻¹) at final harvest of four maize hybrids grown with 0 or 270 kg N ha⁻¹ when rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Treatment	Total crop dry matter (t ha ⁻¹)			Grain yield (t ha ⁻¹)		
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean
Rain fed	12.1	20.9	16.5	5.6	10.7	8.2
Irrigated	15.8	27.5	21.7	8.3	13.7	11.0
Mean	14.0	24.2	19.1	6.9	12.2	9.6
P value	P<0.001		P<0.012	P<0.001		P<0.050
SE	0.70		0.40	0.40		0.17
CV (%)	17.9			15.7		

Table 4.2: Crop harvest index of four maize hybrids grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

kg N ha ⁻¹	Crop harvest index					
	Hybrid				Water	
	'P39K38' (sgr 6)	'P38V12' (sgr 7)	'P38F70' (sgr 8)	'P38G43' (sgr 9)	Rain fed	Irrigated
0	0.46	0.46	0.46	0.47	0.44	0.51
270	0.50	0.51	0.51	0.49	0.48	0.50
P value	P<0.027				P<0.001	
SE	0.006				0.004	
CV (%)	3.1					

4.5.3 Yield components

4.5.3.1 Kernel weight per ear (g)

The kernel weight per ear increased ($P<0.001$) from 80 (± 4.1) g to 130 (± 4.1) g when 270 kg N ha⁻¹ was applied. It also showed a tendency ($P<0.054$) to increase with irrigation from 88 (± 1.9) g to 119 (± 1.9) g. Kernel weight per ear (g), however, did not differ among the hybrids ($P<0.361$) and was 103.6 (± 5.80) g.

4.5.3.2 Number of kernels per ear

The number of kernels per ear was influenced by all treatment factors but not their interaction (Table 4.3). It increased ($P < 0.001$) from 290 to 430 with addition of N, and from 320 to 390 ($P < 0.030$) with applied irrigation. Among the hybrids, 'P38V12' (sgr 7) filled 21% more ($P < 0.003$) kernels per ear than the other hybrids.

Table 4.3: Number of kernels per ear of four maize hybrids grown with 0 or 270 kg N ha⁻¹ and either rainfed or irrigated at Lincoln University, New Zealand, during 2008.

Hybrid	Number of kernels per ear				Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Rain fed	Irrigated	
'P39K38' (sgr 6)	270	400	310	360	340 _b
'P38V12' (sgr 7)	340	480	360	450	410 _a
'P38F70' (sgr 8)	240	430	300	380	340 _b
'P38G43' (sgr 9)	290	390	300	380	340 _b
Mean	290	430	320	390	360
P value	$P < 0.001$		$P < 0.030$		$P < 0.003$
SE	10.2		9.5		14.4
CV (%)	14.0				

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

4.5.3.3 Seed weight

Seed weight was influenced by a hybrid x N interaction (Table 4.4). The seed weight (mg) of 'P38F70' (sgr 8) increased ($P < 0.034$) by 11% when N was provided compared with between 26 and 30% for the other hybrids. Seed weight was also increased ($P < 0.025$) by irrigation from 270 to 290 mg. Among the hybrids, 'P38V12' (sgr 7) had the lowest ($P < 0.001$) seed weight.

Table 4.4: Individual grain weight (mg) of four maize hybrids grown with 0 or 270 kg N ha⁻¹ and either rain fed or fully irrigated at Lincoln University, New Zealand, during 2008.

Hybrid	Seed weight (mg)				Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Rain fed	Irrigated	
‘P39K38’ (sgr 6)	270	340	290	320	310 _a
‘P38V12’ (sgr 7)	210	270	230	250	240 _c
‘P38F70’ (sgr 8)	280	310	290	310	300 _a
‘P38G43’ (sgr 9)	230	300	250	280	270 _b
Mean	250	310	270	290	280
P value	P<0.034		P<0.025		P<0.001
SE	5.7		2.6		5.7
CV (%)	7.1				

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

4.5.4 Non kernel ear dry matter

The non kernel ear dry matter (rachis, husks and ear shank) (t ha⁻¹) was influenced by all treatment factors (Table 4.5). They increased (P<0.001) from 2.2 to 3.8 t ha⁻¹ with additional N and from 2.6 to 3.4 t ha⁻¹ with irrigation.

Table 4.5: The non kernel ear dry matter (t ha⁻¹) of maize hybrids grown with 0 or 270 kg N ha⁻¹ and either rainfed or irrigated at Lincoln University, New Zealand, during 2008.

Hybrid	Non kernel ear dry matter (t ha ⁻¹)				Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Rain fed	Irrigated	
‘P39K38’ (sgr 6)	2.7	5.0	3.6	4.0	3.8 _a
‘P38V12’ (sgr 7)	2.2	3.2	2.2	3.2	2.7 _b
‘P38F70’ (sgr 8)	2.1	3.4	2.2	3.3	2.8 _b
‘P38G43’ (sgr 9)	1.8	3.7	2.2	3.3	2.8 _b
Mean	2.2	3.8	2.6	3.5	3.0
P value	P<0.001		P<0.023		P<0.006
SE	0.15		0.02		0.22
CV (%)	20.6				

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

The non kernel ear component also differed ($P < 0.006$) among hybrids with ‘P39K38’ (sgr 6) having 3.8 t ha^{-1} which was 36% more non kernel ear dry matter than other hybrids.

4.5.5 Dry matter accumulation

4.5.5.1 Duration to silking and physiological maturity

Silking was earlier ($P < 0.001$) at $690 \text{ }^{\circ}\text{C.d}$ after emergence in ‘P39K38’ (sgr 6) compared with $730 \text{ }^{\circ}\text{C.d}$ in both ‘P38V12’ (sgr 7) and ‘P38G43’ (sgr 9). Application of N fertiliser also hastened ($P < 0.001$) silking by $20 \text{ }^{\circ}\text{C.d}$ (700 vs. $720 \text{ }^{\circ}\text{C.d}$ after emergence), while irrigation had no effect ($P < 0.425$) on the duration to silking. From the fitted logistic function (Section 3.6.6), physiological maturity was determined retrospectively as the time of maximum dry matter accumulation ($1470 \text{ }^{\circ}\text{C.d}$ after emergence) which also coincided with time of maximum kernel dry weight.

4.5.5.2 Total dry matter

There were no hybrid differences in the pattern of dry matter accumulation. Hence, the temporal partitioning of the accumulated total dry matter was compared between the fertilised and non fertilised irrigated treatments of each hybrid and illustrated for ‘P39K38’ (sgr 6) and ‘P38G43’ (sgr 9) in Figure 4.1. Data for the other two hybrids (‘P38V12’ (sgr 7) and ‘P38F70’ (sgr 8)) showed a similar trend and are presented in Appendix 1. These data showed that at silking ($710 \text{ }^{\circ}\text{C.d}$), the non fertilised crops had accumulated 5.7 t ha^{-1} , compared with 8.1 t ha^{-1} for the fertilised crops. Accumulated total dry matter then increased ($P < 0.001$) from 16.3 to $28.0 (\pm 0.94) \text{ t ha}^{-1}$, at physiological maturity for the non-fertilised and fertilised crops, respectively.

As a main effect, water had no influence on the mean maximum total crop dry matter accumulated during the vegetative growth stage (Figure 4.2). However, at physiological maturity, the irrigated crops had accumulated on average 4.0 t ha^{-1} more ($P < 0.043$) dry matter than the rain fed crops.

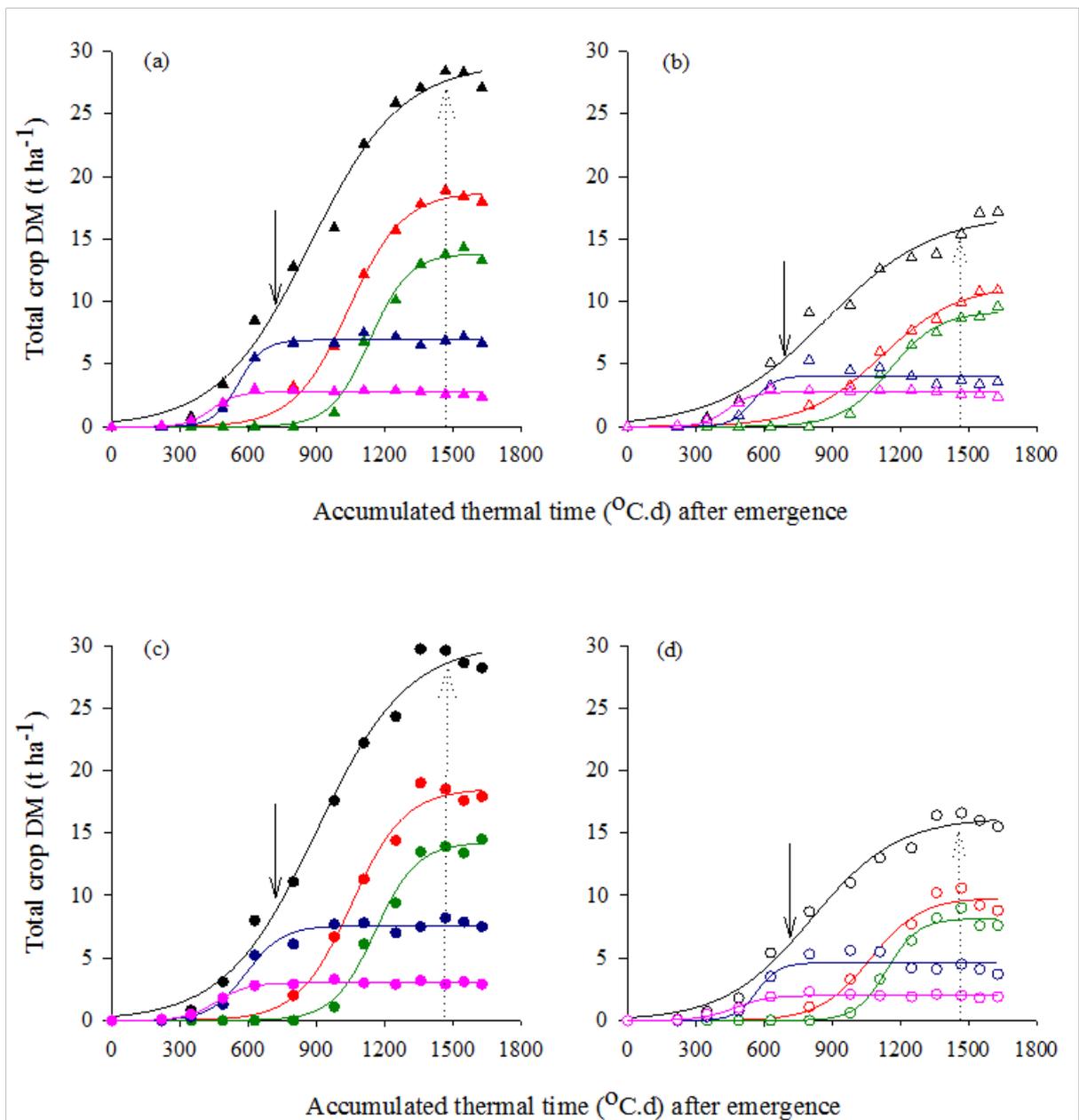


Figure 4.1: Accumulated dry matter (t ha^{-1}) for total crop (black), ears (red), kernels (dark green), stalks (dark blue) and leaves (pink) in fully irrigated crops of ‘P39K38’ (sgr 6) (a and b) and ‘P38G43’ (sgr 9) (c and d), grown at Lincoln University, New Zealand, during 2008. The crops either received 270 (closed symbols) or 0 kg N ha^{-1} (open symbols). The solid arrow represents silking and the dotted physiological maturity (1470 °C.d).

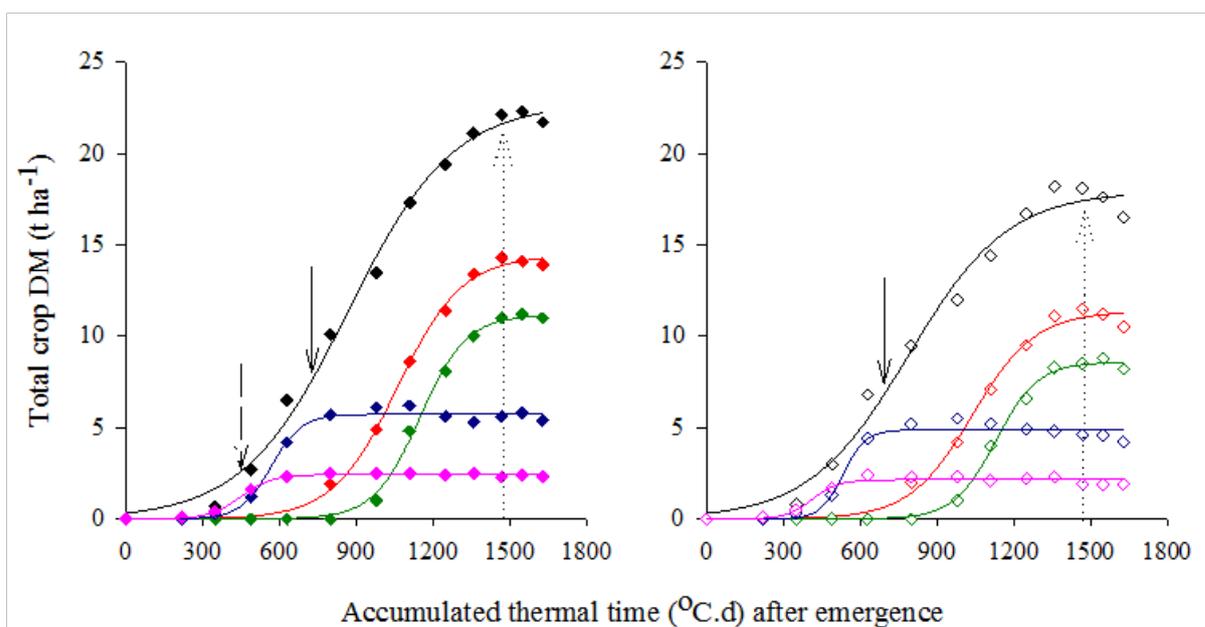


Figure 4.2: Mean accumulated dry matter (t ha^{-1}) of both levels of N for total crop (black), ears (red), kernels (dark green), stalks (dark blue) and leaves (pink) in fully irrigated (closed symbols) and rain fed (open symbols) crops grown at Lincoln University, New Zealand, during 2008. The dashed arrow shows the start of irrigation, the solid silking and the dotted physiological maturity ($1470\text{ }^{\circ}\text{C.d}$).

4.5.5.3 Leaf dry matter

The DUR ($^{\circ}\text{C.d}$) of linear accumulation of leaf dry matter only differed ($P < 0.015$) among hybrids (Table 4.6). ‘P38G43’ (sgr 9) took longer to accumulate 95% of its total leaf dry matter ($480\text{ }^{\circ}\text{C.d}$) compared with ‘P38F70’ (sgr 8) ($350\text{ }^{\circ}\text{C.d}$) and ‘P39K38’ (sgr 6) ($390\text{ }^{\circ}\text{C.d}$). Both N ($P < 0.129$) and water ($P < 0.241$) had no effect on the DUR ($^{\circ}\text{C.d}$) of linear accumulation of leaf dry matter with a mean of $420 (\pm 20.7)\text{ }^{\circ}\text{C.d}$.

The mean maximum leaf dry matter (t ha^{-1}) was recorded $800\text{ }^{\circ}\text{C.d}$ after emergence (Figure 4.1) and increased ($P < 0.001$) from 2.1 to 2.8 t ha^{-1} with added N (Table 4.7). Mean maximum leaf dry matter (t ha^{-1}) was also 23% greater ($P < 0.001$) in ‘P38V12’ (sgr 7) compared with ‘P38F70’ (sgr 8). Irrigation did not affect ($P < 0.328$) the mean maximum leaf dry matter which averaged $2.4 (\pm 0.11)\text{ t ha}^{-1}$.

Table 4.6: The DUR (°C.d) of linear accumulation of leaf dry matter (5-95% of maximum) in four maize hybrids grown at Lincoln University, New Zealand, during 2008.

Hybrid	Duration of linear growth (°C.d)
'P39K38' (sgr 6)	390 _{bc}
'P38V12' (sgr 7)	450 _{ab}
'P38F70' (sgr 8)	350 _c
'P38G43' (sgr 9)	480 _a
P value	P<0.015
SE	29.2
CV (%)	24.2

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

Table 4.7: The mean maximum leaf dry matter (t ha⁻¹) of maize hybrids grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Hybrid	Mean maximum leaf dry matter (t ha ⁻¹)		
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean
'P39K38' (sgr 6)	2.1	2.8	2.5 _b
'P38V12' (sgr 7)	2.2	3.2	2.7 _a
'P38F70' (sgr 8)	1.8	2.6	2.2 _c
'P38G43' (sgr 9)	2.1	2.7	2.4 _{bc}
Mean	2.1	2.8	2.5
P value	P<0.001		P<0.001
SE	0.05		0.07
CV (%)	9.6		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

4.5.5.4 Stalk dry matter

Maximum stalk dry matter (t ha⁻¹) was recorded 980 °C.d after emergence (Figure 4.1), when the N fertilised crops had accumulated (P<0.001) 6.5 (\pm 0.13) t ha⁻¹ compared with 5.0 (\pm 0.13) t ha⁻¹ in the unfertilised crops (Table 4.8). 'P38G43' (sgr 9) accumulated 17% more (P<0.008) stalk dry matter (t ha⁻¹) than 'P39K38' (sgr 6) with the other two hybrids intermediary.

Table 4.8: Maximum accumulated stalk dry matter (t ha⁻¹) in four maize hybrids grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Hybrid	Maximum stalk DM (t ha ⁻¹)		Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	
‘P39K38’ (sgr 6)	4.5 _c	6.2 _b	5.4 _c
‘P38V12’ (sgr 7)	5.2 _{ab}	6.8 _a	6.0 _{ab}
‘P38F70’ (sgr 8)	5.0 _b	6.1 _b	5.6 _{bc}
‘P38G43’ (sgr 9)	5.4 _a	6.9 _a	6.2 _a
Mean	5.0	6.5	5.8
P value	P<0.001		P<0.008
SE	0.18		0.13
CV (%)	10.6		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

At physiological maturity, stalk dry matter (t ha⁻¹) increased (P<0.001) from 3.9 to 6.3 t ha⁻¹ with added N while it was 28% heavier (P<0.018) for ‘P38G43’ (sgr 9) than ‘P39K38’ (sgr 6) (Table 4.9). Irrigation did not affect (P<0.115) the stalk dry matter at physiological maturity which averaged 5.1 (± 0.20) t ha⁻¹.

Table 4.9: Stalk dry matter (t ha⁻¹) at physiological maturity (1470 °C.d) in four maize hybrids grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Hybrid	Stalk dry matter (t ha ⁻¹)		Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	
‘P39K38’ (sgr 6)	3.3 _c	5.8 _b	4.6 _b
‘P38V12’ (sgr 7)	3.9 _b	6.3 _b	5.1 _{ab}
‘P38F70’ (sgr 8)	3.9 _b	5.9 _b	4.9 _b
‘P38G43’ (sgr 9)	4.5 _a	7.2 _a	5.9 _a
Mean	3.9	6.3	5.1
P value	P<0.001		P<0.018
SE	0.19		0.28
CV (%)	18.7		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

4.5.5.5 Ear DM

The relationship between ear dry matter (t ha^{-1}) accumulation and thermal time ($^{\circ}\text{C.d}$) had an initial lag phase, before it increased rapidly over the linear phase at a mean rate of 18.8 kg ha^{-1} per $^{\circ}\text{C.d}$ for $700 (\pm 18.1) ^{\circ}\text{C.d}$ (Figure 4.1 and 4.2). A maximum ear dry matter of $16.9 (\pm 0.46) \text{ t ha}^{-1}$ was achieved in the presence of N compared with $8.9 (\pm 0.46) \text{ t ha}^{-1}$ when no N was applied. Irrigation also increased ($P < 0.022$) the maximum ear dry matter from $11.1 (\pm 0.32)$ to $14.7 (\pm 0.32) \text{ t ha}^{-1}$. However, it did not differ ($P < 0.801$) among the hybrids and averaged $12.9 (\pm 0.65) \text{ t ha}^{-1}$.

Total crop dry matter (t ha^{-1}) after silking was strongly related to ear dry matter (Figure 4.3a). Ears began to develop when the fertilised crops had accumulated 9.3 t ha^{-1} compared with 6.9 t ha^{-1} for the unfertilised crops. Greater remobilization of crop dry matter occurred with no applied N as demonstrated by the difference ($P < 0.001$) in the slope of the regression of total dry matter on ear dry matter. Remobilization of crop dry matter into the ear also differed ($P < 0.045$) between the water treatments (Figure 4.3b).

4.5.5.6 Grain growth

In all hybrids, kernel dry matter accumulation (t ha^{-1}) against thermal time ($^{\circ}\text{C.d}$) followed a characteristic sigmoid growth pattern (Figure 4.1 and Appendix 1). Maximum kernel dry matter (t ha^{-1}) was recorded at physiological maturity and was increased ($P < 0.001$) from 7.1 to $12.4 (\pm 0.51) \text{ t ha}^{-1}$ by the addition of N. Applied irrigation also increased ($P < 0.033$) the maximum kernel dry matter from 8.2 to $11.3 \text{ t ha}^{-1} (\pm 0.31)$. However, it did not differ ($P < 0.325$) among the hybrids and averaged $9.8 (\pm 0.71)$. Total kernel dry matter (t ha^{-1}) was strongly related ($R^2 = 0.98$) to total crop dry matter (t ha^{-1}) in the N fertilised crop but the relationship was weaker ($R^2 = 0.87$) for the non-fertilised crops (Figure 4.4a). Kernel dry matter (t ha^{-1}) was also strongly related ($R^2 = 0.99$) to ear dry matter (t ha^{-1}) and kernels began to grow rapidly when the ears had accumulated 4.8 t ha^{-1} in the fertilised crops and 2.4 t ha^{-1} in the unfertilised crops, respectively (Figure 4.4b).

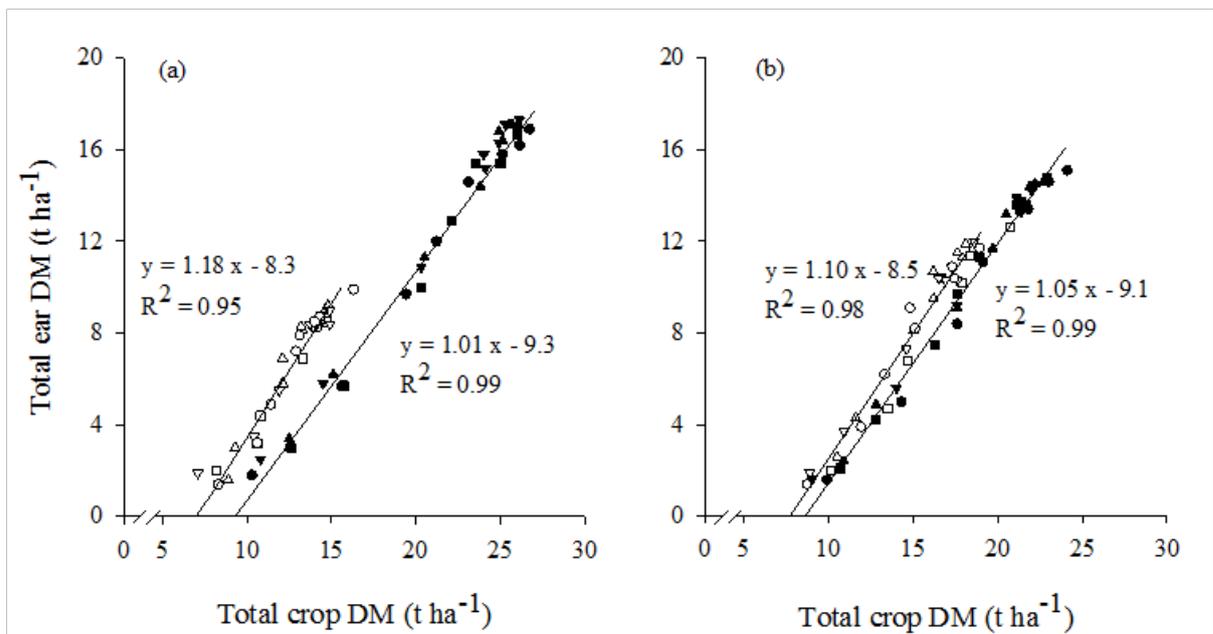


Figure 4.3: Ear dry matter (t ha^{-1}) versus total crop dry matter (t ha^{-1}) for ‘P39K38’ (sgr 6) (Δ), ‘P38V12’ (sgr 7) (\square), ‘P38F70’ (sgr 8) (∇) and ‘P38G43’ (sgr 9) (\circ) maize hybrids grown with (a) 0 (open symbols) or with 270 kg N ha^{-1} (closed symbols) and (b) irrigated (closed symbols) or rain fed (open symbols) at Lincoln University, New Zealand, during 2008.

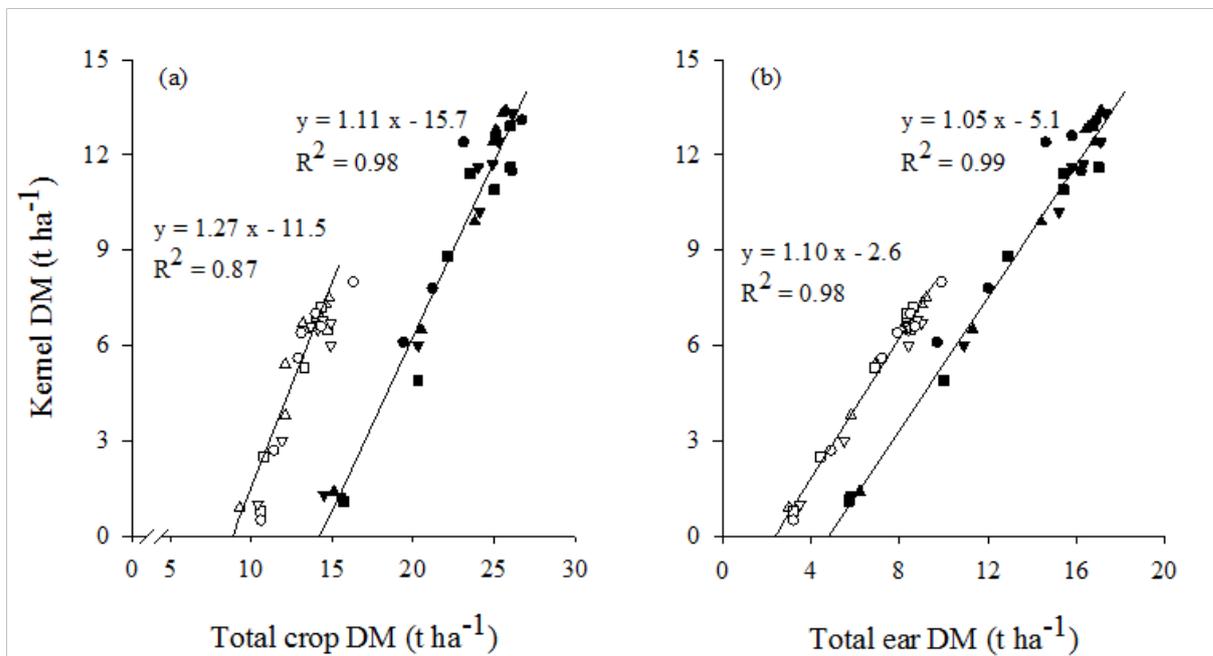


Figure 4.4: Kernel dry matter (t ha^{-1}) versus (a) total dry matter (t ha^{-1}) and (b) total ear dry matter (t ha^{-1}) for ‘P39K38’ (sgr 6) (Δ), ‘P38V12’ (sgr 7) (\square), ‘P38F70’ (sgr 8) (∇) and ‘P38G43’ (sgr 9) (\circ) maize hybrids grown with 0 (open symbols) or 270 kg N ha^{-1} (closed symbols) at Lincoln University, New Zealand, during 2008.

4.6 Discussion

4.6.1 Total crop DM and grain yield (t ha^{-1})

Total accumulated dry matter and grain yield (t ha^{-1}) did not differ amongst the hybrids at physiological maturity (Sections 4.5.5.1 and 4.5.5.6), which suggests a similar pattern of dry matter accumulation. This was in contrast with the anticipated greater yield from the high ‘stay-green’ hybrids (Section 2.6) because of their lengthened leaf area duration and expected greater PAR interception (Section 2.3.4.1). It appears that the ‘stay-green’ trait did not lengthen the leaf area duration or that the photosynthetic efficiency of the leaves may have declined by the time the extra PAR was intercepted. Alternatively, the low ‘stay-green’ hybrids (sgr 6 and 7) may have altered their temporal and spatial pattern of PAR interception and compensated for the reduction in leaf area duration. These scenarios will be examined further in Chapters 5-7.

In contrast, total accumulated dry matter and grain yield at final harvest was increased by the addition of N (Table 4.1). The influence of N on grain yield was related to an improved harvest index (Table 4.2), increased number of kernels per ear (Table 4.3) and heavier kernels (Table 4.4). These findings are consistent with those of Vos *et al.* (2005) and Muchow and Davies (1988) who all obtained increased dry matter yield with N application in maize.

To explain the effect of water deficits on dry matter accumulation and partitioning (Figure 4.2), a quantitative measure of drought severity was necessary (Section 2.3.4.6). In Experiment 1, the rain fed crops experienced water stress from late December, 2008 (~ 500 °C.d), and reached a maximum potential soil moisture deficit ($D_{p_{\max}}$) of 380 mm at the end of the season (Figure 3.3). This was 230 mm above the critical deficit (D_c) of 150 mm (Section 3.6.5). Because this water stress developed towards the end of the period of leaf area development, leaf and stalk dry matter accumulation were unaffected (Section 4.5.5.2 and 4.5.5.3). However, ear and kernel dry matter were increased by irrigation (Sections 4.5.5.5 and 4.5.5.6), which suggests that water stress influenced total dry matter through kernel growth rates. Further evidence to support this observation was derived from the enhanced crop harvest index (Table 4.2) and number of kernels per ear in the irrigated crops (Table 4.3). Over all, the results from this study were similar with those of Jamieson and Francis (1991) who obtained a dry matter increase from 15.2 to 20.6 t ha^{-1} and grain yield increase from 9.5 to 11.5 t ha^{-1} , respectively with irrigation in their crop of maize.

4.6.2 Crop harvest index

Crop harvest index did not differ among the hybrids and the mean of 0.48 (\pm 0.010) recorded was consistent with a stable harvest index in maize (Bänziger *et al.* 2002). Crop harvest index was influenced by the interaction of water and N (Table 4.2). The crop harvest index was highest when additional N was provided without irrigation. Two factors may have been responsible for this observation. First, the unusually high rainfall received in February (Figure 3.3) coincided with the start of grain filling; a period that has been reported to be critical for yield development in maize (Andrade *et al.* 2002). Cakir (2004), reported increments in the seed weight of a water stressed crop of maize that received a single or double irrigation during grain filling and attributed this to the greater filling of fewer grains that had been set. Secondly, the water stressed crops remobilised proportionately more dry matter towards grain filling (Figure 4.3b). This observation was consistent with the work of Sadras *et al.* (1993) in sunflower (*Helianthus annuus* L.) and Westgate (1994) in maize who have also reported a strong dependence of seed filling on remobilised dry matter in water stressed plants.

Crop harvest index also declined when the crops were fertilised and irrigated. Total dry matter at final harvest for the fertilised and irrigated crops was 32% higher than the fertilised but unirrigated crops (Table 4.1). A large biomass in maize has been associated with increased respiratory costs (Cirilo & Andrade 1994) due to the increase in maintenance respiration (Amthor 2000). Similarly, Fletcher and Jamieson (2009), also observed a negative linear relationship between the rate of change of harvest index and biomass in wheat.

4.6.3 Number of kernels per ear and the seed weight (mg)

The number of kernels per ear was increased by both additional N and irrigation (Table 4.3) as a consequence of more kernels being initiated and filled. Both kernel set and the quantity of assimilate partitioned to the kernels during the post-silking growth phase determine the number of kernels per ear and hence yield (Cirilo & Andrade 1994; Otegui & Bonhomme 1998). Water stress and nutrient deficiency have both been reported to lengthen the anthesis silking interval so that pollen was shed before the silks were receptive which increases the number of unfertilised florets (Section 2.4.2).

Seed weight was inversely related to kernel number per ear (Table 4.4). 'P38V12' (sgr 7) set a larger number of kernels but had the lowest seed weight. This was consistent with yield component compensation and the inherent plasticity in the determination of grain yield in cereals (Hay 1999; Tollenaar & Dwyer 1999).

4.6.4 Non kernel ear dry matter (t ha^{-1})

The large proportion of dry matter partitioned to the non kernel ear fraction in 'P39K38' (sgr 6) compared with the other hybrids (Table 4.5), may indicate a hybrid variation in the partitioning of assimilate during grain filling (Tollenaar 1977). Non kernel ear dry matter was also increased by both N and irrigation because these factors had a greater influence on ear dry matter than on crop harvest index, suggesting a sink limitation on yield under these conditions.

4.6.5 Crop growth and DM partitioning

4.6.5.1 Total dry matter

Dry matter accumulation and partitioning data showed that under non limiting conditions of N and water, total crop yield appeared to be sink limited. This observation was deduced from the lack of remobilization of vegetative dry matter towards grain filling (Figures 4.1a, c), and suggests that current photosynthate was sufficient for grain filling. However, remobilization of stalk dry matter in N stressed crops commenced soon after silking (900 °C.d) in 'P39K38' (sgr 6) (Figure 4.1b), but later during grain filling (1200 °C.d) in 'P38G43' (sgr 9). Thus, when N was withheld, the crops were source limited, and remobilised more of their carbon reserves. Overall, the low 'stay-green' hybrids ('P39K38' (sgr 6) and 'P38V12' (sgr 7)) remobilised their stalk dry matter earlier than the high 'stay-green' hybrids ('P38F70' (sgr 8) and 'P38G43' (sgr 9)). These data are consistent with other sink-source relationships in cereals (Sections 2.3.3.2 and 2.3.3.3).

4.6.5.2 Leaf dry matter

Among the hybrids, 'P38V12' (sgr 7) accumulated more leaf dry matter (Table 4.7) probably by partitioning a greater proportion of its resources into the development of leaves because leaf dry matter increased mainly as a consequence of the increase in leaf area (Yang *et al.*

2004). Hence, factors that governed leaf area increase affected leaf dry matter accumulation (Stone *et al.* 1999). 'P38G43' (sgr 9) took longer to accumulate 5-95% of its leaf dry matter compared with the other hybrids (Table 4.6). This suggests a slower development of leaf area and reflects an inherent genotypic characteristic specific to this hybrid with respect to dry matter accumulation and partitioning (Egli 1998; Jones *et al.* 1996).

4.6.5.3 Stalk dry matter

Maximum stalk dry matter (t ha^{-1}) was 15% higher in 'P38G43' (sgr 9) than in 'P39K38' (sgr 6) (Table 4.8) which is consistent with the greater partitioning of dry matter as suggested in Section 4.6.5.2. An examination of the maximum stalk dry matter (Table 4.8) and at physiological maturity (Table 4.9) shows that remobilization of dry matter occurred during grain filling. Among the hybrids, the decline in stalk dry matter was 15% for the low 'stay-green' hybrids ('P39K38' (sgr 6), 'P38V12' (sgr 7)), 12.5% for 'P38F70' (sgr 8) and 5% for 'P38G43' (sgr 9). These, differences in stalk dry matter amongst the hybrids at physiological maturity reflect differences in the extent of remobilization under low and high N conditions.

Maximum stalk dry matter (t ha^{-1}) was recorded 260 °C.d after silking (Figures 4.1 and 4.2). This suggests excess carbohydrate was synthesized during early grain filling and was temporarily stored in the stalk (Below *et al.* 1981; Swank *et al.* 1982). Cliquet *et al.* (1990a) used isotope labelling techniques and confirmed the role of the stalk as an important temporary reservoir of fixed carbon in maize.

4.6.5.4 Kernel growth

Changes in the ear dry matter (Section 4.5.5.5) were mainly a consequence of increased kernel dry matter (Figure 4.4b), therefore only kernel growth will be considered here. Kernel dry matter (t ha^{-1}) was strongly related ($R^2 = 0.98$) to total crop dry matter (t ha^{-1}) and accounted for all crop dry matter (t ha^{-1}) increase after silking in the fertilised crops (Figure 4.4a). In contrast, greater remobilisation of reserves occurred in the N deficient crops. Most of the remobilised dry matter originated from the stalk (Section 4.6.5.3), with a smaller proportion from the leaves (Figure 4.1). Other workers have also reported greater remobilisation of stored reserves during late grain filling in unfertilised crops (Egli 1981; Tollenaar & Dwyer 1999).

The response of kernel dry matter accumulation to addition of N (Section 4.5.5.6) resulted from its influence on the sink capacity as reflected by the increase in the number of kernels per ear (Table 4.3). Thus, increments in kernel dry matter could be attributed to the positive effect of N on spikelet differentiation (Jacobs & Pearson 1991), cell division, expansion and enzymatic activity during kernel development (Lawlor 2002). Further, addition of N has also been reported to reduce the number of unfertilised florets (Tollenaar 1977). N fertilization also led to an increase in kernel weight (Table 4.4) which was consistent with the reported influence of N on the potential sink size and its growth rate in maize (Melchiori & Caviglia 2008). Lastly, irrigation may have increased the number of fertilised florets as a result of the better synchrony between anthesis and silking as earlier suggested by Fischer and Palmer (1984). These results are consistent with those of Muchow *et al.* (1990) who report that most of the carbon fixed after silking was directed towards ear development.

4.7 Conclusions

- Total accumulated dry matter and grain yield did not differ amongst the hybrids. However, differences in yield components suggest that accumulated dry matter was partitioned differently. For example, ‘P38G43’ (sgr 9) accumulated more dry matter in the stalk but had less expansion of leaf area.
- Under non limiting conditions of nitrogen and water, hybrid maize crops are sink limited, but under N or water stress are source limited.
- The stalk is the most important reservoir for excess carbohydrates synthesized during the lag phase of grain filling (≤ 210 °C.d after silking). If growth conditions are insufficient to meet sink demand, these reserves are remobilised as a source for growing grains.
- Stalk dry matter remobilization occurred earlier and to a greater extent under N deficiency in the low ‘stay-green’ hybrids (‘P39K38’ (sgr 6) and ‘P38V12’ (sgr 7)) than the high ‘stay-green’ hybrids (‘P38F70’ (sgr 8) and ‘P38G43’ (sgr 9)).

Dry matter accumulation has been related to the spatial and temporal development of leaf area and the concomitant capture of environmental resources e.g. light and CO₂. These factors will be considered in the next chapter.

Chapter 5

Light interception and the development of green area in hybrid maize of different 'stay-green' rating

5.1 Introduction

Total accumulated dry matter can be described as the product of the rate of biomass increase and the duration of growth. While the rate of biomass increase is influenced by the amount of solar radiation intercepted (Muchow & Carberry 1989), the duration of growth is directly proportional to temperature (Kiniry *et al.* 1991). Crop biomass is therefore the temporal integral of the seasonal net gain in CO₂ of individual leaves (Westgate *et al.* 2004). Such a quantitative relationship between resource capture and growth allows dry matter to be expressed as the product of the total quantity of incident solar radiation received, the fraction that is intercepted by the canopy and its efficiency of conversion into dry matter (Equation 1.1).

In Chapter 4, total accumulated dry matter and grain yield did not differ among the hybrids (Table 4.5.1). However, there were differences in yield components and total accumulated leaf and stalk dry matter (Sections 4.5.3 and 4.5.5). This infers that the mechanisms by which dry matter accumulation occurred differed between the hybrids. In this chapter, the quantity of iPAR by the hybrids is examined. Green leaf area influences the rate of biomass increase through the amount of iPAR (Dwyer & Stewart 1986b), and its development and maintenance determine the proportion of iPAR (Muchow & Carberry 1989).

The objectives of this chapter were to investigate and quantify any contribution by the hybrid 'stay-green' characteristic to total iPAR. Total iPAR was evaluated in terms of the development and maintenance of canopy green area, which in turn was related to the leaf appearance rate and individual leaf size. In the next chapter the efficiency of use of iPAR in the accumulation of dry matter will be considered.

5.2 Materials and methods

A detailed description of the experiment was given in Section 3.2.2.

5.2.1 Measurements

Leaf appearance was followed as described in Section 3.4. Green leaf area index (GLAI) and the instantaneous measurements of the fraction of transmitted PAR (β) were also monitored (Section 3.4.2). A set of six readings were taken per plot following the procedure of Gallo and Daughtry (1986), and the average plot reading of the fraction of incident PAR transmitted and the calculated GAI was logged.

5.2.2 Calculations and data analysis

Thermal time was calculated as described in Section 3.6.1. The phyllochron, defined as the interval between the appearance of successive leaf tips or ligules (Hay & Porter 2006), was calculated as described in Section 3.6.2. The fraction of iPAR (τ) and total accumulated PAR were also calculated (Section 3.6.4). PAR extinction coefficient (k_{par}) was derived by fitting an exponential function to the relationship between τ and GAI (Gallo *et al.* 1993; Maddonni & Otegui 1996) as shown in Equation 5.1.

$$\tau = a*(1 - e^{-k_{\text{par}}\text{GAI}}) \quad \text{Equation 5.1}$$

Where, a is the asymptote of τ and k_{par} the extinction coefficient

The PAR extinction coefficient (k_{par}) is related to the total solar radiation extinction coefficient (k_s) by Equation 5.2 (Stockle & Kemanian 2009).

$$k_s = 0.62 k_{\text{par}}^{0.86} \quad \text{Equation 5.2}$$

Green area duration (GAD) between successive harvests (days) was estimated as (Hunt 1982):

$$\text{GAD} = (\text{GAI}_1 + \text{GAI}_2) \times (t_2 - t_1)/2 \quad \text{Equation 5.3}$$

Where, t_1 and t_2 is the time in days.

In addition, a logistic function was used to examine the development of GAI between emergence and silking. Thereafter, linear regression was most appropriate to quantify the relationship between thermal time ($^{\circ}\text{C}\cdot\text{d}$) and the decline in GAI.

5.3 Results

As in Chapter 4, there were no significant three way interactions among the treatments for any of the variables under consideration in this chapter. Since the fraction of iPAR measurements used to compute total iPAR were obtained using the SunScan, a calibration check was required. On two occasions a comparison was made between the leaf area measurements obtained from the leaf area meter and those calculated by the SunScan. The two instruments were found to be in close agreement (Appendix 2), hence the GAI data obtained using the SunScan were considered appropriate.

5.3.1 Total intercepted PAR

Daily iPAR (MJ m^{-2}) was calculated using Equation 3.2 and summed to derive the seasonal iPAR (MJ m^{-2}). Total iPAR (MJ m^{-2}) differed between the N treatments and among the hybrids (Table 5.1). The fertilised crops intercepted 17% more ($P<0.001$) total PAR (MJ m^{-2}) compared with the unfertilised crops. Among the hybrids, the low ‘stay-green’ hybrids, (‘P39K38’ (sgr 6) and ‘P38V12’ (sgr 7)), intercepted on average 5% more ($P<0.005$) total PAR (MJ m^{-2}) compared with the high ‘stay-green’ hybrids (‘P38F70’ (sgr 8) and ‘P38G43’ (sgr 9)). Irrigation had no effect ($P<0.525$) on the total iPAR with both the irrigated and rain fed crops intercepting $900 (\pm 13.7) \text{ MJ PAR m}^{-2}$.

The relationship between total iPAR (MJ m^{-2}) and time (DAE) was linear once the establishment phase (up to 7 fully expanded leaves), when measurements were not possible, was completed. The linear rate of increase in total iPAR ($\text{MJ m}^{-2} \text{ day}^{-1}$) with time was influenced by the water x N interaction (Table 5.2). It was increased ($P<0.003$) 10% with irrigation when the crops were not fertilised. However, when fertiliser N was provided, water had no effect. The linear rate of increase in total iPAR ($\text{MJ m}^{-2} \text{ day}^{-1}$) was 5% slower ($P<0.047$) in ‘P38G43’ (sgr 9) than the other hybrids.

Table 5.1: Total intercepted photosynthetically active radiation (MJ m⁻²) of four maize hybrids grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Treatment	Total intercepted PAR (MJ m ⁻²)		
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean
‘P39K38’ (sgr 6)	840	980	910 _a
‘P38V12’ (sgr 7)	860	1000	930 _a
‘P38F70’ (sgr 8)	810	930	870 _b
‘P38G43’ (sgr 9)	800	950	880 _b
Mean	830	970	900
P value	P<0.001		P<0.005
SE	8.5		11.9
CV (%)	4.6		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

Table 5.2: The linear rate of increase of total intercepted PAR (MJ m⁻² day⁻¹) between 40 and 150 days after sowing in hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Treatment	Linear rate of increase of total intercepted PAR (MJ m ⁻² day ⁻¹)		
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean
Rain fed	6.89	8.29	7.59
Irrigated	7.55	8.37	7.96
P value	P<0.003		P<0.048
SE	0.085		0.059
‘P39K38’ (sgr 6)	7.24	8.35	7.80 _{ab}
‘P38V12’ (sgr 7)	7.42	8.52	7.97 _a
‘P38F70’ (sgr 8)	7.24	8.20	7.72 _{ab}
‘P38G43’ (sgr 9)	6.98	8.24	7.61 _b
Mean	7.22	8.33	7.78
P value	P<0.001		P<0.047
SE	0.063		0.087
CV (%)	3.9		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

The duration from emergence to physiological maturity lasted 150 days or 1470 °C.d. An analysis of the intercepts of the linear increase in total iPAR ($\text{MJ m}^{-2} \text{ day}^{-1}$) with time (days) revealed that the rate of increase of total iPAR was influenced by the duration during which iPAR (MJ m^{-2}) was estimated to be zero (lag phase) (Figure 5.1). The low ‘stay-green’ hybrids had a shorter ($P < 0.001$) lag phase compared with the high ‘stay-green’ hybrids (Table 5.3). Both irrigation ($P < 0.081$) and N ($P < 0.311$) had no effect.

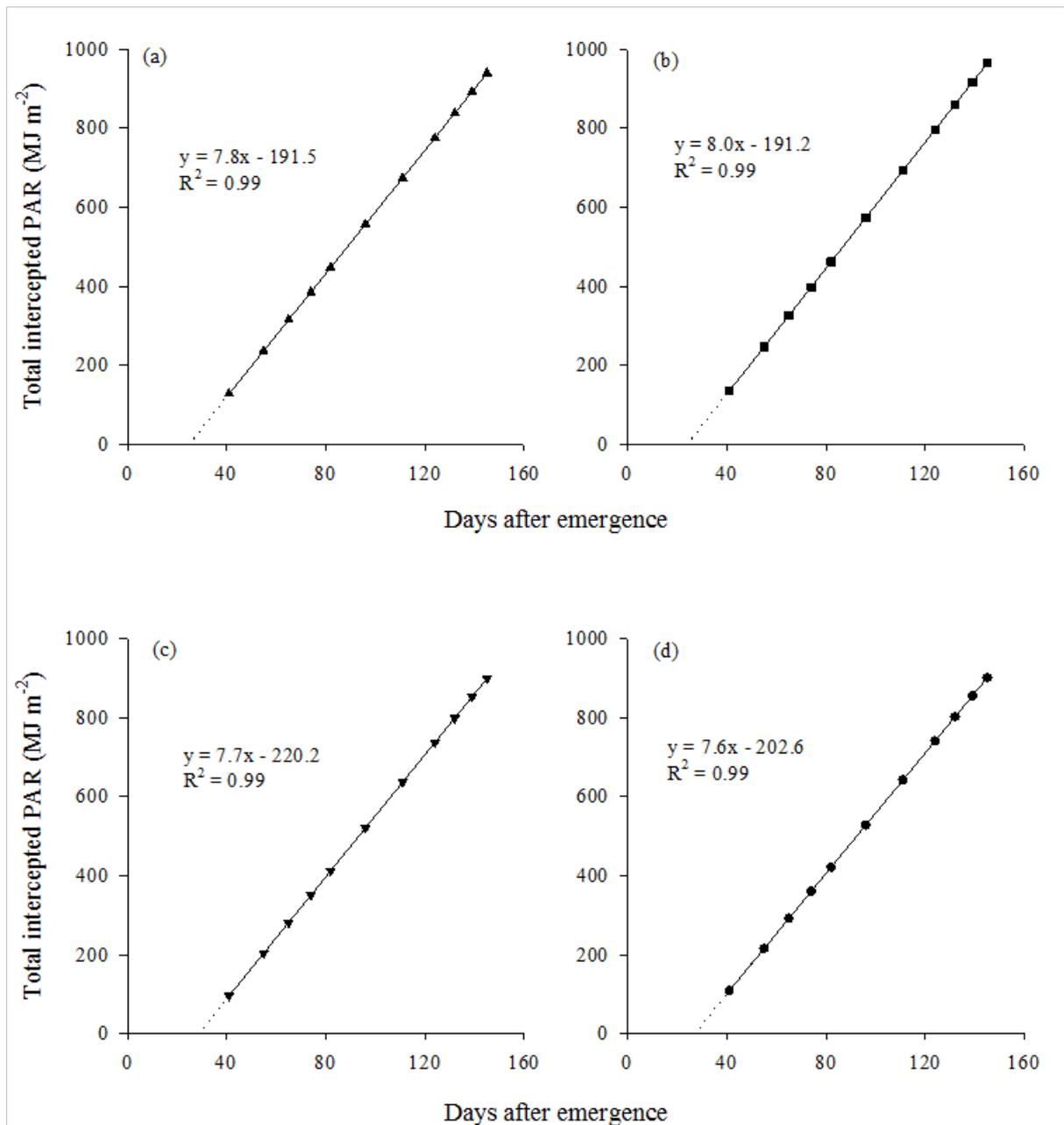


Figure 5.1: Total intercepted photosynthetically active radiation (MJ m^{-2}) versus days after emergence for (a) ‘P39K38’ (sgr 6), (b) ‘P38V12’ (sgr 7), (c) ‘P38F70’ (sgr 8) and (d) ‘P38G43’ (sgr 9) maize hybrids grown at Lincoln University, New Zealand, during 2008. The solid line represents the fitted regression while the dotted the extrapolation to the x-axis.

Table 5.3: The duration of the lag phase (days) for accumulation of PAR (MJ m⁻²) for hybrid maize either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Treatment	Duration of the lag phase (days)		
	Rain fed	Irrigated	Mean
'P39K38' (sgr 6)	22	28	25 _c
'P38V12' (sgr 7)	21	27	24 _c
'P38F70' (sgr 8)	26	31	29 _a
'P38G43' (sgr 9)	24	30	27 _b
Mean	23	29	26
P value	P<0.081		P<0.001
SE	1.2		0.6
CV (%)	7.7		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

5.3.2 Canopy extinction coefficient (kpar)

The extinction coefficient (kpar) of individual hybrids was derived using Equation 5.1. There were no differences in kpar; hence a common function was fitted to the relationship between τ and GAI (Figure 5.2). From the exponential relationship, a value of 0.77 was determined for kpar which is equivalent to a ks of 0.50. Using Equation 5.1, the critical GAI (GAI at which 95% of incident PAR is intercepted) was calculated to be 4.5 (± 0.10).

5.3.3 Green area development

In this study, kpar (-0.77) did not differ ($P<0.356$) among the hybrids; hence, differences in the proportion of iPAR could be attributed to development of GAI.

5.3.3.1 Green area index

Green area index was slow during crop establishment and was >1.0 at 350 °C.d after emergence (Figure 5.3). After this initial lag phase it accelerated and peaked around silking. Peak GAI was above the critical value of 4.5 (calculated from kpar = 0.77) in all the fertilised crops; while in the N deficient crops the critical GAI was not attained by any hybrid.

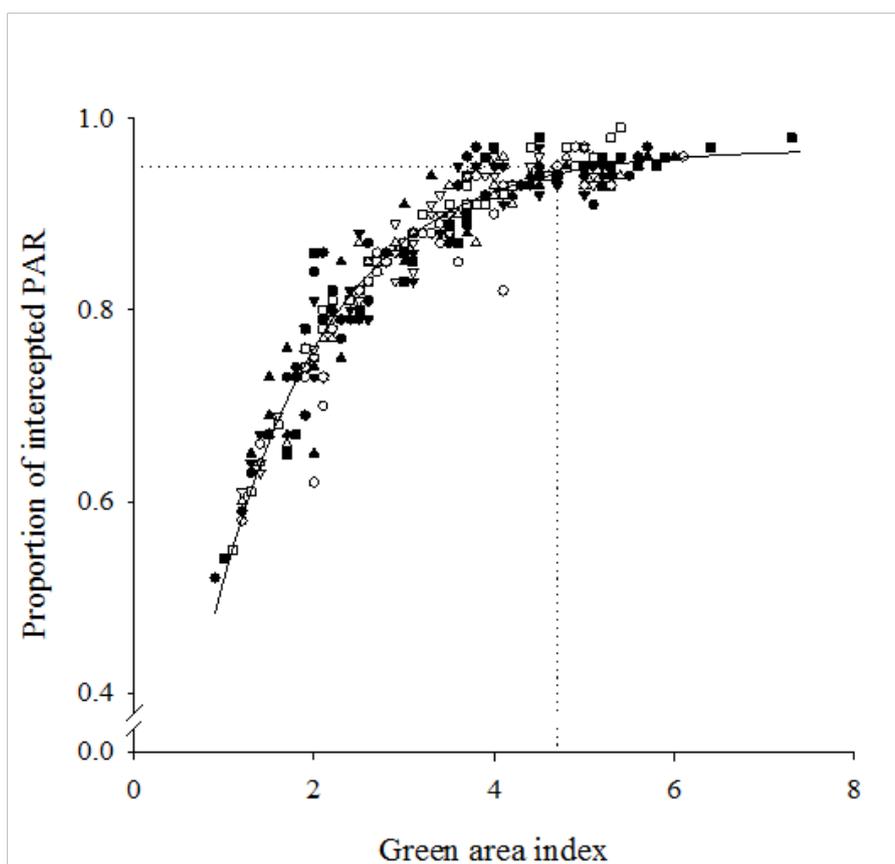


Figure 5.2: Proportion of intercepted photosynthetically active radiation versus the green area index for ‘P39K38’ (sgr 6, Δ), ‘P38V12’ (sgr 7, \square), ‘P38F70’ (sgr 8, ∇) and ‘P38G43’ (sgr 9, \circ) maize hybrids grown with 0 (open symbols) or 270 kg N ha⁻¹ (closed symbols) at Lincoln University, New Zealand, during 2008. The solid line represents the fitted regression $y = 0.98(1 - e^{-0.77x})$; $R^2 = 0.93$ and the dotted 95% PAR absorptance and critical green area index, respectively.

To examine the duration ($^{\circ}\text{C.d}$) required to reach the critical GAI, Equation 3.6 (Section 3.6.6) was rearranged and thermal time (X) made the subject as shown on Equation 5.4.

$$X = \left[\frac{\ln\left(\frac{c}{y-1}\right)}{-b} \right] + M \quad \text{Equation 5.4}$$

Using Equation 5.4, the duration ($^{\circ}\text{C.d}$) required to attain critical GAI was examined only in the fertilised crops (Table 5.4). The duration ($^{\circ}\text{C.d}$) to critical GAI differed ($P < 0.001$) among the hybrids but was unaffected ($P < 0.769$) by the water regime. ‘P38V12’ (sgr 7) required 605 $^{\circ}\text{C.d}$ to attain the critical GAI compared with 715 $^{\circ}\text{C.d}$ for ‘P38F70’ (sgr 8).

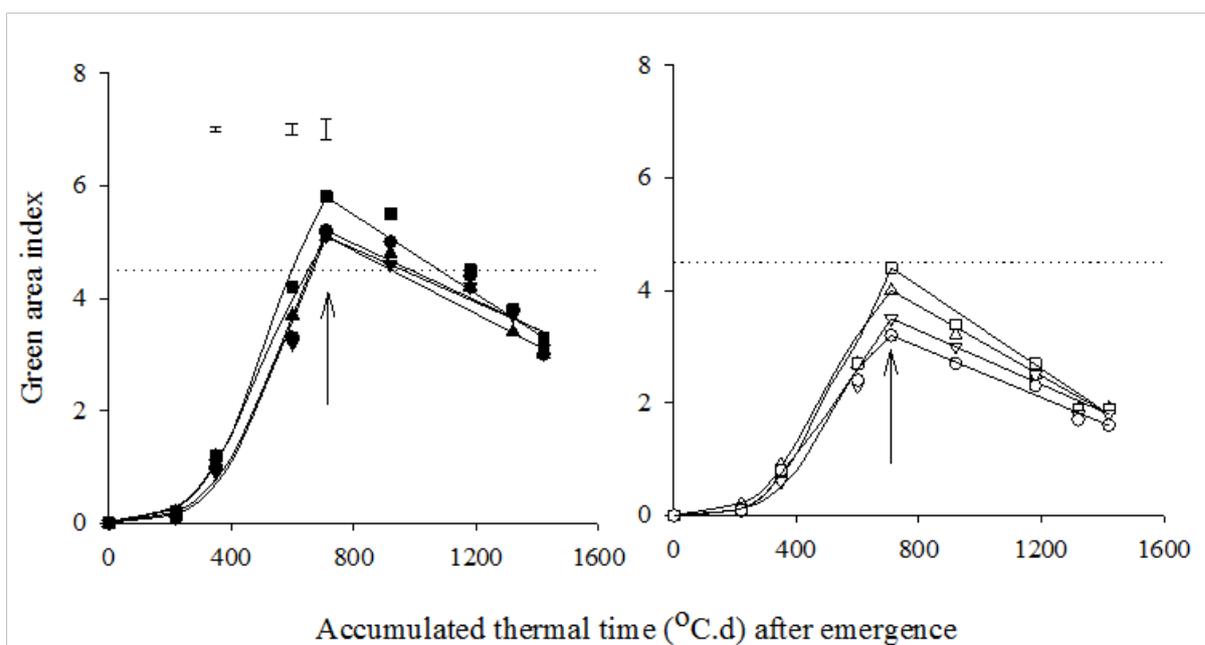


Figure 5.3: Green area index against accumulated thermal time ($^{\circ}\text{C.d}$) after emergence for ‘P39K38’ (sgr 6, \triangle), ‘P38V12’ (sgr 7, \square), ‘P38F70’ (sgr 8, ∇) and ‘P38G43’ (sgr 9, \circ) maize hybrids grown with 270 (closed symbols) or 0 (open symbols) kg N ha^{-1} at Lincoln University, New Zealand, during 2008. The dotted line represents the critical green area index, the arrows silking date and the error bars the standard error of the means at each harvest date.

Table 5.4: The duration ($^{\circ}\text{C.d}$) to critical green area index in hybrid maize grown with 270 kg N ha^{-1} and either rain fed or fertilised at Lincoln University, New Zealand, during 2008.

Treatment	Duration ($^{\circ}\text{C.d}$) to critical GAI		
	Rain fed	Irrigated	Mean
‘P39K38’ (sgr 6)	660	660	660 _b
‘P38V12’ (sgr 7)	600	610	605 _c
‘P38F70’ (sgr 8)	710	720	715 _a
‘P38G43’ (sgr 9)	690	680	685 _a
Mean	665	670	670
P value	P<0.769		P<0.001
SE	9.8		7.7
CV (%)	2.8		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

Maximum green area index was recorded at 800 $^{\circ}\text{C.d}$ and influenced by N and hybrid (Table 5.5). It increased ($P<0.001$) from 3.74 to 5.27 with added N, and was 20% higher ($P<0.021$)

in ‘P38V12’ (sgr 7) compared with ‘P38G43’ (sgr 9). Water had no effect ($P < 0.151$) on mean GAI which was $4.51 (\pm 0.102)$.

Table 5.5: Mean green area index ($\text{m}^2 \text{m}^{-2}$) at 800 °C.d of four maize hybrids grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand during 2008.

Treatment	Green area index ($\text{m}^2 \text{m}^{-2}$)		
	0 kg N ha^{-1}	270 kg N ha^{-1}	Mean
‘P39K38’ (sgr 6)	3.95	5.13	4.54 _{ab}
‘P38V12’ (sgr 7)	4.35	5.68	5.02 _a
‘P38F70’ (sgr 8)	3.48	5.08	4.28 _b
‘P38G43’ (sgr 9)	3.18	5.18	4.18 _b
Mean	3.74	5.27	4.51
P value	P<0.001		P<0.021
SE	0.14		0.19
CV (%)	14.7		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

To investigate the source of variation in GAI among the hybrids, a coefficient that related the calculated leaf area (length by width), with their measured leaf area was determined (Section 3.4) at silking (Appendix 3). A coefficient of 0.65 was obtained and used to calculate total leaf area per plant. Leaves were then separated into three cohorts (Section 3.4). The lower leaves of ‘P38V12’ (sgr 7) were larger ($P < 0.001$) than those of the other hybrids (Table 5.6). Within the middle leaf stratum, the low ‘stay green’ hybrids ‘P39K38’ (sgr 6) and ‘P38V12’ (sgr 7) had larger ($P < 0.001$) leaves than both ‘P38F70’ (sgr 8) and ‘P38G43’ (sgr 9). ‘P39K38’ (sgr 6) also had larger ($P < 0.001$) top leaves than the other hybrids.

Total leaf area per plant was also affected by the water x N interaction in which water increased ($P < 0.029$) total leaf area per plant by 19% without N but only by 5% when N was provided (Appendix 4). This interaction was considered of a lesser significance than the main effects of N and hybrid because the F value for the interaction was close to two orders of magnitude lower.

Table 5.6: Total and the cohort leaf area (cm² per plant) at 800 °C.d of four hybrids grown at Lincoln University, New Zealand, during 2008.

Treatment	Leaf area (cm ² per plant)			Total
	Lower leaves	Middle leaves	Top leaves	
‘P39K38’ (sgr 6)	1000 _c	1560 _a	1160 _a	3720 _b
‘P38V12’ (sgr 7)	1500 _a	1560 _a	1050 _b	4110 _a
‘P38F70’ (sgr 8)	1090 _{bc}	1410 _b	920 _c	3420 _c
‘P38G43’ (sgr 9)	1200 _b	1380 _b	1010 _{bc}	3590 _{bc}
P value	P<0.001	P<0.001	P<0.001	P<0.001
SE	44.7	25.0	36.5	72.9
CV (%)	12.9	5.9	12.2	6.8

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

To quantify the decline in GAI after silking (Figure 5.2), a linear regression was fitted to the relationship between GAI and thermal time (°C.d) from silking to physiological maturity (Table 5.7). The rate of decline in GAI accelerated ($P < 0.012$) from 2.84 ($\times 10^{-3}$) to 3.60 ($\times 10^{-3}$) ($\text{m}^2 \text{m}^{-2}$) per °C.d when additional N was provided. It was also higher ($P < 0.008$) for ‘P38V12’ (sgr 7) at 4.10 ($\times 10^{-3}$) ($\text{m}^2 \text{m}^{-2}$) per °C.d than for other hybrids. Green area index decline between the water treatments was similar ($P < 0.164$) at 3.2 (± 0.23) ($\times 10^{-3}$) ($\text{m}^2 \text{m}^{-2}$) per °C.d.

Table 5.7: The rate of decline ($\text{m}^2 \text{m}^{-2}$) (°C.d⁻¹) in GAI after silking for hybrid maize crops grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Treatment	Rate of GAI decline (°C.d ⁻¹) ($\times 10^{-3}$) ($\text{m}^2 \text{m}^{-2}$)		
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean
‘P39K38’ (sgr 6)	2.89	3.39	3.14 _b
‘P38V12’ (sgr 7)	3.44	4.76	4.10 _a
‘P38F70’ (sgr 8)	2.70	2.67	2.68 _b
‘P38G43’ (sgr 9)	2.33	3.59	2.96 _b
Mean	2.84	3.60	3.22
P value	P<0.012		P<0.008
SE ($\times 10^{-3}$)	0.199		0.282
CV (%)	20.5		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

5.3.3.2 Green area duration (days)

Green area duration was influenced by all treatment factors as main effects (Table 5.8). It increased ($P < 0.001$) from 272 to 422 days when N was applied. GAD also increased ($P < 0.048$) from 317 to 377 days with irrigation and was highest ($P < 0.013$) at 377 days in ‘P38V12’ (sgr 7).

Table 5.8: Green area duration (days) in hybrid maize grown with 0 or 270 kg N ha⁻¹ and either irrigated or rain fed at Lincoln University, New Zealand, during 2008.

Hybrid	Green area duration (days)				Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Rain fed	Irrigated	
‘P39K38’ (sgr 6)	297	419	322	394	358 _{ab}
‘P38V12’ (sgr 7)	299	455	342	412	377 _a
‘P38F70’ (sgr 8)	251	393	308	336	322 _c
‘P38G43’ (sgr 9)	242	419	294	368	331 _{bc}
Mean	272	422	317	377	347
P value	P<0.001		P<0.048		P<0.013
SE	7.8		3.3		11.0
CV (%)	9.0				

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

5.3.4 Leaf appearance rate

5.3.4.1 Leaf tips

The relationship between the number of visible leaf tips and accumulated thermal time (°C.d) after emergence was bilinear and consisted of two distinct phases. During the first phase (up to 465 °C.d after emergence), the phyllochron_(tip) was 6% larger ($P < 0.001$) for the unfertilised than the N fertilised crops (Table 5.9). Similarly, it was 6% larger ($P < 0.011$) in ‘P38V12’ (sgr 7) compared with ‘P38F70’ (sgr 8). Irrigation had no effect ($P < 0.460$) on the phyllochron_(tip) during this stage. However, during Stage 2 (465 -700 °C.d after emergence), the phyllochron_(tip) of ‘P39K38’ (sgr 6) was longer ($P < 0.033$) than that of the other hybrids, while the leaf tips of the unfertilised crops appeared faster ($P < 0.041$) than those of the N fertilised crops (Table 5.10).

Table 5.9: The phyllochron_(tip) (°C.d) during Stage 1 (up to 465 °C.d after emergence) for maize hybrids grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Treatment	Phyllochron (°C.d)		Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	
‘P39K38’ (sgr 6)	35.7	34.1	34.9 _{ab}
‘P38V12’ (sgr 7)	37.3	35.0	36.2 _a
‘P38F70’ (sgr 8)	35.5	32.5	34.0 _b
‘P38G43’ (sgr 9)	36.9	35.0	36.0 _a
Mean	36.4	34.2	35.3
P value	P<0.001		P<0.011
SE	0.34		0.47
CV (%)	4.7		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

Table 5.10: The phyllochron_(tip) (°C.d) during Stage 2 (465 -700 °C.d after emergence) for maize hybrids grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Treatment	Phyllochron (°C.d)		Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	
‘P39K38’ (sgr 6)	78.0	86.9	82.5 _a
‘P38V12’ (sgr 7)	62.6	69.0	65.8 _b
‘P38F70’ (sgr 8)	63.6	68.6	66.1 _b
‘P38G43’ (sgr 9)	63.4	69.6	66.5 _b
Mean	66.9	73.5	70.2
P value	P<0.041		P<0.033
SE	3.89		5.51
CV (%)	20.4		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

As the rate of appearance of leaf tips differed in the presence of added N and among hybrids, separate functions were fitted to these relationships. The point of inflection was similar (P<0.194) for the N treatments (Figure 5.4) and occurred at 465 (± 5.4) °C.d after emergence. However, at the point of inflection, the fertilised crops had one more (P<0.001) visible leaf tip

per plant (Table 5.11). The point of inflection was also consistent ($P < 0.435$) among the hybrids and occurred at $465 (\pm 7.7) ^\circ\text{C.d}$ after emergence (Figure 5.5). At the point of inflection ‘P38G43’ (sgr 9) and ‘P38V12’ (sgr 7) had 0.7 less ($P < 0.001$) leaf tips per plant than the other hybrids.

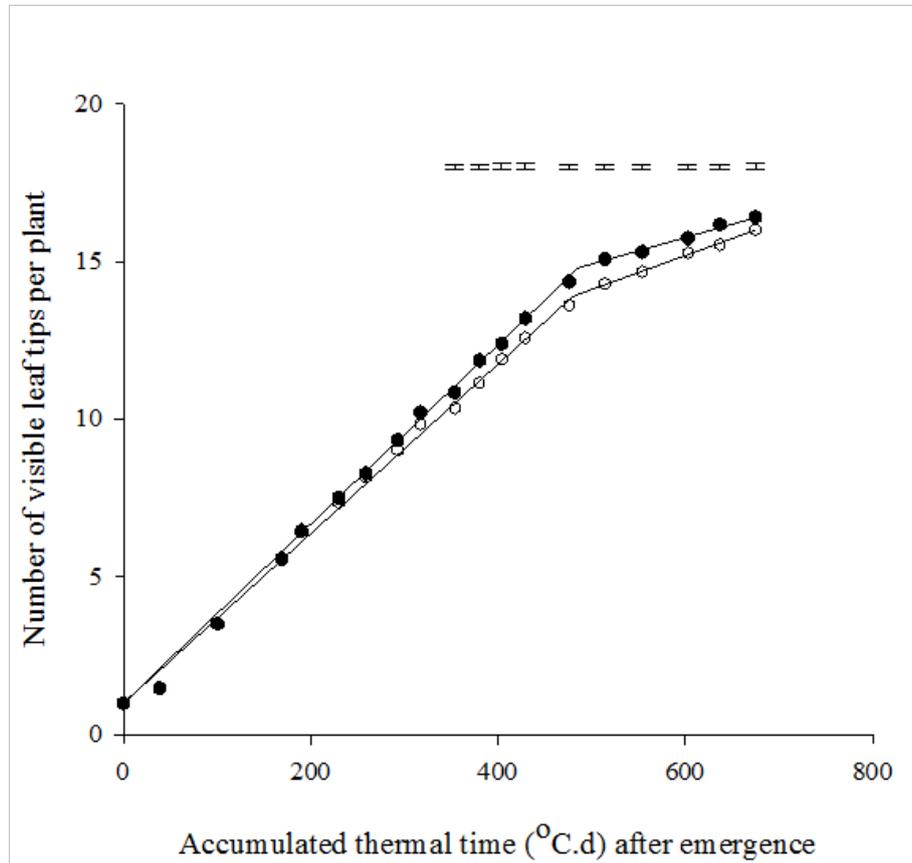


Figure 5.4: Number of visible leaf tips per plant versus accumulated thermal time ($^\circ\text{C.d}$) in hybrid maize grown with 0 (open symbols) or 270 (closed symbols) kg N ha^{-1} at Lincoln University, New Zealand, during 2008. The error bars represent the standard error of the means at each harvest date (leaf tips). Stage 1 equations were: $y = 0.0275x + 1$ and $y = 0.0292x + 1$, $R^2 = 0.99$ for the unfertilised and N fertilised crops, respectively.

Table 5.11 Number of visible leaf tips per plant at the point of inflection (up to 465 °C.d after emergence) in maize hybrids grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Treatment	Number of visible leaf tips per plant at the point of inflection		
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean
‘P39K38’ (sgr 6)	13.1	14.2	13.6 _a
‘P38V12’ (sgr 7)	12.2	13.6	12.9 _b
‘P38F70’ (sgr 8)	13.1	14.1	13.6 _a
‘P38G43’ (sgr 9)	12.4	13.3	12.9 _b
Mean	12.7	13.8	13.3
P value	P<0.001		P<0.001
SE	0.16		0.23
CV (%)	4.2		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

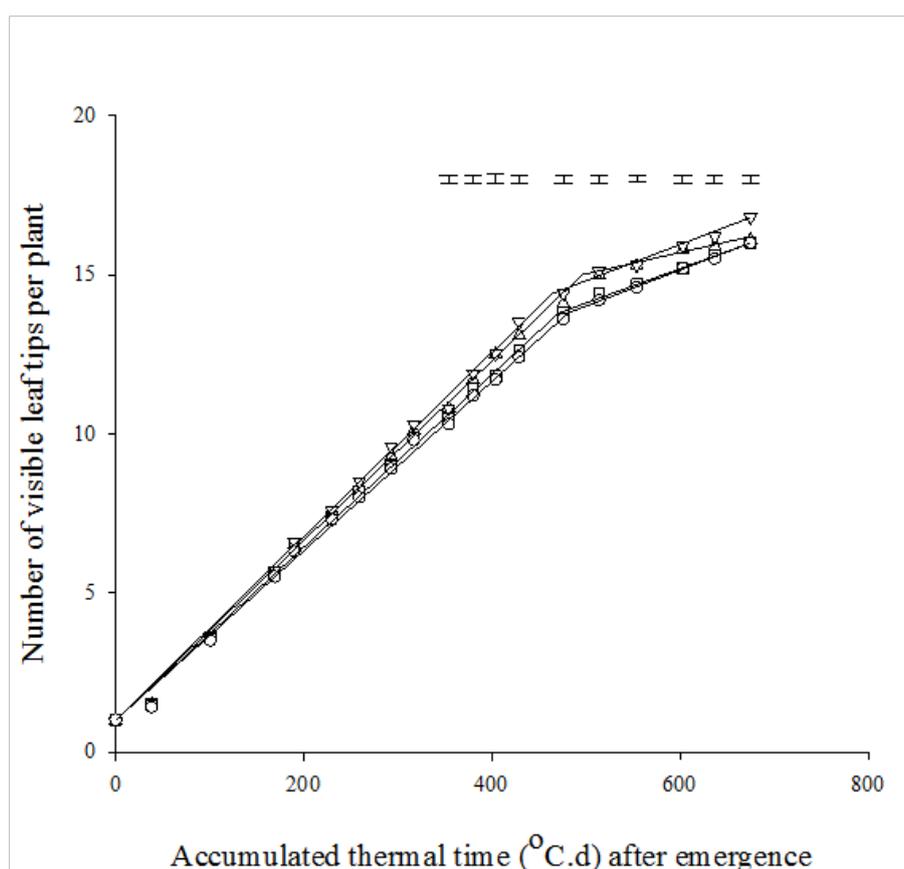


Figure 5.5: Number of visible leaf tips per plant versus accumulated thermal time (°C.d) after emergence in maize hybrids ‘P39K38’ (sgr 6, Δ), ‘P38V12’ (sgr 7, \square), ‘P38F70’ (sgr 8, ∇) and ‘P38G43’ (sgr 9, \circ) grown at Lincoln University, New Zealand, during 2008. The error bars represent the standard error of the means at each harvest date (leaf tips). Stage 1 equations were as follows: $y = 0.0286x + 1$ (sgr 6), $y = 0.0276x + 1$ (sgr 7), $y = 0.0294x + 1$ (sgr 8) and $y = 0.0277x + 1$ (sgr 9); $R^2 = 0.99$.

5.3.4.2 Fully expanded leaves

Fully expanded leaves emerged at a constant rate against accumulated thermal time ($^{\circ}\text{C.d}$) in a similar pattern to the appearance of visible leaf tips (Section 5.3.4.1). The first phase was longer and leaves emerged at a slower rate compared with the second phase. In contrast with the appearance of leaf tips, fully expanded leaves emerged at a faster rate during the second phase. During the first phase, the phyllochron_(ligule) declined ($P < 0.001$) from 57.4 $^{\circ}\text{C.d}$ to 54.1 $^{\circ}\text{C.d}$ per leaf when N was provided (Table 5.12). The phyllochron_(ligule) was also shorter ($P < 0.002$) in ‘P38F70’ (sgr 8) than in the other hybrids. In contrast, the phyllochron_(ligule) was unaffected by water ($P < 0.327$) during this phase.

Table 5.12: The phyllochron_(ligule) ($^{\circ}\text{C.d}$) during Stage 1 in hybrid maize grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Treatment	Phyllochron ($^{\circ}\text{C.d}$)		Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	
‘P39K38’ (sgr 6)	57.2	54.5	55.9 _a
‘P38V12’ (sgr 7)	59.8	54.8	57.3 _a
‘P38F70’ (sgr 8)	54.9	50.9	52.9 _b
‘P38G43’ (sgr 9)	57.8	56.1	56.9 _a
Mean	57.4	54.1	55.8
P value	P < 0.001		P < 0.002
SE	0.57		0.80
CV (%)	5.0		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

During the second phase, the treatments had no effect ($P < 0.216$) on the phyllochron and fully expanded leaves appeared at a constant $31.5 (\pm 0.46)$ $^{\circ}\text{C.d}$. As the phyllochron_(ligule) differed between the N treatments, separate functions were fitted to the relationship between the duration of appearance of successive fully expanded leaves against thermal time ($^{\circ}\text{C.d}$) (Figure 5.6). The point of inflection occurred earlier ($P < 0.003$) in N fertilised than the unfertilised crops (Table 5.13). However, at each point of inflection, the number of fully expanded leaves per plant were similar ($P < 0.626$) at 9.2.

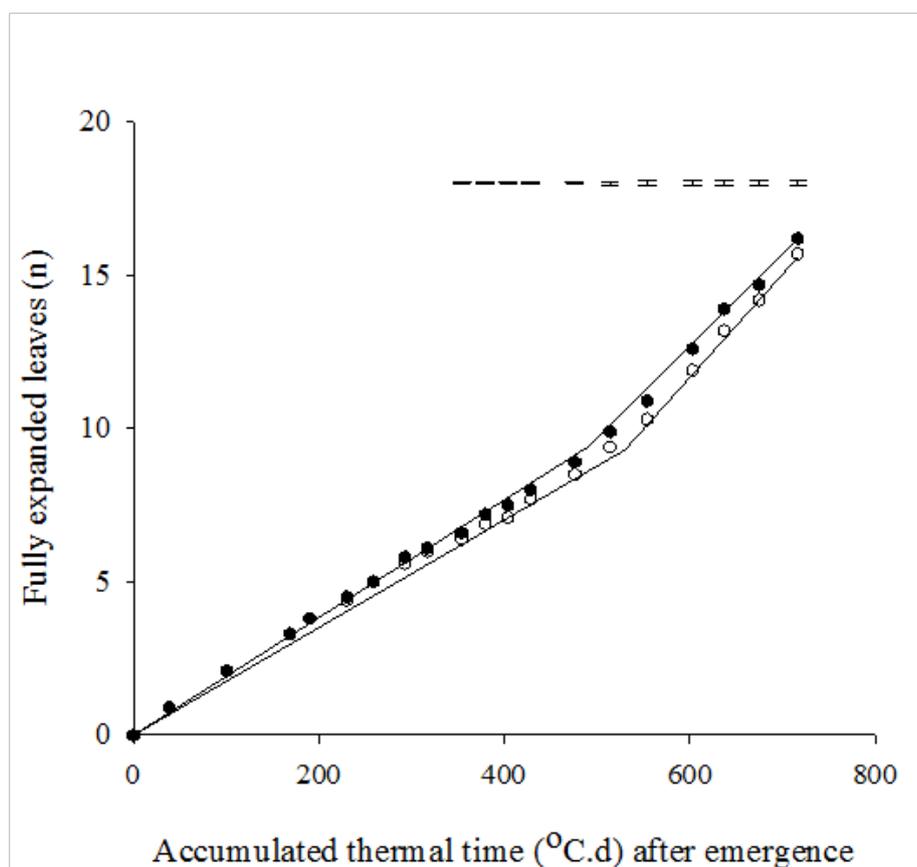


Figure 5.6: Number (n) of fully expanded leaves versus accumulated thermal time ($^{\circ}\text{C.d}$) in hybrid maize grown with 0 (open symbols) or 270 (closed symbols) kg N ha^{-1} at Lincoln University, New Zealand, during 2008. The error bars represent the standard error of the means at each harvest date (leaves). Stage 1 equations were: $y = 0.0174x$ and $y = 0.0185x$; $R^2 = 0.99$ for the unfertilised and N fertilised crops, respectively.

Table 5.13: The point of inflection ($^{\circ}\text{C.d}$) in the rate of appearance of ligules of hybrid maize grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.

Treatment	Point of inflection ($^{\circ}\text{C.d}$)		Mean
	0 kg N ha^{-1}	270 kg N ha^{-1}	
'P39K38' (sgr 6)	510	470	490 _b
'P38V12' (sgr 7)	560	530	550 _a
'P38F70' (sgr 8)	520	470	490 _b
'P38G43' (sgr 9)	520	500	510 _b
Mean	530	490	510
P value	P<0.003		P<0.002
SE	7.56		10.69
CV (%)	7.3		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

Similarly, separate functions were fitted to the $\text{phyllochron}_{(\text{ligule})}$ against accumulated thermal time data for the hybrids (Figure 5.7). ‘P38V12’ (sgr 7) required 550 °C.d to reach the point of inflection in leaf appearance or about 10% longer ($P < 0.002$) than other hybrids (Table 5.13). The point of inflection did not differ ($P < 0.813$) between the irrigation treatments and occurred 510 °C.d after emergence. However, the rain fed plants had developed half a leaf per plant more ($P < 0.001$) than the irrigated plants (Table 5.14).

There were also differences ($P < 0.006$) in the number of leaves per plant among the hybrids at the point of inflection. Interestingly, ‘P38V12’ (sgr 7) had a similar number of leaves per plant as ‘P38F70’ (sgr 8) despite a 60 °C.d difference in the duration required to reach the point of inflection by ‘P38V12’ (sgr 7).

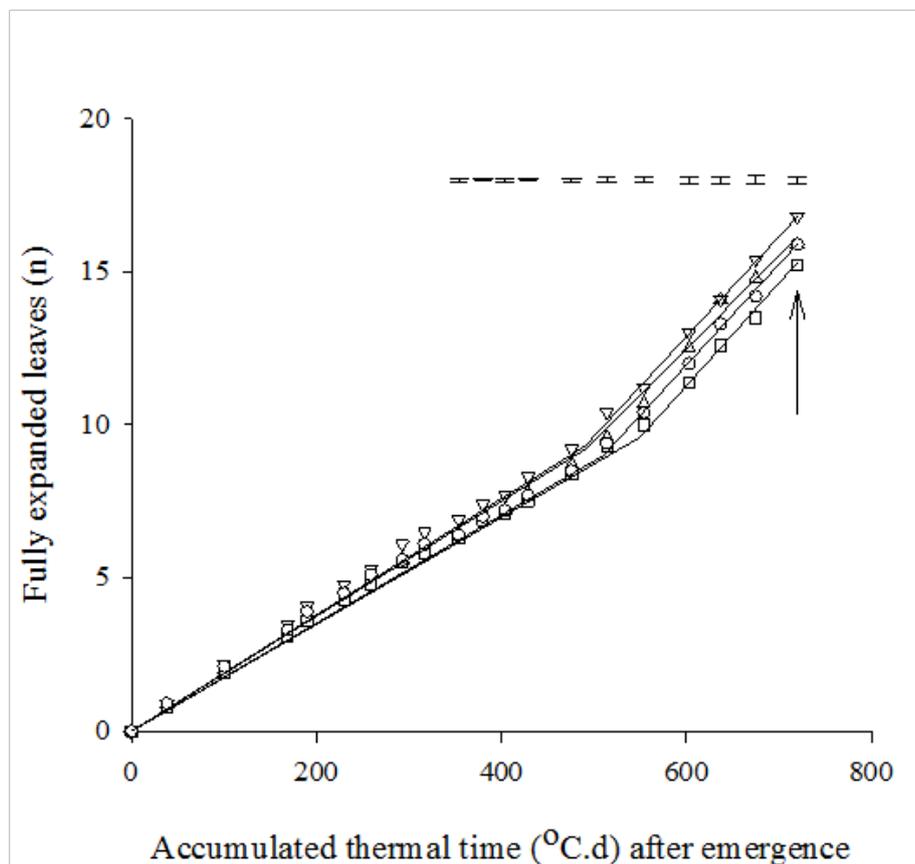


Figure 5.7: Number (n) of fully expanded leaves versus accumulated thermal time (°C.d) after emergence in maize hybrids ‘P39K38’ (sgr 6, Δ), ‘P38V12’ (sgr 7, \square), ‘P38F70’ (sgr 8, ∇) and ‘P38G43’ (sgr 9, \circ) grown at Lincoln University, New Zealand, during 2008. The arrow indicates silking and the error bars the standard error of the means (leaves). Stage 1 equations were as follows: $y = 0.0179x$ (sgr 6), $y = 0.0175x$ (sgr 7), $y = 0.0189x$ (sgr 8) and $y = 0.0176x$ (sgr 9); $R^2 = 0.99$.

Table 5.14: The number of leaves per plant at the point of inflection in the rate of appearance of fully expanded leaves of hybrid maize either rainfed or irrigated at Lincoln University, New Zealand, during 2008.

Treatment	Number of leaves per plant at the point of inflection		
	Rain fed	Irrigated	Mean
'P39K38' (sgr 6)	8.6	8.9	8.8 _c
'P38V12' (sgr 7)	9.9	9.2	9.6 _a
'P38F70' (sgr 8)	9.6	9.1	9.4 _{ab}
'P38G43' (sgr 9)	9.3	8.6	9.0 _{bc}
Mean	9.4	9.0	9.2
P value	P<0.001		P<0.006
SE	0.01		0.16
CV (%)	6.1		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

The final number of fully expanded leaves per plant also differed among the hybrids (Table 5.15) with one less ($P<0.001$) leaf for 'P39K38' (sgr 6), than the other hybrids.

Table 5.15: Number of fully expanded leaves per plant of four maize hybrids grown at Lincoln University, New Zealand, during 2008.

Hybrid	Fully expanded leaves per plant
'P39K38' (sgr 6)	16.1 _b
'P38V12' (sgr 7)	17.2 _a
'P38F70' (sgr 8)	17.2 _a
'P38G43' (sgr 9)	16.9 _a
P value	P<0.001
SE	0.14
CV (%)	2.0

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

5.4 Discussion

In Chapter 4, the total dry matter at final harvest was unaffected by the hybrid (Section 4.5.1). Differences were recorded in the yield components (Section 4.5.3) which suggests there were differences in the partitioning of dry matter amongst hybrids. Dry matter accumulation by crops is related to the accumulated PAR, which in turn is dependent on the canopy development of leaf area and its spatial distribution. Thus, each component of canopy expansion was examined to explain the mechanism(s) through which total dry matter at final harvest may have converged.

Total iPAR was calculated from the daily estimates of the proportion of iPAR and LAI (Section 3.6.4), hence, a functional relationship between the two components needed to be established (Appendix 1). A negative exponential function of the form illustrated in Equation 5.1, was consistent with other relationships for maize (Maddonni & Otegui 1996), wheat (Hippes *et al.* 1983) and sunflower (Trapani *et al.* 1992).

5.4.1 Canopy light interception

5.4.1.1 Total intercepted PAR

In this study, the low 'stay-green' hybrids, 'P39K38' (sgr 6) and 'P38V12' (sgr 7), accumulated on average 50 MJ m⁻² more total PAR than the high 'stay-green' hybrids 'P38F70' (sgr 8) and 'P38G43' (sgr 9) (Table 5.1). Given their extinction coefficients did not differ (Section 5.3.1), this was because the low 'stay-green' hybrids developed larger canopies (Table 5.6) that intercepted more PAR. It is plausible to assume the faster canopy development from individual leaf area per plant occurred as a result of a longer duration of leaf expansion, faster rate of leaf expansion or a combination of both (Stewart & Dwyer 1994).

An examination of the rate of increase in total iPAR (MJ m⁻² day⁻¹) (Table 5.2) showed an N by water interaction. Specifically irrigation in the absence of fertiliser N increased the rate of total PAR accumulation by 10%. However, when N was provided, irrigation had no effect on the rate of PAR accumulation, which suggests that leaf area expanded to its maximum in the absence of water stress. Furthermore, N exerts a stronger influence on leaf growth and leaf area (Section 2.3.3.2), via the synthesis of amino acids necessary for cell growth and division

(Lawlor *et al.* 1988). Water, however, had less effect on leaf area increase, as moderate water stress only affects cell extension and not cell number (Section 2.3.3.3). This can be illustrated by the greater increase in the rate of total PAR accumulation from 7.24 to 8.35 MJ m⁻² per day with fertiliser N compared with from 7.59 to 7.96 MJ m⁻² per day when irrigation was provided. These results are consistent with previous observations that N deficiency reduced radiation interception principally through diminished leaf expansion rates and consequently leaf area (Lawlor *et al.* 1988; Uhart & Andrade 1995).

5.4.1.2 Extinction coefficient (kpar)

The extinction coefficient of PAR (kpar) was consistent among the hybrids and averaged 0.77 which was equivalent to an extinction coefficient of total solar (ks) of 0.50 (Figure 5.2). This suggests a homogenous canopy was achieved through the similarity in canopy architecture among the hybrids. This was consistent with the work of Maddonni *et al.* (2001), who observed no variation in the extinction coefficient between two maize hybrids once the critical green area index was achieved in populations ≥ 9 plants m⁻². The kpar recorded in this study is close to the value of 0.70 reported by Plenet *et al.* (2000b) in maize and within the 0.45-0.90 range normally observed for most field crops (Stockle & Kemanian 2009).

5.4.2 Leaf area development

In Section 5.4.1.1, differences in total iPAR and its rate of increase between the N treatments or among the hybrids were attributed to the temporal pattern of leaf area development. Similarly GAI increase can be considered to be the product of the rate and duration of leaf expansion. The rate of leaf expansion is governed mainly by temperature and can be considered a developmental event (Section 2.3.2). However, the duration of expansion is modified by other environmental variables such as the availability of nutrients and water and derives a growth component (Section 2.3.3.3). Therefore, growth and development interact to determine the spatial and temporal pattern of leaf area development.

5.4.2.1 Canopy establishment

The relationship between GAI and thermal time (°C.d) during the vegetative phase was curvilinear (Figure 5.3). Green area index was slow during the establishment phase which lasted for up to 350 °C.d or until a green area index of 1.0 was attained. This pattern of

development was attributed to the mild late spring and early summer temperatures in 2008 (Table 3.3). For example, the mean temperatures for November and December were 13.8 °C and 15.4 °C, respectively, compared with a near optimum temperature of ~20 °C reported by Bos *et al.* (2000) for leaf area expansion under controlled environment conditions.

Yang *et al.* (2004), observed that early vegetative growth in maize is driven by leaf area expansion which is itself under the control of temperature. To hasten the rate of development during crop establishment in New Zealand, Stone *et al.* (1999), utilized transparent polythene sheets to raise the soil temperature and successfully accelerated the rate of leaf appearance. This led to a closer alignment between the time of peak radiation interception and its occurrence and as a consequence increased total iPAR (Stone *et al.* 1999). Studies in temperate zones have also confirmed the reduction in leaf area expansion and hence GAI as a result of low temperatures during crop establishment (Bollero *et al.* 1996; Wilson *et al.* 1995).

5.4.2.2 Canopy development

The mean maximum GAI was recorded shortly after silking because by then leaf appearance and expansion were complete and large scale leaf senescence had not began. Only the N fertilised crops attained the critical green area index of 4.5 (Section 5.4.1.2). To discern any hybrid differences, the duration to critical GAI was examined in these crops. The GAI for the low ‘stay-green’ hybrids, (‘P39K38’ (sgr 6) and ‘P38V12’ (sgr 7)), accelerated faster ($P < 0.001$) towards critical GAI and was reached, on average, 70 °C.d earlier than in the high ‘stay-green’ hybrids (‘P38F70’ (sgr 8) and ‘P38G43’ (sgr 9)) (Table 5.4). The acceleration was sustained by the development of larger leaves by the low ‘stay-green’ hybrids as already suggested (Section 5.4.1.2). This acceleration in leaf area development ensured an earlier start in the accumulation of total PAR (Table 5.3). Hence, the period of maximum radiation occurrence (Figure 3.1) was more synchronised with the duration of maximum GAI and culminated in these hybrids intercepting the highest amount of total PAR (Table 5.1) (Stone *et al.* 1999).

The mean maximum GAI differed between the N treatments and among the hybrids (Table 5.5). The fertilised crops had greater GAI compared with those not receiving N because of the influence of N on leaf area development (Section 2.3.3.2). Among the hybrids, the low ‘stay-

green' hybrids on average developed a higher GAI compared with the high 'stay-green' hybrids and consequently the GAD was longer in these hybrids (Table 5.8). In essence, this advantage for sgr 6 and 7 was achieved through development of larger middle and upper section leaves (Table 5.6) which maximized light interception because of their size and inclination (Maddonni & Otegui 1996). Of note was the observation that water had no effect on the mean maximum GAI (Section 5.3.3.1).

5.4.2.3 Green area index decline

The total accumulated PAR differential between the low and the high 'stay-green' hybrids was a consistent ~ 50 MJ PAR m^{-2} until physiological maturity. This amount was predominantly accumulated during the vegetative growth phase, but an accelerated decline in GAI amongst the low 'stay-green' hybrids after silking meant there were no further gains (Table 5.7). Green area index also declined at a faster rate in the fertilised than in the unfertilised crops presumably due to greater demand for remobilised N by the kernels of these crops (Section 2.3.4). Furthermore, the fertilised crops had a higher GAI (Figure 5.3), and a likelihood of greater filtration of the iPAR. Lers (2007) reported that a reduction in the fraction of PAR in the light perceived by leaves accelerates leaf senescence. Other workers have also observed greater loss of leaf under high N compared with low conditions (Muchow 1994).

5.4.3 Leaf appearance

5.4.3.1 Leaf tips

The appearance of leaf tips against accumulated thermal time ($^{\circ}C.d$) was bilinear (Figures 5.4 and 5.5), with a clear transition from one stage to the other. Phyllochrons_(tip) differed among the hybrids during this initial stage (Stage 1) in the appearance of leaf tips (Table 5.9). For example, each leaf tip of 'P38V12' (sgr 7), required 36.2 $^{\circ}C.d$ to emerge from its whorl compared with 34.0 $^{\circ}C.d$ for the other hybrids. This delay in the appearance of leaf tips among the low 'stay-greens' was a consequence of the initiation of larger leaves (Tables 5.5 and 5.6) which took longer to expand. Leaf tips appeared at a faster rate during the first stage because the internodes were shorter and leaf sheaths smaller. Therefore the distance traversed from the point of leaf initiation to the point of emergence was shorter (Robertson 1994). Stage

2 involved fewer leaf tips (~3-4) which took longer to emerge because of the slower rate of internode elongation of nodes >8 (Robertson 1994) (Table 5.10).

Further evidence to suggest the development of larger leaves by the low 'stay-green' compared with the high 'stay-green' hybrids was derived from the consistency in the duration to the point of inflection among the hybrids which occurred $465 (\pm 7.7) ^\circ\text{C.d}$ after emergence. However, 'P38V12' (sgr 7) had the lowest number of emerged leaf tips at this point (Table 5.11). Further, this hybrid required the longest duration to reach silking (Section 4.5.5.1) which usually signals the completion of leaf appearance (Kiniry & Bonhomme 1991). These data were in agreement with those of Birch *et al.* (1998b) who reported only a minor difference in the maize phyllochron_(tip) in a number of hybrids grown across a wide range of environments.

The phyllochron_(tip) was also delayed by $2.2 ^\circ\text{C.d}$ per leaf tip when the crops were not fertilised (Table 5.9). This was probably because leaf tip appearance is a developmental event which can be influenced by extreme N deficiency (Section 2.3.2) because of the role N plays in protein synthesis, hence leaf area expansion (Section 5.4.1.2). This observation supports the existence of a growth component which modifies development in leaf appearance as conceptualised by Birch *et al.* (1998b).

5.4.3.2 Fully expanded leaves

Fully expanded leaves emerged in a similar pattern to the appearance of leaf tips. However, they emerged at a faster rate during the second stage of leaf expansion (Figures 5.8 and 5.9). Consistent with the appearance of leaf tips, both N and hybrid influenced the rate of emergence of fully expanded leaves. Additional N accelerated the emergence of fully expanded leaves and produced a phyllochron_(ligule) of 54.1 compared with $57.4 ^\circ\text{C.d}$ (Table 5.12). Similarly, the fully expanded leaves of 'P38V12' (sgr 7) emerged at a slower rate compared with those of 'P38F70' (sgr 8). Ligule appearance rate differed among the hybrids and between the N treatments for similar reasons as the leaf tips (Section 5.4.3.1). Similar bilinear relationships between fully expanded leaves and thermal time ($^\circ\text{C.d}$) have also been reported by Muchow and Carberry (1989).

The delay in the emergence of fully expanded leaves of ‘P38V12’ (sgr 7), due to their larger leaf size (Section 5.4.4.1), also delayed its point of inflection by 50 °C.d compared with the other hybrids (Table 5.13). This delay partly explains the longer duration to silking in this hybrid (Section 4.5.5.4). Even though ‘P39K38’ (sgr 6) had a longer phyllochron_(ligule) (Table 5.12), it was the earliest to silk (Table 4.13) because it initiated one less leaf per plant than the other hybrids (Table 5.14).

These data have important implications in crop modelling. In simulation models e.g. CERES-Maize, phenology is modelled by assuming a constant phyllochron_(ligule) from emergence to the end of the vegetative phase (Kiniry & Bonhomme 1991). In this study, however, ligule appearance was a two-step process with the point of inflection 510 °C.d after emergence (Table 5.13). Further, the point of inflection in the appearance of ligules occurred early (9.2 leaves per plant) (Table 5.14), suggesting that the use of a constant phyllochron_(ligule) for a crop that initiates 17 leaves (as in this study) will introduce errors in the estimation of the duration to silking. Similarly, leaf tips appeared at a slower rate during Stage 2 (Table 5.10) compared with Stage 1 (Table 5.9), thus the use of a constant phyllochron_(tip) would underestimate the duration to silking.

5.5 Conclusions

- The low ‘stay-green’ hybrids intercepted more PAR (Table 5.1) by reaching critical GAI earlier than the high ‘stay-green’ hybrids (Table 5.4). This was achieved through the development of larger mid section leaves (Table 5.5).
- As a result of the larger leaves developed, the low ‘stay-green’ hybrids achieved a higher maximum GAI. However, GAI declined at a faster rate after silking in these hybrids (Table 5.7) and limited any further gains in light interception from the initially larger GAI.
- The lack of consistency in the leaf appearance rate among the low ‘stay-green’ hybrids (Tables 5.9, 5.10 and 5.12) was attributed to the development of one less leaf per plant in ‘P39K38’ (sgr 6) compared with ‘P38V12’ (sgr 7) (Table 5.15). This led to a smaller emergence to anthesis duration in ‘P39K38’ (sgr 6).
- The appearance of fully expanded leaves was a two-step process and the use of a constant phyllochron_(ligule) in simulation modeling could introduce errors in the estimation of the silking date.

Chapter 6

Radiation use efficiency and crop N content

6.1 Introduction

In Chapter 4, the total dry matter produced was not different between low (sgr 6 and 7) and high (sgr 8 and 9) 'stay-green' hybrids at any stage of the crop growth cycle. However, total iPAR differed between the N treatments and among hybrids (Chapter 5). Total iPAR was higher in the 'low stay-green' hybrids due to differences in the spatial and temporal development of GAI (Section 5.3.3.1). Therefore, by definition, there should be differences in RUE. This chapter quantifies these differences and identifies the mechanisms for the compensatory influence of RUE in the high 'stay-green' hybrids. Further, the close relationship between the total intercepted radiation and crop growth observed by Bonhomme (2000b) has been shown by Sinclair and Horie (1989) to be a consequence of the strong relationship between SLN concentration (g m^{-2}) and leaf CO_2 assimilation rates. RUE was therefore examined with specific emphasis on the influence of the SLN on potential CO_2 fixation. Of particular interest is the role played by the hybrid 'stay-green' rating on N remobilisation and its consequence for leaf senescence.

6.2 Materials and methods

The experimental design was described in detail in Section 3.2.2.

6.3 Measurements

Total above ground dry matter was harvested at 14 day intervals from a 3-plant subsample during the growing season. Instantaneous measurements of the proportion of iPAR were made as described in Section 3.4.1. Leaf chlorophyll content in each cohort of leaves (Section 3.4.2) was also monitored from the start of silking until physiological maturity (Section 3.4.3). N content was determined by automated dry combustion-gas chromatography (Section 3.4.6).

Data are presented for three key measurement dates which represented the approximate timings of silking (800 °C.d), late grain filling (1360 °C.d) and physiological maturity (1470 °C.d) which was determined retrospectively (Section 4.5.5.7).

6.4 Calculations and data analysis

Cumulative iPAR was calculated as described in Section 3.6.4. Absorbed PAR was assumed to equal 0.85 of the total iPAR (Monteith 1972; Sinclair & Muchow 1999). RUE was determined as the slope of the linear regression between total biomass accumulated and cumulative PAR absorbed (Plenet *et al.* 2000b; Sinclair & Muchow 1999). The regression was constrained to intercept the axis at the origin where total biomass and absorbed PAR for individual crops is equal to zero (Fletcher *et al.* 2008b). The relationship between the number of senesced leaves and thermal time (after emergence) was examined using an exponential function (Muchow & Carberry 1989).

A simple estimate of N remobilisation was derived from the assumption that N uptake during reproductive growth was directed towards grain filling (Rajcan & Tollenaar 1999b), and that N lost from the leaves and stalk was remobilised to the developing grains (Przulj & Momcilovic 2001). Thus, N remobilised from the either leaves or stalks was calculated following the approach of Cox *et al.* (1986) and shown in Equation 6.1. Further, N translocation efficiency (%) (Equation 6.2) and nitrogen harvest index (%) (Equation 6.3) were also determined following the procedure of Przulj and Momcilovic (2001). Finally, the SLN (g m^{-2}) was derived from the ratio of leaf N concentration (g N kg^{-1} dry matter) and specific leaf area ($\text{m}^2 \text{kg}^{-1}$ dry matter) (Garnier *et al.* 1997; Muchow 1994). These values were then analysed using ANOVA to examine treatment effects.

$$\text{N translocation (kg ha}^{-1}\text{)} = \text{Total plant N content (kg ha}^{-1}\text{) at anthesis} - \text{non grain N content (kg ha}^{-1}\text{) at physiological maturity} \quad \text{Equation 6.1}$$

$$\text{N translocation efficiency (proportion of pre silking N translocated to the kernels)} = \text{N translocation} / \text{Total plant N content at silking} \quad \text{Equation 6.2}$$

$$\text{Nitrogen harvest index (NHI)} = \text{Grain N} / \text{Total N content in above ground parts at physiological maturity} \times 100 \quad \text{Equation 6.3}$$

6.5 Results

6.5.1 RUE

Radiation use efficiency (RUE) was influenced by the water x N and water x hybrid interactions. However, these were considered of minor importance because the N main effect variance ratio was two orders of magnitude greater than those for the interactions (199 vs. 6.40). Thus, only the main effects are presented here. RUE of the high ‘stay-green’ hybrids (sgr 8 and 9) was 8% higher ($P < 0.041$) than that of the low ‘stay-green’ hybrids (sgr 6 and 7) (Table 6.1). RUE also increased ($P < 0.001$) with N fertiliser from 2.08 to 3.07 g dry matter MJ^{-1} PAR absorbed.

Table 6.1: Radiation use efficiency (g dry matter MJ^{-1} PAR absorbed) in maize grown with 0 or 270 kg N ha^{-1} and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Hybrid	RUE (g dry matter MJ^{-1} PAR absorbed)				Mean
	0 kg N ha^{-1}	270 kg N ha^{-1}	Rain fed	Irrigated	
‘P39K38’ (sgr 6)	1.91	3.08	2.32	2.67	2.50 _b
‘P38V12’ (sgr 7)	2.01	2.89	2.42	2.48	2.45 _b
‘P38F70’ (sgr 8)	2.20	3.18	2.39	2.99	2.69 _a
‘P38G43’ (sgr 9)	2.21	3.13	2.31	3.03	2.67 _a
Mean	2.08	3.07	2.36	2.79	2.58
P value	$P < 0.001$		$P < 0.023$		$P < 0.041$
SE	0.049		0.047		0.070
CV (%)	9.4				

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

Similarly, irrigation also increased ($P < 0.023$) the RUE from 2.36 to 2.79 g dry matter MJ^{-1} PAR absorbed. Of note, RUE appeared to be systematically lower than the mean value for both N treatments prior to the absorption of 200 MJ m^{-2} of PAR (Figure 6.1).

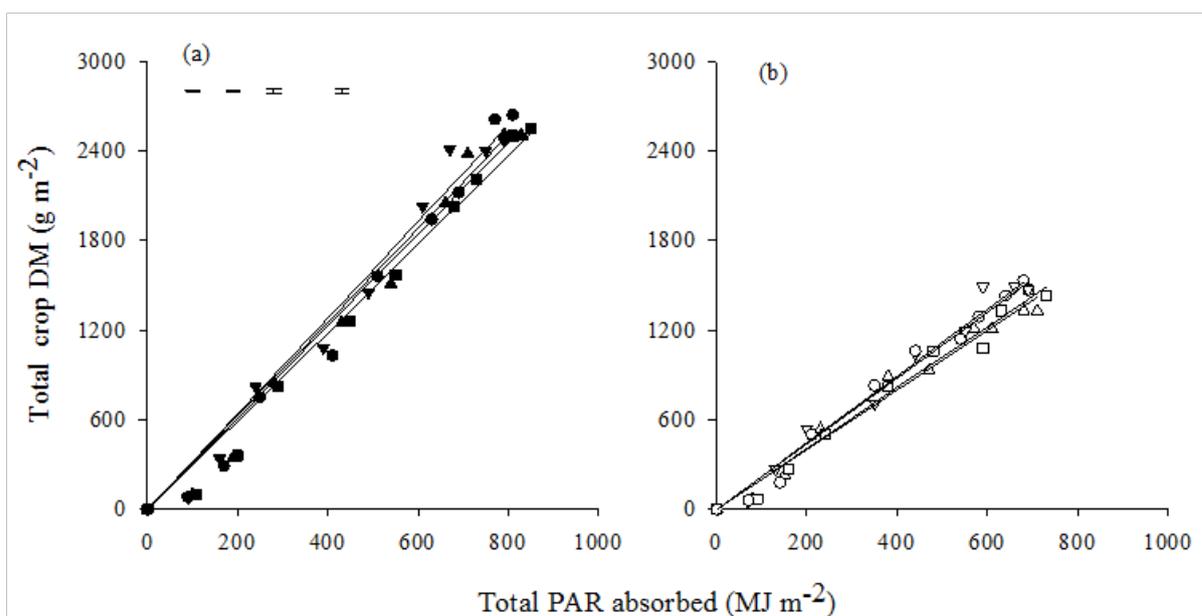


Figure 6.1: Radiation use efficiency (g dry matter MJ⁻¹ PAR absorbed) in ‘P39K38’ (sgr 6, Δ), ‘P38V12’ (sgr 7, \square), ‘P38F70’ (sgr 8, ∇) and ‘P38G43’ (sgr 9, \circ) maize hybrids grown with 0 (open symbols) or 270 (closed symbols) kg N ha⁻¹ at Lincoln University, New Zealand, during 2008. The error bars represent the standard error of the hybrid means (g m⁻²) at each sample date.

6.5.2 Chlorophyll content

In this study, leaf chlorophyll content was used as a non destructive indicator of leaf N concentration (Section 2.2.5.4), while leaf senescence provided a means of assessing the degree of N remobilisation during grain filling. It was essential that a relationship between the SPAD readings and a constituent of chlorophyll was established to provide a basis for the analysis. The relationship between the SLN concentration (g m⁻²) and SPAD readings at 800 °C.d was an asymptotic exponential ($R^2 = 0.89$) (Figure 6.2). At this measurement date SPAD meter readings and samples for chemical N analysis were taken concurrently. Throughout the next 56 day measurement period, SPAD readings continuously declined and differed ($P < 0.05$) between the water and N treatments.

Prior to grain filling (800 °C.d); when the GAI began to decline (Figure 5.2), the average SPAD readings per leaf from the fertilised crops were 62% higher ($P < 0.001$) than those from the 0 kg N ha⁻¹ plots (Table 6.2). Based on the relationship between SPAD units and SLN concentration (g m⁻²), this was equivalent to a SLN concentration of 1.97 (± 0.024) g m⁻² and 1.04 (± 0.024) g m⁻², for the fertilised and unfertilised crops, respectively. SPAD readings from the irrigated crops were also 13% (0.24 g N m⁻²) higher ($P < 0.008$) than those of the rain

fed crops. SPAD readings did not differ ($P < 0.094$) amongst the hybrids and averaged $43.7 (\pm 1.33)$ SPAD units, which was equivalent to $1.47 (\pm 0.035)$ g N m⁻².

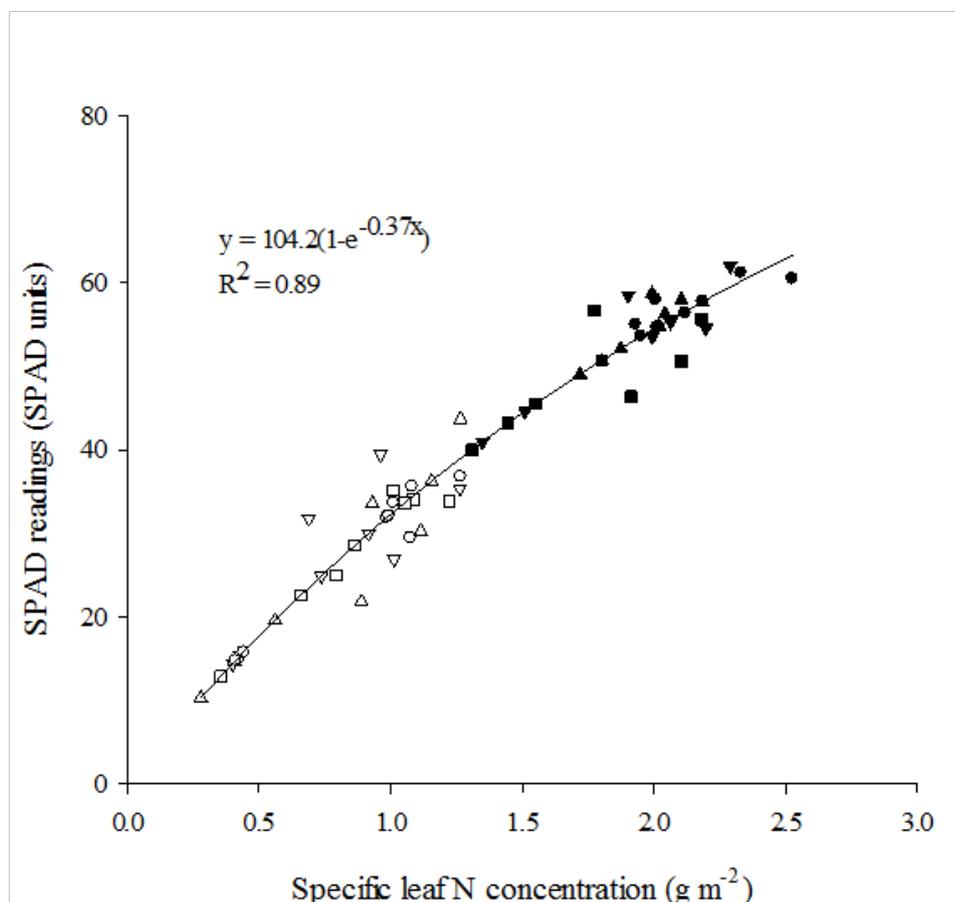


Figure 6.2: SPAD readings (SPAD units) per leaf versus specific leaf N concentration (g m⁻²) for ‘P39K38’ (sgr 6, △), ‘P38V12’ (sgr 7, □), ‘P38F70’ (sgr 8, ▽) and ‘P38G43’ (sgr 9, ○) maize hybrids grown with 0 (open symbols) or 270 (closed symbols) kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Similarly, at physiological maturity (1470 °C.d), trends in mean SPAD readings per leaf were consistent with those observed at 800 °C.d. SPAD readings increased ($P < 0.001$) from 23.2 (0.68 ± 0.024 g N m⁻²) to 44.4 (1.50 ± 0.024 g N m⁻²) SPAD units per leaf when fertiliser N was provided (Table 6.3). They also increased ($P < 0.003$) from 29.8 (0.91 ± 0.009 g N m⁻²) to 37.7 (1.21 ± 0.009 g N m⁻²) SPAD units per leaf when the crops were irrigated. Hybrid had no effect ($P < 0.270$) on the SPAD readings per leaf at this period and averaged $33.8 (1.06 \pm 0.035)$ g N m⁻² SPAD units per leaf.

Table 6.2: Average SPAD readings (SPAD units) per leaf at 800 °C.d after emergence in hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Hybrid	SPAD readings (SPAD units) per leaf				Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Rain fed	Irrigated	
‘P39K38’ (sgr 6)	31.1	54.7	41.1	44.7	42.9
‘P38V12’ (sgr 7)	32.1	50.3	38.5	43.9	41.2
‘P38F70’ (sgr 8)	35.1	56.6	43.2	48.5	45.9
‘P38G43’ (sgr 9)	35.1	54.4	41.6	47.9	44.8
Mean	33.4	54.0	41.1	46.3	43.7
P value	P<0.001		P<0.008		P<0.094
SE	0.94		0.34		1.33
CV (%)	10.6				

Table 6.3: Average SPAD readings (SPAD units) per leaf at 1470 °C.d after emergence in hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Hybrid	SPAD readings (SPAD units) per leaf				Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Rain fed	Irrigated	
‘P39K38’ (sgr 6)	19.2	44.5	27.6	36.1	31.8
‘P38V12’ (sgr 7)	24.8	41.7	29.8	36.6	33.2
‘P38F70’ (sgr 8)	23.5	45.7	31.0	38.2	34.6
‘P38G43’ (sgr 9)	25.2	45.6	30.8	40.0	35.4
Mean	23.2	44.4	29.8	37.7	33.8
P value	P<0.001		P<0.003		P<0.270
SE	0.94		0.33		1.33
CV (%)	13.7				

6.5.3 Leaf senescence

6.5.3.1 Number of senesced leaves

From silking to physiological maturity, the number of senesced leaves per plant was influenced by the N x hybrid interaction. As an illustration of this, data at silking and

physiological maturity are presented. When the crops were unfertilised, all hybrids had senesced on average 7.3 (\pm 0.1) leaves per plant at silking (Table 6.4). In contrast, when fertiliser N was provided, ‘P38G43’ (sgr 9) had senesced one less ($P < 0.001$) leaf per plant, than all the other hybrids.

A similar trend was observed at physiological maturity (1470 °C.d) when ‘P38G43’ (sgr 9) had 1-2 fewer ($P < 0.046$) senesced leaves per plant than the other hybrids but only when fertiliser N was provided. In the absence of fertiliser at least 10 leaves had senesced at physiological maturity, for all hybrids.

Table 6.4: Number of senesced leaves per plant at silking (710 °C.d) and physiological maturity (1470 °C.d) in hybrid maize grown with either 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Hybrid	Number of senesced leaves per plant			
	Silking (710 °C.d)		Physiological maturity (1470 °C.d)	
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	0 kg N ha ⁻¹	270 kg N ha ⁻¹
‘P39K38’ (sgr 6)	7.4	3.0 _a	10.7	10.0 _a
‘P38V12’ (sgr 7)	7.5	3.0 _a	11.0	9.4 _a
‘P38F70’ (sgr 8)	7.0	3.1 _a	11.2	9.2 _a
‘P38G43’ (sgr 9)	7.5	2.1 _b	10.6	8.0 _b
Hybrid x N	P<0.001		P<0.035	
SE	0.18		0.31	
CV (%)	8.9		7.7	

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

For the fertilised crops, the relationship between the numbers of senesced leaves per plant and thermal time was exponential and of the form shown by Equation 6.4 (Figure 6.3). In contrast, the relationship between senesced leaves per plant and thermal time for the non fertilised crops was logarithmic, with a steeper earlier phase of leaf loss followed by a slower decline towards physiological maturity.

$$Y = ae^{bTt}$$

Equation 6.4

Where Y = number of senesced leaves per plant, a = intercept with Y – axis (senesced leaves), b represents the degree of curvature (dimensionless) and Tt = thermal time after emergence (Section 6.4).

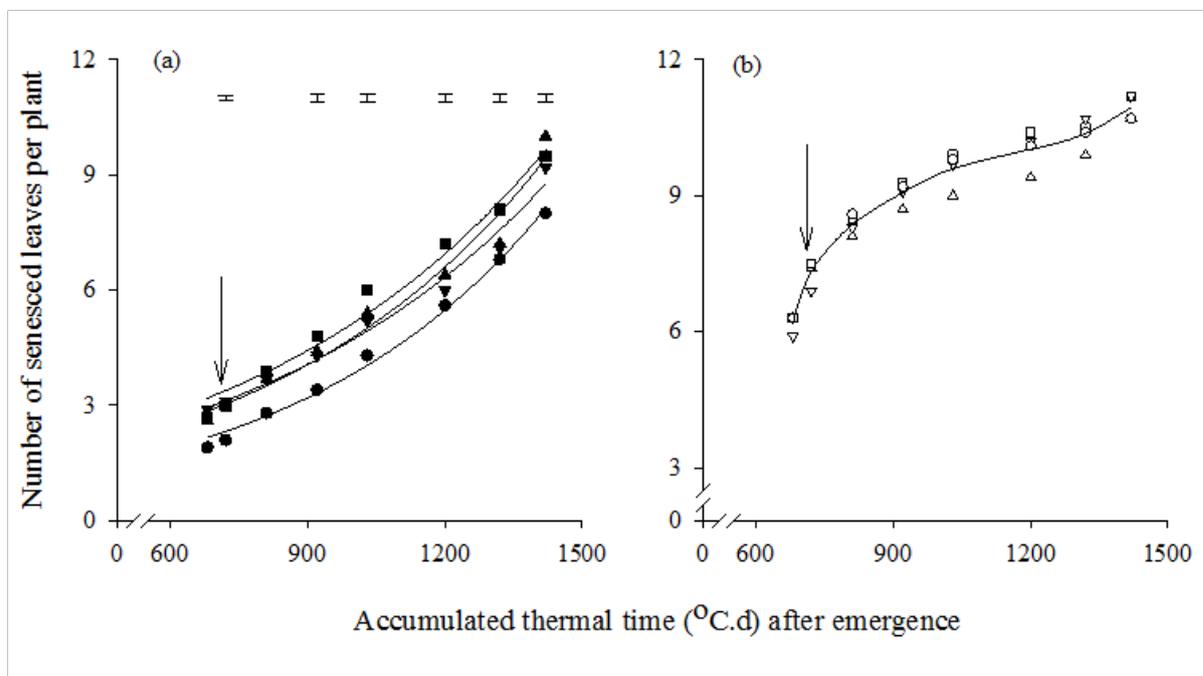


Figure 6.3: Number of senesced leaves per plant versus accumulated thermal time ($^{\circ}\text{C.d}$) in ‘P39K38’ (sgr 6, Δ), ‘P38V12’ (sgr 7, \square), ‘P38F70’ (sgr 8, ∇) and ‘P38G43’ (sgr 9, \circ) maize hybrids grown with 0 (open symbols) or 270 (closed symbols) kg N ha^{-1} at Lincoln University, New Zealand, during 2008. For the fertilised crops, the respective equations for the hybrids were; $y = 0.95e^{0.0016Tt}$; $y = 1.15e^{0.0015Tt}$; $y = 1.08e^{0.0015Tt}$ and $y = 0.64e^{0.0018Tt}$; $R^2 = 0.98$. The arrow indicates silking and the error bars represent the standard error of the hybrid means (leaves per plant) at each sample date.

The number of senesced leaves per plant was also affected by the water x N interaction from silking to physiological maturity. At silking (710 $^{\circ}\text{C.d}$), the control crop had 7.8 senesced leaves per plant, this decreased ($P < 0.042$) to 3.0 with the application of fertiliser N and to 6.8 with irrigation (Table 6.5). However, when both were provided, the number of senesced leaves per plant reduced even further to 2.6 leaves per plant.

At 1470 $^{\circ}\text{C.d}$, N application reduced ($P < 0.001$) the number of senesced leaves per plant from 11.8 to 11.0 without water but from 9.9 to 7.3 when water was provided. The fertilised crops senesced proportionately more leaves per plant compared with the unfertilised between

silking and physiological maturity which was consistent with the observed faster rate of decline of leaf dry matter by the fertilised crop (Section 5.3.4.1).

Table 6.5: Number of senesced leaves per plant at silking (710 °C.d) and physiological maturity (1470 °C.d) in hybrid maize grown with either 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Treatment	Number of senesced leaves per plant			
	Silking (710 °C.d)		Physiological maturity (1470 °C.d)	
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	0 kg N ha ⁻¹	270 kg N ha ⁻¹
Rain fed	7.8	3.0	11.8	11.0
Irrigated	6.8	2.6	9.9	7.3
W x N	P<0.042		P<0.001	
SE	0.13		0.22	
CV (%)	8.9		7.7	

6.5.4 Crop N dynamics

6.5.4.1 Total crop N (kg ha⁻¹)

Total crop N (kg ha⁻¹) at final harvest was influenced by both N and water but not hybrid or any of the interactions. Total crop N (kg ha⁻¹) more than doubled (P<0.001) from 138 to 308 kg ha⁻¹ when additional N was provided (Figure 6.4 and Appendix 5). It also increased 39% when irrigation was provided (Figure 6.5). The quantity of N accumulated by the hybrids at final harvest did not differ (P<0.087) and averaged 223 (± 12.4) kg ha⁻¹.

At physiological maturity (1470 °C.d), only additional N increased (P<0.001) total crop N from 135 to 320 kg ha⁻¹. Neither hybrid (P<0.091) nor water (P<0.134) had an effect on total crop N which both averaged 228 (± 12.2) kg ha⁻¹.

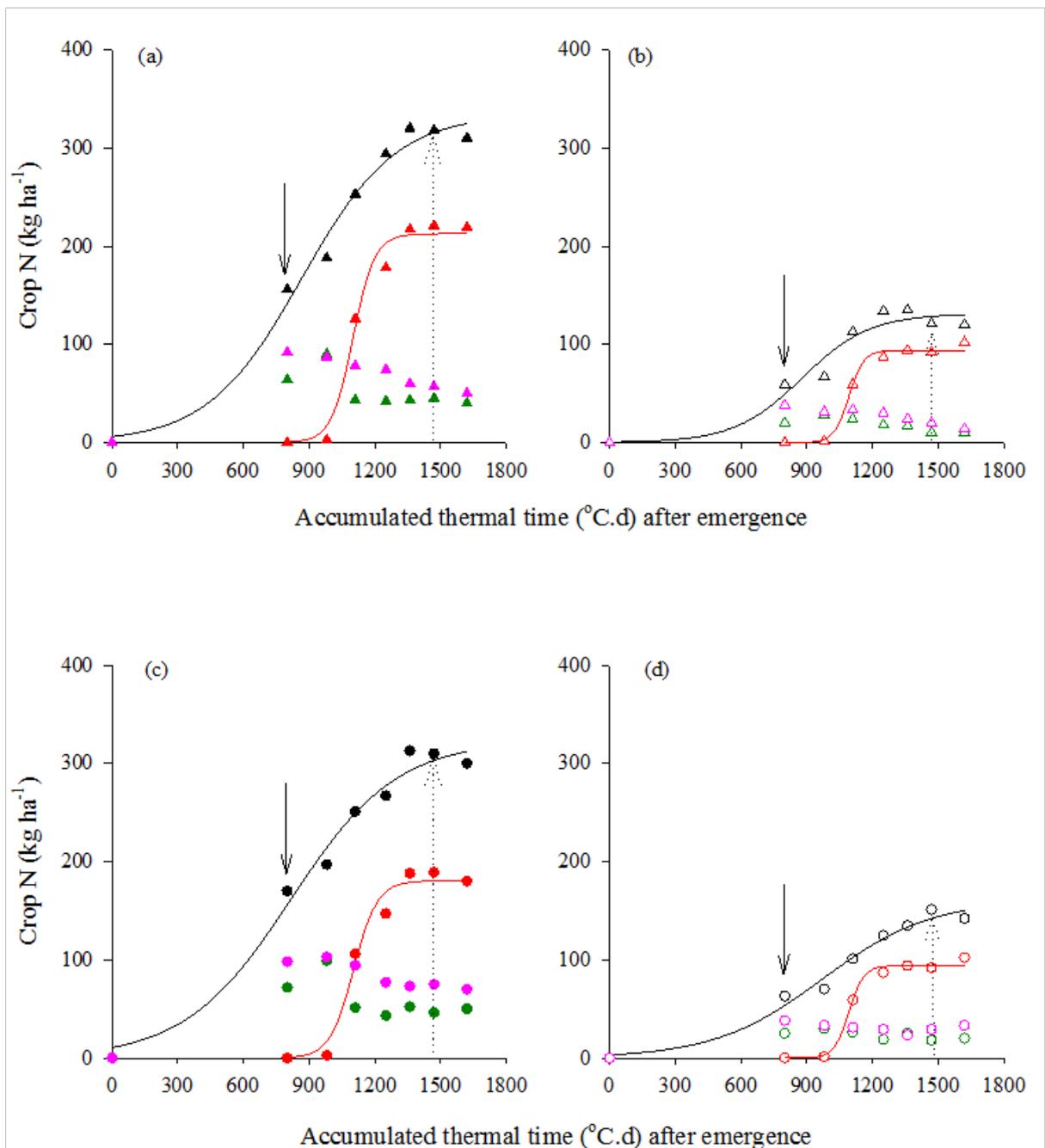


Figure 6.4: Mean N content (kg ha⁻¹) for total crop (black), kernels (red), stalk (dark green), and leaves (pink) against accumulated thermal time (°C.d) after emergence in irrigated crops of 'P39K38' (sgr 6) (a and b) and 'P38G43' (sgr 9) (c and d), grown with 270 (solid symbols) or 0 kg N ha⁻¹ (open symbols) at Lincoln University, New Zealand, during 2008. The solid arrow represents 7 days after silking (800 °C.d) and the dotted physiological maturity (1470 °C.d).

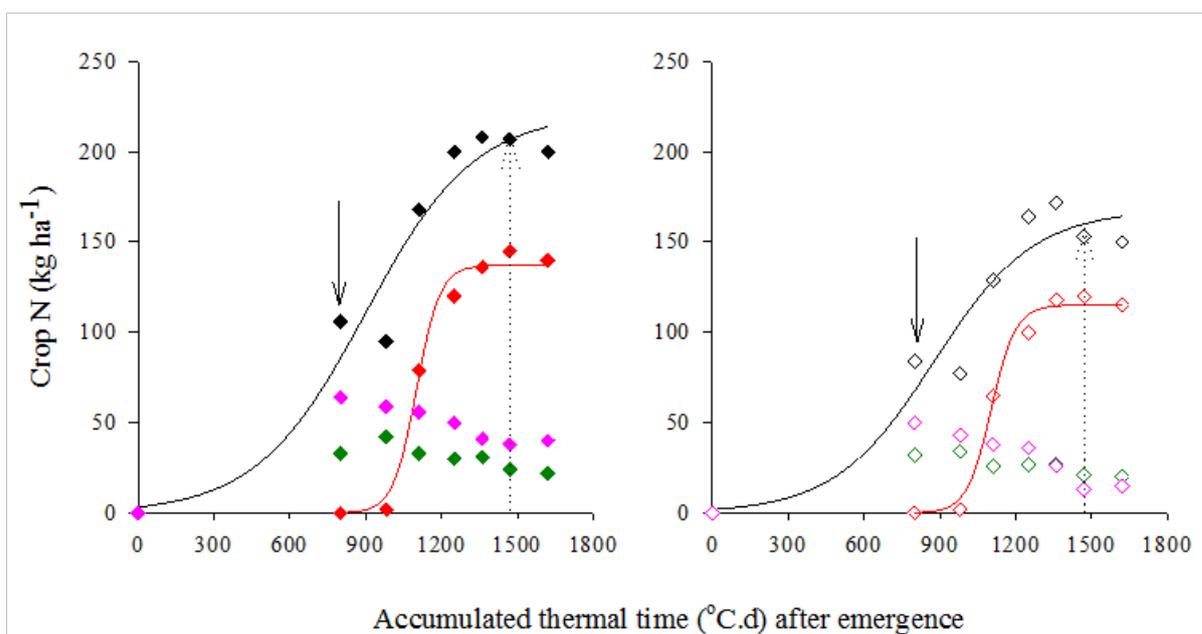


Figure 6.5: Mean N content (kg ha^{-1}) for total crop (black), kernels (red), stalk (dark green), and leaves (pink) against accumulated thermal time ($^{\circ}\text{C.d}$) after emergence in irrigated (solid symbols) or rain fed (open symbols) crops grown at Lincoln University, New Zealand, during 2008. The solid arrow represents 7 days after silking (800°C.d) and the dotted physiological maturity (1470°C.d).

6.5.4.2 Kernel N

Averaged across N and water treatments, grain N (%) at final harvest was highest ($P < 0.005$) at 1.43% in ‘P39K38’ (sgr 6) compared with 1.29% for ‘P38G43’ (sgr 9) with the other two hybrids intermediate. Grain N (kg ha^{-1}) at final harvest also differed between the N treatments and among the hybrids. Maximum N accumulated in the kernels of the unfertilised crops was 80 kg ha^{-1} compared with 190 kg ha^{-1} in the fertilised crops (Table 6.6). The kernels of ‘P39K38’ (sgr 6) accumulated 155 kg N ha^{-1} which was more ($P < 0.045$) than all the other hybrids. Irrigation had no effect ($P < 0.084$) on the total N accumulated in the kernels at final harvest which averaged $135 (\pm 3.8) \text{ kg ha}^{-1}$ (Figure 6.5).

During grain filling the rate of increase in kernel N ($\text{kg ha}^{-1} \text{ day}^{-1}$) was essentially linear up to 64 days after silking (1360°C.d) (Figure 6.4 and Appendix 5) and influenced by N and hybrid main effects. Provision of fertiliser N accelerated ($P < 0.001$) the rate of N acquisition by 130% while ‘P39K38’ (sgr 6) had the fastest ($P < 0.047$) rate of kernel N increase at 2.29 kg ha^{-1} per day (Table 6.7). Provision of water also promoted the uptake of N by the kernels with the rate

of N accumulated by the irrigated crops being 28% higher ($P < 0.050$) than that of the rain fed crops.

Table 6.6: Total kernel N (kg ha^{-1}) at final harvest in hybrid maize grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.

Hybrid	Total kernel N (kg ha^{-1})		
	0 kg N ha^{-1}	270 kg N ha^{-1}	Mean
'P39K38' (sgr 6)	90	220	155 _a
'P38V12' (sgr 7)	80	180	130 _b
'P38F70' (sgr 8)	80	170	125 _b
'P38G43' (sgr 9)	70	190	130 _b
Mean	80	190	135
P value	P<0.001		P<0.045
SE	5.4		7.7
CV (%)	15.9		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

Table 6.7: Rate of increase of kernel N ($\text{kg ha}^{-1} \text{ day}^{-1}$) from silking to physiological maturity in hybrid maize grown with 0 or 270 kg N ha^{-1} and either irrigated or rain fed at Lincoln University, New Zealand, during 2008.

Treatment	Rate of increase of kernel N ($\text{kg ha}^{-1} \text{ day}^{-1}$)				Mean
	0 kg N ha^{-1}	270 kg N ha^{-1}	Rain fed	Irrigated	
'P39K38' (sgr 6)	1.36	3.22	2.11	2.47	2.29 _a
'P38V12' (sgr 7)	1.17	2.67	1.83	2.01	1.92 _b
'P38F70' (sgr 8)	1.19	2.53	1.50	2.22	1.86 _b
'P38G43' (sgr 9)	1.04	2.66	1.52	2.18	1.85 _b
Mean	1.19	2.77	1.74	2.22	1.98
P value	P<0.001		P<0.050		P<0.047
SE	0.081		0.027		0.114
CV (%)	16.3				

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

NHI (%) was influenced by both water and hybrid. The rain fed crops partitioned 11% more ($P<0.044$) of their above ground N into the kernels compared with the irrigated crops (Table 6.8). Similarly, ‘P39K38’ (sgr 6) translocated 10% more ($P<0.001$) N to its kernels than ‘P38G43’ (sgr 9). N fertilisation had no effect ($P<0.156$) on the proportion of N partitioned to the kernels with an average of 75 (± 0.8)% of the total above ground N recovered from the kernels of both crops.

Table 6.8: Nitrogen harvest index (%) in hybrid maize either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Hybrid	Nitrogen harvest index (%)		Mean
	Rain fed	Irrigated	
‘P39K38’ (sgr 6)	82	72	77 _a
‘P38V12’ (sgr 7)	80	72	76 _a
‘P38F70’ (sgr 8)	79	73	76 _a
‘P38G43’ (sgr 9)	74	65	70 _b
Mean	79	71	75
P value	P<0.044		P<0.001
SE	0.4		1.2
CV (%)	4.4		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

6.5.4.3 Stalk N

Stalk N (kg ha^{-1}) content in the fertilised crops peaked at 980 °C.d, but immediately declined to a relatively constant value at 1100 °C.d (Figure 6.4 and Appendix 5). At 800 °C.d (7 days after silking), stalk N (kg ha^{-1}) increased ($P<0.001$) from 23 to 83 kg ha^{-1} with the provision of fertiliser N (Table 6.9). However, stalk N did not differ ($P<0.054$) among the hybrids at 800 °C.d (7 days after silking) and averaged 53 (± 2.6) kg ha^{-1} . Similarly, it did not differ ($P<0.156$) with irrigation at this time and averaged 53 (± 1.8) kg ha^{-1} .

At physiological maturity (1470 °C.d), the quantity of N recovered from the stalks of the fertilised crops was more than threefold ($P<0.001$) the quantity recovered from the stalks of the non fertilised crop. Also, the stalks of ‘P38G43’ (sgr 9) had 14 kg N ha^{-1} more ($P<0.005$)

than those of both ‘P38V12’ (sgr 7) and ‘P38F70’ (sgr 8). Stalk N (kg ha^{-1}) did not differ ($P < 0.285$) with irrigation at physiological maturity ($1470\text{ }^{\circ}\text{C.d}$) and averaged $23 (\pm 1.3)\text{ kg ha}^{-1}$.

Translocated N from stalks differed between the N and hybrid treatments. The fertilised crops translocated $49\text{ kg of N ha}^{-1}$ which was more ($P < 0.001$) than the $13\text{ kg of N ha}^{-1}$ from non fertilised crops (Table 6.10). The low ‘stay-green’ hybrids (‘P39K38’ (sgr 6) and ‘P38V12’ (sgr 7)) translocated at least $20\text{ kg of N ha}^{-1}$ more ($P < 0.020$) stalk N than the high ‘stay-green’ (‘P38G43’ (sgr 9)) hybrid. Water had no effect ($P < 0.138$) on the N translocated from the stalks which averaged $31 (\pm 0.7)\text{ kg N ha}^{-1}$.

Table 6.9: Stalk N (kg ha^{-1}) at $800\text{ }^{\circ}\text{C.d}$ and physiological maturity ($1470\text{ }^{\circ}\text{C.d}$) for hybrid maize grown with 0 or 270 kg N ha^{-1} at Lincoln University, New Zealand, during 2008.

Hybrid	Stalk N (kg ha^{-1})					
	800 $^{\circ}\text{C.d}$			Physiological maturity		
	0 kg N ha^{-1}	270 kg N ha^{-1}	Mean	0 kg N ha^{-1}	270 kg N ha^{-1}	Mean
‘P39K38’ (sgr 6)	24	90	57	10	32	21 _b
‘P38V12’ (sgr 7)	23	87	55	8	30	19 _b
‘P38F70’ (sgr 8)	22	70	46	10	28	19 _b
‘P38G43’ (sgr 9)	23	85	54	16	50	33 _a
Mean	23	83	53	11	35	23
P value	$P < 0.001$		$P < 0.054$	$P < 0.001$		$P < 0.005$
SE	1.9		2.6	1.8		2.5
CV (%)	13.9			32.0		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

Both ‘P39K38’ (sgr 6) and ‘P38V12’ (sgr 7) translocated stalk N more ($P < 0.036$) efficiently (65 and 64%) than ‘P38G43’ (sgr 9), which only translocated 42% of its stalk N. Neither N ($P < 0.383$) nor water ($P < 0.916$) had an effect on the stalk N translocation efficiency which averaged $56 (\pm 3.9)\%$.

Table 6.10: Stalk N (kg ha⁻¹) translocation and its efficiency (%) during grain filling in hybrid maize grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Hybrid	Stalk N translocated (kg ha ⁻¹)			Translocation efficiency (%)
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean	
‘P39K38’ (sgr 6)	16	58	37 _a	65 _a
‘P38V12’ (sgr 7)	14	58	36 _a	64 _a
‘P38F70’ (sgr 8)	12	43	28 _{ab}	54 _{ab}
‘P38G43’ (sgr 9)	10	37	24 _b	42 _b
Mean	13	49	31	56
P value	P<0.001		P<0.020	P<0.036
SE	2.4		3.4	5.5
CV (%)	30.9			27.8

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

6.5.4.4 Leaf N content

(a) Silking to physiological maturity

Total leaf N (kg ha⁻¹) content at 800 °C.d (7 days after silking), differed between the N and water treatments as main effects. It increased (P<0.001) from 30 to 84 kg ha⁻¹ when fertiliser N was provided (Table 6.11). The leaves of the irrigated treatments also had 14 kg ha⁻¹ more (P<0.044) than the rain fed crops at this time. In contrast, hybrid had no effect (P<0.139) on total leaf N content which averaged 57 (± 2.8) kg ha⁻¹.

Total leaf N (kg ha⁻¹) at physiological maturity (1470 °C.d) was influenced by the water x hybrid interaction. Except in ‘P38F70’ (sgr 8), irrigation more than doubled (P<0.001) the amount of N recovered from the leaves (Table 6.12). Further, the leaves of ‘P38G43’ (sgr 9) held 35 kg ha⁻¹, which was higher (P<0.001) than the average of ~25 kg ha⁻¹ found in the leaves of both ‘P39K38’ (sgr 6) and ‘P38V12’ (sgr 7). Total leaf N (kg ha⁻¹) at physiological maturity was also influenced by the water x N interaction. Fertiliser N increased (P<0.001) the amount of N recovered from the leaves of the rain fed crops by only 14 kg ha⁻¹. However, it increased it by 31 kg ha⁻¹ when they were irrigated.

Table 6.11: Total leaf N (kg ha⁻¹) 7 days after silking (800 °C.d) in hybrid maize grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Hybrid	Total leaf N at 800 °C.d (kg ha ⁻¹)				Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Rain fed	Irrigated	
‘P39K38’ (sgr 6)	29	85	50	64	57
‘P38V12’ (sgr 7)	32	89	54	67	61
‘P38F70’ (sgr 8)	27	75	46	56	51
‘P38G43’ (sgr 9)	32	86	50	68	59
Mean	30	84	50	64	57
P value	P<0.001		P<0.044		P<0.139
SE	2.0		0.7		2.8
CV (%)	13.7				

Table 6.12: Total leaf N (kg ha⁻¹) at physiological maturity (1470 °C.d) in hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Water	Total leaf N (kg ha ⁻¹)				kg N ha ⁻¹	
	Hybrid				0	270
	‘P39K38’ (sgr 6)	‘P38V12’ (sgr 7)	‘P38F70’ (sgr 8)	‘P38G43’ (sgr 9)		
Rain fed	10	15	12	21	7	22
Irrigated	39	37	22	49	21	53
P value	P<0.001				P<0.001	
SE	2.6				2.0	
CV (%)	12.3					

The quantity of N translocated from the leaves was influenced by the water x N interaction. Crops translocated a similar quantity of N when they were unfertilised (Table 6.13). However, when fertiliser N was provided, irrigation reduced (P<0.007) the quantity of N translocated from the leaves by 16 kg ha⁻¹. N translocation from the leaves during grain filling was also influenced by the hybrid main effect. ‘P38G43’ (sgr 9) translocated the least (P<0.044) amount of its leaf N compared with the other hybrids (Table 6.14). Leaf N translocation efficiency (%) was affected by the water x hybrid interaction. Irrigation had the least (P<0.020) effect on the efficiency of leaf N translocation by ‘P38F70’ (sgr 8).

Table 6.13: Total leaf N (kg ha⁻¹) translocated from silking to physiological maturity (grain filling) in hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Water	Leaf N translocated (kg ha ⁻¹)	
	0 kg N ha ⁻¹	270 kg N ha ⁻¹
Rain fed	19	54
Irrigated	17	38
P value	P<0.024	
SE	3.0	
CV (%)	24.2	

Table 6.14: Leaf N (kg ha⁻¹) translocated from silking to physiological maturity (grain filling) in hybrid maize grown with 0 or 270 kg N ha⁻¹ and its efficiency (%) of translocation in rain fed or irrigated crops grown at Lincoln University, New Zealand, during 2008.

Hybrid	Leaf N translocated (kg ha ⁻¹)			Translocation efficiency (%)	
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean	Rain fed	Irrigated
'P39K38' (sgr 6)	18	48	33 _a	80	42
'P38V12' (sgr 7)	20	52	36 _a	73	46
'P38F70' (sgr 8)	19	50	35 _a	73	61
'P38G43' (sgr 9)	15	34	25 _b	62	29
Mean	18	46	32	72	45
P value	P<0.001		P<0.044	P<0.020	
SE	1.9		2.8	4.3	
CV (%)	24.2			13.4	

Due to the relationship between the SLN concentration (g m⁻²) and RUE (Section 2.3.4.2), this component was considered the most relevant in the analysis of the influence of N on crop growth and development. As an illustration, SLN data 7 days after silking (800 °C.d) and late grain filling (1360 °C.d) are presented. However, only the general trend of decline amongst the hybrids was illustrated graphically.

(b) Specific leaf N concentration (g m^{-2})

(i) Lower leaves

SLN concentration (g m^{-2}) differed between the N and irrigation treatments seven days after silking (800 °C.d). It increased ($P<0.001$) from 0.91 to 1.85 g m^{-2} when N fertiliser was provided (Table 6.15). Irrigation also increased ($P<0.007$) the SLN from 1.29 to 1.47 g m^{-2} . However, SLN did not differ ($P<0.859$) among the hybrids at this time and averaged 1.38 (± 0.071) g m^{-2} .

Table 6.15: Specific leaf N concentration (g m^{-2}) of the lower leaves at 800 °C.d for hybrid maize grown with 0 or 270 kg N ha^{-1} and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Hybrid	Specific leaf N concentration (g m^{-2})				Mean
	0 kg N ha^{-1}	270 kg N ha^{-1}	Rain fed	Irrigated	
‘P39K38’ (sgr 6)	0.94	1.72	1.28	1.38	1.33
‘P38V12’ (sgr 7)	0.96	1.80	1.26	1.50	1.38
‘P38F70’ (sgr 8)	0.87	1.91	1.34	1.44	1.39
‘P38G43’ (sgr 9)	0.87	1.97	1.28	1.56	1.42
Mean	0.91	1.85	1.29	1.47	1.38
P value	$P<0.001$		$P<0.007$		$P<0.859$
SE	0.050		0.002		0.071
CV (%)	14.5				

While SLN of the lower leaves declined in all hybrids during grain filling (Figure 6.6), there was a sharp decline between 800 and 980 °C.d. This initial decline appeared to be steeper in ‘P38V12’ (sgr 7) than in the other hybrids. It then declined more gently towards physiological maturity.

At late grain filling (1360 °C.d), all two way interactions significantly influenced the SLN of the lower leaves. SLN was influenced ($P<0.003$) by the N x hybrid interaction in which fertiliser N increased the SLN of both ‘P38V12’ (sgr 7) and ‘P38F70’ (sgr 8) by 0.50 g m^{-2} . In contrast, fertiliser N increased the SLN of ‘P39K38’ (sgr 6) by only 0.24 g m^{-2} compared with 0.97 g m^{-2} for ‘P38G43’ (sgr 9) (Table 6.16). SLN of the lower leaves was also affected by

the water x hybrid interaction at this time. Irrigation increased ($P < 0.029$) SLN in all hybrids except 'P38V12' (sgr 7) where SLN declined by 0.1 g m^{-2} .

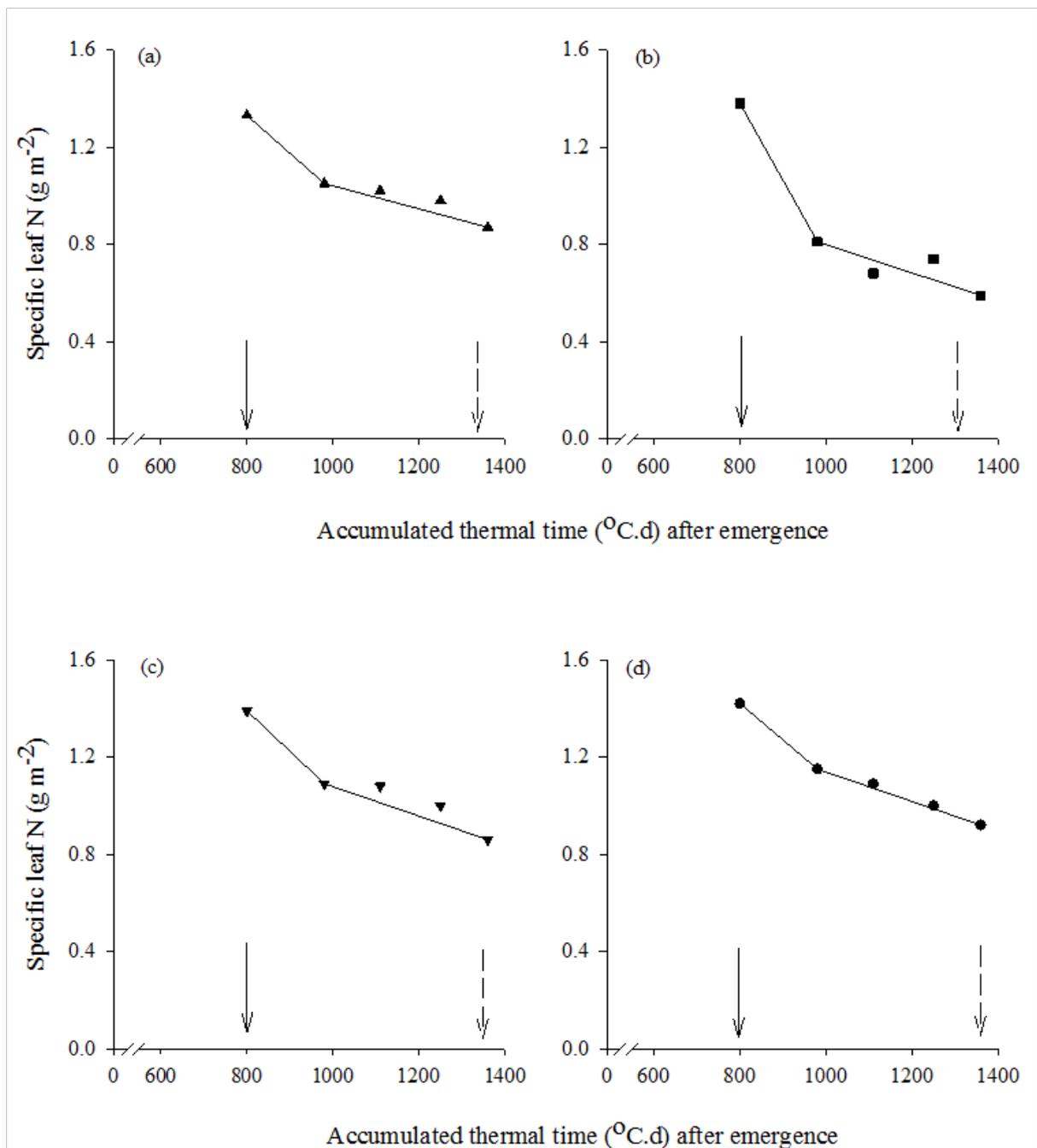


Figure 6.6: Mean (across N and irrigation levels) specific leaf N concentration (g m^{-2}) during grain filling of the lower leaves of (a) 'P39K38' (sgr 6), (b) 'P38V12' (sgr 7), (c) 'P38F70' (sgr 8) and (d) 'P38G43' (sgr 9) grown at Lincoln University, New Zealand, during 2008. The solid arrow indicates 7 days after silking ($800 \text{ }^{\circ}\text{C.d}$) and the dashed late grain filling ($1360 \text{ }^{\circ}\text{C.d}$).

Table 6.16: Specific leaf N concentration (g m^{-2}) of the lower leaves at 1360 °C.d for hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Hybrid	Specific leaf N concentration (g m^{-2})				Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Rain fed	Irrigated	
'P39K38' (sgr 6)	0.75	0.99	0.81	0.92	0.87 _a
'P38V12' (sgr 7)	0.34	0.84	0.64	0.54	0.59 _b
'P38F70' (sgr 8)	0.61	1.11	0.70	1.02	0.86 _a
'P38G43' (sgr 9)	0.43	1.40	0.73	1.11	0.92 _a
Mean	0.53	1.09	0.72	0.90	0.81
P value	P<0.003		P<0.029		P<0.003
SE	0.107		0.096		0.054
CV (%)	18.7				

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

Similarly, fertiliser N increased ($P<0.001$) the SLN by 57% from 0.56 to 0.88 g m^{-2} when the crops were rain fed (Table 6.17). However, when the crops were irrigated, N increased the SLN by 160% from 0.50 to 1.29 g m^{-2} .

Table 6.17: Specific leaf N concentration (g m^{-2}) of the lower leaves at 1360 °C.d for hybrid maize grown with 0 or 270 kg N ha⁻¹ and either irrigated or rain fed at Lincoln University, New Zealand, during 2008.

Water	Specific leaf N concentration (g m^{-2})		
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean
Rain fed	0.56	0.88	0.72
Irrigated	0.50	1.29	0.90
Mean	0.53	1.08	0.81
P value	P<0.001		P<0.001
SE	0.307		0.042
CV (%)	18.7		

(ii) Middle leaves

The SLN of the middle leaves at 800 °C.d was influenced by all treatment factors but not their interactions. Fertiliser N increased ($P < 0.001$) the SLN, from 1.27 to 1.97 g m⁻² (Table 6.18). Irrigation also increased ($P < 0.033$) the SLN from 1.59 to 1.64 g m⁻². Among the hybrids, ‘P38G43’ (sgr 9) had the highest ($P < 0.001$) SLN at 1.77 g m⁻² and ‘P38V12’ (sgr 7) was also lower (1.50 g m⁻²) than ‘P38F70’ (sgr 8).

Table 6.18: Specific leaf N concentration (g m⁻²) of the middle leaves at 800 °C.d for hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Hybrid	Specific leaf N concentration (g m ⁻²)				Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Rain fed	Irrigated	
‘P39K38’ (sgr 6)	1.21	1.89	1.53	1.56	1.55 _{bc}
‘P38V12’ (sgr 7)	1.19	1.81	1.49	1.51	1.50 _c
‘P38F70’ (sgr 8)	1.26	2.02	1.56	1.72	1.64 _b
‘P38G43’ (sgr 9)	1.40	2.14	1.78	1.76	1.77 _a
Mean	1.27	1.97	1.59	1.64	1.62
P value	P<0.001		P<0.033		P<0.001
SE	0.024		0.002		0.034
CV (%)	6.0				

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

Consistent with the SLN of the lower leaves, that of the middle leaves also declined during grain filling. However, the decline in SLN did not show a consistent trend among the hybrids (Figure 6.7). Except for ‘P38V12’ (sgr 7), SLN declined more steadily in the other hybrids between 800 °C.d and 1100 °C.d. After mid grain filling (1110 °C.d), the pattern of SLN decline was consistent among the hybrids.

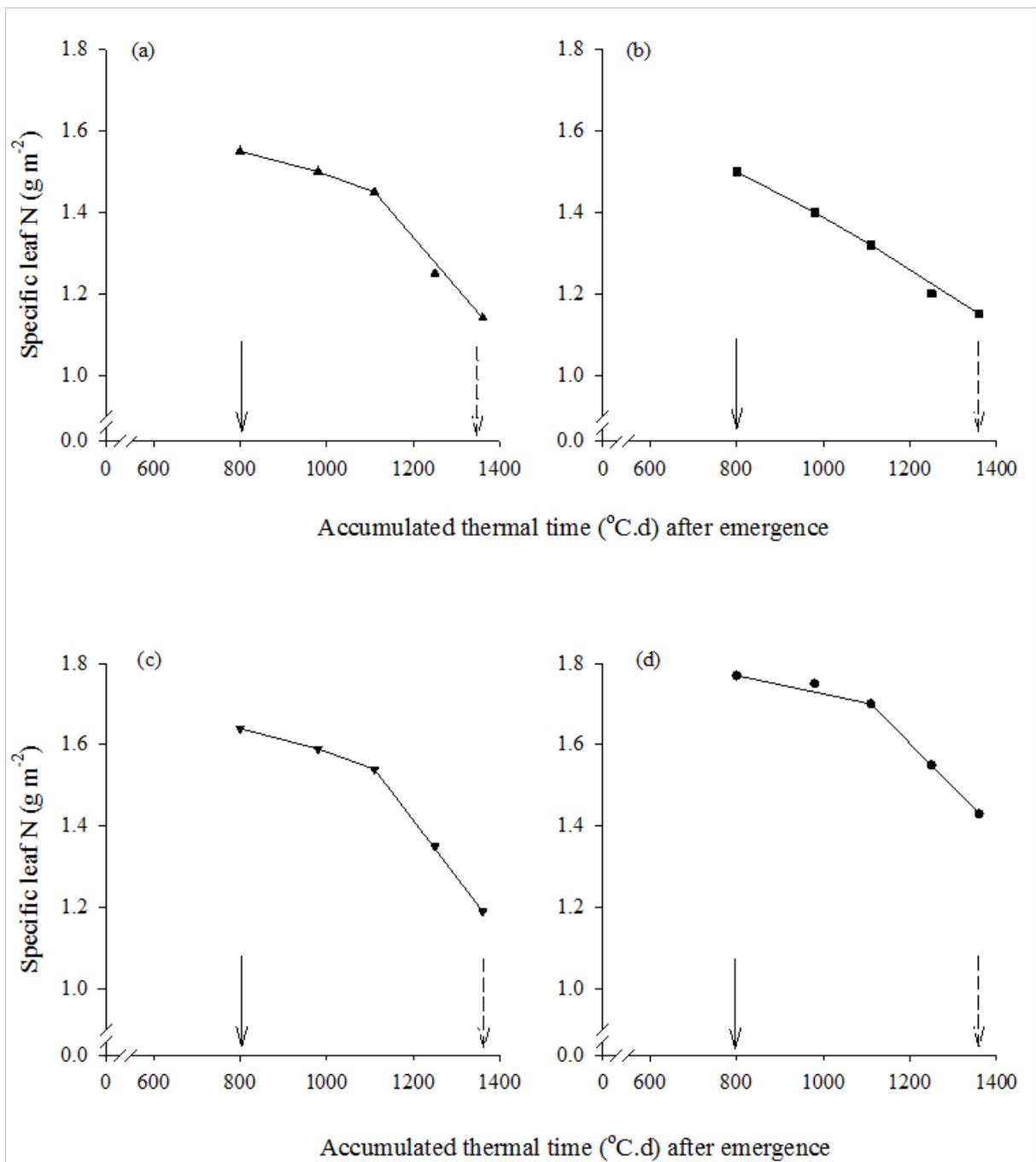


Figure 6.7: Mean (across N and irrigation levels) specific leaf N concentration (g m^{-2}) during grain filling of the middle leaves of (a) 'P39K38' (sgr 6), (b) 'P38V12' (sgr 7), (c) 'P38F70' (sgr 8) and (d) 'P38G43' (sgr 9) grown at Lincoln University, New Zealand, during 2008. The solid line represents 7 days after silking (800 $^{\circ}\text{C.d}$) and the dashed late grain filling (1360 $^{\circ}\text{C.d}$).

At 1360 $^{\circ}\text{C.d}$, SLN increased ($P < 0.001$) from 0.80 to 1.65 g m^{-2} in the presence of fertiliser N, while the SLN of 'P38G43' (sgr 9) was 1.43 g m^{-2} and higher ($P < 0.044$) than that of the other hybrids ($\leq 1.19 \text{ g N m}^{-2}$) (Figure 6.19). Irrigation again had no effect ($P < 0.110$) on SLN and at this stage it averaged $1.23 (\pm 0.036) \text{ g m}^{-2}$, regardless of treatment.

Table 6.19: Specific leaf N concentration (g m^{-2}) across irrigation treatments of the middle leaves at 1360 °C.d for hybrid maize grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Hybrid	Specific leaf N concentration (g m^{-2})		
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean
‘P39K38’ (sgr 6)	0.75	1.51	1.14 _b
‘P38V12’ (sgr 7)	0.78	1.51	1.15 _b
‘P38F70’ (sgr 8)	0.75	1.62	1.19 _b
‘P38G43’ (sgr 9)	0.91	1.95	1.43 _a
Mean	0.80	1.65	1.23
P value	P<0.001		P<0.044
SE	0.052		0.074
CV (%)	17.0		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

(iii) Top leaves

SLN of the top leaves at 800 °C.d was affected by the hybrid and N treatments. Fertiliser N increased ($P<0.001$) SLN from 1.25 to 2.36 g m^{-2} , while among the hybrids ‘P38G43’ (sgr 9) had the highest ($P<0.036$) SLN of 1.95 g m^{-2} (Table 6.20). Irrigation had no effect ($P<0.208$) on SLN at this stage which averaged 1.81 (± 0.048) g m^{-2} .

SLN at 1360 °C.d differed between the N treatments and among the hybrids. Fertiliser N increased ($P<0.001$) SLN from 1.07 to 1.62 g m^{-2} while the two higher rated ‘stay-green’ hybrids had higher ($P<0.025$) SLN when compared with the two low ‘stay-green’ hybrids (Table 6.21). Water had no effect ($P<0.975$) on the SLN which averaged 1.35 (± 0.160) g m^{-2} . SLN of the top leaves declined continuously during grain filling. The decline was faster ($P<0.041$) at 0.0012 g m^{-2} per °C.d in ‘P39K38’ (sgr 6) compared with an average of 0.0007 \pm (0.00013) g m^{-2} per °C.d in the other hybrids (Figure 6.8).

Table 6.20: Specific leaf N concentration (g m^{-2}) of the top leaves at 800 °C.d for hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Hybrid	Specific leaf N concentration (g m^{-2})				Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Rain fed	Irrigated	
‘P39K38’ (sgr 6)	1.21	2.38	1.70	1.90	1.80 _{ab}
‘P38V12’ (sgr 7)	1.20	2.22	1.64	1.78	1.71 _b
‘P38F70’ (sgr 8)	1.23	2.31	1.70	1.84	1.77 _b
‘P38G43’ (sgr 9)	1.36	2.53	1.80	2.10	1.95 _a
Mean	1.25	2.36	1.71	1.91	1.81
P value	P<0.001		P<0.208		P<0.036
SE	0.036		0.048		0.051
CV (%)	7.9				

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

Table 6.21: Specific leaf N concentration (g m^{-2}) of the top leaves at 1360 °C.d for hybrid maize grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Hybrid	Specific leaf N concentration (g m^{-2})			Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹		
‘P39K38’ (sgr 6)	0.89	1.38		1.14 _b
‘P38V12’ (sgr 7)	1.11	1.50		1.31 _{ab}
‘P38F70’ (sgr 8)	1.14	1.80		1.47 _a
‘P38G43’ (sgr 9)	1.12	1.79		1.46 _a
Mean	1.07	1.62		1.35
P value	P<0.001			P<0.025
SE	0.054			0.077
CV (%)	16.2			

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

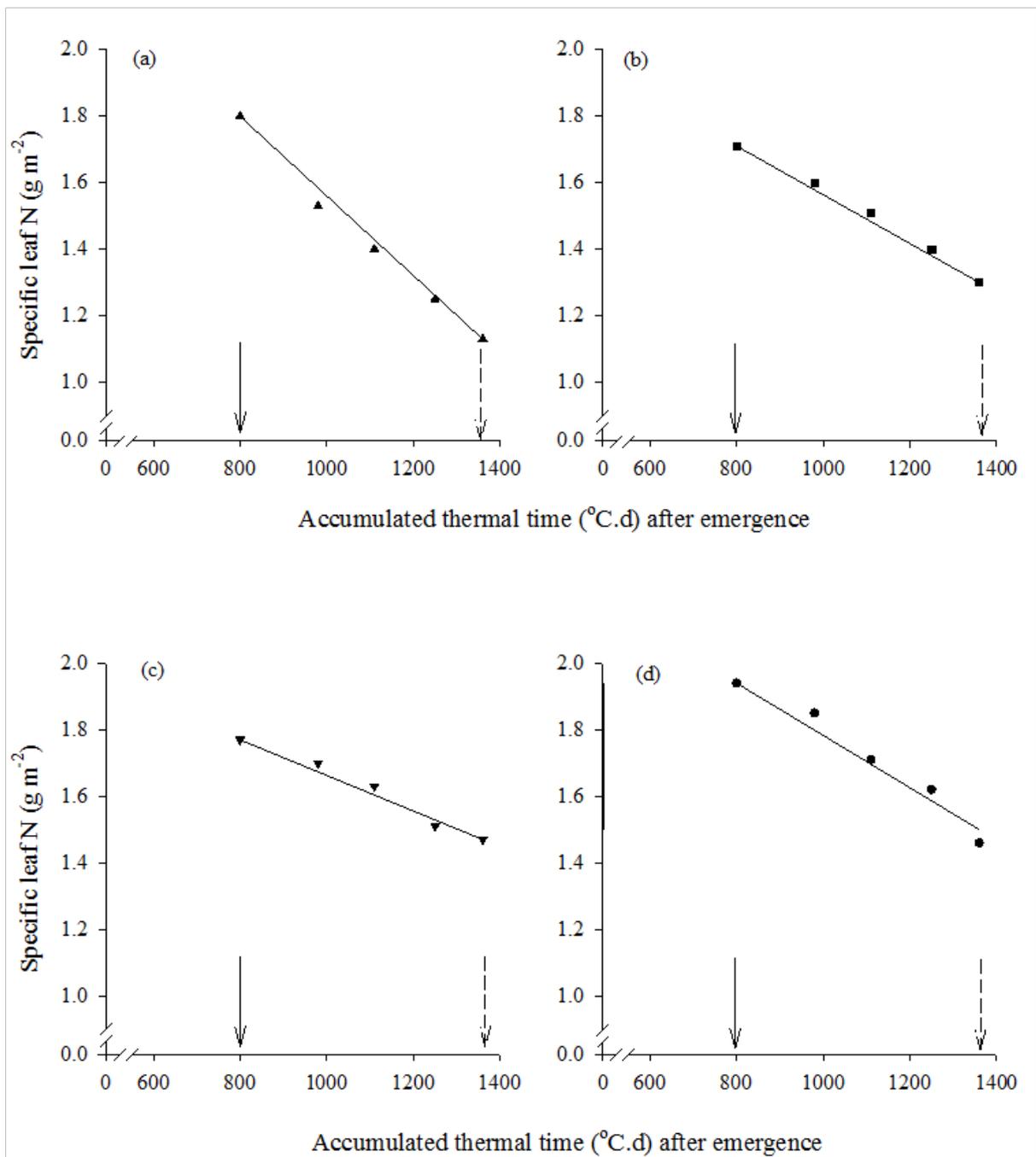


Figure 6.8: Mean (across N and irrigation levels) specific leaf N concentration (g m^{-2}) during grain filling of the top leaves of (a) 'P39K38' (sgr 6), (b) 'P38V12' (sgr 7), (c) 'P38F70' (sgr 8) and (d) 'P38G43' (sgr 9) grown at Lincoln University, New Zealand, during 2008. The respective equations were: (a) $y = 2.71 - 0.0012x$; $R^2 = 0.99$, (b) $y = 2.31 - 0.0007x$; $R^2 = 0.99$, (c) $y = 2.24 - 0.0006x$; $R^2 = 0.98$ and (d) $y = 2.64 - 0.0008x$; $R^2 = 0.97$. The solid line represents 7 days after silking (800 °C.d) and the dashed late grain filling (1360 °C.d).

6.6 Discussion

6.6.1 RUE

The 'stay-green' trait positively influenced RUE, and the high 'stay-green' hybrids (sgr 8 and 9) utilised iPAR more efficiently than the lower 'stay-green' rated hybrids. Specifically, RUE of the high 'stay-green' hybrids (sgr 8 and 9) was 8% higher than the low 'stay-green' hybrids (sgr 6 and 7) (Table 6.1). The lower RUE for 'P39K38' (sgr 6), was probably related to a decline in photosynthetic rate during grain filling as a result of the reduction in SLN of its middle and upper leaves (Tables 6.19 and 6.21). Part of the decline in RUE also reflects greater demand for N by its kernels (Table 6.8) and the high energy costs associated with the synthesis of products rich in N (Sinclair & Muchow 1999; Trapani *et al.* 1992). Dale (1992), provides a value of 2.35 g of glucose per gram of N compound synthesized compared with 1.15 g of glucose per gram of polysaccharide. Interestingly, using the production value (PV, gram of product/ gram of glucose used) approach (McDermitt & Loomis 1981), these values are consistent with the 0.40 and 0.83, calculated by Penning de Vries *et al.* (1974), for the synthesis of nitrogenous compounds and polysaccharides, respectively.

For 'P38V12' (sgr 7), the lower RUE was associated with the steeper decline in SLN of its lower leaves between 800 and 980 °C.d (Figure 6.6b), and that of the middle and upper leaves during grain filling as a consequence of the development of more grains per ear (Table 4.3). The greater demand for N by the grains of 'P38V12' (sgr 7) was likely to have reduced the photosynthetic capacity of the lower leaves (first 10 leaves) and its efficiency to utilize absorbed PAR. This is consistent with the lower seed weight (mg) recorded in 'P38V12' (sgr 7) (Table 4.4). These results support the idea of enhanced photosynthetic efficiency by N reported by Tollenaar and Bruulsema (1988), through the maintenance of a higher SLN (Sections 2.3.4.3).

The low 'stay-green' hybrids (sgr 6 and 7) also accumulated more green area than the high 'stay-green' hybrids (sgr 8 and 9) (Figure 5.2). Given an inherent negative correlation between photosynthetic capacity and leaf area (Pellny *et al.* 2004), the reduction in RUE among the low 'stay-green' hybrids may be related to an increase in the respiratory costs associated with the maintenance and growth of this green area (Amthor 2000). Respiratory costs are considered proportional to total gross photosynthesis (Andrade *et al.* 1992), and may consume up to 50% of the total carbon fixed in C₃ plants (Gifford *et al.* 1984).

6.6.2 Chlorophyll content and leaf senescence

Leaf chlorophyll content (SPAD units) soon after silking (800 °C.d) was strongly indicative ($R^2 = 0.89$) of SLN (Figure 6.2). Therefore, SPAD meter readings can be used as a quick reference of the leaf N content under field conditions (Chapman & Barreto 1997; Markwell *et al.* 1995). Leaf chlorophyll content did not differ between the hybrids seven days after silking (800 °C.d) or at physiological maturity (1470 °C.d) (Tables 6.2 and 6.3). This observation could be related to the SPAD measurements that were derived from an average from three leaf cohorts (Section 3.4.3). An examination of the chlorophyll content of the bottom leaf cohort at seven days after silking showed differences among the low and high ‘stay-green’ hybrids (Appendix 6). Thus, the lack of difference in chlorophyll content amongst the hybrids seems to contradict the observed differences in RUE among the hybrids (Section 6.6.1). However, it is unlikely that an instantaneous measure of the chlorophyll content could have a bearing on RUE which is determined as a seasonal integral (Section 6.4).

The number of senesced leaves per plant increased consistently from silking until physiological maturity (Figure 6.3). Amongst the hybrids ‘P38G43’ (sgr 9), senesced fewer leaves per plant but only when the crops were N fertilised (Table 6.4). This suggests the expression of the ‘stay-green’ trait was dependent on an adequate supply of N as previously suggested by Subedi and Ma (2005). Around silking, there appeared to be an accelerated leaf loss among the N stressed crops (Figure 6.3b). This is consistent with the strong N demand at sink establishment observed by Tollenaar and Dwyer (1999). However, once the sink size was determined, the rate of leaf loss declined in accordance with sink demands. Similarly, the fertilised but rain fed crops senesced more leaves per plant between silking and physiological maturity than the irrigated crops (Table 6.5), which was related to the greater efficiency of N translocation (Table 6.14). This was reflected by the larger amount of leaf N translocated (Table 6.13), in agreement with the results obtained by Wolfe *et al.* (1988a) in their study in maize.

6.6.3 N uptake and partitioning during grain filling

Over 60% of total crop N had accumulated in the kernels of each crop by final harvest but hybrids differed in the absolute amount (Table 6.6). ‘P39K38’ (sgr 6) accumulated more N in its kernels than the other hybrids. To produce high grain N, ‘P39K38’ (sgr 6), either partitioned a greater proportion of its N to grain filling or remobilized more of the vegetative

N (Borrell *et al.* 2001). Total crop N at final harvest (Figures 6.4, 6.5 and Appendix 5) and at silking did not differ among the hybrids (Appendix 7), which suggests greater N remobilisation by 'P39K38' (sgr 6). Table 6.7 shows that 'P39K38' (sgr 6), had a faster rate of N accumulation in the grains (Table 6.7), and consequently the highest NHI (Table 6.8). NHI was 7% higher in 'P39K38' (sgr 6), compared with 'P38G43' (sgr 9). These data agree with those of Subedi and Ma (2005), who also found no differences in N uptake among three maize hybrids of different 'stay-green' rating. However, they contrast with the observations of Borrell and Hammer (2000), in grain sorghum and Rajcan and Tollenaar (1999b), in maize who reported greater N sequestration by the 'stay-green' hybrids during grain filling. The implication is that the mechanisms responsible for the qualitative 'stay-green' trait may differ between these two species.

The results from this study support greater remobilisation of vegetative N towards grain filling in 'P39K38' (sgr 6). Evidence for this observation was derived from the greater proportion and efficiency of stalk N (kg ha^{-1}) translocation during grain filling (Tables 6.9 and 6.10). The low 'stay-green' hybrids (sgr 6 and 7) translocated stalk N more efficiently than the high 'stay-green' hybrids (sgr 8 and 9). For example, 'P39K38' (sgr 6) translocated 23% more stalk N than 'P38G43' (sgr 9). Additionally, the low 'stay-green' hybrids (sgr 6 and 7), also translocated $\sim 10 \text{ kg ha}^{-1}$ more of their leaf N compared with 'P38G43' (sgr 9) (Table 6.14). These results are consistent with those of Ta and Weiland (1992), who also reported greater remobilisation of vegetative N from an early senescent than a late senescent maize hybrid.

6.6.4 Specific leaf N concentration (g m^{-2})

A detailed examination of SLN concentration (g m^{-2}) was undertaken because of its potential role in the expression of the 'stay-green' trait (Section 2.6). Thus, leaf N dynamics are likely to have a profound influence on the SLN.

6.6.4.1 Lower leaves

SLN concentration (g m^{-2}) of the lower leaves did not differ among the hybrids at $800 \text{ }^{\circ}\text{C.d}$ (Table 6.15). This suggests that N supply was adequate to meet the total crop requirements at this time. Alternately, any shortfall may have been met from remobilisation from the stalk.

Indeed, there was a tendency for the stalk N to differ between the hybrids at this time (Table 6.9) which indicates that it is the initial source of remobilised N (Ta & Weiland 1992). Crops appear to have remobilised N in the most economical manner starting with N in the stalks as reported by Nooden *et al.* (1997).

With the advance in kernel growth, N demand appears to have exceeded supply and remobilisation from the lower leaves had advanced by late grain filling (1360 °C.d), when SLN in the lower leaves of ‘P38V12’ (sgr 7) had declined by 57% (Table 6.16). At 1360 °C.d, the SLN of the unfertilised crops had attained a constant minimum value of ~0.50 g m⁻² which is indicative of the structural N component (Anten *et al.* 1995; Li *et al.* 2006). During late grain filling, the SLN of the lower leaves was also influenced by an N x water interaction (Table 6.17), which illustrates the important role played by water in N uptake (Section 2.3.3.3).

6.6.4.2 Middle leaves

The SLN concentration (g m⁻²) of the middle leaves declined during grain filling and differed among the hybrids (Tables 6.18 and 6.19). Throughout this period, ‘P38G43’ (sgr 9) consistently maintained the highest SLN of all hybrids. Similarly, the low ‘stay-green’ hybrids (sgr 6 and 7) had the least SLN on each measurement date, suggesting greater remobilisation of N which is consistent with their lower RUE (Table 6.1). The decline in SLN between 800 °C.d and 1110 °C.d (mid grain filling) amongst the hybrids was minimal ~2-12% (Figure 6.7). This suggests plants maintained high photosynthetic rates within this stratum of leaves where most of the crop’s carbohydrates are synthesized (Tollenaar & Daynard 1978). These leaves also received a higher PFD than those below and may have allocated proportionately more N to maximize dry matter accumulation (Grindlay 1997).

6.6.4.3 Top leaves

SLN concentration (g m⁻²) of the top leaves also declined during grain filling (Figure 6.8). The rate of decline was greater in ‘P39K38’ (sgr 6) compared with the other hybrids. It follows that the top leaves represent an important source of remobilisable N for grain filling in this hybrid. SLN declined 37% between 800 °C.d and 1360 °C.d (Tables 6.20 and 6.21). It is also noteworthy that the mean SLN of the top leaves at late grain filling (1360 °C.d) was 1.35 g m⁻² (Table 6.23) compared with 1.23 g m⁻² for the middle leaves (Table 6.21). Yet the top

leaves senesced earlier than those in the middle stratum. This indicates that the senescence of the top leaves may not solely be a consequence of N remobilisation, as suggested by Rajcan and Tollenaar (1999a), but probably also linked with the dry down of the portion of stalk that subtends the male inflorescence.

6.7 Conclusions

- Radiation use efficiency differed among the hybrids most likely due to differences in the SLN concentration (g m^{-2}) during grain filling when most of the total crop dry matter was accumulated.
- Hybrids accumulated an equal amount of N in fertilized or unfertilized conditions but partitioned it differently. Across N and water treatments, more N was partitioned into the kernels of 'P39K38' (sgr 6) compared with the other hybrids.
- Greater remobilisation of N occurred from the lower and top leaves of the low 'stay-green' hybrids (sgr 6 and 7) than from the high 'stay-green' hybrids (sgr 8 and 9).
- By retaining N in their vegetative parts during grain filling, the high 'stay-green' hybrids developed grain of lower N content.
- The 'stay-green' trait was exhibited only when N fertilizer was provided to the crops. In non fertilized crops hybrids senesced leaves at a similar rate.
- Senescence of the top leaves may be triggered by physiological factors other than just N remobilisation *per se*.

Chapter 7

Experiment 2: DM accumulation, light interception, RUE and N content

7.1 Introduction

In Experiment 1, total dry matter at final harvest did not differ among the hybrids (Section 4.5.1), though both total iPAR (Section 5.3.2) and RUE (Section 6.5.1) did. Effectively the hybrids had different strategies in their accumulation of dry matter. The low ‘stay-green’ hybrids (‘P39K38’, (sgr 6) and ‘P38V12’ (sgr 7)) accumulated more leaf area, and therefore intercepted more PAR compared with the high ‘stay-green’ hybrids (‘P38F70’ (sgr 8) and ‘P38G43’ (sgr 9)). Conversely, the high ‘stay-green’ hybrids were conservative in their leaf area, but maintained a higher SLN concentration (g m^{-2}) (Section 6.5.4.4) and hence a higher RUE. Experiment 2 was conceived to further explore the mechanisms of difference between these two categories of hybrids. In Experiment 1, both ‘P39K38’ (sgr 6) and ‘P38G43’ (sgr 9) consistently expressed phenotypic characteristics associated with their ‘stay-green’ rating. Thus, in Experiment 2, the growth, development, N uptake and partitioning of both ‘P39K38’ (sgr 6) and ‘P38G43’ (sgr 9) were examined under four N treatments ranging from low to high.

7.2 Materials and methods

7.2.1 Experimental design and treatments

The experimental design and treatments were described in detail in Section 3.3.1. Briefly, the experimental design was a randomised complete block with three replicates, four levels of N fertiliser (0, 0 (V6) + 50 (V12), 150 (V6) + 0 (V12) and 150 (V6) + 50 (V12)) (kg N ha^{-1}) and two hybrids (‘P39K38’ (sgr 6) and ‘P38G43’ (sgr 9)). The development stage V6 represents six fully expanded leaves while V12 is 12 fully expanded leaves (Section 3.3.1). Thus, in the 150 (V6) + 0 (V12) treatment, 150 kg N ha^{-1} was provided when six leaves had fully expanded with no further N applications at the 12 leaf stage. Both hybrids had a comparative relative maturity (CRM) of 87 (Table 3.2).

7.2.2 Crop establishment

The crops were established on a Templeton silt loam soil whose classification and nutrient status were outlined in Section 3.2.1. Paddock selection was based on its cropping history (Section 3.2.1). Sowing date was delayed to 12 November by intermittent rainfall during October and early November, 2009. Cardinal temperatures at crop establishment were below the long term means (Table 3.3) and may have influenced the germination rate. The average plant population after thinning was only 7 plants m⁻² against a target of 10 plants m⁻². The low plant population and reduced temperature restricted early canopy development. Additional N applications were timed to occur at critical stages of crop development to examine the pattern of seasonal N demand (Section 7.2.1). Unfortunately the perennial ryegrass (2005-2008) and barley (2008-2009) crops failed to create the low N environment envisaged (Section 3.2.1). Further, the preliminary available N test (up to 15 cm), done prior to sowing indicated a low available soil N level (82 kg N ha⁻¹). However, when the deep N analysis results were obtained after sowing, the background N level at depth was found to be high (Table 3.1).

7.3 Measurements

All measurements taken for Experiment 1 were also taken for Experiment 2. In addition, gross photosynthetic rates were measured using the LI-6400 portable photosynthesis system (Licor Inc., Lincoln, NE, USA) on the ear leaf of a single plant in each plot on two dates (Section 3.4.4). The first measurements were taken immediately after silking (22/2/2010 or 850 °C.d after emergence) and the second during late grain filling (22/4/2010 or 1390 °C.d after emergence). Grain filling occurred during autumn when temperatures had started to decline and progress towards physiological maturity was therefore slow (Wilson *et al.* 1995).

In this study, total above ground dry matter accumulation was assumed to follow a logistic growth form (Section 3.6.6). The final harvest, thus, serves to determine in retrospect the time of physiological maturity. To investigate leaf dry matter accumulation between the hybrids, dry matter (t ha⁻¹) accumulation by three leaf cohorts was examined at silking when maximum leaf dry weight occurred (Section 3.4.2).

As in Experiment 1 (Section 5.3.1), a calibration check was performed to synchronise the measurements of GAI from the SunScan and those of the leaf area meter. In this experiment, the two measurements were also found to closely agree (Appendix 8).

7.4 Calculations and data analyses

Calculations and data analysis during this season were similar to those described in Section 3.6. However, statistical analyses used a randomised complete block design (Section 3.6.7). As in Experiment 1, the duration to maximum kernel dry matter was used as an indication of the duration of grain filling to physiological maturity (Section 4.5.5.7).

7.5 Results

The low plant population (Section 7.2.2) and cool conditions meant yields were lower in 2009/10 than in 2008/09. As a consequence of the high background N level, N fertiliser had no effect on all variables examined except the N content of the stalks. Therefore, with the exception of this variable, only the hybrid means are presented. The lack of N response effectively meant there were 12 replicates for hybrid as a main effect. This provides a statistically powerful and physiologically unique opportunity to examine differences in the responses of these contrasting hybrids.

7.5.1 Dry matter accumulation

7.5.1.1 Final harvest

At the last harvest, which was 30 days after physiological maturity, crops showed visual symptoms of decay and leaves were considerably shredded because of the excess rainfall received after physiological maturity (Figure 3.4). At this point total dry matter (t ha^{-1}) ($P < 0.088$), seed yield (t ha^{-1}) ($P < 0.093$) and crop harvest index ($P < 0.943$) did not differ between hybrids. Total dry matter and seed yield averaged $20.7 (\pm 0.52) \text{ t ha}^{-1}$ and $10.1 (\pm 0.26) \text{ t ha}^{-1}$, respectively, giving a crop harvest index of $0.49 (\pm 0.010)$.

Both the number of kernels per ear ($P < 0.232$) and the seed weight ($P < 0.113$) were also unaffected by the hybrid. The number of kernels per ear averaged $460 (\pm 11.8)$ while the seed

weight was 310 (\pm 3.0) mg. The kernel weight per ear also did not differ ($P < 0.232$) between hybrids and averaged 140 (\pm 5.3) g. In contrast to these results from the last harvest, total dry matter, seed yield and its components all differed between hybrids at physiological maturity.

7.5.1.2 Non kernel ear dry matter

Throughout the post-silking development phase, the non kernel ear dry matter (rachis, husks and ear shank) was greater ($P < 0.001$) in ‘P39K38’ (sgr 6) than in ‘P38G43’ (sgr 9) (Table 7.1). Finally 800 °C.d after silking, the non kernel ear dry matter of ‘P39K38’ (sgr 6) was 39% higher ($P < 0.001$) than that of ‘P38G43’ (sgr 9).

Table 7.1: Non kernel ear dry matter ($t\ ha^{-1}$) at 250, 370, 620, and 800 °C.d after silking in maize hybrids grown at Lincoln University, New Zealand, during 2009.

Hybrid	Non kernel ear dry matter ($t\ ha^{-1}$)			
	Accumulated thermal time (°C.d) after silking			
	250	370	620	800
‘P39K38’ (sgr 6)	5.39	5.18	5.11	4.04
‘P38G43’ (sgr 9)	3.91	3.79	3.30	2.91
P value	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$
SE	0.155	0.162	0.172	0.152
CV (%)	11.6	12.5	14.2	15.1

7.5.2 Dry matter accumulation

7.5.2.1 Duration to silking and physiological maturity

The duration to silking did not differ ($P < 0.100$) between the N treatments nor between the hybrids ($P < 0.139$) and occurred 790 (\pm 3.1) °C.d after emergence. Physiological maturity was determined as in Experiment 1 (Section 4.5.5.1) and occurred 160 days or 1450 °C.d after emergence.

7.5.2.2 Total dry matter

In Experiment 2, hybrids differed in the pattern of dry matter (t ha^{-1}) accumulation, therefore, separate logistic functions were used to describe the relationship between total crop dry matter (t ha^{-1}) accumulated and thermal time ($^{\circ}\text{C.d}$) after emergence (Figure 7.1). ‘P39K38’ (sgr 6) accumulated a maximum dry matter of $22.5 (\pm 0.51) \text{ t ha}^{-1}$, which was higher ($P < 0.013$) than the $20.5 (\pm 0.51) \text{ t ha}^{-1}$ by ‘P38G43’ (sgr 9).

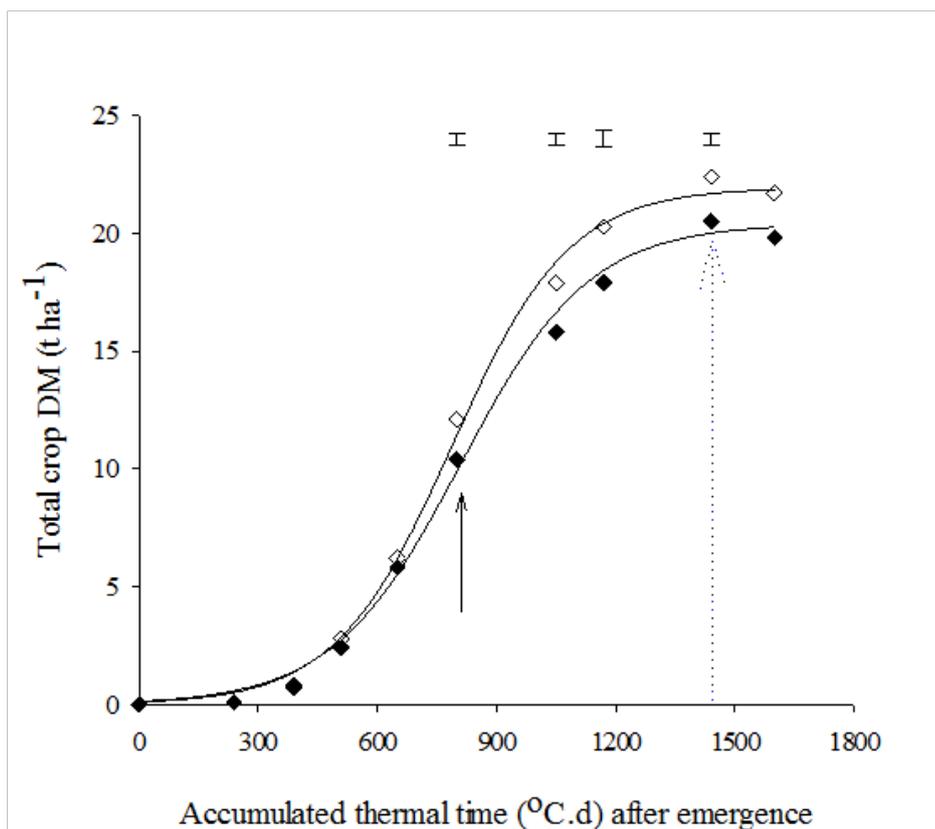


Figure 7.1: Total dry matter (t ha^{-1}) versus accumulated thermal time ($^{\circ}\text{C.d}$) for ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The solid and dotted arrows indicate silking and physiological maturity, respectively. The error bars represent the standard error of the means (t ha^{-1}) at each sample date.

7.5.2.3 Leaf dry matter

In both hybrids, maximum leaf dry matter was recorded at silking (Figure 7.2), when ‘P39K38’ (sgr 6) had accumulated 0.20 t ha^{-1} more ($P < 0.030$) dry matter than ‘P38G43’ (sgr 9). Total leaf dry weight did not differ ($P < 0.554$) for the lower leaves of both hybrids (Table 7.2). However, the dry weight (t ha^{-1}) of the middle leaves of ‘P39K38’ (sgr 6) was 13%

higher ($P < 0.001$) than those of ‘P38G43’ (sgr 9). Similarly, the dry weight ($t\ ha^{-1}$) of the top leaves of ‘P39K38’ (sgr 6) was 22% higher ($P < 0.009$) than those of ‘P38G43’ (sgr 9).

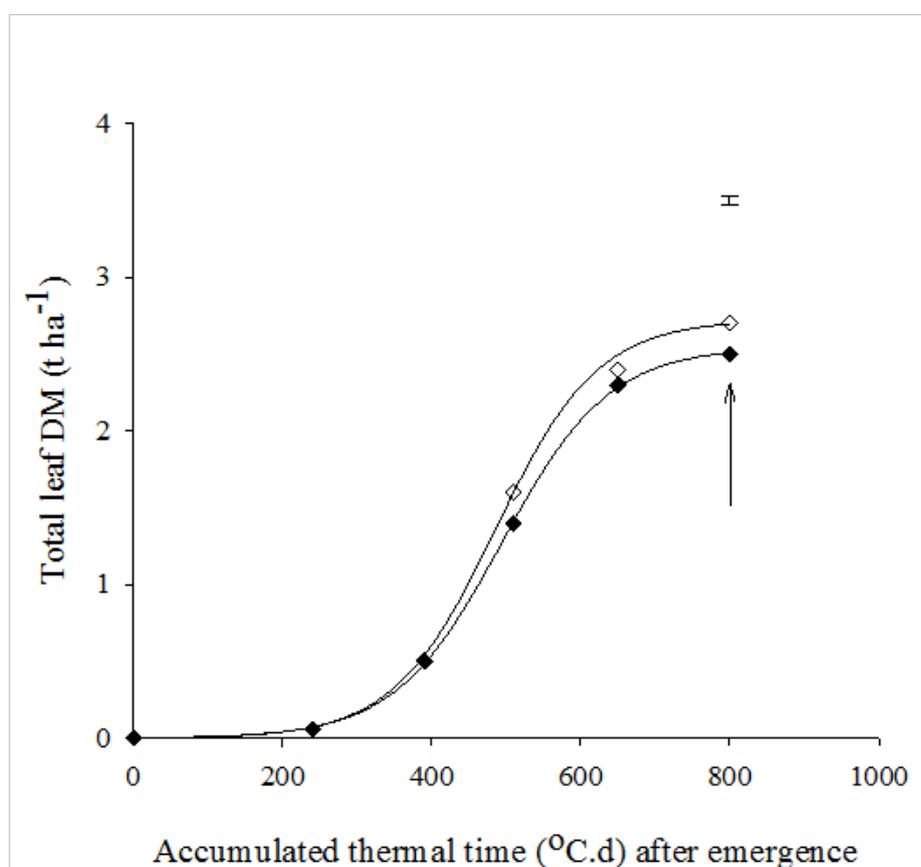


Figure 7.2: Total leaf dry matter ($t\ ha^{-1}$) accumulation versus thermal time ($^{\circ}C.d$) for ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The arrow indicates silking while the error bar represents the standard error of the means ($t\ ha^{-1}$).

Table 7.2: Total dry weight ($t\ ha^{-1}$) of the bottom, middle and top leaves at silking of maize hybrids grown at Lincoln University, New Zealand, during 2009.

Hybrid	Leaf dry matter ($t\ ha^{-1}$)			Total
	Bottom	Middle	Top	
‘P39K38’ (sgr 6)	0.87	1.02	0.79	2.68
‘P38G43’ (sgr 9)	0.90	0.91	0.65	2.46
P value	$P < 0.554$	$P < 0.001$	$P < 0.009$	$P < 0.030$
SE	0.037	0.018	0.031	0.063
CV (%)	14.4	6.3	14.9	8.5

7.5.2.4 Stalk dry matter

The pattern of stalk dry matter accumulation did not differ ($P < 0.898$) between the two hybrids. A common logistic curve was therefore used to describe the relationship between accumulated stalk dry matter (t ha^{-1}) and thermal time ($^{\circ}\text{C.d}$) from emergence until maximum stalk dry matter was accumulated (Figure 7.3). Stalk dry matter (t ha^{-1}) peaked at 1000°C.d after emergence and averaged $6.89 (\pm 0.201) \text{ t ha}^{-1}$.

Stalk dry matter then declined towards final harvest. At physiological maturity (1450°C.d), it did not differ ($P < 0.663$) between the hybrids but had declined 15% to $5.89 (\pm 0.224) \text{ t ha}^{-1}$.

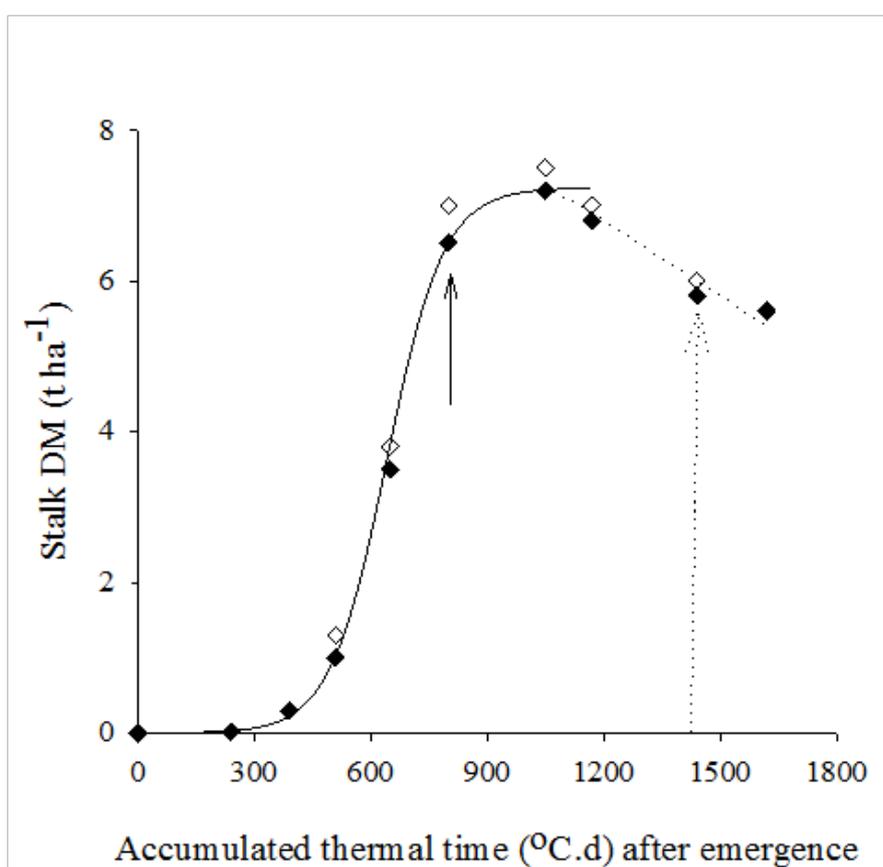


Figure 7.3: Stalk dry matter (t ha^{-1}) accumulation against thermal time ($^{\circ}\text{C.d}$) for ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The solid and dotted arrows indicate silking and physiological maturity, respectively. The dotted line represents the decline in stalk dry matter ($y = 10.61 - 0.0032x$, $R^2 = 0.96$).

7.5.2.5 Ear dry matter

The maximum ear dry matter differed ($P < 0.001$) between the hybrids with 'P39K38' (sgr 9) yielding 15.5 t ha^{-1} compared with 12.5 t ha^{-1} for 'P38G43' (sgr 9) (Figure 7.4a). The slopes of the regression of ear dry matter (t ha^{-1}) on total crop dry matter (t ha^{-1}) between the two hybrids were similar (Figure 7.4b). However, the ears began to develop when 'P39K38' (sgr 6) had accumulated $10.2 \text{ t dry matter ha}^{-1}$ compared with ($P < 0.034$) $9.5 \text{ t dry matter ha}^{-1}$ in 'P38G43' (sgr 9).

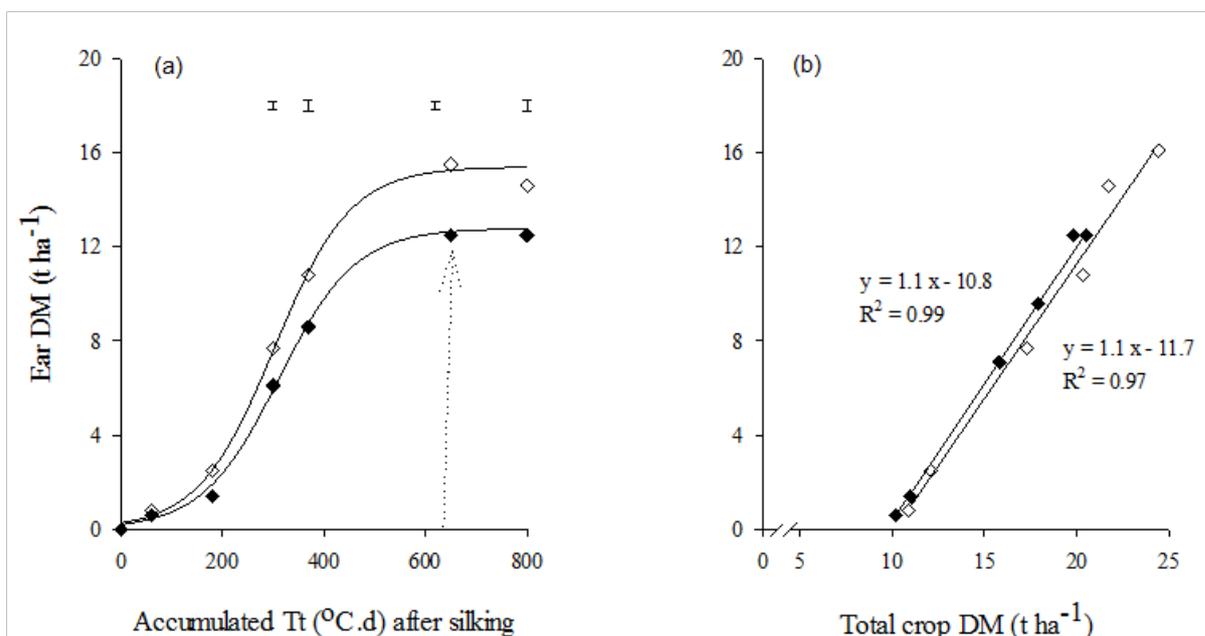


Figure 7.4: Ear dry matter (t ha^{-1}) versus accumulated thermal time ($^{\circ}\text{C.d}$) after silking (a) and against total crop dry matter (b) for 'P39K38' (sgr 6, ◇) and 'P38G43' (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009. The dotted line indicates physiological maturity while the error bars represent the standard error of the means (t ha^{-1}).

7.5.2.6 Kernel growth

Separate logistic curves were also used to describe kernel dry matter (t ha^{-1}) accumulation by the two hybrids (Figure 7.5a), which increased with increasing accumulated thermal time ($^{\circ}\text{C.d}$) after an initial lag phase and peaked at physiological maturity (660 $^{\circ}\text{C.d}$ after silking). Maximum kernel dry matter (t ha^{-1}) differed ($P < 0.001$) between the hybrids being $11.0 (\pm 0.27) \text{ t ha}^{-1}$ for 'P39K38' (sgr 6) and $9.2 (\pm 0.27) \text{ t ha}^{-1}$ for 'P38G43' (sgr 9).

The slopes of the regression of kernel dry matter (t ha^{-1}) against ear dry matter (t ha^{-1}) in both hybrids were similar (Figure 7.5b). However, kernel dry matter accumulation in ‘P39K38’ (sgr 6) began when the ears had accumulated 5.5 t ha^{-1} compared with ($P < 0.030$) 4.4 t ha^{-1} in ‘P38G43’ (sgr 9).

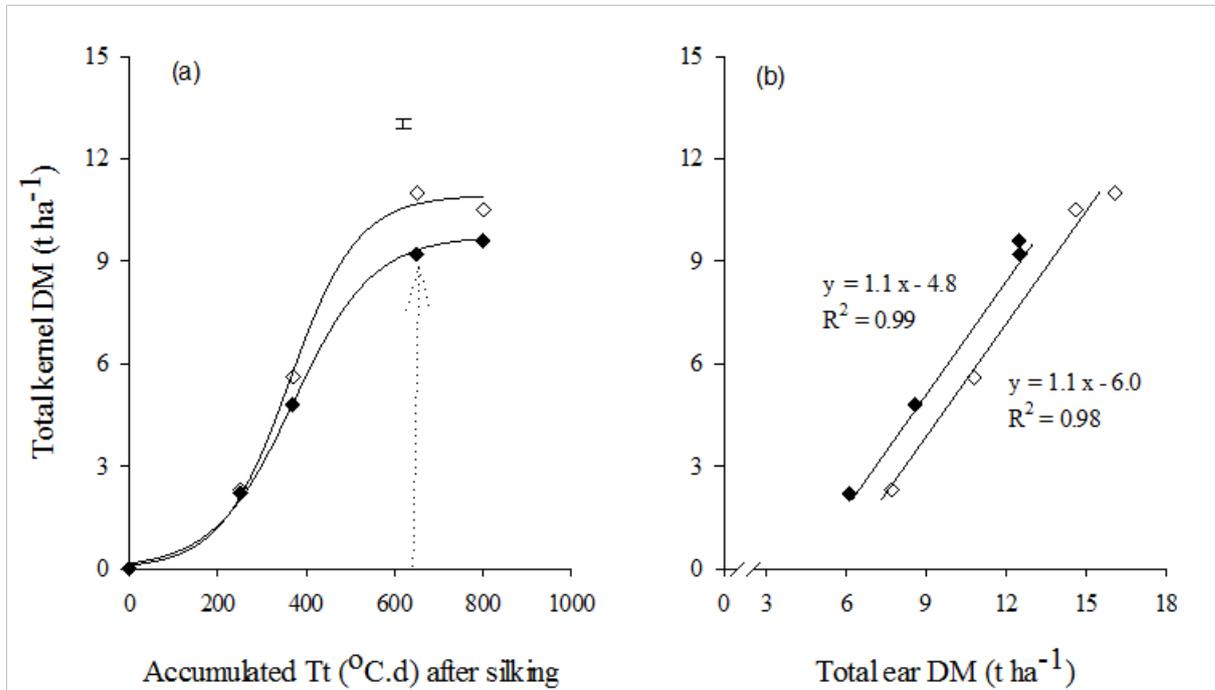


Figure 7.5: Total kernel dry matter (t ha^{-1}) versus (a) accumulated thermal time ($^{\circ}\text{C.d}$) after silking and (b) total ear dry matter (t ha^{-1}) for ‘P39K38’ (sgr 6, \diamond) and P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The dotted line indicates physiological maturity while the error bar represents the standard error of the means (t ha^{-1}) at physiological maturity.

7.5.3 Light interception

7.5.3.1 Total intercepted PAR

Total accumulated iPAR during Experiment 2 was higher ($P < 0.001$) for 'P39K38' (sgr 6) at $970 (\pm 5.7)$ MJ PAR m^{-2} compared with $910 (\pm 5.7)$ MJ PAR m^{-2} for 'P38G43' (sgr 9). An initial exponential phase as temperatures rose was followed by a linear phase. Finally there was a slow decline related to cool temperatures at the end of the season (Figure 7.6).

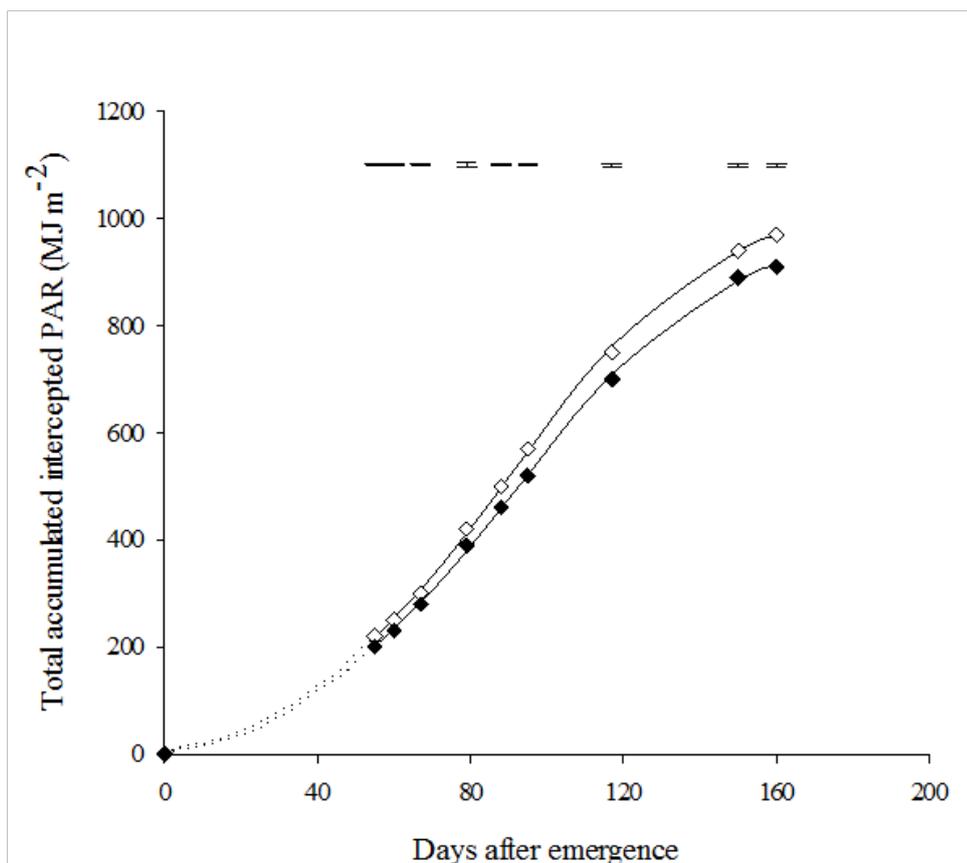


Figure 7.6: Total accumulated intercepted photosynthetically active radiation (MJ m^{-2}) versus time in 'P39K38' (sgr 6, \diamond) and 'P38G43' (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The respective equations for the solid lines were $y = 1040.0/(1+e^{(-0.0373(x-90.3)})}$ and $y = 988.6/(1+e^{(-0.0367(x-92.0)})}$, $R^2 = 0.99$. The dotted lines represent the extrapolated pattern of increase before the start of measurements. The error bars represent the standard error (MJ m^{-2}) at each sample date.

7.5.3.2 Canopy extinction coefficient (kpar)

The extinction coefficient (kpar) was derived from the slope of the exponential relationship between the proportion of intercepted PAR (τ) and green area index (Section 5.2.2). In

Experiment 2, k_{par} was 0.74 (Figure 7.7), equivalent to an extinction coefficient for total solar (k_s) of 0.48 (Equation 5.3). From the fitted regression equation, the critical GAI was determined to be $4.7 (\pm 0.10)$ (Section 5.3.2).

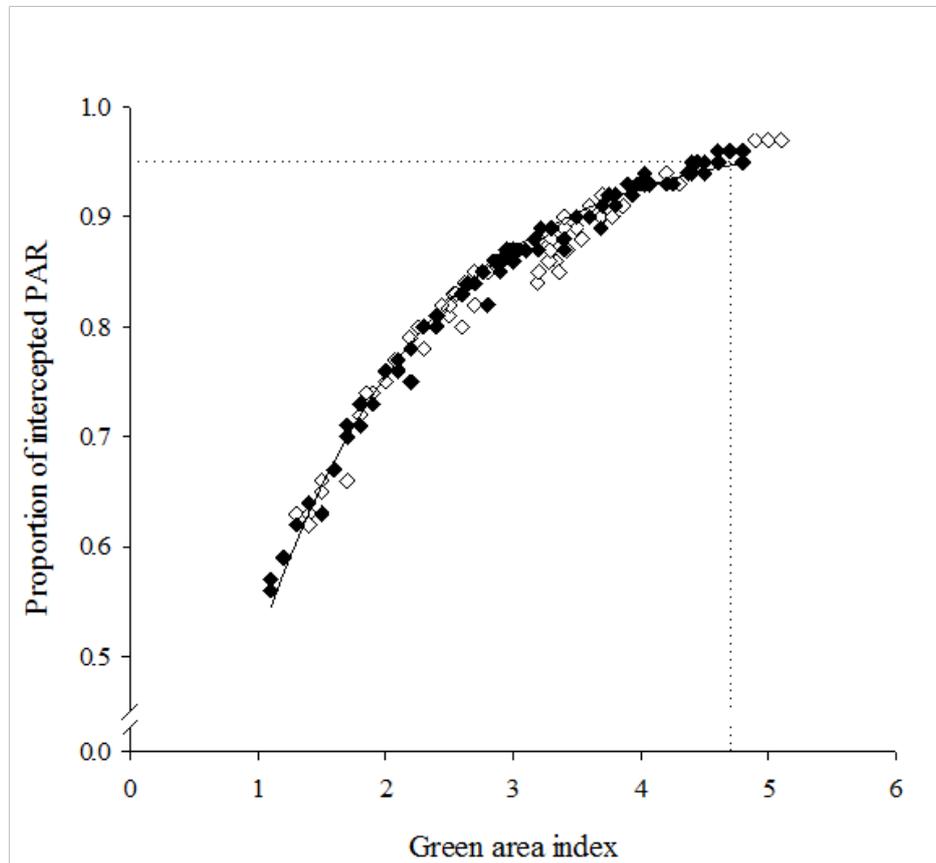


Figure 7.7: Proportion of intercepted photosynthetically active radiation versus the green area index for ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The solid line represents the fitted regression $y = 0.98(1 - e^{-0.74x})$, $R^2 = 0.99$, and the dotted 95% PAR absorptance and critical green area index, respectively.

7.5.4 Green area development

7.5.4.1 Green area index increase

Green area index followed a similar trend as in Experiment 1. The initial increase was slow (<300 °C.d after emergence) but accelerated thereafter and peaked shortly after silking (880 °C.d) (Figure 7.8). There were no differences ($P > 0.05$) on any sampling date for GAI prior to maximum GAI. However, the maximum GAI of ‘P39K38’ (sgr 6) was 4% greater ($P < 0.016$) than that of ‘P38G43’ (sgr 9) (Table 7.3).

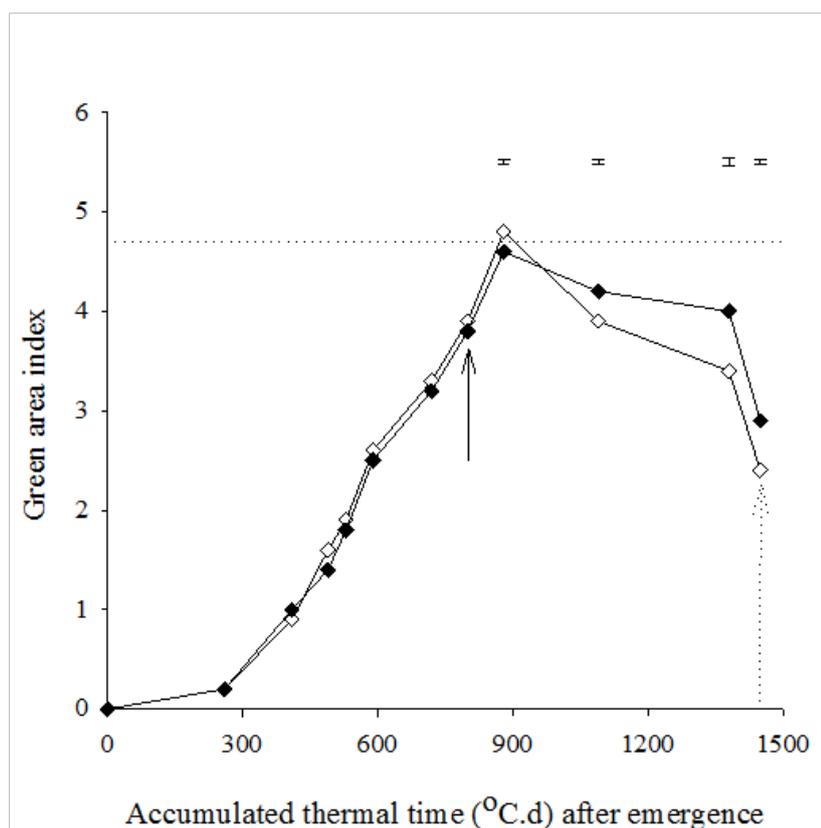


Figure 7.8: Green area index versus thermal time ($^{\circ}\text{C.d}$) after emergence in ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The solid arrow indicates silking while the dotted line represents the critical green area index. The dotted arrow indicates physiological maturity and the error bars represent the standard error of the means ($\text{m}^2 \text{m}^{-2}$) at each sample date.

Table 7.3: Maximum green area index in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.

Treatment	Maximum green area index		
	‘P39K38’ (sgr 6)	‘P38G43’ (sgr 9)	Mean
N1†	4.73	4.53	4.63
N2	4.73	4.73	4.73
N3	4.87	4.57	4.72
N4	4.70	4.70	4.70
Mean	4.76	4.63	4.70
P value	P<0.016		P<0.454
SE	0.032		0.046
CV (%)	2.4		

†N1 = 0, N2 = 0 (V6) + 50 (V12), N3 = 150 (V6) + 0 (V12) and N4 = 150 (V6) + 50 (V12) kg N ha $^{-1}$. See Section 7.2.1 for a description of treatments.

To examine the cause of the difference ($P < 0.016$) in maximum GAI, a relationship between calculated and measured leaf area was derived (Section 3.4.2). Using the coefficient of 0.71 (Appendix 9), individual leaf area was estimated and related to its position on the plant. The leaves of 'P39K38' (sgr 6) in positions 8-14 were on average 10% larger ($P < 0.05$) than those of 'P38G43' (sgr 9) (Figure 7.9). Cumulatively, the total leaf area per plant was also 10% more ($P < 0.001$) in 'P39K38' (sgr 6) than in 'P38G43' (sgr 9) (Table 7.4).

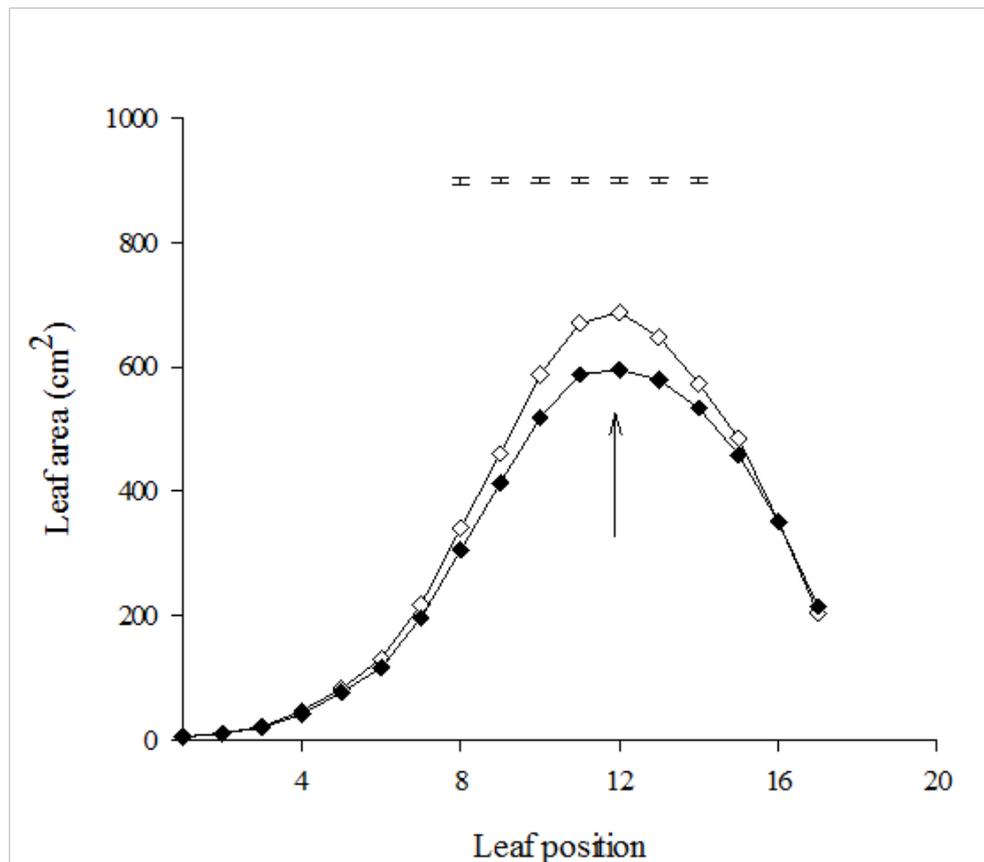


Figure 7.9: Leaf area (cm²) versus leaf position in 'P39K38' (sgr 6, \diamond) and 'P38G43' (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The arrow indicates the position of the ear leaf and the error bars represent the standard error of the means (cm²) for each leaf position.

7.5.4.2 Green area index decline

Post maximal decline in GAI in Experiment 2 (Table 7.5) was consistent with that observed in Experiment 1. At physiological maturity (1450 °C.d), the GAI of 'P38G43' (sgr 9) was 26% greater ($P < 0.001$) than that of 'P39K38' (sgr 6). This difference in GAI resulted from a slower ($P < 0.001$) rate of GAI decline in 'P38G43' (sgr 9) during grain filling (Table 7.6). The decline was 0.0023 (m² m⁻²) per °C.d in 'P38G43' (sgr 9) compared with 0.0036 (m² m⁻²) per

°C.d in ‘P39K38’ (sgr 6). During the grain filling period of ~660 °C.d, the GAI of ‘P39K38’ (sgr 6) decreased by 2.3 units compared with 1.5 unit decrease in ‘P38G43’ (sgr 9).

Table 7.4: Total leaf area per plant in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.

Treatment	Total leaf area per plant (cm ²)		
	‘P39K38’ (sgr 6)	‘P38G43’ (sgr 9)	Mean
N1†	5460	4950	5205
N2	5430	4850	5140
N3	5630	5160	5395
N4	5580	5140	5360
Mean	5525	5025	5275
P value	P<0.001		P<0.251
SE	70.1		99.2
CV (%)	4.6		

†N1 = 0, N2 = 0 (V6) + 50 (V12), N3 = 150 (V6) + 0 (V12) and N4 = 150 (V6) + 50 (V12) kg N ha⁻¹. See Section 7.2.1 for a description of treatments.

Table 7.5: Green area index at physiological maturity (1450 °C.d) in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.

Treatment	Green area index at physiological maturity (1450 °C.d)		
	‘P39K38’ (sgr 6)	‘P38G43’ (sgr 9)	Mean
N1†	2.30	2.77	2.54
N2	2.35	2.90	2.63
N3	2.62	3.01	2.82
N4	2.37	3.09	2.73
Mean	2.41	2.94	2.68
P value	P<0.001		P<0.137
SE	0.058		0.082
CV (%)	7.5		

†N1 = 0, N2 = 0 (V6) + 50 (V12), N3 = 150 (V6) + 0 (V12) and N4 = 150 (V6) + 50 (V12) kg N ha⁻¹. See Section 7.2.1 for a description of treatments.

Table 7.6: Green area index decline (per °C.d) during grain filling in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.

Treatment	Green area index decline per °C.d (x10 ⁻²)		
	‘P39K38’ (sgr 6)	‘P38G43’ (sgr 9)	Mean
N1†	3.6	2.4	3.0
N2	3.6	2.4	3.0
N3	3.5	2.1	2.8
N4	3.6	2.4	3.0
Mean	3.6	2.3	3.0
P value	P<0.001		P<0.820
SE (x 10 ⁻⁴)	4.0		1.4
CV (%)	16.7		

†N1 = 0, N2 = 0 (V6) + 50 (V12), N3 = 150 (V6) + 0 (V12) and N4 = 150 (V6) + 50 (V12) kg N ha⁻¹. See Section 7.2.1 for a description of treatments.

7.5.4.3 Leaf appearance

(a) Leaf tips

Leaf tip appearance in Experiment 2 followed a similar pattern as in Experiment 1 (Section 5.3.5.1). The rate of appearance of leaf tips was unaffected by the hybrid during both Stages 1 (P<0.636) and 2 (P<0.689) (Figure 7.10). The phyllochron_(tip) was 37.8 °C.d and 74.3 °C.d per leaf tip during Stage 1 and 2, respectively. ‘P38G43’ (sgr 9) reached the point of inflection 560 °C.d after emergence or earlier (P<0.001) than the 610 °C.d for ‘P39K38’ (sgr 6).

(b) Fully expanded leaves

Fully expanded leaves per plant also appeared in a consistent manner with that observed during Experiment 1 (Section 5.3.5.2). The rate of appearance of fully expanded leaves was unaffected (P<0.495) by the hybrid and a constant phyllochron_(ligule) of 53.6 (± 1.07) °C.d per leaf was recorded prior to the point of inflection (Stage 1) (Figure 7.11). After the point of inflection (Stage 2), the fully expanded leaves of ‘P38G43’ (sgr 9) appeared after 28.5 °C.d which was faster (P<0.002) than the 31.3 °C.d for ‘P39K38’ (sgr 6). These slower rates were consistent with the development of larger leaves by ‘P39K38’ (sgr 6) (Figure 7.9). Hybrids

also differed ($P < 0.001$) in the duration from emergence to the point of inflection, in which 'P39K38' (sgr 6) required 560 °C.d compared with 590 °C.d for 'P38G43' (sgr 9).

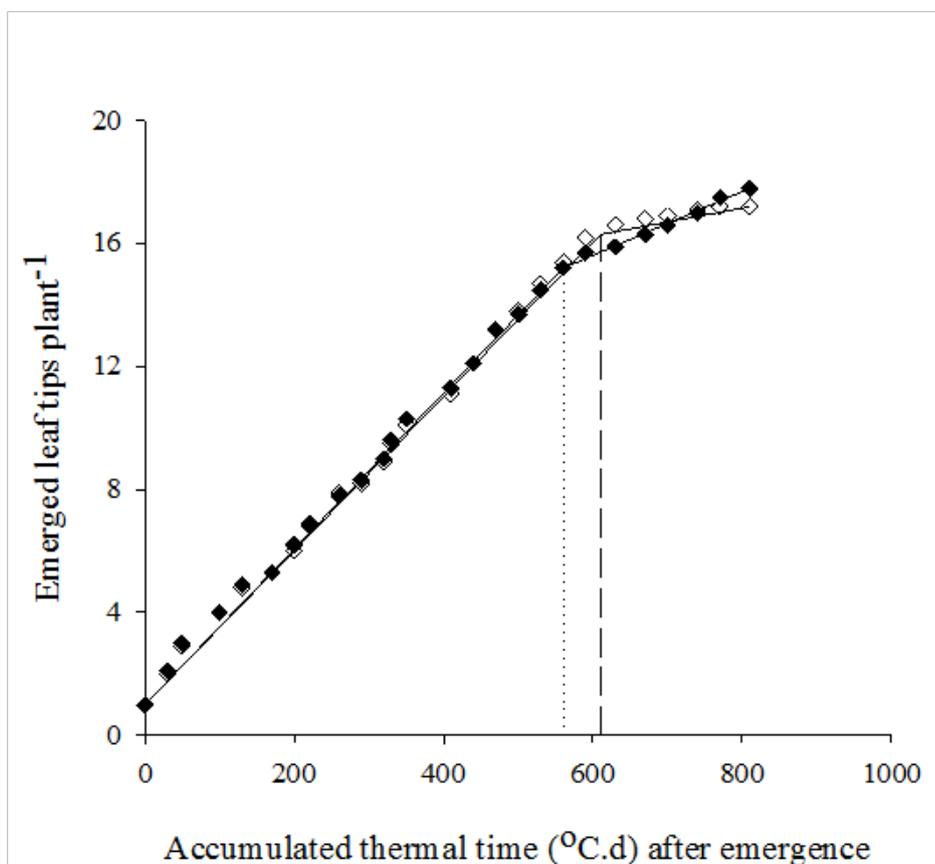


Figure 7.10: Number of visible leaf tips per plant versus accumulated thermal time (°C.d) in 'P39K38' (sgr 6, \diamond) and 'P38G43' (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The dashed and dotted lines represent the duration (°C.d) to the point of inflection in 'P39K38' (sgr 6) and 'P38G43' (sgr 9), respectively. The graph was constrained to intercept the y axis at (0, 1).

Hybrids differed ($P < 0.004$) in the total number of fully expanded leaves initiated per plant (Table 7.7) with 17.8 for 'P38G43' (sgr 9) and 17.3 for 'P39K38' (sgr 6).

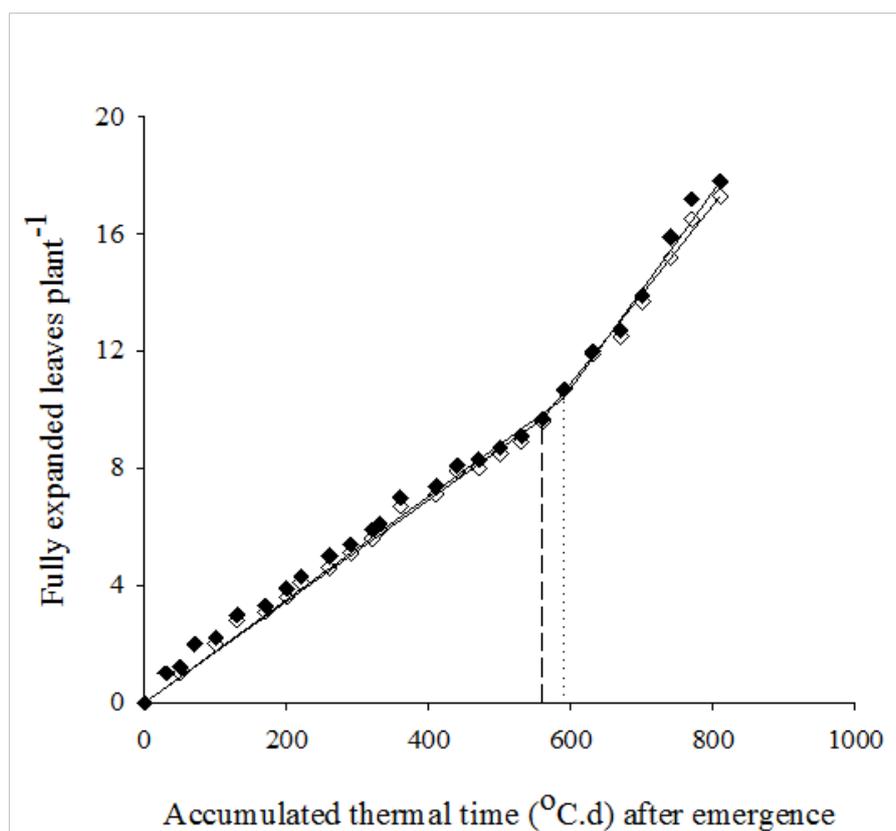


Figure 7.11: Number of fully expanded leaves per plant versus accumulated thermal time ($^{\circ}\text{C.d}$) in ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The dashed and dotted lines represent the duration ($^{\circ}\text{C.d}$) to the point of inflection in ‘P39K38’ (sgr 6) and ‘P38G43’ (sgr 9), respectively. The graph was constrained to intercept the axis at the origin.

Table 7.7: Final number of leaves per plant in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.

Treatment	Final leaf number per plant	
	‘P39K38’ (sgr 6)	‘P38G43’ (sgr 9)
N1†	17.4	18.0
N2	17.2	17.5
N3	17.3	17.8
N4	17.1	17.8
Mean	17.3	17.8
P value	P<0.004	
SE	0.11	
CV (%)	2.1	

†N1 = 0, N2 = 0 (V6) + 50 (V12), N3 = 150 (V6) + 0 (V12) and N4 = 150 (V6) + 50 (V12) kg N ha⁻¹. See Section 7.2.1 for a description of treatments.

7.5.5 RUE

Seasonal RUE (g dry matter MJ⁻¹ absorbed PAR) was determined following the method described in Section 6.4. In contrast to Experiment 1, RUE did not differ ($P < 0.634$) between the hybrids and averaged 3.03 (± 0.033) g dry matter per MJ of absorbed PAR (Figure 7.12). It appears that the relationship between total crop dry matter (g m⁻²) and total absorbed PAR (MJ m⁻²) was bilinear with a steeper slope between 200–400 °C.d, and a decline thereafter (dotted line).

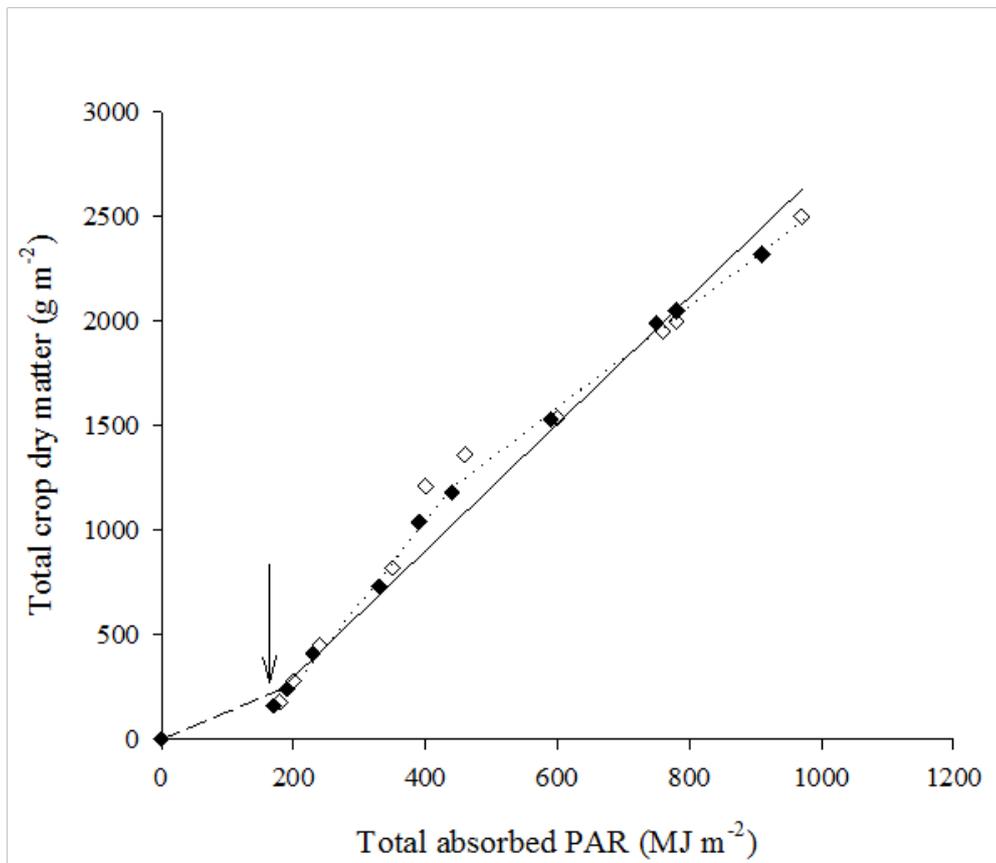


Figure 7.12: Radiation use efficiency (g dry matter per MJ absorbed PAR) in ‘P39K38’ (sgr 6, \diamond) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand during 2009. The equation for the regression of total crop dry matter (g m⁻²) on total absorbed PAR (MJ m⁻²) was $y = 3.03x - 309.2$ (>8 fully expanded leaves), $R^2 = 0.99$. The dashed line represents the extrapolated RUE before 8 fully expanded leaves (shown by arrow) and the dotted the bilinear response.

7.5.6 Gross photosynthesis

The rate of gross photosynthesis was unaffected by either N ($P < 0.482$) or hybrid ($P < 0.079$) shortly after silking (22/02/2010 or 850 °C.d after emergence) and averaged $39.2 (\pm 0.41) \mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Table 7.8).

At the second measurement close to physiological maturity (22/04/2010 or 1390 °C.d after emergence), gross photosynthetic rate ($\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) also did not differ ($P < 0.111$) between the hybrids, but had declined on average 37%.

Table 7.8: Gross photosynthesis rate ($\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in maize hybrids grown at Lincoln University, New Zealand, during 2009.

Treatment	Gross photosynthesis ($\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)			
	850 °C.d after emergence		1390 °C.d after emergence	
	'P39K38' (sgr 6)	'P38G43' (sgr 9)	'P39K38' (sgr 6)	'P38G43' (sgr 9)
N1†	42.7	41.1	19.8	22.8
N2	40.0	36.3	24.5	27.1
N3	39.2	38.5	24.8	28.0
N4	36.3	39.3	23.6	26.0
Mean	39.6	38.8	23.2	26.0
P value	$P < 0.482$		$P < 0.111$	
SE	0.70		1.09	
CV (%)	5.1		12.5	

†N1 = 0, N2 = 0 (V6) + 50 (V12), N3 = 150 (V6) + 0 (V12) and N4 = 150 (V6) + 50 (V12) kg N ha⁻¹. See Section 7.2.1 for a description of treatments.

7.5.7 Chlorophyll content

SPAD meter readings during Experiment 2 commenced prior to silking to examine the pattern of change in chlorophyll content over time. Throughout the 80 days of measurement, the SPAD meter readings from the ear leaves of 'P38G43' (sgr 9) were consistently higher ($P < 0.001$) than those of 'P39K38' (sgr 6) (Figure 7.13). Ear leaf SPAD readings peaked at silking when the ear leaves of 'P38G43' (sgr 9) recorded 64.5 SPAD units compared with 61.6 for 'P39K38' (sgr 6). Towards physiological maturity (140 DAE), SPAD readings of the ear leaves of 'P38G43' (sgr 9) were 9% higher ($P < 0.001$) than those of 'P39K38' (sgr 6).

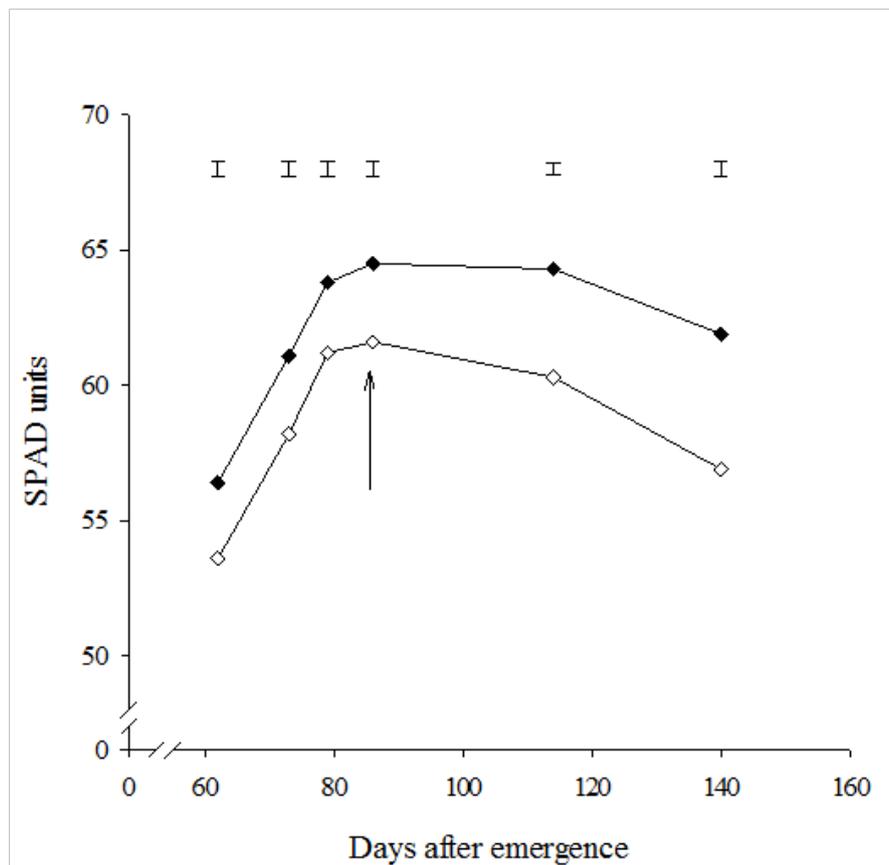


Figure 7.13: Ear leaf SPAD readings (SPAD units) versus time (DAE) for 'P39K38' (sgr 6, \diamond) and 'P38G43' (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The arrow indicates silking while the error bars represent the standard error of the means (SPAD units) at each sample date.

7.5.8 Leaf senescence

The number of senesced leaves per plant increased at a constant rate ($P < 0.112$) of 0.007 leaves per $^{\circ}\text{C}\cdot\text{d}$ (Figure 7.14). In 'P39K38' (sgr 6), senescence commenced 320 $^{\circ}\text{C}\cdot\text{d}$ after emergence which was 80 $^{\circ}\text{C}\cdot\text{d}$ earlier ($P < 0.015$) than in 'P38G43' (sgr 9).

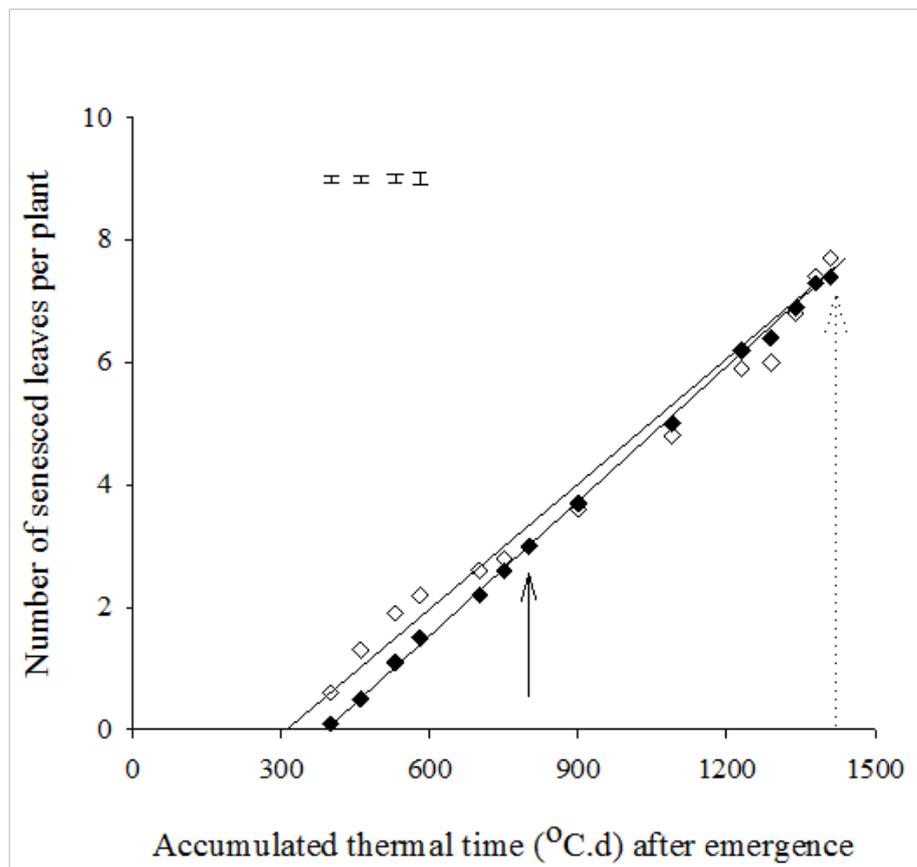


Figure 7.14: Number of senesced leaves per plant versus thermal time (°C.d) in ‘P39K38’ (sgr 6, \triangle) and ‘P38G43’ (sgr 9, \blacklozenge) maize hybrids grown at Lincoln University, New Zealand, during 2009. The respective equations were $y = 0.0068x - 2.20$; $R^2 = 0.95$ and $y = 0.0073x - 2.92$; $R^2 = 0.99$. The solid arrow indicates silking and the dotted physiological maturity. The error bars represent the standard error of the means (leaves per plant) at each sample date.

7.5.9 Crop N content

7.5.9.1 Final harvest

Total crop N at final harvest did not differ ($P < 0.074$) between the hybrids and averaged $246 (\pm 11.7)$ kg ha^{-1} , with 62-67% accumulated in the kernels (Figure 7.15a). Both the leaf ($P < 0.360$) and stalk ($P < 0.872$) N content also did not differ between the hybrids and averaged $45.6 (\pm 2.62)$ and $34.5 (\pm 2.60)$ kg ha^{-1} , respectively (Figures 7.15c and d). In contrast, the kernels of ‘P39K38’ (sgr 6) accumulated 19% more ($P < 0.007$) N than those of ‘P38G43’ (sgr 9) (Figure 7.15b).

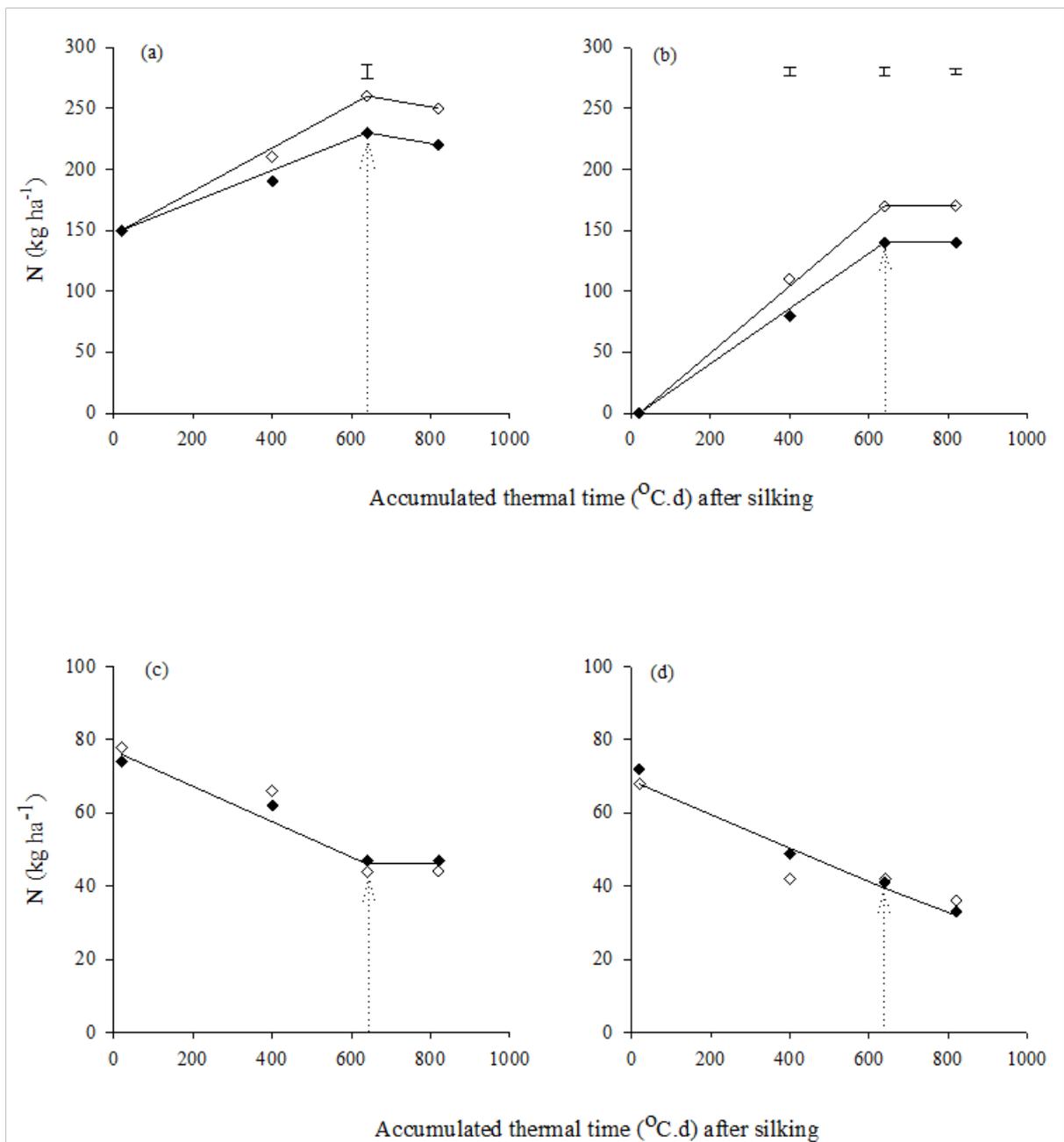


Figure 7.15: Mean N content (kg ha⁻¹) for total crop (a), kernel (b), leaves (c) and stalk (d) against accumulated thermal time (°C.d) after silking in 'P39K38' (sgr 6, △) and 'P38G43' (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009. The dotted arrows indicate physiological maturity and the error bars the standard error of the means (kg ha⁻¹) at each sample date.

7.5.9.2 Silking to physiological maturity

Total crop N (kg ha⁻¹) increased from silking to physiological maturity (650 °C.d after silking) Figure 7.15a) as a result of N accumulation in the kernels which peaked at physiological

maturity (Figure 7.15b). Both leaf and stalk N content (kg ha^{-1}) declined during the same period (Figures 7.15c and d) due to remobilisation of stored N.

At silking, the crops that received more than 150 kg N ha^{-1} accumulated a greater ($P < 0.006$) proportion of this N in their stalks when compared with those that received no added N or only 50 kg N ha^{-1} at V12 (Table 7.9). However, hybrids did not differ ($P < 0.386$) in their stalk N content at silking and averaged $70.2 (\pm 2.85) \text{ kg ha}^{-1}$. Leaf N content also did not differ ($P < 0.322$) between the hybrids at silking and averaged $76.3 (\pm 2.49) \text{ kg ha}^{-1}$.

Table 7.9: Stalk N content (kg N ha^{-1}) at silking ($790 \text{ }^\circ\text{C.d}$) and physiological maturity ($1450 \text{ }^\circ\text{C.d}$) in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.

Treatment	Stalk N content (kg N ha^{-1})					
	790 $^\circ\text{C.d}$			1450 $^\circ\text{C.d}$		
	'P39K38' (sgr 6)	'P38G43' (sgr 9)	Mean	'P39K38' (sgr 6)	'P38G43' (sgr 9)	Mean
N1†	58.4	62.2	60.3 _b	34.4	37.4	35.9 _b
N2	57.4	58.4	57.9 _b	34.5	36.3	35.4 _b
N3	78.4	90.8	84.6 _a	52.3	51.4	51.9 _a
N4	78.9	76.7	77.8 _a	45.8	43.8	44.8 _{ab}
Mean	68.3	72.0	70.2	41.8	42.2	42.0
P value	P<0.386		P<0.006	P<0.893		P<0.035
SE	2.85		4.04	2.46		3.47
CV (%)	11.5			21.7		

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$. †N1 = 0, N2 = 0 (V6) + 50 (V12), N3 = 150 (V6) + 0 (V12) and N4 = 150 (V6) + 50 (V12) kg N ha^{-1} . See Section 7.2.1 for a description of treatments.

Consistent with silking, at physiological maturity, the crops that received 150 kg N ha^{-1} at V6 accumulated about 65% more ($P < 0.035$) N in their stalks than those which received no N at V6 and 50 kg N ha^{-1} (Table 7.9). Hybrids also did not differ ($P < 0.893$) in the amount of N contained in their stalks at this period which averaged $42.0 (\pm 2.46) \text{ kg ha}^{-1}$.

However, kernel N content (kg ha^{-1}) at physiological maturity was greater ($P < 0.002$) in ‘P39K38’ (sgr 6) at 170 kg ha^{-1} compared with 140 kg N ha^{-1} for ‘P38G43’ (sgr 9) (Figure 7.15b). Similarly, the kernels of ‘P39K38’ (sgr 6) contained ($P < 0.001$) 1.63% N and those of ‘P38G43’ (sgr 9) 1.45%.

7.5.9.3 Specific leaf N concentration (g m^{-2})

Specific leaf N concentration (g m^{-2}) declined in all leaf cohorts between silking ($790 \text{ }^\circ\text{C.d}$) (Table 7.10) and physiological maturity ($1450 \text{ }^\circ\text{C.d}$) (Table 7.11). At silking, SLN differed between the hybrids only within the cohort of lower leaves. It was 1.82 g m^{-2} in ‘P39K38’ (sgr 6) compared with ($P < 0.043$) 2.34 g m^{-2} in ‘P38G43’ (sgr 9). Within the cohort of middle leaves, SLN was similar ($P < 0.353$) between the hybrids and averaged $2.16 (\pm 0.056) \text{ g m}^{-2}$. Similarly, SLN of the cohort of top leaves did not differ ($P < 0.113$) between the hybrids and averaged $1.97 (\pm 0.117) \text{ g m}^{-2}$.

Table 7.10: Specific leaf N concentration (g m^{-2}) in the lower, middle and top leaves at silking ($790 \text{ }^\circ\text{C.d}$) in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.

Treatment	Specific leaf N concentration (g m^{-2})					
	Lower leaves		Middle leaves		Top leaves	
	‘P39K38’ (sgr 6)	‘P38G43’ (sgr 9)	‘P39K38’ (sgr 6)	‘P38G43’ (sgr 9)	‘P39K38’ (sgr 6)	‘P38G43’ (sgr 9)
N1†	1.82	2.16	2.20	2.32	2.18	1.78
N2	1.57	2.50	1.98	2.15	2.18	2.11
N3	1.87	2.50	2.02	2.22	2.11	1.80
N4	2.02	2.20	2.28	2.08	2.01	1.59
Mean	1.82	2.34	2.12	2.19	2.12	1.82
P value	P<0.043		P<0.353		P<0.113	
SE	0.151		0.056		0.117	
CV (%)	20.5		7.3		16.7	

†N1 = 0, N2 = 0 (V6) + 50 (V12), N3 = 150 (V6) + 0 (V12) and N4 = 150 (V6) + 50 (V12) kg N ha^{-1} . See Section 7.2.1 for a description of treatments.

Specific leaf N concentration (g m^{-2}) at physiological maturity (1450 °C.d) showed a consistent trend with that observed at silking. Only the SLN of the cohort of lower leaves differed between the hybrids. It was 0.850 g m^{-2} in ‘P39K38’ (sgr 6) and lower ($P < 0.003$) than the 1.18 g m^{-2} in ‘P38G43’ (sgr 9) (Table 7.11). SLN in the middle leaf cohort did not differ ($P < 0.134$) between the hybrids and averaged $1.51 (\pm 0.089) \text{ g m}^{-2}$, while that of the top leaves ($P < 0.596$) was $1.21 (\pm 0.107) \text{ g m}^{-2}$.

Table 7.11: Specific leaf N concentration (g m^{-2}) in the lower, middle and top leaves at physiological maturity (1450 °C.d) in maize hybrids grown with four levels of N at Lincoln University, New Zealand, during 2009.

Treatment	Specific leaf N concentration (g m^{-2})					
	Lower leaves		Middle leaves		Top leaves	
	‘P39K38’ (sgr 6)	‘P38G43’ (sgr 9)	‘P39K38’ (sgr 6)	‘P38G43’ (sgr 9)	‘P39K38’ (sgr 6)	‘P38G43’ (sgr 9)
N1†	0.830	1.05	1.21	1.73	1.07	1.34
N2	0.740	1.07	1.32	1.51	1.25	1.26
N3	0.980	1.27	1.59	1.58	1.22	1.26
N4	0.850	1.32	1.48	1.63	1.12	1.14
Mean	0.850	1.18	1.40	1.61	1.17	1.25
P value	P<0.003		P<0.134		P<0.596	
SE	0.051		0.089		0.107	
CV (%)	14.2		16.7		25.1	

†N1 = 0, N2 = 0 (V6) + 50 (V12), N3 = 150 (V6) + 0 (V12) and N4 = 150 (V6) + 50 (V12)

kg N ha⁻¹. See Section 7.2.1 for a description of treatments.

7.6 Discussion

As a consequence of the supraoptimal N content encountered in Experiment 2 (Section 3.2.1), none of the parameters measured, responded to N except the stalk N content. Therefore this discussion focuses on the hybrid main effects observed in Experiment 2 with reference made to the comparable fully irrigated and fertilised treatments of Experiment 1.

7.6.1 Dry matter accumulation

Except for the stalk, the pattern of dry matter accumulation differed between the low ('P39K38', sgr 6) and high ('P38G43', sgr 9) 'stay-green' hybrids in Experiment 2 (Section 7.5.2). Consequently, maximum accumulated dry matter at physiological maturity was 10% higher in 'P39K38' (sgr 6) than in 'P38G43' (sgr 9) (Figure 7.1). These results contrast with those obtained in Experiment 1 (Section 4.5.5.1) where total dry matter at physiological maturity did not differ between these hybrids. This suggests that at supraoptimal N levels (Section 3.2.1), the 'stay-green' trait appeared to influence yield negatively. Perhaps 'P38G43' (sgr 9) is a relatively lower yielding hybrid that uses the 'stay-green' trait to deliver a competitive yield only when under N or water stress.

Post-silking dry matter accumulation was dependent solely on ear dry matter accumulation (Figure 4.1). Thus, greater dry matter accumulation by 'P39K38' (sgr 6) can be attributed to the larger maximum GAI (Table 7.3), that led to the interception of more PAR (Figure 7.7). Specifically, the middle and top leaf cohorts in 'P39K38' (sgr 6) developed 10% more green area than 'P38G43' (sgr 9), as a consequence of larger leaves in positions 8-14 (Figure 7.9). This observation is consistent with the report by Tetio-Kagho and Gardner (1988) and Tollenaar and Daynard (1978), that within the crop canopy these strata of leaves absorb the largest quantity of PAR, and hence provide a substantial proportion of assimilates for ear development (Fairey & Daynard 1978; Pearson *et al.* 1984). Additionally, the greater remobilisation of N from the lower leaves of 'P39K38' (sgr 6) (Tables 7.10 and 7.11), would supply N to sustain higher crop growth rates and thus, more dry matter accumulation by its ears. Other studies have also demonstrated a close relationship between the biomass partitioned for ear development, plant available N and crop growth rates in maize (Borras *et al.* 2007; D'Andrea *et al.* 2008; Uhart & Andrade 1995). It appears that adequate N supply means total dry matter accumulation is greater in crops with a canopy structure that enables them to intercept more PAR (Wall & Kanemasu 1990).

Green area index at physiological maturity (1450 °C.d) was greater in ‘P38G43’ (sgr 9) than in ‘P39K38’ (sgr 6) (Table 7.4) because ‘P39K38’ (sgr 6) lost green area at a faster rate (Table 7.5). This observation shows that the high ‘stay-green’ hybrid (‘P38G43’ (sgr 9)), had a longer leaf area duration which is consistent with previous reports (Borrell *et al.* 2000a; Thomas & Smart 1993). However, this was not advantageous for PAR interception because it occurred late in the season (Figure 7.8) when solar radiation receipts were declining (Figure 3.1). Evidence to support this assertion was derived from the similarity in gross photosynthesis between hybrids during late grain filling (Table 7.8). Further, because photosynthetic efficiency declines with leaf age (Masclaux-Daubresse *et al.* 2008; Vietor & Musgrave 1979), any gains in dry matter derived from the extra PAR intercepted would be negligible.

These data demonstrate that with sufficient N, the influence of a larger leaf size on dry matter accumulation overrode the higher SLN. Under such conditions the ‘stay-green’ trait was detrimental to crop productivity as shown by the lower maximum total dry matter accumulated by ‘P38G43’ (sgr 9) in this experiment (Figure 7.1). Furthermore, any decline in dry matter accumulation as a result of lower total PAR interception was unlikely to be compensated for by a longer duration of dry matter accumulation. To compensate for any decline in PAR interception among the high ‘stay-green hybrids, a higher plant population may be required.

7.6.2 Crop N content

The N content (kg ha^{-1}) of the leaves, stalk and kernels at the final harvest of Experiment 2 showed a consistent trend with those observed in Experiment 1. In both experiments, both leaf (Figure 7.15c) and stalk (Figure 7.15d) N content declined during grain filling while that of the kernels increased during the same period (Figure 7.15b). This suggests that N was remobilised from the vegetative structures into the kernels during grain filling. Despite the similarity in total leaf N (kg ha^{-1}) content between the hybrids during the grain filling period (Figure 7.15c), the SLN of the lower leaves of ‘P38G43’ (sgr 9) was higher at silking and at physiological maturity than that of ‘P39K38’, (sgr 6) (Tables 7.10 and 7.11). This observation was partly related to the smaller leaves of ‘P38G43’ (sgr 9) (Figure 7.9), which contained more N per unit leaf area.

In both experiments, total kernel N content (kg ha^{-1}) was consistently higher in ‘P39K38’ (sgr 6) than in ‘P38G43’ (sgr 9) (Table 6.6 and Figure 7.15b). An examination of the rates of N uptake by the kernels showed that ‘P39K38’ (sgr 6) accumulated N at a faster rate compared with ‘P38G43’ (sgr 9) (Table 6.7). Greater remobilisation of N from the lower leaves of ‘P39K38’ (sgr 6), as shown by the lower SLN (Tables 7.10 and 7.11), appears to have provided a steady supply of N for grain filling. These results are consistent with those of Lhuillier *et al.* (1999), who reported that seed N concentration in pea (*Pisum sativum* L.) was dependent on its rate of accumulation as directed by N availability in the plant. Similarly, the reliance of grain N content on its efficient redistribution within the plant has been demonstrated in wheat (*Triticum aestivum* L.) by Beninati and Busch (1992).

The chlorophyll content (SPAD units) during grain filling showed a consistent pattern between the low and high ‘stay-green’ hybrids. The ear leaves of ‘P38G43’ (sgr 9) had consistently higher concentrations of chlorophyll than those of ‘P39K38’ (sgr 6) (Figure 7.13). Because of the relationship between chlorophyll content (SPAD units) and SLN (Figure 6.2), the high chlorophyll concentration was indicative of a higher SLN, which could explain the delay in the commencement of leaf senescence in ‘P38G43’ (sgr 9) compared with ‘P39K38’ (sgr 6) (Figure 7.14).

7.6.3 Radiation use efficiency

In Experiment 2, RUE was similar between the hybrids (Section 7.5.5). The high background N level in Experiment 2 (Section 3.2.1) means N availability probably did not constrain dry matter accumulation (Muchow & Davies 1988). Subsequently, luxury N had a greater effect on dry matter accumulation than the hybrid ‘stay-green’ trait as shown by the gross photosynthesis measurements which did not differ between the hybrids soon after silking and close to physiological maturity (Table 7.8). However, gross photosynthesis may also have been similar because the measurements were made on the ear leaf where SLN during grain filling remained similar between the hybrids (Tables 7.10 and 7.11). The ear leaf was also the largest leaf (Figure 7.9), and probably well illuminated, thus had proportionately more leaf N allocated to it (Grindlay 1997).

Overall RUE in Experiment 2 was 10% lower than in Experiment 1 (Table 6.1 and Section 7.5.5). The lower radiation receipts in 2009/10 compared with 2008/09 are partly responsible for this observation (Table 5.1 and Section 7.5.3.1). It may also be related to the cooler environment experienced around silking when mean air temperature was 16.6 °C (February) compared with 18.7 °C (January) for Experiment 1 (Table 3.3). Andrade *et al.* (1992) observed that the seasonal differences in RUE for their maize crop in Balcarce, Argentina, were due to low temperature (15-18 °C) during the vegetative growth stage. They associated this observation to the influence of temperature on photosynthesis in agreement with the data presented on Figure 2.3.

7.6.4 Non kernel ear dry matter

In both experiments, the proportion of the non kernel ear dry matter was greater in ‘P39K38’ (sgr 6) compared with ‘P38G43’ (sgr 9) (Tables 4.5 and 7.1). This may suggest a greater partitioning of dry matter or limited post anthesis translocation from this pool. ‘P39K38’ (sgr 6), had a higher maximum GAI (Table 7.8), and probably synthesised carbohydrates in excess of its daily requirements prior to active grain filling (Pearson *et al.* 1984; Swank *et al.* 1982; Wardlaw & Willenbrink 1994). However, once the kernels began to develop, most of its requirements were met from current photosynthates (Muchow *et al.* 1990), and the shortfall from reserves in the stalk (Figure 7.3). Consequently the contribution of the non kernel ear dry matter reserves was limited to ~10% (Figure 7.5b). In Experiment 2, this would have been supplied entirely from stalk reserves (Section 7.2.5.3) which are preferable because its carbohydrates are stored mainly as water soluble sugars (Wardlaw 1990), and are therefore, readily available for remobilisation unlike the cellulose in the non kernel ear dry matter (Cliquet *et al.* 1990b).

A reduction in the proportion of dry matter incorporated into the non kernel dry matter accumulated by ‘P39K38’ (sgr 6), could minimise the amount of N that needs to be remobilised from the leaves (Masclaux-Daubresse *et al.* 2008). This would elevate the SLN of its lower leaves and also unlock other vital resources such as carbohydrates for use in grain filling.

7.7 Conclusions

- Dry matter accumulation, yield and grain N were higher in ‘P39K38’ (sgr 6) compared with ‘P38G43’ (sgr 9) because of the faster rate of dry matter accumulation as a consequence of more PAR interception by the low ‘stay-green’ hybrid (sgr 6) compared with the high ‘stay-green’ hybrid (sgr 9).
- ‘P39K38’ (sgr 6) intercepted more PAR compared with ‘P38G43’ (sgr 9) because it had larger leaves in positions 8-14.
- Remobilisation of N from the lower leaves of ‘P39K38’ (sgr 6) may have sustained higher growth rates which led to higher total dry matter and kernel yield at physiological maturity.
- The greater proportion of N recovered in the kernels of ‘P39K38’ (sgr 6) was associated with the faster rate of GAI decline post-silking, probably due to N remobilisation.
- RUE and gross photosynthesis did not differ between the hybrids or the N levels, because N was at luxury levels.
- More N could have been remobilised from the stalk of both hybrids to increase grain N content with no expected consequence in crop yield.

Chapter 8

General discussion and conclusions

In this study, dry matter accumulation in maize was expressed as a function of the total absorbed radiation and its efficiency of utilization (RUE). Consistent with studies in sorghum (*Sorghum bicolor* L. Moench) (Muchow & Davies 1988; Sinclair & Muchow 1999), soybean (*Glycine max* L. Merr.) and rice (*Oryza sativa* L.) (Sinclair & Horie 1989), RUE in maize declines during grain filling from a maximum at silking due to N remobilization (Section 2.3.4.4). ‘Stay-green’ hybrids offer the potential to intercept and utilize more solar radiation during grain filling and accumulate more dry matter (Section 2.3.4.1), as they were selected to increase dry matter yield through an increase in leaf area duration (Tollenaar & Aguilera 1992). Most of the recent research with the ‘stay-green’ trait in Australia and New Zealand was carried out on grain sorghum (*Sorghum bicolor* L. Moench). Experimental results from this research indicated a yield advantage with the incorporation of this trait (Section 2.6). However, no such data have been reported for maize (*Zea mays* L.). Further, the physiological basis of this trait remains unclear despite the development of a possible framework in sorghum (*Sorghum bicolor* L. Moench) (Borrell *et al.* 2001; Borrell *et al.* 2003).

The objectives of this study were to firstly quantify the yield potential accrued from the incorporation of the ‘stay-green’ trait. Secondly, to examine how different N and moisture levels influence the response of maize hybrids of different ‘stay-green’ rating. Lastly to understand the physiological mechanism(s) which underlie the expression of this trait in maize hybrids.

8.1 Influence of the hybrid ‘stay-green’ trait

8.1.1 Dry matter and grain yield

In Experiment 1, total dry matter and grain yield at physiological maturity did not differ among the hybrids used (Sections 4.5.5.1 and 4.5.5.6). However, data from Experiment 2 showed that both total dry matter and seed yield at physiological maturity were greater in the low (‘P39K38’ (sgr 6)) than in the high ‘stay-green’ (‘P38G43’ (sgr 9)) hybrid (Figures 7.1 and 7.5a). This observation was hypothesised to be related to higher crop growth rates

attained by these low ‘stay-green’ crops as a consequence of increased PAR interception (Section 7.5.3.2) and efficient redistribution of plant available N (Section 7.5.9.3).

The Canterbury region of New Zealand is considered a marginal and risky region for maize grain (*Zea mays* L.) production (Wilson *et al.* 1994). Despite this, at physiological maturity, the fertilised and irrigated crops in Experiment 1 achieved an average dry matter yield of 28.0 t ha⁻¹, while those of Experiment 2 averaged 21.5 t ha⁻¹. Grain yields also averaged 14.0 and 10.1 t ha⁻¹, respectively. Hence, as part of a crop sequence, maize (*Zea mays* L.) can make a major contribution towards the targeted production of 45 t of dry matter ha⁻¹ per year as set as a stretch target by the dairy industry (de Ruiter *et al.* 2009). These yields were comparable with the 30.7 t ha⁻¹ and 24.9 t ha⁻¹ obtained in a two year experiment in a farmer’s field in the Waikato region of New Zealand (Densley *et al.* 2006). The higher yields from the warm Waikato region were attributed to the use of hybrids with a longer maturity (Densley *et al.* 2006), since seasonal dry matter accumulation is positively correlated with the relative maturity rating of the hybrid (Tollenaar & Dwyer 1999). In summary, no yield advantage was gained from the use of these specific ‘stay-green’ hybrids in Canterbury and in the second cooler, season the ‘stay-green’ hybrid with the lower rating had higher yields.

8.1.2 Dry matter accumulation

Chapters 5 and 6 described how the low and high ‘stay-green’ hybrids adopted different mechanisms in their capture and utilization of resources to achieve a similar yield at physiological maturity. In this section the pattern of dry matter accumulation will be explained using general mechanism(s) consistent across both experiments in each category of ‘stay-greens’ starting from canopy development and light interception to N remobilisation. For consistency, the hybrids were categorized broadly as low and high ‘stay-green’ and represented mainly by ‘P39K38’ (sgr 6) and ‘P38G43’ (sgr 9), respectively.

Work on ‘stay-green’ sorghum has identified the maintenance of SLN above a critical threshold as a possible mechanism for the expression of the ‘stay-green’ trait (Borrell & Hammer 2000), because during their vegetative growth, crops partitioned N in favour of either leaf expansion or SLN (Vos *et al.* 2005). Partitioning of more N towards leaf development would potentially favour greater light interception, while the maintenance of a

higher SLN would enhance photosynthetic efficiency. Evidence exists to associate the high 'stay-green' hybrids with the maintenance of a higher SLN (Section 2.6). However, it is unclear if the low 'stay-green' hybrids partition more of the N taken up during vegetative growth towards leaf area development.

8.1.2.1 Canopy development

In both Experiments 1 and 2 the low 'stay-green' hybrid ('P39K38', (sgr 6)), had a higher GAI (Tables 5.5 and 7.3) from the development of more leaf area per plant (Tables 5.6 and 7.4) compared with the high 'stay-green' hybrid ('P38G43' (sgr 9)). This was related to the larger leaves in positions 8-14 in 'P39K38' (sgr 6) than 'P38G43' (sgr 9) (Figure 7.9). For the major part of leaf appearance (<13.2 leaf tips) in Experiment 1, the phyllochron_(tip) did not differ between 'P39K38' (sgr 6) and 'P38G43' (sgr 9) (Table 5.9). Similarly, fully expanded leaf appearance rates were similar between the two hybrids (Table 5.12). This was also observed in Experiment 2 (Section 7.5.4.3). The implication is that 'P39K38' (sgr 6) developed a larger GAI as a result of a reduced plastochron, faster rate or longer duration of leaf area expansion (Birch *et al.* 2007; Birch *et al.* 2003; Plenet *et al.* 2000a).

Studies in wheat (*Triticum aestivum* L.) (Hay 1999) and maize (*Zea may* L.) (Vos *et al.* 2005), have shown that the plastochron was approximately half the phyllochron, and therefore can be expected to follow a similar pattern of development as the phyllochron. Thus, its influence on GAI can be discounted. This leaves the rate and duration of extension of the lamina as the most probable causes of the differences in leaf area between these hybrids. Several studies have shown that genetic and environmental variables mainly influenced leaf size through its rate of expansion and not the duration of expansion (Dale 1988; Monteith & Elston 1983; Tardieu *et al.* 1999). In this regard, the influence of the duration of expansion was ignored and the rate of expansion of individual leaf area was considered the most important reason for the differences in leaf area between these hybrids.

Lamina extension rate is determined by tissue expansion rate and epidermal cell division (Dale 1988, 1992). While tissue expansion rate is dependent on the cell wall rheological properties (plastic extensibility and yield threshold) (Cosgrove 1986; Dale 1992), cell division is governed by genetic factors but modified by environmental variables e.g. N availability

(Gastral & Nelson 1994; Lawlor 2002). It seems most likely that ‘P39K38’ (sgr 6) had a lower minimum threshold requirement for cell wall extension (Equation 2.8), or maintained a higher cell turgor pressure through the synthesis of osmotically active compounds e.g. proteins (Cosgrove 1986), than ‘P38G43’ (sgr 9). More importantly, the low ‘stay-green’ hybrid ‘P39K38’ (sgr 6), may have attained the faster rates of cell division by partitioning proportionately more N towards leaf area development (Lemaire *et al.* 2007). Support for this observation is provided in Section 8.1.4.2. Furthermore, Tardieu *et al.* (1999), and Volonec and Nelson (1984), show that N has a large influence on the rate of leaf area development through its stimulation of cell production. Thus, the accelerated rate of cell division and expansion associated with the greater leaf area in ‘P39K38’ (sgr 6), though under genetic control, was modified by differential N allocation as suggested by Dale (1988).

Green area index declined more rapidly in the low than in the high ‘stay-green’ hybrids (Tables 5.7 and 7.6). This was consistent with more leaves senesced in these hybrids (Table 6.4 and Figure 7.8) and provides support for a longer green area duration among the high ‘stay-green’ hybrids when N was provided.

8.1.2.2 Post-silking dry matter accumulation

Post-silking dry matter increase was solely driven by ear dry matter accumulation (Section 7.5.2.5), as a result of kernel growth (Figure 7.5a) as reported by both Borrás *et al.* (2007) and Tollenaar and Dwyer (1999). Thus, differences in kernel growth rates between hybrids were responsible for the differences in post-silking accumulated total dry matter. Similar results were reported by Wilkinson and Hill (2003), who attributed the lower ear dry matter of the ‘stay-green’ hybrids to a limited sink capacity for photosynthate.

Evidence to suggest a weaker sink capacity can be deduced from the lower total and percent N in the grains of the high ‘stay-green’ hybrids in both experiments (Table 6.6 and Section 7.5.9.2). As N is delivered into the grains as amino acids (Feller & Fischer 1994; Tollenaar & Dwyer 1999), the osmotic concentration of the expanding grain cells is influenced by the quantity of N deposited. The larger the quantity of amino acids deposited, the greater the absorption of water and the corresponding sink size (Egli 1998; Fraser *et al.* 1982; Westgate 1994). Additionally, early silking in ‘P39K38’ (sgr 6) (Section 4.5.5.1) meant that this hybrid

had a longer duration of grain filling, therefore greater dry matter accumulation by the kernels of this hybrid. This was in agreement with NeSmith and Ritchie (1992), who report that reductions in kernel dry weight were the result of a shortened linear phase of kernel filling.

8.1.3 Light interception and RUE

8.1.3.1 Light interception

Larger leaf area increments in ‘P39K38’ (sgr 6) compounded over time, particularly during the vegetative growth phase more than in ‘P38G43’ (sgr 9) (Section 8.1.2.1). This advanced the development of GAI such that critical GAI was reached earlier than in ‘P38G43’ (sgr 9) (Figure 5.3 and Table 5.4). Canopy closure was therefore accelerated and consequently ‘P39K38’ (sgr 6) absorbed more PAR (Table 5.1 and Section 7.5.3.2). The additional leaf area in ‘P39K38’ (sgr 6) was strategically invested within the canopy to make the maximum return on PAR interception. Thus, leaves in positions 8-14 were larger in ‘P39K38’ (sgr 6) than those of ‘P38G43’ (sgr 9) in a similar position. Leaves in this position intercepted the most solar radiation (Tetio-Kagho & Gardner 1988) and also provided a large proportion of the photosynthate for the developing ear (Section 7.6.1).

More importantly, the acceleration of canopy closure in ‘P39K38’ (sgr 6) synchronized the attainment of maximum GAI with the period of greatest solar radiation occurrence (Figure 3.1). Stone *et al.* (1999), report a 20% increase ($P < 0.05$) in total solar radiation intercepted by a crop of maize compared with the control when the time of peak GAI was synchronized with that of maximum solar radiation occurrence. Notwithstanding the extended leaf area duration in ‘P38G43’ (sgr 9) during Experiment 2 (Figure 7.8), total intercepted PAR was still below that of ‘P39K38’ (sgr 6) (Section 7.5.3.2). This implies that the additional PAR intercepted by ‘P38G43’ (sgr 9) during late grain filling was insufficient to compensate for the loss of capacity incurred due to the delay in canopy closure and the lower maximum GAI (Tables 5.5 and 7.3). The inability to bridge the gap in PAR interception can partly be attributed to the decline in the quantity of irradiance received as the season progressed towards autumn (Figure 3.1).

In summary, the investment in early canopy closure by ‘P39K38’ (sgr 6) paid more dividend in PAR interception than the delayed leaf area duration as a result of the ‘stay-green’ trait in

'P38G43' (sgr 9). Based on these results, the 'stay-green' trait had a negative impact on total PAR interception.

8.1.3.2 RUE

Section 8.1.3.1 indicated total PAR interception was compromised by the 'stay-green' trait. Given the close relationship between PAR interception and dry matter accumulation (Section 2.3.4.1), the high 'stay-green' hybrids (e.g. 'P38G43' (sgr 9)) were anticipated to accumulate less dry matter yield. However, in Experiment 1, total dry matter and grain yield at physiological maturity did not differ between the low and high 'stay-green' hybrids (Section 4.5.5.1). This implies that there was a trade off in these high 'stay-green' hybrids between high RUE and the low PAR interception. Table 6.2 shows that 'P38G43' (sgr 9) had a higher RUE than 'P39K38' (sgr 6).

In Experiment 2, however, RUE did not differ between the low and high 'stay-green' hybrids (Section 7.5.5), which explains why 'P39K38' (sgr 6) had a higher total dry matter at physiological maturity (Figure 7.1). The similarity in RUE between the hybrids in Experiment 2 could be related to the interacting physiological processes which determine RUE at the canopy level (Reynolds *et al.* 2000; Tollenaar & Aguilera 1992). N availability probably enhanced the photosynthetic capacity and delayed leaf senescence in 'P39K38' (sgr 6), thus, increasing its RUE. The similarity in gross photosynthesis rate between these hybrids during late grain filling provides support for this assumption (Table 7.8).

8.1.4 Nitrogen dynamics

One drawback of the simple N balance method used in this study was its lack of precision in the determination of the proportion of N derived from soil uptake or remobilisation because both processes occurred concurrently during grain filling as reported earlier by Gallais *et al.* (2007). However, consistent trends in N uptake and remobilisation emerged from both experiments.

8.1.4.1 N uptake

It has been suggested that ‘stay-green’ hybrids maintain a higher SLN through the greater uptake of N during grain filling (Section 2.6). In 2008/09, total N uptake did not differ between the hybrids at silking (Appendix 7) and at physiological maturity (Section 6.5.4.1). These results are in agreement with those of Subedi and Ma (2005), who report no differences in total N uptake between early and late senescent hybrids grown under controlled environment conditions. However, it contrasted with the work of Rajcan and Tollenaar (1999b), who observed greater N sequestration during grain filling in a ‘stay-green’ hybrid under field conditions. In their study, greater N uptake during grain filling was attributed to a higher rate of dry matter accumulation by the ‘stay-green’ hybrid (Rajcan & Tollenaar 1999b), probably from an enhanced leaf photosynthesis rate (Masclaux *et al.* 2001). In the present study, gross photosynthetic rates were similar between the hybrids (Table 7.8), which could explain why N uptake during grain filling was similar. For the 2009/10 crop, total N content at silking was similar between the hybrids but ‘P39K38’ (sgr 6) accumulated more N than ‘P38G43’ (sgr 9) at physiological maturity (Figure 7.15a) probably due to luxury N uptake associated with a larger green area.

8.1.4.2 N remobilisation

Remobilization of N may commence soon after full leaf expansion or during grain filling if current N uptake is insufficient to meet crop requirements (Section 2.4.6). In this study, it appears that during vegetative growth, leaf N turnover was faster in the low ‘stay-green’ hybrid (‘P39K38’, sgr 6) than in the high ‘stay-green’ hybrid (‘P38G43’, sgr 9). For example in Experiment 1, the SLN of the lower leaves at 800 °C.d did not differ among the hybrids (Table 6.15). However, the SLN of the middle leaves of ‘P39K38’ (sgr 6) was lower than that of ‘P38G43’ (sgr 9) at this time (Table 6.18). This indicates that N may have been remobilised from this strata to support the expansion of the top leaves. Indeed the SLN of the top leaves of these two hybrids was higher than that of the other hybrids at this time (Table 6.20).

Thus, it can be hypothesized that once a leaf of ‘P39K38’ (sgr 6) was fully expanded, its N concentration was lowered to a critical minimum threshold and any surplus N was rapidly transported to the younger expanding leaves (Section 6.6.4). This cycle of events was then repeated sequentially until all the leaves were fully expanded and may explain why ‘P39K38’

(sgr 6) developed larger leaves in positions 8-14. These leaves were initiated and developed after the plant became autotrophic (Duncan 1975), consistent with the temporal operation of such a mechanism. Both Lhuillier *et al.* (1999) and Beninati and Busch (1992), have demonstrated that the efficiency of N redistribution within the plant had a more profound effect on crop growth rates than its total quantity. Thus, crops that efficiently remobilise N, sustain increased catalytic activity (Lawlor 2002), and have enhanced cell division and expansion rates (Gastral & Lemaire 2002).

In Experiment 1 both the stalk and leaves remobilised $\sim 30 \text{ kg N ha}^{-1}$ towards grain filling (Tables 6.10 and 6.14). However, more N was remobilised from the stalks of the low ‘stay-green’ (‘P39K38’, (sgr 6) and ‘P38V12’ (sgr 7)) than from the high ‘stay-green’ (‘P38F70’ (sgr 8) and ‘P38G43’ (sgr 9)) hybrids (Table 6.10). Similarly, the low ‘stay-green’ hybrids remobilised more of their leaf N towards grain filling than ‘P38G43’ (sgr 9) (Table 6.14). Surprisingly ‘P38F70’ (sgr 8) also remobilised a large proportion of its leaf N towards grain filling. This variation could be related to its tendency to accumulate less stalk N (Table 6.9). To compensate it appears to have remobilised more N from its leaves. For ‘P39K38’ (sgr 6), the demand for N from the kernels (Table 6.6) was responsible for the greater remobilization of N from the vegetative structures. ‘P38G43’ (sgr 9), therefore, retained more N in its leaves during grain filling (Table 6.14), which lead to a higher SLN (g m^{-2}) and longer retention of leaves when the crops were fertilised.

These results demonstrate that during grain filling the high ‘stay-green’ hybrids withheld N in their stalk and leaves to the detriment of the grain N content. Furthermore, in extreme situations there might not be enough N to reach minimum grain N content so grain yield will also decrease. As a consequence feed formulations with ‘P38G43’ (sgr 9) as an ingredient may be lower in N than those from hybrids of lower ‘stay-green’ rating. Moot *et al.* (2007), reported that maize has a low N content, hence, the use of ‘P38G43’ (sgr 9) with an even lower grain N% in feed formulation may be counterproductive.

8.2 N partitioning strategy for cool temperate climates

Observations from Experiment 2 suggest that the productivity of the low ‘stay-green’ hybrids could be increased through an increase in canopy photosynthesis. This increase in canopy

photosynthesis was mediated through an increase in total leaf area in agreement with the strong evidence that suggests the interception of solar radiation had a more profound influence on dry matter accumulation and yield (Gallagher & Biscoe 1978; Monteith 1981) than an enhanced rate of photosynthesis (Richards 2000). Attempts to increase dry matter accumulation through an enhanced efficiency of the photosynthetic system have yielded unsatisfactory results because of its complexity and feedback regulatory mechanisms (Gifford *et al.* 1984). Thus, under the conditions experienced during the vegetative growth stage in this study (mean temperature <19 °C) (Table 3.3), an enhanced photosynthetic capacity was unlikely to be advantageous because leaf photosynthesis for C₄ crops declines with temperature (Duncan & Hesketh 1968) and was below the optimum mean temperature of 25-34 °C for most of the growing season (Edwards & Walker 1983; Muchow *et al.* 1990). Further, Andrade *et al.* (1992), report that the RUE of maize grown under cool temperate conditions (<16 °C) was, mainly dependent on the temperatures during the vegetative growth phase.

The low 'stay-green' hybrids showed a remarkable ability to remobilise N acquired during the vegetative growth stage towards grain filling (Tables 6.10 and 6.14). These hybrids would be suitable for the New Zealand environment where intensive dairy farming has led to the accumulation of soil nitrate (Di & Cameron 2002). An efficient remobilisation of N would therefore reduce N inputs, lower the cost of production and limit environmental degradation due to nitrate leaching (Masclaux-Daubresse *et al.* 2008). However, by holding on to N during grain filling, the enhanced 'stay-green' hybrids risk relying on absorbed N and requiring greater N inputs.

In summary, Richards (2000), asserts that no meaningful gain in the improvement of the photosynthetic system below that of the leaf canopy development was currently feasible. Therefore, in the absence of limitations, crops with an intrinsic ability to develop larger surfaces for light interception are expected to yield higher than those reliant on an efficient photosynthetic system (Ayaz *et al.* 2004). The findings from this study and those of Richards (2000), emphasize the need for the selection of crops whose duration of growth and timing of developmental events are synchronised with the radiation and temperature regime experienced during growth.

8.3 Whither 'stay-green'?

In Experiment 1, dry matter accumulation and grain yield were similar between the hybrids (Section 4.5.1). However, 'P39K38' (sgr 6) accumulated more dry matter and grain yield than 'P38G43' (sgr 9) in Experiment 2 (Figure 7.5). This was in contrast to the anticipated greater yields from the high 'stay-green' hybrids (Section 2.6). Given the influence of temperature on both photosynthesis and RUE (Figure 2.3 and Section 8.2), these results were not surprising. Under the marginal conditions for maize growth experienced in Canterbury (Section 8.1.1), environmental conditions appear to have had a greater impact on the accumulation of dry matter and grain yield than the inherent genetic characteristics of the hybrids. Wilkinson and Hill (2003) reached a similar conclusion in their work on maize in England.

Apart from their potential to increase dry matter yields, 'stay-green' hybrids were also selected because of their tolerance to stress, particularly increased plant population (Tollenaar 1991) and late season plant health (Cavalieri & Smith 1985). Late season plant health may confer improved disease resistance (Wilkinson & Hill 2003) due to cell integrity (Crafts-Brandner *et al.* 1984). However, Havilah and Kaiser (1994), report a lower whole plant dry matter content in these hybrids, which eroded any gains from a healthier crop. Increased plant population could enhance the productivity of the high 'stay-green' hybrid ('P38G43' (sgr 9)) because of the potential for increased N remobilisation from its leaves and stalk. This is consistent with the work of Tollenaar (1991), who in a comparison of an old (senescent) and new hybrid ('stay-green'), showed that a higher plant population increased loss of vegetative weight and accelerated leaf senescence in the new than the old hybrid. Furthermore, a higher plant population was suggested as an option to increase the quantity of intercepted PAR by the high 'stay-green' hybrids (Section 7.6.1). While this may justify a recommendation for a higher seed rate, the ultimate beneficiaries may be the seed producers because a similar yield can be attained with a lower plant population of the low 'stay-green' hybrids.

Perhaps the ability of the high 'stay-green' hybrids to retain green leaves for longer when N was available (Tables 6.5 and 7.5) and thus provide an opportunity for a prolonged harvest window as suggested by Havilah and Kaiser (1994), may be its greatest asset. Occasionally farm operations e.g. harvesting maize for silage preparation may be delayed by unfavourable weather or contractors' busy schedule. Under these circumstances the high 'stay-green' hybrids can still be harvested with minimal adverse effect on its quality.

8.4 Maize ideotype

The need to develop crop ideotypes in cereals evolved from the realisation that production potential was maximised when the plant characteristics influenced photosynthesis, growth and grain production (Donald 1968). In maize for example, the faster development of leaf area is a critical component of an ideal maize crop (Mock & Pearce 1975). In the present study, the low 'stay-green' hybrids had accelerated development of their leaf area and reached critical GAI earlier than the high 'stay-green' hybrids (Table 5.4). Furthermore, their maximum GAI was higher (Tables 5.5 and 7.3). Consequently these crops were able to intercept more solar radiation and, in Experiment 2, 'P39K38' (sgr 6) yielded more than 'P38G43' (sgr 9) (Figure 7.1). A potential maize ideotype should therefore possess the inherent ability for rapid canopy closure, as exhibited in general by the low 'stay-green' hybrids but more specifically 'P39K38' (sgr 6). The ideal maize crop should also build sufficient N reserves during vegetative growth and remobilize a large proportion of this towards grain filling as suggested by Masclaux *et al.* (2001). In this study, the low 'stay-green' hybrid 'P39K38' (sgr 6) remobilised more of its leaf and stalk N reserves than 'P38G43' (sgr 9) (Tables 6.10 and 6.14).

An ideal maize crop should also utilize its photosynthate more efficiently. Under non limiting conditions of water and nutrients, dry matter accumulation during grain filling is sink limited (Figure 4.1 and 4.2). Hence, in agreement with Richards (2000), there is potential to increase dry matter yield through partitioning of the surplus carbohydrate for the initiation of more kernels or larger kernel size. Alternatively, prolific hybrids could also be bred to utilize the excess carbohydrate as suggested by Mock and Pearce (1975).

The findings from this study show the existence of sufficient diversity among the hybrids to suggest that the incorporation of suitable traits from each category of hybrids may provide potential for the development of a maize ideotype for cool temperate environments.

8.5 Scope for further research

8.5.1 Exploring the productivity of extremely low rated ‘stay-green’ hybrids

In Experiment 2, the low ‘stay-green’ hybrid (‘P39K38’ (sgr 6)), accumulated more dry matter and grain yield than the high ‘stay-green’ hybrid (‘P38G43’ (sgr 9)) (Section 7.5.2.2) by accelerating its canopy development and attaining critical GAI earlier (Section 5.3.3.1). Similarly, ‘P39K38’ (sgr 6), probably had a faster rate of N turnover during the vegetative growth stage compared with ‘P38G43’ (sgr 9) (Section 8.1.4.2). In the Canterbury region of New Zealand, seasonal variation in temperature and solar radiation means the duration of crop growth is crucial in determining productivity. Hence, hybrids able to reach critical GAI earlier through manipulation of their N economy may yield higher than those with no similar mechanism. Thus, there is need to evaluate the agronomic performance of extremely low rated ‘stay-green’ hybrids (e.g. ‘sgr’ 4-5), the assumption being the lower the ‘stay-green’ rating, the greater the degree of N remobilisation and faster canopy development.

8.5.2 Increased plant population and remobilization of leaf N

Results from Experiment 1 show that ‘P38G43’ (sgr 9), remobilized less N from its leaves and stalk than ‘P39K38’ (sgr 6) (Section 8.1.4.2). One of the factors for the selection of high ‘stay-green’ hybrids was their tolerance to increased plant population (Section 8.3). Thus, an increase in plant population would create more competition for available resources e.g. N and probably cause these crops to remobilise more of the N acquired during the vegetative growth stage towards grain filling. An increase in plant population would also increase the GAI of these crops and advance canopy closure, enabling them to intercept more solar radiation. Potentially, this would increase both dry matter and grain yield due to the increase in RUE (Westgate *et al.* 1997).

8.5.3 Reduction of the non kernel ear dry matter

In both experiments, ‘P39K38’ (sgr 6) partitioned proportionately more of the dry matter synthesized prior to linear grain filling into the husks, rachis and shank than the other hybrids (Tables 4.5 and 7.1). The greater dry matter accumulated prior to active grain filling by ‘P39K38’ (sgr 6) was related to the greater green area developed by these crops (Tables 5.5 and 7.4). However, it is unclear why only a small proportion was remobilised for grain growth or stored in the stalk, where it is readily available for translocation (Fairey & Daynard 1978).

8.6 Conclusions

Under the marginal conditions for maize growth and development experienced at Lincoln University, New Zealand, environmental factors e.g. temperature and solar radiation played a major role in the accumulation of total dry matter and grain yield. Consequently, the following conclusions can be drawn from this study.

- Higher hybrid 'stay-green' rating either had no influence or was associated with a decline in dry matter accumulation and grain yield because of a reduction in total PAR intercepted. In contrast under low N conditions high 'stay-green' rating improved RUE but this was not sufficient to counter the reduced PAR interception.
- The low 'stay-green' hybrids developed more leaf area in early crop growth leading to an accelerated canopy closure, thus attaining the critical GAI early. This improved synchronisation between light interception and the solar radiation regime.
- Hybrids did not show any preferential N uptake during grain filling, suggesting that their pattern of uptake was similar, but its redistribution within the crops differed.
- The high 'stay-green' hybrids had a higher SLN but the same total leaf N (kg ha^{-1}) because they developed smaller leaves. Additionally, because N remobilization from the leaves of 'P38G43' (sgr 9) occurred to a lesser degree, a higher leaf N concentration was maintained for longer.
- The low 'stay-green' hybrids efficiently remobilised N from their leaves and stalk towards grain filling. N remobilization appears to have occurred earlier during vegetative growth in 'P39K38' (sgr 6) and may be responsible for the enlarged leaves in positions 8-14, which contributed to the interception of more solar radiation.
- The selection for high 'stay-green' rating may have led to a decline in the partitioning of N to the kernels and consequently contributed to lower grain N levels.

At best the hybrid 'stay-green' trait may only provide an opportunity for a prolonged harvest window before crops are ensiled. At worst it had a negative effect on dry matter yield and grain protein content.

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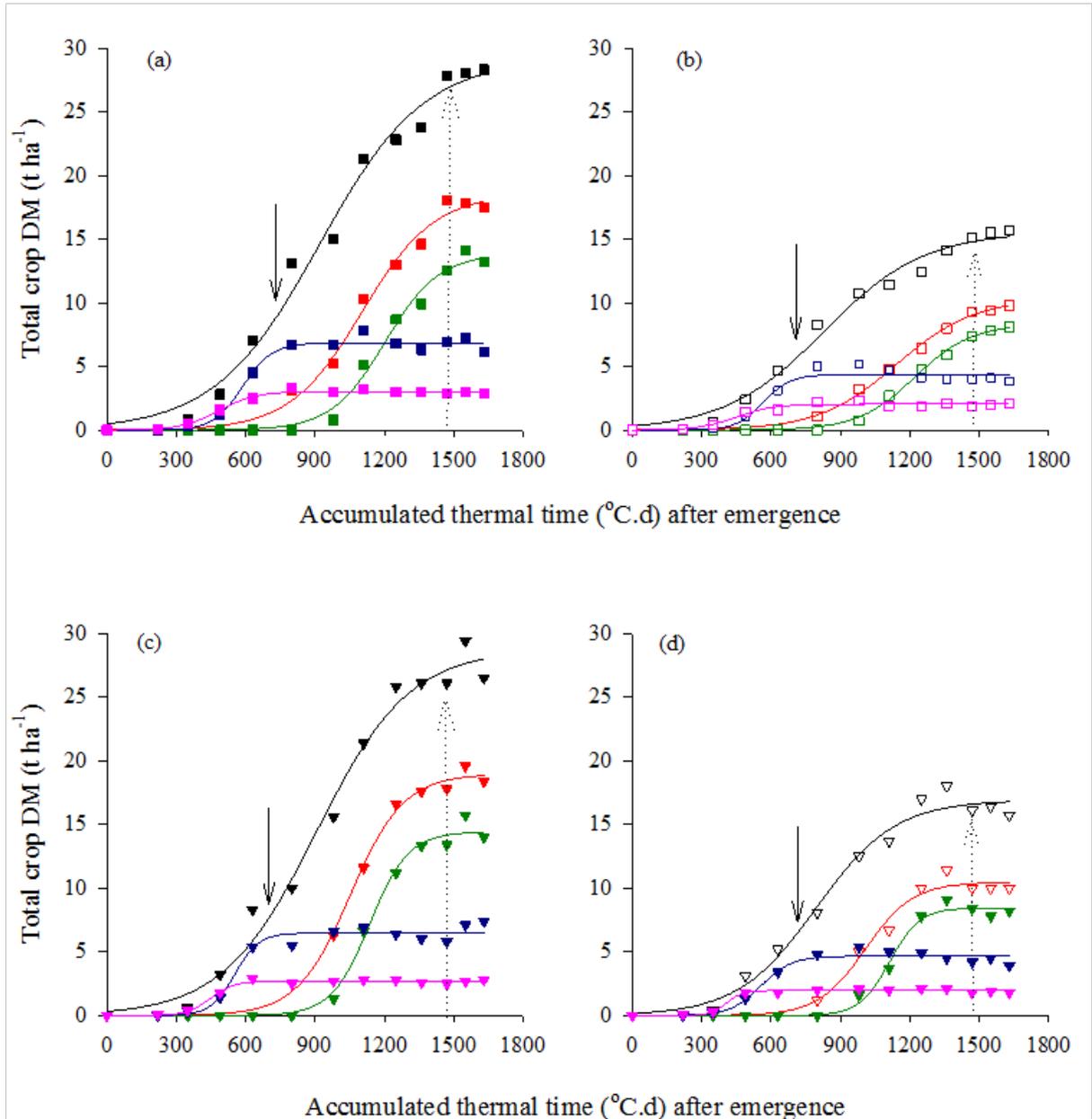
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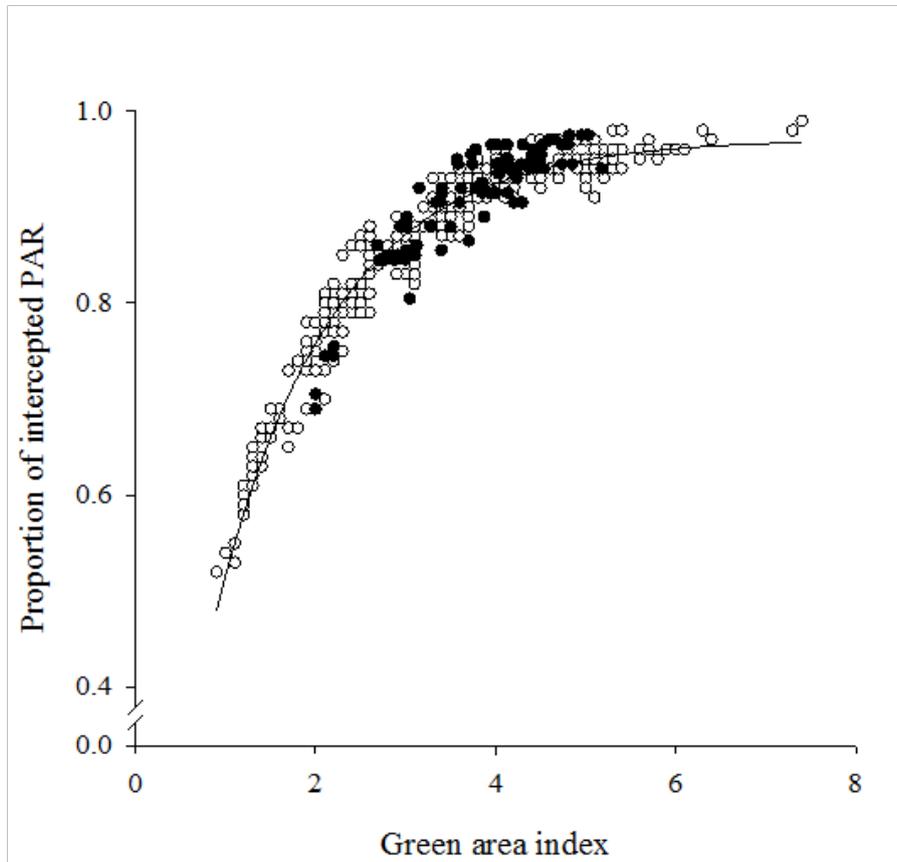
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Appendices

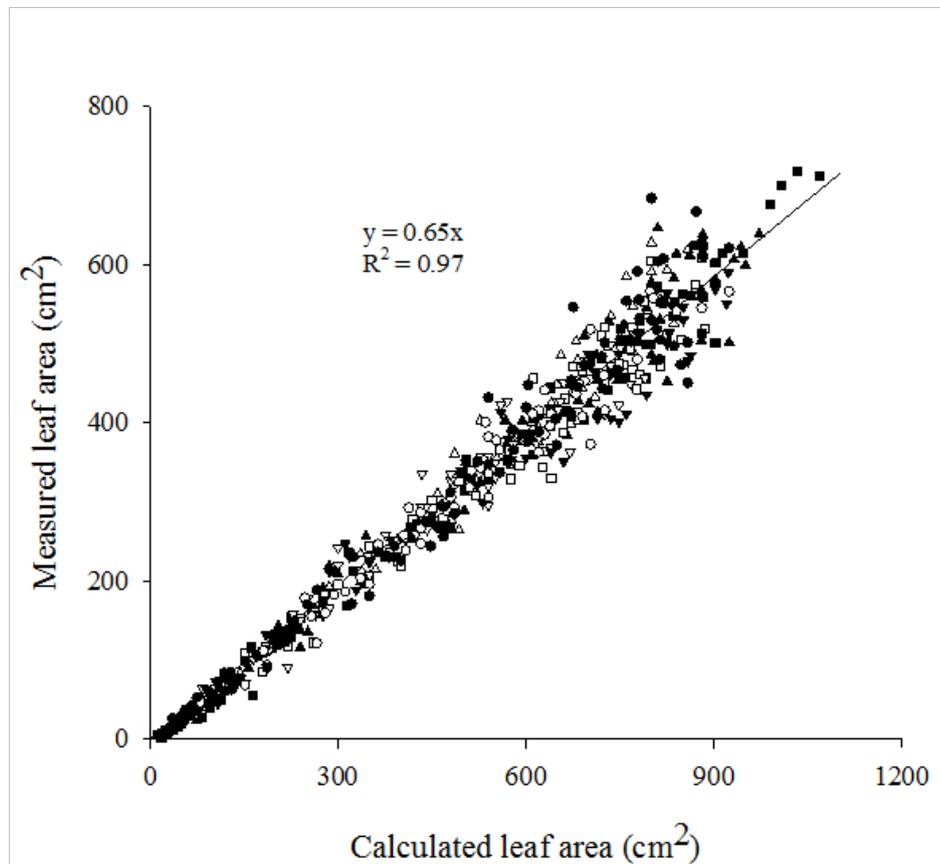
Appendix 1: Accumulated dry matter for total crop (black), ear (red), kernel (dark green), stalk (dark blue) and leaves (pink) in fully irrigated crops of ‘P38V12’ (sgr 7) (a and b) and ‘P38F70’ (sgr 8) (c and d), grown at Lincoln University, New Zealand, during 2008. The crops either received 270 (solid symbols) or 0 (open symbols) kg N ha⁻¹. The solid arrow represents silking and the dotted physiological maturity (1470 °C.d).



Appendix 2: Measurements of green area index obtained using the SunScan (open symbols) and leaf area meter (closed symbols) for maize hybrids grown at Lincoln University, New Zealand, during 2008. The solid line indicates the fitted regression $y = 0.97(1 - e^{-0.76x})$; $R^2 = 0.96$.



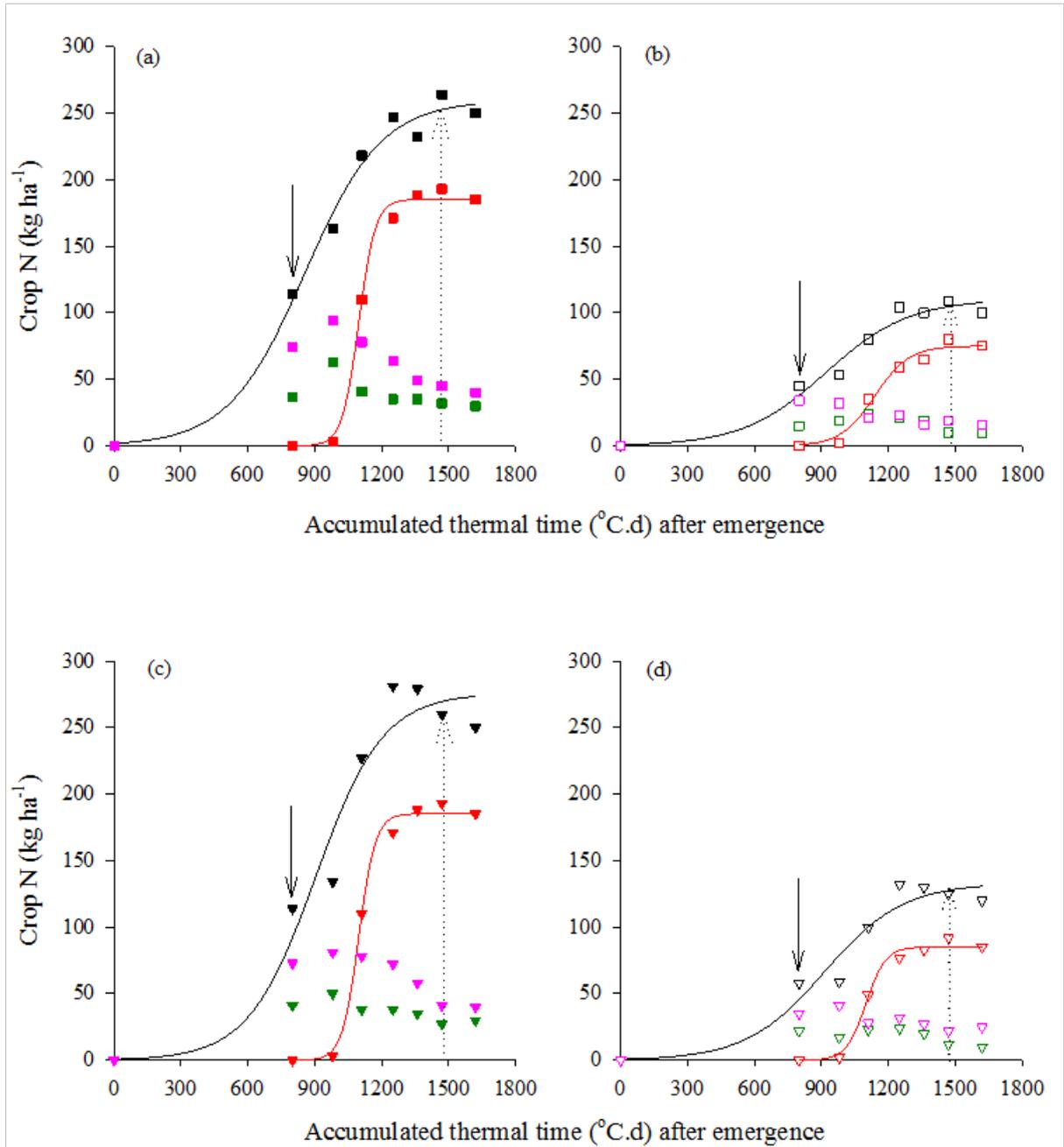
Appendix 3: Regression of the calculated against the measured leaf area (cm²) for ‘P39K38’ (sgr 6, △), ‘P38V12’ (sgr 7, □), ‘P38F70’ (sgr 8, ▽) and ‘P38G43’ (sgr 9, ○) maize hybrids grown with 0 (open symbols) or 270 (closed symbols) kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.



Appendix 4: Total leaf area (cm²) per plant at 800 °C.d of hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

Treatment	Leaf area (cm ²) per plant	
	0 kg ha ⁻¹	270 kg N ha ⁻¹
Rain fed	2880	4170
Irrigated	3420	4380
P value	P<0.029	
SE	138.5	
CV (%)	6.8	

Appendix 5: Mean N content (kg ha^{-1}) for total crop (black), kernels (red), stalk (dark green), and leaves (pink) against accumulated thermal time ($^{\circ}\text{C.d}$) after emergence in irrigated crops of ‘P38V12’ (sgr 7) (a and b) and ‘P38F70’ (sgr 8) (c and d), grown with 270 (solid symbols) or 0 kg N ha^{-1} (open symbols) at Lincoln University, New Zealand, during 2008. The solid arrow represents 7 days after silking (800 $^{\circ}\text{C.d}$) and the dotted physiological maturity (1470 $^{\circ}\text{C.d}$).



Appendix 6: SPAD readings (SPAD units per leaf) of the lower leaves at 800 °C.d after emergence in hybrid maize grown with 0 or 270 kg N ha⁻¹ and either rain fed or irrigated at Lincoln University, New Zealand, during 2008.

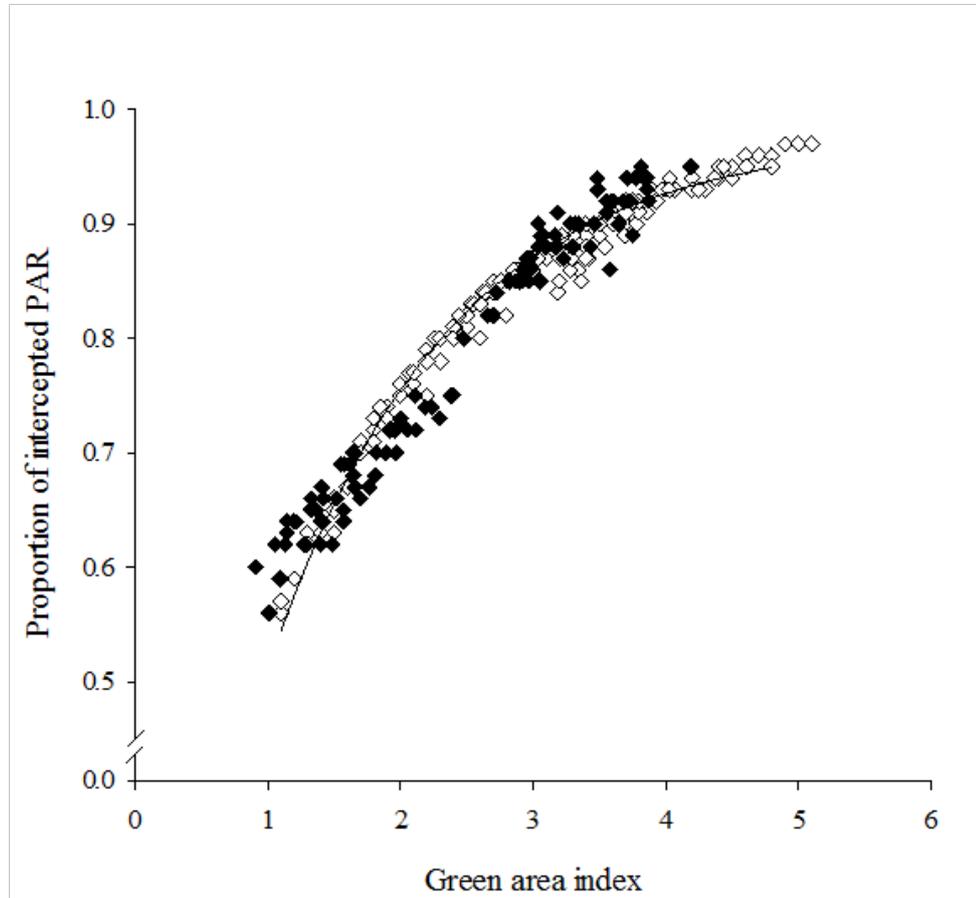
Hybrid	SPAD readings (SPAD units) per leaf				Mean
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Rain fed	Irrigated	
'P39K38' (sgr 6)	23.7	56.6	37.7	42.6	40.2 _{ab}
'P38V12' (sgr 7)	23.4	53.2	36.2	40.5	38.3 _b
'P38F70' (sgr 8)	29.0	56.4	40.7	44.7	42.7 _a
'P38G43' (sgr 9)	27.6	57.6	39.9	45.3	42.6 _a
Mean	25.9	56.0	38.6	43.3	41.0
P value	P<0.001		P<0.047		P<0.047
SE	0.84		0.74		1.18
CV (%)	10.0				

Means with letter subscripts in common are not significantly different at $\alpha = 0.05$.

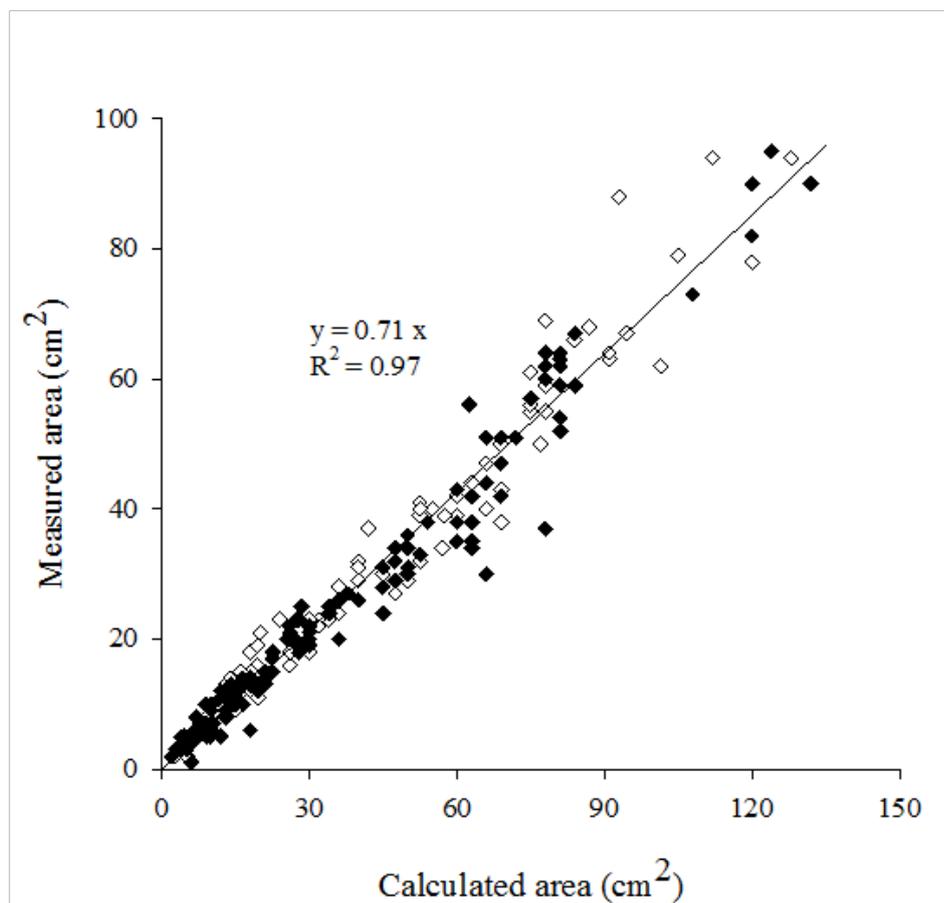
Appendix 7: Total crop N (kg ha⁻¹) 7 days after silking (800 °C.d) in hybrid maize grown with 0 or 270 kg N ha⁻¹ at Lincoln University, New Zealand, during 2008.

Hybrid	Total crop N (kg ha ⁻¹) at silking		
	0 kg N ha ⁻¹	270 kg N ha ⁻¹	Mean
'P39K38' (sgr 6)	56	175	116
'P38V12' (sgr 7)	57	177	117
'P38F70' (sgr 8)	51	146	99
'P38G43' (sgr 9)	58	170	114
Mean	56	167	112
P value	P<0.001		P<0.078
SE	3.7		5.2
CV (%)	13.2		

Appendix 8: Proportion of intercepted photosynthetically active radiation versus green area index measurements obtained from the SunScan (open symbols) and leaf area meter (closed symbols) in maize hybrids grown at Lincoln University, New Zealand, during 2009. The solid line represents the fitted regression $y = 0.98(1 - e^{-0.74x})$, $R^2 = 0.99$.



Appendix 9: Calculated versus measured leaf area (cm²) in ‘P39K38’ (sgr 6, ◇) and ‘P38G43’ (sgr 9, ◆) maize hybrids grown at Lincoln University, New Zealand, during 2009.



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