Early vigour - Its role in enhancing the productivity of wheat grown in South Australia

A thesis submitted for the degree of Doctor of Philosophy

Department of Agronomy and Farming Systems

The University of Adelaide

David Sloane

November 1999

TABLE OF CONTENTS

Abstract vii

Declaration viii

Acknowledgments ix

List of figures x

List of tables xiv

List of abbreviations xvi

1. General introduction 1

2. Review of literature 4

- 2.1 Introduction 4
- 2.2 Wheat growing in a Mediterranean environment 4
  - 2.2.1 Climatic constraints 4
  - 2.2.2 Adaptation 5
- 2.3 Definition of early vigour 6
- 2.4 The role of early vigour 7
  - 2.4.1 Improving water use efficiency and dry matter production 8
    - 2.4.1.1 Early ground cover 8
    - 2.4.1.2 Partitioning of water use 12
    - 2.4.1.3 Remobilisation of stored assimilates 14
    - 2.4.1.4 Soil influences 15
    - 2.4.1.5 Weed competition 16
  - 2.4.2 Other benefits of increased early vigour 18
    - 2.4.2.1 Nitrogen leaching 18
    - 2.4.2.2 Erosion control 19
- 2.5 Methods of stimulating early vigour 19
  - 2.5.1 Agronomic methods of promoting early vigour 20
    - 2.5.1.1 Plant density 20
    - 2.5.1.2 Plant arrangement 24
    - 2.5.1.3 Plant Nutrition 26
    - 2.5.1.4 Sowing techniques 30
      - 2.5.1.4.1 Time of sowing 31
      - 2.5.1.4.2 Sowing depth 32
  - 2.5.2 Genetic potential for improving early vigour 33
    - 2.5.2.1 Genetic variation 33
    - 2.5.2.2 Traits which promote early vigour 35
      - 2.5.2.2.1 Rate of emergence 35
      - 2.5.2.2.2 Specific leaf area 37
      - 2.5.2.2.3 Leaf angle and canopy architecture 38
      - 2.5.2.2.4 Leaf size 40

- 2.5.2.2.5 Phyllochron interval........41
- 2.5.2.2.6 Tillering ability........42
- 2.5.2.2.7 Dwarfing genes........44
- 2.5.3 Parental seed source effects........45
  - 2.5.3.1 Seed nutrient content........45
  - 2.5.3.2 Seed size........47
  - 2.5.3.3 Stresses during parental seed maturation........49
- 2.6 Screening techniques for early vigour........49
  - 2.6.1 Scoring for early vigour........50
  - 2.6.2 Photography........51
  - 2.6.3 Canopy reflectance........51
  - 2.6.4 Light interception........54
- 2.7 Summary........55

3. General materials and methods........59

- 3.1 Introduction........59
- 3.2 Site descriptions........59
  - 3.2.1 Soils........59
  - 3.2.2 Climate........60
- 3.3 Agronomy........61
- 3.4 Data analysis........62
- 3.5 Soil moisture monitoring........62
  - 3.5.1 Method........62
  - 3.5.2 Calibration........63
- 3.6 Remote sensing for vigour estimation........64
  - 3.6.1 Multi-spectral radiometer........64
  - 3.6.2 Ceptometer........65

4. Promoting early vigour by agronomic means........67

- 4.1 Introduction........67
- 4.2 The effect of increased sowing rate and nitrogen application on early vigour and grain yield........68
  - 4.2.1 Materials and methods........68
    - 4.2.1.1 Experiment 1: Roseworthy 1993........68
    - 4.2.1.2 Experiments 2 - 5: Roseworthy and Kapunda 1994, 1995........69
  - 4.2.2 Results........70
    - 4.2.2.1 Experiment 1........70
      - 4.2.2.1.1 Early vigour........70
      - 4.2.2.1.2 Moisture supply........71
      - 4.2.2.1.3 Grain yield........71
    - 4.2.2.2 Experiments 2 - 5: Roseworthy and Kapunda 1994, 1995........73
      - 4.2.2.2.1 Early vigour........73
      - 4.2.2.2.2 Grain yield........75
  - 4.2.3 Discussion........76
    - 4.2.3.1 Experiment 1........76
    - 4.2.3.2 Experiments 2-5........78
- 4.3 Genotypic responses to high and low combinations of sowing rate and nitrogen supply........79
  - 4.3.1 Materials and methods........80

4.3.1.1 Experiments 6 & 7 ... 80
4.3.2 Results ... 81
4.3.2.1 Experiments 6 & 7 ... 81
4.3.2.1.1 Early vigour ... 81
4.3.2.1.2 Grain yield ... 83
4.3.3 Discussion ... 84
4.4 General discussion ... 85
4.4.1 Early vigour ... 85
4.4.2 Grain yield ... 87
4.4.3 Genotypic effects ... 88
4.4.4 Viability of promoting early vigour agronomically ... 88
4.5 Conclusions ... 89

5. The effect of plant density on early vigour and grain yield in high and low tillering genotypes. ... 91

5.1 Introduction ... 91
5.2 Experiment 1: Plant density x tillering ability ... 92
5.2.1 Materials and methods ... 93
5.2.2 Results ... 94
5.2.2.1 Early Vigour ... 94
5.2.2.2 Leaf senescence ... 100
5.2.2.3 Grain Yield ... 101
5.2.2.4 Harvest index (HI) ... 104
5.2.2.5 Tiller mortality ... 105
5.2.2.6 Yield Components ... 106
5.3 Experiment 2: Glasshouse vigour studies ... 109
5.3.1 Materials and methods ... 110
5.3.2 Results ... 111
5.4 General Discussion ... 114
5.4.1 Early vigour ... 114
5.4.1.1 Measurement of early vigour ... 114
5.4.1.2 Genotypic vigour differences ... 115
5.4.1.3 Agronomy versus genotype ... 116
5.4.2 Relationship of early vigour with grain yield ... 116
5.4.2.1 Agronomic effects ... 117
5.4.2.2 Genotypic effects ... 118
5.4.2.3 Genotype x density effects ... 120
5.5 Conclusions ... 122

6. Genetic variability in early vigour: Field studies ... 123

6.1 Introduction ... 123
6.2 Initial screening of Roseworthy breeding lines for early vigour ... 124
6.2.1 Materials and methods ... 124
6.2.1.1 Data analysis ... 125
6.2.2 Results ... 125
6.2.3 Discussion ... 129
6.3 Field vigour studies of selected breeding lines ... 131
6.3.1 Introduction ... 131
6.3.2 Method ... 131

6.3.2.1 Data analysis 132
6.3.3 Results 133
6.3.3.1 Early vigour 133
6.3.3.2 Grain yield 136
6.3.3.3 Comparison of 1995 / 1996 results 141
6.4 Discussion 143
6.4.1.1 Early vigour 143
6.4.1.2 Early vigour x grain yield 144
6.4.1.3 Genotype x environment 147
6.4.1.4 Methods of early vigour assessment 148
6.5 Conclusions 149

7. Plant characteristics which promote early vigour: Glasshouse studies 150

7.1 Introduction 150
7.2 Experiment 1: Traits which promote early vigour 151
7.2.1 Materials and methods 152
7.2.1.1 Pot experiment 152
7.2.1.2 Embryo size 153
7.2.1.3 Coleoptile length 154
7.2.1.4 Analysis 154
7.2.2 Results 154
7.3 Experiment 2: Root growth 165
7.3.1 Materials and methods 165
7.3.2 Results 166
7.4 Comparison of vigour experiments 167
7.5 Discussion 170
7.5.1 Differences in early vigour 170
7.5.2 Traits which promote early vigour 171
7.5.3 Initial size versus rate of growth 174
7.5.4 Genotype x environment interaction 174
7.6 Conclusions 175

8. Identifying quantitative trait loci (QTLs) for traits which promote early vigour 177

8.1 Screening of a doubled haploid population 178
8.1.1 Materials and methods 179
8.1.1.1 Glasshouse experiment 179
8.1.2 Results 180
8.1.2.1 Leaf area 181
8.1.2.2 Leaf width 181
8.1.2.3 Leaf length 182
8.1.2.4 Specific leaf weight 183
8.1.2.5 Kernel weight 184
8.1.2.6 Root weight 185
8.2 Discussion 185
8.2.1 Early vigour traits 185
8.2.2 Benefits to plant breeding 187
8.3 Conclusions 189

9. General Discussion **190**
- 9.1 Improving early vigour 191
- 9.2 Plant traits which promote early vigour 192
- 9.3 Selection tools for early vigour 193
- 9.4 Conclusions 195

10. References **196**

Appendicies **221**
- A. Potting mixes 221
  - University of California mix 221
  - Lucern / Medic mix without perlite 221
- B. Fertilisers 222
  - Nitrophoska Analysis 222
  - Aquasol^{TM} soluble fertiliser 222
- C. Light interception and yield ranking 223

ABSTRACT

The cropping regions of South Australia experience cool wet winters and hot dry summers, and grain filling is usually carried out under moisture stress. During early vegetative growth the soil surface can remain wet for long periods and as much as 30-40% of growing season rainfall can be lost to soil evaporation. Given a water use efficiency for grain yield of 20 kg/ha/mm, this represents a sizeable loss in potential yield. This investigation explored the role of crop agronomy and genotype in improving early vigour with a view to increasing grain yield.

Agronomic studies showed that increased plant density and nitrogen supply gave significant increases in early vigour and anthesis biomass, however the effect on grain yield was variable. Higher agronomic inputs increased interplant competition and supplementary irrigation and rainout shelters showed that the variable yield response was due to moisture availability in the post anthesis period.

Rapid screening techniques were used to identify vigorous and non-vigorous lines within the Roseworthy Wheat Breeding Program and selections were made which reflected high and low yielding types. Investigation using these selections revealed that early vigour was significantly correlated with grain yield, however, early vigour on its own was only a moderate determinant of grain yield. Factors which influenced harvest index, such as phenology, plant height and tillering ability were equally important for yield in this environment.

Glasshouse studies using these high and low vigour selections showed that genotypic differences in growth could be detected as early as early as 207 °Cd from sowing (6 days after emergence). Leaf width was most strongly correlated with early leaf area development and this trait was also highly correlated with specific leaf weight and large embryo size. A doubled haploid population was used to identify QTLs for leaf length, SLW and kernel weight, and there is good potential for using marker assisted selection to improve early vigour.

DECLARATION

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

24/2/2000

David H.G. Sloane

ACKNOWLEDGMENTS

I am fortunate to have received assistance from many people and I am particularly grateful for the contribution from my supervisors; Tim Reeves, Gil Hollamby, Gurjeet Gill and Glenn McDonald. I thank Tim for getting me started and pointing me in the right direction; I thank Gil and all the staff in the Roseworthy Plant Breeding Program for their helpful hints and practical support; and I thank Gurjeet and Glenn for their academic guidance and editorial comments in the preparation of this thesis. It has been a team effort from which I have learned a lot and benefited greatly.

To the original cast members Brett, Grant and Darren, thanks for all the good times and happy memories. At least I wasn't the last one to finish the race! To all staff and colleagues in the AFS department, thanks for all the help, it has been fun working with you and best wishes for the future.

To my darling Annie, thank you for your support and patience - I couldn't have done it without you. The road has been long but we have travelled it together and now let it be paved in gold.

I also wish to thank the Grains Research and Development Corporation for their financial support and provision of a research scholarship.

LIST OF FIGURES

Figure 3.1 NDVI versus LAI for two radiometer calibrations; 1996 (O) y = 1.3425x - 0.3654 and 1997 (●) y = 1.5466x - 0.2573. Equations are highly significant (P < 0.01) with r values of 0.95 and 0.98 respectively....................65

Figure 3.2 Ceptometer calibration for light interception versus LAI. Y = 0.3477ln(x) + 0.3921. R = 0.91 (P < 0.01) 66

Figure 4.3 Percentage increase in tillering DM and grain yield due to the HV treatment growing under rainfed conditions in 1993 (■); or sowing rate (●) and nitrogen (O) at Roseworthy and Kapunda in 1994 and 1995.................86

Figure 5.1 Normalised difference vegetation index (NDVI) at (a) 40 DAS and (b) 60 DAS for genotype and density treatment averages. Error bars indicate LSD. 95

Figure 5.2 Percent light interception at (a) 59 DAS and (b) 98 DAS. Light interception values in (b) have been arcsine transformed to remove skew in the data. Error bars indicate LSD. 95

Figure 5.3 Dry matter versus plant density at 57 DAS for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 97

Figure 5.4 Leaf area index 57 DAS versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 97

Figure 5.5 Tiller number per plant at 57 DAS for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 98

Figure 5.6 Dry matter per plant 57 DAS versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 99

Figure 5.7 Estimated percentage of leaf area which was green 142 DAS for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 100

Figure 5.8 Grain yield versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 102

Figure 5.9 Grain yield per plant versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 102

Figure 5.10 Grain yield versus above ground dry matter at anthesis for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). 103

Figure 5.11 Grain yield versus time to anthesis. The four data points for each cultivar represent averages for densities of 100, 200, 300 and 400 plants/m^2. Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). $r = 0.541$ ($P < 0.01$). 104

Figure 5.12 Harvest index versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 105

Figure 5.13 Percentage of tillers present at 57 DAS which formed spikes at anthesis for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 106

Figure 5.14 Spikes per m^2 versus plant density for experimental lines (a) and commercial cultivars (b); grains per spike versus plant density for experimental lines (c) and commercial cultivars (d); and grain weight versus plant density for experimental lines (e) and commercial cultivars (f). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 107

Figure 5.15 Number of grains per m^2 versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 108

Figure 5.16 Percent screenings (grain width < 1.9 mm) versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD. 109

Figure 5.17 Average number of leaves per plant versus time. Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Halberd (▼). 114

Figure 6.1 Grain yield versus light interception (66 DAS) for raw data. Breeding lines are represented by (.), check varieties are indicated by (•) and lines selected for further study are indicated by numbers (see Table 6.7). ($r = 0.48$, $P < 0.01$) 126

Figure 6.2 Grain yield versus light interception for data adjusted using TwoD nearest neighbour analysis with plant density as a covariate for light interception. Breeding lines are indicated by (.), average of check varieties are indicated by (•) and lines selected for further study are indicated by numbers (see Table 6.7). ($r = 0.11$, ns) 127

Figure 6.3 Dry matter (57 DAS) versus grain yield. Plots are averages listed by line number or CV name (Table 6.7). ($r = 0.28$, $P > 0.05$). However, the regression equation becomes highly significant ($r = 0.52$, $P < 0.01$) if lines 1, 8, and 16 are removed. 137

Figure 6.4 Early vigour measured as NDVI using a spectral radiometer (40 DAS) versus grain yield. ($r = 0.42$, $P < 0.05$). Regression equation becomes highly significant ($r = 0.61$, $P < 0.01$) if lines 8 and 16 are removed 137

Figure 6.5 Anthesis dry matter versus grain yield. The symbols (●) represent named cultivars. 139

Figure 6.6 Harvest index versus grain yield. ($r = 0.60$, $P < 0.01$) 139

Figure 6.7 Time to anthesis versus harvest index. ($r = 0.49$, $P < 0.01$) 140

Figure 6.8 Harvest index versus percentage (a) tiller survival (57 DAS - maturity), (b) plant height. Correlations for (a) $r = 0.58$ ($P < 0.01$), (b) $r = 0.67$ ($P < 0.01$). 140

Figure 6.9 Vigour score (48 DAS) versus time to anthesis. ($r = -0.51$, $P < 0.01$) 141

Figure 6.10 Comparison of TwoD adjusted LI (66 DAS) in 1995 versus LI (60 DAS) in 1996. ($r = 0.35$, $P < 0.10$). 142

Figure 6.11 Comparison of grain yields between 1995 TwoD adjusted data and 1996 averages. ($r = 0.56$, $P < 0.01$) 142

Figure 6.12 Comparison of the number of days from sowing to anthesis for cultivars grown in 1995 and 1996. ($r = 0.87$, $P < 0.01$) 143

Figure 7.1 Coleoptile length versus time to 50% emergence ($r = 0.47$, $P < 0.05$) 155

Figure 7.2 Thermal time to 50% emergence versus total leaf area at H1 (a) and H2 (b). Correlation for (a) $r = 0.44$ ($P < 0.05$), (b) is ns ($P > 0.05$). 158

Figure 7.3 Thermal time to 50% emergence versus total DM at H1 (a) and H2 (b). Correlations are not significant ($P > 0.05$). 158

Figure 7.4 Embryo weight versus (a) shoot DM at H2; (b) leaf area at H2. Correlation for (a) $r = 0.62$ ($P < 0.01$), (b) $r = 0.52$ ($P < 0.01$). 159

Figure 7.5 Growth rate comparisons for (a) shoot growth rate (GR 1) from emergence-H1 versus GR 2 from H1-H2; (b) leaf expansion rate (LER 1) from emergence-H1 versus LER 2 from H1-H2. Correlation for (a) $r = 0.36$ ($P < 0.05$), (b) $r = 0.48$ ($P < 0.01$). 160

Figure 7.6 Relative growth rate comparisons for (a) RGR versus DM at 400 °Cd; (b) RLER versus LA at 400 °Cd. Correlation for (a) $r = 0.55$ ($P < 0.01$), (b) $r = 0.69$ ($P < 0.01$). 160

Figure 7.7 Leaf width versus LA at 400 °Cd for (a) leaf 1; (c) leaf 2; (e) leaf 3. Leaf length versus LA at 400 °Cd for (b) leaf 1; (d) leaf 2; (f) leaf 3. Correlations for (a) $r = 0.77$; (b) $r = 0.89$; (c) $r = 0.92$; (d) $r = 0.83$; (e) $r = 0.84$; (f) $r = 0.42$. Significance for (a), (b), (c), (d), (e) is ($P < 0.01$); (f) is ($P < 0.05$). 162

Figure 7.8 The effect of (a) cumulative leaf length and (b) cumulative leaf width on LA at harvest 2. Correlation for (a) ns ($P > 0.05$); (b) $r = 0.79$ ($P < 0.01$). 163

Figure 7.9 Leaf width versus SLW at 400 °Cd for (a) leaf 1; (c) leaf 2; (e) leaf 3. Leaf length versus SLW at 400 °Cd for (b) leaf 1; (d) leaf 2; (f) leaf 3. Correlations for (a) $r = 0.56$; (c) $r = 0.68$, (e) $r = 0.87$. Significance for (a), (c) and (e) is ($P < 0.01$); (b), (d) and (f) are ns ($P > 0.05$). 164

Figure 7.10 Leaf number versus days after sowing. 165

Figure 7.11 Root DM versus shoot DM 405 °Cd. ($r = 0.69$, $P < 0.01$) 167

Figure 7.12 Comparison of SLW and leaf area between the 1996 and 1997 glasshouse experiments, (a) SLW leaf 1; (b) LA leaf 1; (c) SLW leaf 2; (d) LA leaf 2; (e) SLW leaf 3; (f) LA leaf 3. Correlations for (a) ns; (b) $r = 0.87$, (c) $r = 0.44$, (d) $r = 0.91$, (e) $r = 0.56$, (f) ns. Significance level for (b), (d) and (e) is ($P < 0.01$); (c) is ($P < 0.05$); (a) and (f) are ns ($P > 0.05$). Dotted line (....) indicates 1:1 169

Figure 8.1 LOD plots for markers correlated with area of (a) 1st leaf and (b) 2nd leaf. The markers are mapping to chromosome 2D in each case. 181

Figure 8.2 LOD plots for markers correlated with length of (a) 1st leaf and (b) 2nd leaf. The markers are mapping to chromosome 2D in each case. 182

Figure 8.3 LOD plots for markers mapping to (a) chromosome 7A which are correlated with the length of leaf 1; and (b) chromosome 6B which are correlated with the length of leaf 2. 183

Figure 8.4 LOD plots for markers correlated with SLW of (a) 1st leaf and (b) 2nd leaf. The markers are possibly mapping to chromosome 1 but this requires confirmation. 184

Figure 8.5 LOD plots for markers correlated with kernel weight. Markers are mapping to (a) chromosome 3 and (b) chromosome 1, however these chromosome locations require verification. 185

LIST OF TABLES

Table 3.1 Soil descriptions for the topsoil (0-10cm) from each trial site. 59

Table 3.2 Average monthly rainfall statistics for Roseworthy and Kapunda trial sites, including the growing season (April-October) sub-total and long term averages. 60

Table 3.3 Average monthly maximum and minimum temperatures for Roseworthy and Kapunda trial sites. 61

Table 3.4 Calibration equations for the neutron moisture meter in Roseworthy paddock East 7, 1993 64

Table 3.5 Calibration equations for the neutron moisture meter in Roseworthy paddock Buckby's 7, 1995 64

Table 4.1 Timing of destructive harvests and remote sensing for early vigour estimation in Experiments 2 - 5. 70

Table 4.2 Dry matter and leaf area measurements in the period from before the onset of tillering until anthesis 70

Table 4.3 Pre and post-anthesis moisture supply (rainfall + irrigation) for plants grown under rain-out shelters, natural rainfall and supplementary irrigation. Rainfall was calculated between sowing and final harvest. 71

Table 4.4 Grain yield, dry matter, water use efficiency and yield components at maturity. Error terms are based on the interaction of vigour treatment with post-anthesis moisture availability. 72

Table 4.5 The effect of plant density and nitrogen fertiliser on the normalised difference vegetation index (NDVI) and percent light interception as an estimate of early vigour for field experiments at Roseworthy and Kapunda in 1994 and 1995. 73

Table 4.6 The effect of high and low plant density and high and low nitrogen application on early vegetative biomass and final grain yield for plants grown in two locations in each of two years. 74

Table 4.7 The interaction of high and low plant density with high and low nitrogen application on grain yield of wheat grown at Kapunda in 1994 and 1995........ 76

Table 4.8 Estimates of early vigour using the normalised difference vegetation index and percent light interception for plants grown in field experiments at Roseworthy and Kapunda in 1994. Data represent the interaction of cultivar with high and low vigour treatment and the main treatment effect. 81

Table 4.9 Vegetative biomass and leaf area at mid tillering for plants grown in field experiments at Roseworthy and Kapunda in 1994. Data represent the interaction of cultivar with vigour treatment as well as the main vigour treatment effects. 82

Table 4.10 Grain yield and thousand grain weight for plants grown in field experiments at Roseworthy and Kapunda in 1994. Data represent the interaction of cultivar with vigour treatment as well as the main vigour treatment effects. 83

Table 5.1 Morphology and origin of experimental lines and commercial cultivars used in field experiments. 93

Table 5.2 Correlations between different estimates of early vigour........98

Table 5.3 Correlation between early vigour and grain yield........101

Table 5.4 Time to 50% emergence, leaf DM and root growth up to the 3 leaf stage for high and low tillering genotypes grown in the glasshouse........112

Table 5.5 Dimensions of the first three leaves for high and low tillering genotypes........112

Table 5.6 Correlation coefficients between leaf dimensions and leaf area of the first 3 leaves at Harvest 2. 113

Table 6.7 Crossing numbers and pedigrees of selected vigorous and non-vigorous breeding lines. Pedigrees identified as in Purdy *et al* (1966). 128

Table 6.8 Vigour rankings in the period from tillering to anthesis based on measurements with a spectral radiometer (NDVI), ceptometer (LI), and destructive sampling. 1 = most vigorous, 28 = least vigorous. 134

Table 6.9 Growth measurements and yield components for 20 breeding lines and 8 named cultivars grown at Roseworthy in 1996. 135

Table 6.10 Correlations between methods of early vigour measurement........136

Table 7.1 Seed , embryo and coleoptile measurements for seed used in Experiment 1 and Experiment 2 156

Table 7.2 Emergence and growth results for breeding lines and named cultivars at Harvest 1 (207 °Cd) and Harvest 2 (400 °Cd) from Experiment 1 and root growth from Experiment 2. 157

Table 7.3 Specific leaf weight and leaf dimensions. Leaf length and width were measured using a ruler, where leaves 1-3 were fully expanded and leaf 4 was taken at 400 °Cd. 161

Table 7.4 Glasshouse environmental conditions. Figures are averages for each experiment. 168

Table 7.5 Correlation matrix between early vigour (DM and LA), and quantitative growth traits. 171

Table 8.1 Range in response variables illustrating the amount of segregation, number of QTLs and explained variance for each trait. 180

Table C.1 Light interception and yield ranking for raw and TwoD adjusted data from Chapter 6, Experiment 1. 223

LIST OF ABBREVIATIONS

AFLP	Amplified fragment length polymorphism
°Cd	Day degrees
CT	Coleoptile tiller
DAS	Days after sowing
DH	Doubled haploid
DM	Dry matter
Dm_{anth}	Dry matter at anthesis
E_{sc}	Soil evaporation
ET	Evapotranspiration
ET_{dm}	Evapotranspiration for dry matter production
Et_{max}	Maximum evapotranspiration
ET_{total}	Total evapotranspiration
GAI	Green area index
GR	Growth rate
GW	Grain weight
GY	Grain yield
HI	Harvest index
K	Extinction coefficient
LAI	Leaf area index
LER	Leaf expansion rate
LI	Light interception
LOD	Log likelihood of difference
MAS	Marker assisted selection
NDVI	Normalised difference vegetation index
NIR	Near infrared
NMM	Neutron moisture meter
PAR	Photosynthetically active radiation
PI	Phyllochron interval
QTL	Quantitative trait loci
RCBD	Randomised complete block design
RFLP	Restricted fragment length polymorphism
RGR	Relative growth rate
RLER	Relative leaf expansion rate
RO	Reverse osmosis
RUE	Radiation use efficiency
SLA	Specific leaf area
SLW	Specific leaf weight
SR	Simple ratio
T	Transpiration
TGW	Thousand grain weight
TSAVI	Transformed soil adjusted vegetation index
VPD	Vapour pressure deficit
WUE	Water use efficiency
WUE_{dm}	Water use efficiency for dry matter production
WUE_{gy}	Water use efficiency for grain yield

CHAPTER 1

1. General introduction

The cropping regions of South Australia experience a typically Mediterranean-type climate, with cool, wet winters and hot dry summers (Aschmann, 1973). Annual average rainfall in these regions is generally between 250 - 500 mm (Webber *et al.*, 1976) and the growing season is constrained by the timing of the opening rains and terminal drought. The length of grain filling is further restricted to the period after the risk of frost damage has passed but before the onset of severe moisture stress. Crops rely heavily on rainfall for moisture supply and the soil moisture store is generally depleted by maturity. As a result, grain yields are highly correlated with seasonal rainfall (Karimi and Siddique, 1991b).

The potential transpiration efficiency for grain yield in this environment has been calculated at 20 kg/ha per mm of available moisture (French and Schultz, 1984), however this study found that most crops in the region are well below this value. One of the reasons for this is the high rates of soil evaporation, which can be as much as 30-40% of growing season rainfall (French and Schultz, 1984). Given the severe limitations to water availability and the yield response to rainfall, anything that can be done to reduce this loss, should ultimately benefit grain yield (Richards, 1991).

Early vigour may have a role to play in enhancing the productivity of wheat grown in this environment in two different ways. Firstly, good early ground cover may directly reduce soil evaporative loss through shading of the soil surface (Condon and Richards, 1993). Greater interception of radiation during early growth should partition a greater percentage of total evapotranspiration into transpiration (Siddique *et al.*, 1990b). Secondly, there is a role for early vigour in this environment associated with the yield advantage of early flowering genotypes which have a lower pre:post anthesis partitioning of water use (Siddique *et al.*, 1990b). The role of early vigour is to maintain anthesis biomass despite a shorter period of pre-anthesis growth.

There is good evidence in the literature to suggest that early vigour can be enhanced by altering agronomic inputs such as plant density and nutrition, however, farmers in the local environment have been reluctant to utilise these techniques due to concerns about possible negative effects on grain yield and grain quality (eg. 'haying off', Dann, 1969). If large increases in early vigour could reduce soil evaporation, then it may be possible to gain a positive yield response to increasing early vigour using agronomic means.

Another method of increasing early vigour is to utilise genetic variability. Previous studies have identified large differences in early vigour both between cereal species (López-Castañeda and Richards, 1994a) and within cereal species (Turner and Nicolas, 1987; Whan *et al.*, 1991), and positive correlations between early vigour and grain yield have been identified in each case. However, both vigour comparisons within wheat lines have found some variable yield responses, which were often caused by poor adaptation within the genotypes tested.

Access to the Roseworthy Wheat Breeding program not only provides the opportunity to select vigorous genotypes from a much larger number of lines than the previous studies, but lines contained in the local breeding program should also contain some degree of local adaptation which would allow better evaluation of the relationship between early vigour and grain yield. Closer examination of high and low vigour lines may also provide some insight as to which traits promote early vigour.

The only experiments conducted to identify vigour traits have focussed on comparisons between wheat and barley (López-Castañeda *et al.*, 1995; López-Castañeda *et al.*, 1996). It was found that barley is more vigorous than wheat and that the increased vigour is directly responsible for increasing grain yield (López-Castañeda, 1992; Siddique *et al.*, 1990b). These studies identified traits such as high specific leaf area and large embryo size as being important for promoting early vigour (López-Castañeda and Richards, 1990), however, they have not been tested within a species. It is likely that the variation in vigour traits would be greater between species than within species. For this reason it is necessary to identify the amount of variation in these traits exists between wheat lines and whether they can generate differences in early vigour. Furthermore, if differences in vigour can be generated, then what is their effect on grain yield?

Given the severe limitations of the climate and the beneficial role early vigour could play in this environment, it was decided to investigate the role of early vigour in enhancing the productivity of wheat cropping systems in South Australia.

This study aims to:

1. Understand the effect of stimulating early vigour via agronomic means and the relationship this has with grain yield.
2. Quantify the genetic variability in early vigour in a local breeding population and understand the relationship between genotypic variation in early vigour and grain yield.
3. Identify plant characters which promote early vigour and their effect on grain yield.
4. Provide information about the potential to increase early vigour through wheat breeding.

CHAPTER 2

2. Review of literature

2.1 Introduction

Early vigour has an important role to play in improving the productivity and sustainability of wheat cropping systems in Mediterranean-type climatic regions of Australia. This role will be discussed in relation to the environmental constraints and crop productivity, agronomic methods by which early vigour can be enhanced, and the genetic potential for increasing early vigour.

2.2 Wheat growing in a Mediterranean environment

2.2.1 Climatic constraints

Mediterranean climates are characterised by cool wet winters and hot dry summers. They have between 275-900mm annual rainfall, with at least 65% of the rain falling during the winter period (Aschmann, 1973; Lopez-Bellido, 1992). Rainfall during the early part of the growing season usually exceeds crop evapotranspirational demand and moisture can be lost to evaporation, run-off and deep drainage, or stored in the soil. As the season progresses, however, temperatures rise rapidly and rainfall becomes less frequent, with the result that potential evapotranspiration exceeds actual transpiration. Crops become increasingly reliant on the soil moisture store, which is progressively depleted, and crop growth ends in terminal drought.

Mediterranean climates have a highly variable annual rainfall and several studies have shown that up to 80% of yield variation is due to rainfall variability (Blum and Pnuel, 1990; Cornish, 1950; Greacen and Hignett, 1976; Karimi and Siddique, 1991b). This close relationship of yield to water availability has important implications for improving water use efficiency in these regions, especially early in the season when water is more plentiful and water use efficiency is greater.

Growth can be constrained by both low and high temperatures. Mediterranean winters are cool, with at least one month of average temperatures below 15°C, but not harsh, with less than 3% of the year with temperatures below freezing (Aschmann, 1973). This has the effect of retarding growth over winter with little risk of permanent crop damage due to freezing (Loss and Siddique, 1994). Conversely, the summer period can experience maximum temperatures in excess of 40°C causing inefficient water use and heat stress (Loss and Siddique, 1994). Brief periods of high temperature, usually associated with hot dry winds, are also a common phenomenon which, if they occur during flowering, can cause floret death and yield reductions (Stone *et al.*, 1995).

The length of the growing season is variable, largely because the timing of opening rains may vary by up to 8 weeks, but is ultimately constrained by water deficits at the beginning and end of the season (Richards, 1991). This means there is little room for extension of the growing period by agronomic or genetic means. The length of the grain filling period is also restricted by initially, the timing of the last frost, and by the onset of terminal drought. It is within these climatic constraints that grain yields must be maximised in a Mediterranean wheat cropping system.

2.2.2 Adaptation

Empirical breeding methods have produced steady and significant yield increases in Mediterranean regions over the last 40-50 years (Slafer *et al.*, 1994) as varieties become better adapted to local environments. It is prudent to examine the physiological basis of this improved adaptation in order to assess the potential of early vigour in enhancing future yield gains.

There have been many comparisons between old and modern wheat cultivars in the past which have identified traits leading to yield improvements (Austin *et al.*, 1980a; Calderini *et al.*, 1995; Cox *et al.*, 1988; Kirby *et al.*, 1989; Loss *et al.*, 1989; Perry and D'Antouno, 1989; Siddique *et al.*, 1989a; Siddique *et al.*, 1990a; Siddique *et al.*, 1989b; Slafer and Kernich, 1996; Slafer *et al.*, 1994). Modern cultivars generally produce leaves more quickly, are earlier maturing, have a greater post-anthesis water use, produce more spikes and more grains per spike, and have a greater harvest index.

One essential feature of these historical comparisons is that in each case it has been harvest index and not biological yield which has had the greatest impact on raising yields. While there is still room for further increases in harvest index under Australian conditions, from around 0.35-0.40 (Perry and D'Antouno, 1989; Siddique *et al.*, 1990a; Siddique *et al.*, 1989b) to the European levels of greater than 0.50 (Austin *et al.*, 1989), increases in biological yield remain a possible source for further increases in potential yield. Raising biological yield is nearly always water-limited under Mediterranean conditions so any advances in water use efficiency, whilst maintaining harvest index, should lead to increased productivity. Since early vigour increases T as a proportion of ET (see section 2.4.1), it has an important role to play in this area.

The physiologist's approach to adaptation has been to try and combine the positive traits identified in comparative studies into a single model plant or ideotype (Donald, 1968a). This design and construction approach is becoming more relevant as advanced breeding techniques allow the targeting and incorporation of specific genes and the traits which they produce. Early vigour has been one adaptive mechanism that has been widely suggested as a selection criterion for Mediterranean cereal crop improvement (Acevedo, 1987; Loss and Siddique, 1994; Ludlow and Muchow, 1990; Richards, 1987; Richards, 1991; Turner *et al.*, 1989; Whan *et al.*, 1993).

2.3 Definition of early vigour

The term 'early vigour' has been used to describe early growth over a range of developmental stages and situations, including glasshouse studies and field trials. As a consequence the term is somewhat ambiguous but always implies an advantage through vitality and strength of early growth. In some situations, such as with seed testing, early vigour has a narrower definition. The Association of Official Seed Analysts defined seed vigour in 1979 as being "those properties which determine the potential for rapid uniform emergence and development of normal seedlings under a wide range of field conditions" (McDonald, 1980). The problem for other workers, however, is that early vigour is a less definable concept. Since it is used in a variety of situations there is no ready definition of early vigour.

The 'early' in early vigour is obviously open to interpretation and can vary from seed imbibition (López-Castañeda *et al.*, 1996) up to late tillering (Whan *et al.*, 1991). Glasshouse vigour studies have generally concerned themselves with growth measurements up to the 2-4 leaf stage (Evans and Bhatt, 1977; Lafond and Baker, 1986a; López-Castañeda *et al.*, 1995; López-Castañeda *et al.*, 1996) and frequently measure plant vigour in terms of growth rates and rates of leaf expansion.

The 'vigour' component in early vigour has been measured in a multitude of ways, including dry matter per m^2 (Whan *et al.*, 1991), leaf area index (López-Castañeda and Richards, 1994b), relative growth rates (López-Castañeda and Richards, 1994b; Regan *et al.*, 1992), visual scoring (Regan *et al.*, 1992; Turner and Nicolas, 1987), and using remote sensing techniques (Bellairs *et al.*, 1996; Regan *et al.*, 1992). Field trials have been more concerned with measurements at the mid to late tillering stage and predominantly present early vigour in terms of dry matter and leaf area production on an area or per plant basis. If measurements are taken during early vegetative growth, then LAI and DM can be freely substituted for each other (Aase, 1978). Relative growth rates are also commonly used to assess vigour.

The range in timing and method of measurement which have all been loosely termed as estimates of early vigour means that a single definition is elusive. One point common to all studies, however, is that they all refer to vigour in terms of vegetative growth. Thus a useful working definition to be used for field trials during this study is to assess early vigour as DM and/or LAI before the onset of booting. Glasshouse studies shall require more specific growth period but the vigour definition should still focus on DM and leaf area production.

2.4 The role of early vigour

Many physiologists have proposed that early vigour would be a desirable trait in cereals grown under rainfed conditions in Mediterranean environments (Acevedo, 1987; Dakheel *et al.*, 1993; Loss and Siddique, 1994; Richards, 1987; Richards, 1991). The advantages of early vigour stem mainly from improved water use efficiency but also include increased light use efficiency and an increased yield potential through larger anthesis dry matter (DM_{anth}). Water use efficiency (WUE) can be enhanced by reducing evaporation through soil shading, by reducing deep drainage, better partitioning of water use after anthesis and more efficient gas exchange early in the season when vapour pressure deficits (VPD) are low. Early vigour also increases radiation use efficiency (RUE) as the crop has a greater light interception at a time when photosynthetic area is limiting. This maximises growth rates earlier in the life cycle and the advantage is magnified because of the exponential pattern of growth. The more efficient use of water and light creates a greater yield potential through increased anthesis biomass, a greater sink size and increased stem reserves for translocation during grain filling. Thus, early vigour plays an important role in enhancing the productivity of Mediterranean wheat cropping systems. Such productivity should lead to greater economic stability and the ability to allow more sustainable farming practices.

2.4.1 Improving water use efficiency and dry matter production

2.4.1.1 Early ground cover

Mediterranean climates are characterised by wet winters (see section 2.2.1) where the soil surface remains moist for long periods. The evaporative loss from the system can be up to 60% of the growing season rainfall (Yunusa *et al.*, 1993b) but more commonly losses run at about 30-45% under southern and western Australian conditions (French and Schultz, 1984; Leuning *et al.*, 1994; Perry, 1987; Siddique *et al.*, 1990b). When this evaporative loss is partitioned into stages of the growing season, Cooper (1983) found that in the period from sowing to 50 days after sowing (DAS), when canopies are open, soil evaporation (E_{sc}) accounted for almost 100% of evapotranspiration (ET). This is supported by Leuning (1994) who found E_{sc} accounted for 78% of ET during the first 80 DAS. These losses may be well over 150 mm of growing season rainfall (Leuning *et al.*, 1994) and when they are viewed in terms of a potential transpiration efficiency of 20 kg ha^{-1} of grain per mm of available moisture (French and Schultz, 1984), this represents a sizeable loss in grain yield. Clearly, any reduction in evaporative loss, whilst maintaining water use efficiency, will have a direct benefit to productivity.

Ritchie (1972) proposed a two stage model for predicting evaporation from soil surfaces. Phase one, the constant rate stage, is for predicting the evaporative loss from wet soil surfaces and is appropriate for use early in the growing period when conditions are cool and the soil is constantly wet. This stage of the model is limited only by the supply of energy to the soil surface, meaning any reduction in sunlight reaching the soil through canopy shading should reduce soil evaporation. Monteith (1993) illustrated this through modelling and hypothesised that the most efficient use of water under these conditions will be achieved "by establishing good ground cover quickly". The second stage of evaporation is related to capillary rise of moisture to the soil surface as the soil dries. This stage is not canopy dependent but relies on the hydraulic conductivity of the soil and is applicable to the latter part of the growing season. Thus, it is in the early part of the growing season, when evaporative losses are the greatest, that the potential for reducing them is also highest.

A reduction in E_{sc} has been demonstrated experimentally by a number of authors, where differences in ground cover have been induced in different ways. The common theme in each study has been that when ground cover increases, not only is soil evaporation (E_{sc}) reduced but transpiration through the plant (T) forms a greater proportion of the total ET (see Passioura *et al.*, 1993). This gives greater growth for the same water use and the result is an increase in WUE. This section deals with the effect of increasing ground cover *per se* whereas the methods of increasing ground cover and their effect on growth shall be dealt with in section 2.5.

It is generally accepted that barley has superior early growth compared to wheat (López-Castañeda and Richards, 1994b). Studies have shown that this early growth has translated into a reduction in evaporative loss under field conditions in a Mediterranean environment (López-Castañeda and Richards, 1994c). Acevedo (1989) demonstrated that barley gave a 16% greater ground cover at 40 DAS which resulted in 63% greater transpiration as a proportion of total ET. These results are supported by Siddique *et al.* (1990b), Gregory *et al.* (1992a) and López-Castañeda (1992) who also noted a reduction in E_{sc} and a corresponding rise in T due to the early ground cover afforded by barley over wheat. In the case of Siddique *et al.* (1990b), barley actually consumed less water to produce a greater grain yield. In all cases, greater early ground cover produced a greater WUE.

Vigour differences within wheat varieties and their effect on ground cover and evaporation were demonstrated by Condon and Richards (1993). They found that the more vigorous cultivar ‘Matong’ produced greater early biomass which reduced soil evaporation by 20%. When the less vigorous cultivar ‘Quarrion’ was sown at an increased rate the following year, so as to off-set the vigour differences, the amount of evaporation under the artificially increased canopy was reduced and no differences in E_{sc} were detected. Similar results between old and modern cultivars showed that increased early growth of the modern cultivars reduced soil evaporation and increased water use efficiency (Siddique *et al.*, 1990b).

Where agronomic manipulation has given measurable increases in ground cover, similar increases in T as a percentage of ET have been shown. These include increases in LAI through fertiliser addition (Cooper *et al.*, 1983), plant density (Fischer, 1980) and row spacing (Acevedo and Ceccarelli, 1989). In most cases the total ET was not affected, but more water was partitioned into T at the expense of E_{sc}, providing an increases in WUE. Where total ET was increased, it was generally due to an increased water supply by saving moisture which would otherwise have been lost to the system through drainage.

Another mechanism by which early ground cover confers an advantage under Mediterranean conditions is by increasing the photosynthetic area at a time when the vapour pressure deficit (VPD) is lower and gas exchange is more efficient (Condon *et al.*, 1992; Fischer and Turner, 1978; Siddique *et al.*, 1990b). The increased light interception afforded by early vigour utilises a greater proportion of the limited light source which may be apparent early in the season (when conditions are often overcast for long periods). The resulting effect is an increase in energy capture combined with improved conversion of this energy into DM through greater WUE, resulting in an increase in RUE. This invokes a positive feedback whereby the extra DM produced further increases light interception, which in turn further enhances RUE.

Further increases in LI are possible by selecting plants with larger extinction coefficients (K) as these cultivars intercept a larger amount of radiation for a given ground cover (Siddique *et al.*, 1989a; Yunusa *et al.*, 1993c). However, since most moisture losses occur very early in the season, before K has displayed any large differences between genotypes, its impact will not be as great as for ground cover. This is supported by Gregory *et al.* (1992a) who found that light interception was correlated with ground cover and green area index (GAI) up to anthesis. When we also consider that K for total radiation is less than K for photosynthetically active radiation (PAR), but E_{sc} is driven by total radiation, the impact is further reduced. Thus, larger increases in RUE and reductions in E_{sc} are likely to be gained primarily through improving early vigour.

Sometimes the distinction between early growth and the extinction coefficient can become a little unclear, such as with canopy architecture. Leaf angle and canopy shape certainly affect light interception but may also be seen to improve early growth (scored as ground cover). Acevedo (1987) found that early ground cover is positively correlated with a prostrate growth habit but both traits were subjectively scored. Light interception as a measure of early vigour integrates both leaf area and light extinction and is possibly a better measurement when considering ground cover. Early vigour measured in this way will select for reduced soil evaporation (radiant energy hitting the soil surface) and increased photosynthesis (greater light interception).

If early ground cover is a positive trait, then one may ask how much ground cover is required? For most wheat crops full ground cover is not achieved until LAI approaches a value of 3 (de Witt, 1965; Monteith, 1965). Ritchie (1972) suggests that an $LAI > 2.5$ will restrict soil evaporation to a level equivalent to that if the soil was dry. Therefore, where $LAI < 2.5$, evaporation from the soil surface could be reduced through an increase in ground cover. This is supported by Fischer and Kohn (1966) who found that wheat required an $LAI \geq 3$ for $ET \approx ET_{max}$.

If canopies are sparse, not only will evaporation from wet soil be greater but transpiration will also be greater through the 'clothesline effect' (Ritchie, 1972). This phenomenon causes transpiration to be increased through a lower VPD in the micro-climate around the leaves, caused by air movement through the sparse canopy. The end result is that the plant uses a similar amount of water as a full canopy but losses also occur from the wet soil surface, causing a decrease in water use efficiency. For this reason, leaf area reduction strategies aimed at conserving moisture for grain filling (Passioura, 1977; Richards, 1983) must be viewed with caution. Islam and Sedgley(1981) did demonstrate a positive effect from leaf area reduction but the LAI in the de-tillered plots was similar to the controls for much of the early part of the growing season (when the soil was wet). This trial was also sown relatively late compared to the current practice and hence, most of the advantage attributed to early vigour was lost.

2.4.1.2 Partitioning of water use

The process of photosynthesis converts moisture and carbon dioxide, in the presence of sunlight, to oxygen and carbohydrates for plant growth. This activity requires gas exchange through the stomata in the leaves which also leads to moisture loss (Ludlow, 1980). The amount of water lost through the stomata during this process is related to the VPD or atmospheric dryness (Lange *et al.*, 1971; Ludlow, 1980). Less water will be lost to the environment during times of lower VPD (Fischer and Turner, 1978; Richards, 1987; Sinclair *et al.*, 1984) leaving more moisture available for photosynthesis and a higher WUE will result. Under Mediterranean-type conditions the VPD will be lowest during the early winter months when temperatures are low and the humidity is high. Consequently, WUE will be maximised early in the growing season and progressively decrease towards maturity.

The timing of water use in relation to the growth stage of the crop is critical for yield formation. Equation (1) is a simple model of grain yield (GY), where ET is evapotranspiration, WUE is water use efficiency and HI is harvest index (Fischer and Turner, 1978; Passioura, 1977).

$$\mathrm{GY} = \mathrm{ET} \times \mathrm{WUE} \times \mathrm{HI} \tag{1}$$

Pre-anthesis water use will increase WUE and may increase ET (Armstrong *et al.*, 1996; Richards *et al.*, 1993; Siddique *et al.*, 1990b) whereas an increase in post-anthesis water use will increase HI (Passioura, 1977; Richards and Townley-Smith, 1987; Sadras and Connor, 1991; Siddique *et al.*, 1990b). Both of these components need to be maximised to reach maximum yield but due to the vagaries of the climate, post-anthesis water use has a larger influence. The sharp rise in temperature and reduction in rainfall in the post-anthesis period mean that moisture stress is more severe at this time.

The most effective method for increasing post-anthesis water use is through altering phenology (Conner *et al.*, 1992; Regan *et al.*, 1993; Regan *et al.*, 1997; Siddique *et al.*, 1990b). Earlier flowering will ensure lower temperatures and lower VPDs during grain filling, and increase the likelihood of rainfall in this period. Since the start of the season is limited by the timing of opening rains, earlier sowing is not always possible. In situations where the opening rains are delayed, the best method of inducing early flowering will be through the use of short season cultivars. This presents other problems however, as it will also shorten the pre-anthesis period and allow less time for vegetative growth. The net result will be a high harvest index but reduced anthesis biomass and a lower yield potential.

A remedy for this problem is to use short season cultivars with high early vigour (Regan *et al.*, 1993; Regan *et al.*, 1997). The high initial growth rate of vigorous cultivars will enable similar anthesis biomass compared to later cultivars, with the benefit of greater post-anthesis water use and higher water use efficiency for grain production (WUE_{gy}). The use of vigorous cultivars will also produce more efficient soil water use as pre-anthesis moisture is obtained from the topsoil whilst post-anthesis moisture is obtained from deeper in the profile (Fischer, 1980). The tendency for vigorous cultivars to have an increased root length density in the topsoil will reduce E_{sc} and deep drainage early in the season (Cooper *et al.*, 1987a) whilst allowing any moisture which does penetrate to deeper layers of the soil profile to be conserved for grain filling. If the phenology is not matched to plant vigour, it is possible to deplete the soil moisture reserves too quickly through too much early growth (Passioura, 1977). This is not such a problem in Mediterranean-type climates due to the reduced reliance on stored soil moisture.

In a study comparing old and modern cultivars Siddique (1990b) found the ratio of pre:post anthesis water use has fallen from 5.2:1 to 3:1. This was largely due to a reduction in the number of days to anthesis and increases in early vigour. The total water use was reduced, yet the grain yield increased, giving large increases in water use efficiency between cultivars. The modern cultivars had moisture remaining at the end of the season illustrating that even greater yields could have been achieved if DM_{anth} had been further increased. This highlights the importance of the timing of water use under Mediterranean-type conditions and also the crucial role of early vigour in this system.

2.4.1.3 Remobilisation of stored assimilates

The remobilisation of stem reserves adds a new dimension to the role of early vigour in maximising yields under Mediterranean-type conditions. Under optimal conditions the plant derives most of the assimilates required for grain filling from photosynthesis in the post-anthesis period (Austin *et al.*, 1980b; Bidinger *et al.*, 1977; Pheloung and Siddique, 1991). However, as indicated in the previous section, water use and photosynthesis is sub-optimal in this period and under severe conditions this may lead to supply limited yield reductions (Fischer, 1975; Fischer and Hille Ris Lambers, 1978; Fischer and Laing, 1976; Voltas *et al.*, 1997). One mechanism the plants use to continue grain filling under stressful conditions is to utilise the DM accumulated in the pre-anthesis period as a carbon and nitrogen source for grain filling (Austin *et al.*, 1980b; Wardlaw, 1967). Therefore, increasing the store of these pre-anthesis assimilates should have benefits for grain filling under conditions of terminal drought.

There is ample evidence that wheat plants remobilise reserves from the leaves and stems for use in grain filling (Fischer, 1980; McDonald, 1992; Palta and Fillery, 1995a; Palta *et al.*, 1994). The increased DM provided by more vigorous early growth provides a larger resource of assimilates upon which the plant can draw. Commonly about 5-7% of the anthesis biomass is water soluble sugars which are used for grain filling (Fischer, 1980), although this can be more in drier years. Palta *et al.* (1994) showed that by increasing moisture stress after anthesis through halving the relative humidity, post anthesis carbon assimilation was reduced by 57%. This produced a corresponding increase in remobilisation of pre-anthesis carbon of 36%, with nitrogen remobilisation following the same trend.

Where agronomic methods have been employed to stimulate early vigour, crops have greater spike densities and usually produce more grains per m^2 (Anderson, 1992). This creates a greater sink size which will prolong grain filling under periods of greater stress and utilise the stem reserves more fully (Blum *et al.*, 1988). Using ^{15}N labelled plants, Palta *et al.* (1995a) demonstrated that the contribution of pre-anthesis stem reserves was increased from 60% of grain nitrogen to 95% of grain nitrogen with the use of N fertiliser. This trial also showed that the contribution of early accumulated N was increased due to the increase in early biomass, and hence greater size of early storage organs, combined with a greater sink size and lower post-anthesis assimilation.

2.4.1.4 Soil influences

In Australia, the Mediterranean-type climatic zones are characterised by large areas of duplex soils and deep sands (Belford *et al.*, 1990; Tennant *et al.*, 1992). Each soil type presents distinct problems in crop water relations which require different management strategies to maximise WUE. The wet winters produce more rainfall than the crop requires early in the growing season and this moisture may tend to pond on the clay B horizon as a perched water table (Cox and McFarlane, 1990), or it may be lost to drainage through the soil profile (Gregory *et al.*, 1992b). Plants with vigorous early growth will have an advantage under these conditions as they use water more quickly and have the ability to recover it more thoroughly (Richards *et al.*, 1993). The more developed root systems of these vigorous plants will also be better able to tolerate waterlogged conditions (Setter and Belford, 1990).

The higher water requirement of vigorous plants, stems from an increased photosynthetic area and greater biomass accumulation during this early period. Vigorous plants, displaying advanced canopy growth and light interception, will also maintain higher rates of growth and water use during periods when light may be limiting (Richards *et al.*, 1993). This is especially the case during periods of extended cloud cover associated with rainfall early in the growing season.

While there is genetic variation for root:shoot ratio (Siddique *et al.*, 1990a), for any given cultivar the top growth is proportional to root growth (Hamblin and Tennant, 1987; Klepper *et al.*, 1984) and as such, cultivars which display vigorous top growth should also have vigorous root growth. Early root growth has the effect of further increasing biomass (sink strength for moisture) as well as providing a greater root length density in the topsoil. The effect is a more rapid and thorough extraction of moisture in the topsoil (Cooper *et al.*, 1987a), which may alleviate problems caused by both waterlogging and deep drainage. A deep and expansive root system will provide extraction of moisture held deeper in the profile (Brown *et al.*, 1987a) and a greater vertical area for moisture interception before drainage below the root zone occurs. This may be more relevant in sandy soils where drainage is rapid.

Where waterlogging occurs, growth is retarded due to a lack of oxygen necessary for growth (Dracup *et al.*, 1992; Setter and Belford, 1990). This growth retardation has a compounding effect as water usage declines and more moisture is accumulated in the root zone, exacerbating the problem. Early vigour may possibly reduce this phenomenon by increasing moisture usage before it has a chance to accumulate in the root zone, thus maintaining crop growth rate and yield. If waterlogging persists for any length of time then damage to the root structure and function is possible (McDonald and Gardner, 1987) which may cause moisture stress later in the season and a reduction in harvest index. Thus early vigour may confer an advantage to crop growth and yield under both waterlogged and deep drainage conditions.

2.4.1.5 Weed competition

While it has been shown that early vigour can increase the yield potential of wheat grown under Mediterranean-type growing conditions, there are also benefits associated with the maintenance of yield potential in the face of competition from weeds. The threat of increased weed competition has arisen through the shift towards early sowing in the Mediterranean-type growing regions (Anderson, 1989; Kerr and Arbrecht, 1992; Kerr *et al.*, 1992; Perry *et al.*, 1989; Shackley and Anderson, 1995), which has reduced the time available for mechanical weed control and increased the reliance on selective chemicals. The advent of resistance to these herbicides (Powles *et al.*, 1997) has endangered this strategy and forced a re-think in weed management options, where farmers are now urged to follow a more integrated approach. Improved competitive ability of the crop against weeds will form the cornerstone of any integrated weed management package and it is through good crop vigour that the competitive ability is enhanced.

Many traits which could be broadly regarded as 'vigour traits', such as rapid emergence, high relative growth rate, increased LAI, increased biomass and improved light interception are related to good competitive ability in crops (Cousens, 1996; Garrity *et al.*, 1992; Jordan, 1993; Lemerle *et al.*, 1994). Lemerle *et al* (1996b) actually stated that early vigour was correlated to competitive ability and due to the high cost of conducting competition trials, early vigour could be used as a criterion for selecting more competitive cultivars.

Plant height is another trait which has been implicated in crop competitive ability (Balyan *et al.*, 1991; Blackshaw, 1994; Garrity *et al.*, 1992; Lemerle *et al.*, 1996b) but results are not conclusive, with other authors reporting no (or mixed) effects (Cousens, 1996; Reeves and Brooke, 1977; Wicks *et al.*, 1986). Christensen (1995) showed plant height was related to ground cover and light interception, a fact supported by other authors (Garrity *et al.*, 1992; Richards and Whytock, 1993). Again, this suggests height is positively related to early vigour. Lemerle *et al.* (1996b), despite their positive correlation with height and competitive ability, speculated that increased height would only decrease the HI and may actually have a negative result on grain yield. Instead they hypothesised that increased light interception and early vigour would be a more rewarding selection criteria.

Just as there is large genetic variation in early vigour in wheat (see section 2.5.2.1) so too there is large variation in competitive ability with weeds. This has been demonstrated against annual ryegrass (Cousens, 1996; Lemerle *et al.*, 1994; Lemerle *et al.*, 1979; Lemerle *et al.*, 1995; Lemerle *et al.*, 1996a; Reeves and Brooke, 1977; Reeves *et al.*, 1993); wild oats (Balyan *et al.*, 1991; Lanning *et al.*, 1997); and downey brome (Blackshaw, 1994). Considerable variation in competitive ability exists in other cereals such as barley (Christensen, 1995; Cousens, 1996; Lanning *et al.*, 1997; Lemerle *et al.*, 1995), rice (Garrity *et al.*, 1992) and triticale and oats (Lemerle *et al.*, 1995).

Closer examination of the potential yield losses associated with weed infestations demonstrates the extent of the problem. Losses of up to 100% under a moderate weed infestation were experienced in some cultivars whilst the yields of other cultivars were not affected (Lemerle *et al.*, 1994). This highlights the potential benefit of early vigour in enhancing crop productivity in weedy situations and it will also make cropping more sustainable as chemical control becomes unreliable due to the development of herbicide resistant weeds.

Agronomic practices which enhance early vigour also enhance competitive ability of the crop. Increasing plant density improves early vigour (see section 2.5.1.1) and reduces weed growth (Cousens, 1985; Jordan, 1993; Lemerle *et al.*, 1996a; Medd *et al.*, 1985; Radford *et al.*, 1980). Reducing the row spacing can also have a positive effect on both vigour (section 2.5.1.2) and weed competition (Fischer and Miles, 1973), although Medd *et al* (1985) found that increasing plant density had the greater effect. Increasing nutritional inputs will certainly improve early vigour (section 2.5.1.3) but will only improve competitive ability if the crop has preferential access (Jordan, 1993). In some situations the use of fertiliser may enhance weed competition so banding of fertiliser beneath the crop row may be a better practice.

It is important to note that there is a dual role for early vigour in increasing competition with weeds. On the one hand the crop must be *tolerant* and able to yield well in the presence of weeds through better competitive ability for resources but on the other, it is advantageous if the crop can *suppress* weed seed production. Most competition studies are reported in terms of percentage yield reduction, which is a good measure of crop productivity but may increase the weed load in subsequent crops. If the competition causes a reduction in the weed seed yield, then this will be favourable for sustainability. In this way, early vigour plays a pivotal role in weed competition dynamics and crop competitive ability.

2.4.2 Other benefits of increased early vigour

2.4.2.1 Nitrogen leaching

Nitrogen is a highly mobile element which dissolves readily in water and is easily leached (Glendenning, 1990). In situations where crops are grown on deep sandy soil the rate of water and nitrogen movement down the profile can be very rapid. If, however, water is consumed before it has the chance to exit the root zone then the loss of nitrogen will be greatly reduced as well. In this way, the prolific root development of vigorous plants (outlined in section 2.4.1.4) may reduce nitrogen leaching and improve nutrient recovery, giving improved growth and further increasing vigour. The extent of the nitrogen leaching will depend on many variables and in many cases may not be significant, but whatever the scenario, early vigour improves the balance on a "use it or lose it" principle.

2.4.2.2 Erosion control

Early vigour has a role to play in reducing wind and water erosion through greater early ground cover. The increased root biomass from vigorous plants provides greater root length to physically hold the soil together and prevent it from being eroded, whilst increased top growth affords greater protection to the soil from wind erosion.

There is an absence of literature on this aspect of early plant growth however there is little doubt as to the value of crop cover in reducing the effects of erosion. When we consider that increasing the rate of emergence improves early vigour, we can also appreciate the difference between *some* crop cover and *no* crop cover at all.

2.5 Methods of stimulating early vigour

As outlined in section 2.3, there are many indicators of early vigour and as such there are many factors which improve early vegetative growth. These include agronomic and genetic manipulations which improve the growth of both individual plants and swards. Sometimes, however, there are confounding effects between communities and individuals due to inter-plant competition.

Agronomic methods of increasing early vigour include increasing plant density, adjusting plant arrangement, improving plant nutrition and various factors relating to crop establishment. Genetic methods of stimulating early vigour relate to morphological and physiological characters which affect light interception, water use and growth. Other methods of promoting early vigour are combinations of both genotypic and phenotypic characters such as with seed characteristics (see section 2.5.3.

2.5.1 Agronomic methods of promoting early vigour

2.5.1.1 Plant density

Altering plant density is a powerful agronomic tool which can have a large impact on early vigour and the subsequent growth of the crop. Early in the season, when moisture and nutrients are non-limiting, very large growth rates are possible. Puckridge and Donald (1967) were able to generate a LAI of 2 at four weeks after sowing using a density of 1000 plants/m^2. While excessive, this demonstrates the large effect of sowing rate on early ground cover. Other authors, using more moderate densities, have also shown increases in vigour at higher sowing rates (Anderson, 1992; Fischer, 1980; Fukai *et al.*, 1990; Tompkins *et al.*, 1991; Turner *et al.*, 1994; van den Boogaard *et al.*, 1996b). Due to the asymptotic shape of the density-LAI relationship, the largest increases in ground cover occur when moving from low to moderate densities (TeKrony and Egli, 1991).

Altering plant density will have several implications for water use and yield. Biological yield is dependent on total ET and increases with sowing density up to an environmentally-limited maximum (Donald and Hamblin, 1976). Grain yield, on the other hand, depends on the pattern of water use and is variable depending on the environment. If the crop relies on stored soil moisture then increasing the sowing rate will generally lead to early moisture depletion and a dramatic decline in HI and yield (Passioura, 1977). However, where the crop relies on rain that falls within the growing season, as in Mediterranean-type climates, the pattern of water use can be positively affected by increasing plant density (Doyle and Fischer, 1979). The more common occurrence is a composite situation where the harvest index is reduced through early moisture depletion but the resulting biomass increases due to greater pre-anthesis water use are enough to offset the moisture losses, with a net positive effect on yield (Turner *et al.*, 1994; van den Boogaard *et al.*, 1996b).

Wheat plants can produce far more tillers than fertile ears (Sharma, 1995). While assimilates are translocated back into the fertile tillers from the senescing ones, there is still some net loss of assimilates which is a wasteful use of resources (Palta and Fillery, 1993a; Pheloung and Siddique, 1991). Increasing plant density restricts tiller production per plant through inter-plant competition (Donald, 1963) resulting in smaller plants with fewer tillers but tiller death is also greatly reduced (Darwinkel, 1978). The net effect is an increased total number of heads under higher sowing rates.

$$GY = S \times GS \times GW \tag{2}$$

Equation (2) shows the relationship between total spike number (S), the number of grains per spike (GS), and the grain weight (GW). From this equation we can see that there are many different pathways to yield, depending on the ratios of the yield components. Head size will depend on the assimilate supply between double ridge and terminal spikelet, which should be greater per m^2 under higher sowing rates due to better light interception and WUE at this stage (section 2.4.1). This results in more grains per m^2 being produced under higher sowing rates (Darwinkel, 1978), however, the average spike size is reduced due to the larger number of spikes (Darwinkel, 1978). This phenomenon has been reported by a number of authors where, under high densities, head number is negatively correlated to head size (Anderson, 1986; Anderson and Barclay, 1991; Darwinkel, 1978; Darwinkel *et al.*, 1977; Donald and Hamblin, 1976; Fischer *et al.*, 1976; Lafond and Derksen, 1996). The final component in the yield equation, grain size, can provide some degree of yield compensation and GW will depend on the conditions during grain filling.

The moisture supply during grain filling is largely influenced by phenology (section 2.4.1.2). Fukai *et al* (1990) found that anthesis in barley was advanced 6-7 days by increasing the plant density from 36 to 120 plants/m^2. Such an advancement of anthesis increases the chance of receiving greater post-anthesis rainfall because of a longer grain filling period and such a result is supported by other authors (Nerson, 1980; Puckridge and Donald, 1967; van den Boogaard *et al.*, 1996b). Turner *et al.* (1994) found that this 'earliness' was conferred through a reduction in tillering at high sowing rates leading to fewer heads on later order tillers which flowered later. Their results showed that a wheat crop grown at 200 plants/m^2 reached anthesis up to

20 days earlier than a crop grown at 25 plants/m^2, resulting in reduced moisture stress during grain filling and higher grain yield.

While it is true that water use may be increased in the pre-anthesis period by greater early vigour (Tompkins *et al.*, 1991) this can be off-set by reductions in E_{sc} so that there is no net reduction in soil moisture at anthesis. Doyle and Fischer (1979) demonstrated this concept where early season rainfall was high and the advantages conferred by greater early vigour, induced through early sowing and increased plant density, were maximised and E_{sc} reduced. In years when early rainfall was low, the benefits afforded by early ground cover were not as apparent and the anthesis soil moisture was slightly lower at higher densities. Van den Boogaard *et al.* (1996b) had similar results where a five fold increase in sowing rate produced very large increases in biomass for only marginal increases in soil moisture depletion. The net result was a similar water use and grain yield despite having a larger yield potential and WUE_{dm}.

In some drier environments, strategies designed to reduce water use in the pre-anthesis period by restricting early vigour (Islam and Sedgley, 1981) may be advantageous. However this study used de-tillering to reduce pre-anthesis water use, at similar plant density.

In studies where higher sowing rates (relative to common practice for that site) do not produce a yield advantage, it has been shown that they also produce no penalty in grain yield (Anderson, 1986; Medd *et al.*, 1985; Yunusa *et al.*, 1993a). This allows the formation of a greater yield potential, without the risk of a yield penalty under poor conditions. The danger of producing very small grains under these conditions is also reduced. Screenings (shrivelled grains) are predominantly produced on later order tillers (Hucl and Baker, 1989) formed at lower densities, which flower later and are the most affected by adverse conditions during grain filling (Turner *et al.*, 1994). Grain weight has been shown to be one of the most stable yield components across different plant densities (Anderson and Barclay, 1991; Nerson, 1980). The trend is towards a slightly smaller but more uniform grain size at higher densities.

Plant density will have an impact on yield through the rectangularity of planting pattern and the competition between plants within the crop (Donald, 1963). Inter-plant competition will be reduced as the rectangularity approaches 1:1 (Auld *et al.*, 1983; Fischer and Miles, 1973). This arrangement will allow the crop to approach its yield potential, providing enough time is given for thorough exploration of all available space. Higher sowing rates will increase the rectangularity of planting pattern and inter-plant competition but will reduce the time taken to utilise this space (Kemp *et al.*, 1983). This has important implications for weed competition. Increased sowing rates will have a role to play in occupying ground before weeds can get established, however, Fischer and Miles (1973) argue that extra crop plants only compete with themselves instead of the weeds. Two possible remedies are to decrease the row width and reduce rectangularity at higher sowing rates or to maintain the row width and use less competitive plants (Donald, 1968b) at higher sowing rates. In this way plant space will be utilised more quickly and an advantage conferred under a short seasoned Mediterranean-type climate.

Anderson and Barclay (1991) found that different cultivars have different optimum populations with a tendency for higher yields from higher densities. This is supported by the fact that modern cultivars are more erect with fewer leaves (Siddique *et al.*, 1989a) and there is a trend for erect cultivars to have a higher optimum sowing rate (Fischer *et al.*, 1976; Fischer and Kertesz, 1976). This is in line with the Donald (1968a) ideotype for communal crop plants which proposes high densities of non-competitive plants with a high yield potential and HI. The plant type proposed by Donald was one of limited tillering so that greater control of head numbers was possible and wastage of moisture through tiller death could be avoided.

Ear number is the yield component most highly affected by plant density (Darwinkel, 1978; Puckridge and Donald, 1967) and it is also the component most highly correlated with grain yield (Nerson, 1980). For this reason, greater control over the number of ears, by using limited tillering lines, will allow the full complement of ears to be set at an earlier time. This will improve water relations through earlier flowering and increase uniformity in the crop.

Clearly there is a role for plant density in improving early vigour and yield potential under Mediterranean-type conditions, however, an integrated approach is necessary to achieve the right agronomy package to fulfil this potential. Cultivars adapted for high sowing rates will have an erect canopy, few tillers and faster development rates. This is to counter the effects of increased competition and post-anthesis moisture deficits. In this way, increased plant density can improve the productivity of cropping systems under short seasoned, semi-arid, Mediterranean conditions.

2.5.1.2 Plant arrangement

Any given site has an environmentally limited yield potential and the fulfilment of that potential will depend on the biotic stresses that are imposed (Donald, 1963). Inter-plant competition for light, nutrients and moisture, allows some control over the level of stress the crop encounters and it will be minimised as the rectangularity of plant arrangement approaches 1:1 (Auld *et al.*, 1983; Fischer and Miles, 1973). There are two methods of reducing rectangularity; the first is to reduce the row spacing for a given plant density and the second is to reduce the plant density for a given row spacing.

Reducing rectangularity is important as it maximises the biological space for every plant. The effect is that it will take longer for the plants to interfere and compete with each other, allowing a greater period of unimpeded growth. Amending the rectangularity through a decrease in plant density per row will be counter productive as it will take longer to achieve total ground cover (reducing RUE and allowing greater E_{sc}) and the rate of development will be delayed (see section 2.5.1.1.). Improving rectangularity by decreasing the row spacing for a given density will maintain growth rates and LAI production but increase ground cover and early vigour. The net result will be increased LI, greater partitioning of ET into T and increased WUE_{dm}. It will also preserve moisture for post-anthesis water use since biomass isn't directly increased

The sensitivity of cereals to row spacing will be greatest at lower densities (Auld *et al.*, 1983; Kemp *et al.*, 1983). This is because the plants grow radially outwards from their origin until they come into contact with a neighbour. If the plants are not planted 'on the square' then they will come into contact with their neighbours much sooner and competition will begin earlier, reducing the growth rate before full ground cover is achieved. At higher densities the plants will come into contact with each other very quickly, regardless of the row spacing, and so the response will not be significant. The relationship of row spacing to rectangularity was illustrated in a theoretical analysis by Fischer and Miles (1973) who hypothesised that for a constant sowing rate of 150 kg/ha, halving the row spacing from 18cm to 9cm would reduce rectangularity from 12:1 to 4:1.

The limited effect of row spacing at densities of 200 plants/m^2 or more (Auld *et al.*, 1983; Kemp *et al.*, 1983) is caused by the rate of utilisation of biological space. At higher densities, the plants interact within the row at a very early stage and the yield is not affected by rectangularity. Although narrow row spacing at high density may reduce the time to total ground cover, the differences are so small or they happen early enough in the life cycle, they do not have an effect on grain yield. Fischer *et al.* (1976) found no yield response to row spacing within the 10-45cm range and hypothesised that a response would only become evident if the crop failed to reach 95% light interception before 60 DAS.

Acevedo and Ceccarelli (1989) increased early vigour by reducing row spacing from 30cm to 10cm in a barley crop. Ground cover was improved by 30% and biomass was increased by almost 50% in the narrow rows. This reduced E_{sc} and increased WUE, resulting in 20-30% greater yield. Tompkins *et al.* (1991) also increased early vigour using row spacing, however larger responses were seen when narrower rows were combined with higher plant density. Yunusa *et al.* (1993a) found narrow row spacing increased light interception but the differences weren't large enough to have an impact on E_{sc} or water use efficiency.

The evenness of plants within the rows will also affect rectangularity and competition. Turner *et al.* (1994) found that randomly spaced seeds within the drill row reduced grain yield by 20% compared to evenly planted seeds. Unevenly spaced plants produced fewer tillers and fewer grains. The lower total biomass indicates a lower tillering biomass and it follows that this treatment would have a lower leaf area and ground cover.

Where fertiliser is placed with the seed at planting, the row width will have an effect on the concentration of fertiliser within the row and may affect growth. In narrower rows the effect will be to lower the concentration of fertiliser near the seed. However, at wider row spacings the concentration of fertiliser in the band will be increased and toxicity may be a problem (Glendenning, 1990)

Narrower rows are better for weed suppression than increased plant density as they reduce rectangularity and there is less inter (crop) plant competition (Fischer and Miles, 1973). However seeding equipment may have trouble moving through stubble in narrow rows, particularly in direct-drill situations. Under very narrow rows or higher stubble situations, equipment modifications may be required.

The practicalities associated with mechanical sowing mean that we are limited to row spacing and plant density as a means of controlling rectangularity. Row spacing is a useful tool in promoting plant vigour but the responses are sometimes variable. There is the potential for increased WUE via a reduction in E_{sc} and better partitioning of ET, although in some situations an increase in LI has not delivered the benefits. A systems approach to row spacing is required as it will affect management of other problems such as weed control and tillage.

2.5.1.3 Plant Nutrition

The positive growth response of wheat to fertiliser is well recognised. Large increases in early vigour are possible, especially with the use of nitrogen but the effect on grain yield is not so straight forward. In a Mediterranean-type climate, with limited water supply and post-anthesis moisture deficits, large increases in early growth will have further ramifications for water use, especially in the post-anthesis period. Both positive and negative responses to yield have been recorded under these conditions.

Numerous fertiliser trials have indicated that nitrogen fertiliser will increase early biomass and leaf area production in cereals (Anderson, 1992; Benbi, 1994; Brown *et al.*, 1987b; Cooper *et al.*, 1987a; Cooper *et al.*, 1983; Gregory, 1984; McDonald, 1992; Palta and Fillery, 1993b; Shepherd *et al.*, 1987; Steven *et al.*, 1986; Thorne *et al.*, 1979; Turner *et al.*, 1987; van Herwaarden *et al.*, 1996; Venn *et al.*, 1987). The increased leaf area improves light interception (Steven *et al.*, 1986) and provides the WUE and yield benefits outlined in section 2.4.1.1.

The increased DM produced under high fertility conditions is usually achieved with a similar total water use (Shepherd *et al.*, 1987) or if ET is increased, the DM increases are usually proportionally larger and an increase in $\mathrm{WUE_{dm}}$ will result (Cooper *et al.*, 1987b; McDonald, 1992; Turner *et al.*, 1987). The partitioning of water use will, however, be affected and a greater proportion of ET will be used in the pre-anthesis period. This can deplete soil moisture at anthesis and, where grain filling is dependent on stored soil moisture, negatively affect the final grain yield (Passioura, 1977).

The larger biomass produced with the use of nitrogen fertiliser is due to increased tillering (Aspinall, 1961; Dann, 1969; Gooding and Davies, 1997; Palta and Fillery, 1995b; Venn *et al.*, 1987) and faster leaf appearance (Longnecker *et al.*, 1993). More tillers are produced under high nitrogen conditions and a greater proportion of these are retained to produced fertile heads (Ishag and Taha, 1974; Power and Alessi, 1978). Due to the greater tiller production, there is a variable response for head size but invariably more grains are produced per m^2 (McDonald, 1992; Mossedaq and Smith, 1994; Palta and Fillery, 1995b). The larger sink produced by the greater number of grains can be source limited and the resulting grains may be smaller (McDonald, 1992; Palta and Fillery, 1995b). Another factor which influences grain size is that a larger proportion of the yield is carried on later formed tillers (Fathi *et al.*, 1997; Palta and Fillery, 1995b). This means the grains have a shorter time for filling and may be smaller. The higher VPD experienced during grain filling of the later formed tillers also causes stress and source limited reduction in grain size (Turner *et al.*, 1994).

Fertiliser can affect the rate of development with N stress increasing the time to double ridge and terminal spikelet by 2 days (Longnecker *et al.*, 1993). Conversely, increasing the rate of application of phosphorus to barley reduced the time to anthesis by 11 days (Shepherd *et al.*, 1987). Palta and Fillery (1995b), on the other hand, found no effect of nitrogen on the rate of development in wheat but this trial had a minimum rate of 15 kg/ha N. This indicates that there is possibly a nutrient threshold, above which the rate of development is unaffected. Any increase in the rate of development will positively affect grain yield as it should increase moisture availability in the post-anthesis period.

High nitrogen status allows greater photosynthesis at lower leaf water potentials (van den Boogaard *et al.*, 1997) due to the higher rubisco content of the cells. This allows photosynthesis to continue under drier conditions and will affect the WUE and retention of green leaf after anthesis. This is supported by other authors who have indicated that senescence is delayed under high N (Gooding and Davies, 1997), but only under mild water stress. The increased green area duration under more moderate conditions is positively associated with grain yield as photosynthesis after anthesis goes directly into grain filling (Siddique *et al.*, 1989a).

The right nitrogen balance for the seasonal moisture availability is important as too much nitrogen may be harmful. Since the plants can photosynthesise at lower leaf water potentials under high N conditions, this can make them more sensitive to moisture stress if the stress increases beyond a threshold level. This sensitivity is further enhanced by the greater early soil moisture depletion under high N conditions (van Herwaarden *et al.*, 1996) which may increase the severity of moisture stress and advance leaf senescence, causing haying-off and a reduction in grain yield (van Herwaarden, 1996).

The increase in leaf area associated with the use of fertiliser (Brown *et al.*, 1987b) will have a positive effect on the competitive ability of the crop with weeds (Meyers and Lipsett, 1958). While it is true that the vigour of weed species will also be enhanced by the addition of fertiliser, this can be overcome to some extent by banding fertiliser under the crop row as this will favour access by the crop ahead of the weeds.

Where increased nitrogen has stimulated tiller production in wheat plants, a greater pool of assimilates is available for translocation into the grain (Palta and Fillery, 1995b). Under stressed situations, later tillers tend to be sacrificed and assimilates are translocated into the earlier tillers (Palta *et al.*, 1994). There may be some loss of carbon invested in the cell structures (Austin *et al.*, 1977) and as such, excessive tillering may be a wasteful use of plant resources, especially where there is a risk of moisture stress during grain filling. This is another potential hazard of too much nitrogen.

The timing of nitrogen application will have an effect on early growth and crop yield. The largest response for dry matter production is when the total amount of N is applied at sowing (Anderson, 1985; Darwinkel, 1983). This gives large increases in early biomass but may reduce the harvest index, meaning yields may not be maximised (Anderson, 1985; Darwinkel, 1983). Commonly, the largest response in grain yield is through a split application of N, where some is applied at sowing and the rest is top-dressed during tillering (Venn *et al.*, 1987). This has the effect of improving establishment and increasing early growth without stimulating excessive DM production. Top dressing can increase N supply at the time of head formation, which stimulates the production of larger heads and has a positive effect on grain yield. The combination of early vigour and a larger sink size can improve WUE through the conservation of early moisture and the ability to fill grain at lower leaf water potentials.

Fertiliser induced increases in dry matter production are not restricted to top growth but include root growth as well. Brown *et al.* (1987b) recorded an increase in the root density of barley with the addition of (60 kg/ha N, 26 kg/ha P) fertiliser. The increased root growth was of direct benefit in extracting water quickly. This was of particular importance in the topsoil where the faster rate of uptake increased the amount of moisture available to the crop through a reduction in E_{sc} in the drier soil (Ritchie, 1972).

Adequate nutrient supply is essential for productive wheat growing and the fulfilment of yield potential under Mediterranean-type conditions. The stimulation of early vigour with the use of nitrogen is unquestioned but a managed approach is necessary to maximise the benefits that fertiliser can bring. Increased, but not excessive, early growth will increase WUE through greater ground cover which should increase T, reduce E_{sc} and set up a greater yield potential (Passioura *et al.*, 1993). However, despite a reduction in E_{sc}, the increase in T may also increase the risk of early soil moisture depletion if there is excessive early growth (McDonald, 1989). This can be managed through crop phenology as early flowering reduces the risk of post anthesis moisture deficits (Regan *et al.*, 1997; van Herwaarden *et al.*, 1996). Thus, with the use of early maturing cultivars, the stimulation of early vigour through fertiliser application will also have a positive effect on grain yield.

2.5.1.4 Sowing techniques

It has been shown that, due to exponential growth patterns, very early differences in vegetative biomass are maintained for a large portion of the life of the crop (López-Castañeda and Richards, 1994b; López-Castañeda *et al.*, 1995). One method of achieving early growth is through earlier plant emergence (López-Castañeda *et al.*, 1996; Soetono and Donald, 1980) (see section 2.5.2.2.1). It follows, therefore, that any management practice which promotes early emergence will also promote early vigour.

Seed bed preparation can have a large impact on plant emergence. Cornish (1987) found that direct drilling reduced the speed of emergence due to the less friable seed bed. Poorer seed-soil contact of the direct drilled plots gave slower seed imbibition and coleoptile growth was mechanically impeded. Young (1997) found that mechanical impedance can cause reductions in the rate of leaf elongation, even at high water potentials, giving a direct decease in crop vigour. Changes in microclimate under heavy stubble can also decrease vegetative growth. Yunusa (1994) found that stubble mulching caused a reduction in soil temperature through shading, which in turn reduced the amount of tillering and leaf area production in wheat.

2.5.1.4.1 Time of sowing

Sowing occurs in Mediterranean-type climates in late autumn - early winter, when daily temperatures are decreasing and the days are getting shorter. Early sowing ensures seeds are sown into a warmer seed bed which causes faster germination (Khah *et al.*, 1986) and the longer daylight hours experienced at this time provide greater relative leaf expansion rates and crop growth rates (Rawson, 1991). The longer days and warmer conditions reduce the phyllochron interval (Slafer and Rawson, 1997) which combines with the early emergence to produce a dramatic increase in early vigour compared to later sowings (Richards *et al.*, 1993).

Early sowing has a positive effect on the partitioning of water use as the crop reaches anthesis earlier, allowing grain filling to be completed under lower VPD. The net effect is an increase in harvest index and yield. Yield reductions of up to 200-250 kg/ha per week have been found if sowing is delayed past the optimum date, due to penalties in WUE caused by the sharp rise in VPD later in the season (Coventry *et al.*, 1993; French and Schultz, 1984). Crop simulations for northern Syria showed yield penalties of 4.2% per week delay in sowing past the break of season, and up to 9% per week for delay in anthesis past the optimum time (Stapper and Harris, 1989).

Early sowing ensures that the ground is left bare for a shorter period after the opening rains. As discussed in section 2.4.1.1 large moisture losses occur during this period, therefore promoting early vigour will increase T as a proportion of ET and reduce E_{sc}. The advantages of early ground cover will be magnified when we consider not only an *increase* in ground cover but a comparison between having some ground cover and none at all.

Altering the time of sowing is an effective tool in increasing early vigour and grain yield, with little additional cost. The only change which may be required is associated with weed control, where an increased dependency on chemical control may result. This will, however, be off-set to some degree by the increased vigour and competitive ability of the crop. The risk of frost damage can be countered through the use of cultivars with appropriate vernalisation requirement or photoperiod sensitivity. With such a change in management practice, productivity and yield stability can be increased.

2.5.1.4.2 Sowing depth

The depth of sowing affects the speed of emergence, with deeper sown seeds taking longer to emerge (Hadjichristodoulou *et al.*, 1977; Hucl and Baker, 1990a; Kirby, 1993). The relationship between sowing depth and time to emergence is related to coleoptile length. It is roughly linear up to a depth equal to the maximum length of the coleoptile and any seeds sown deeper than the length of the coleoptile will take disproportionately longer to emerge. Thus, sowing depth may affect early vigour, especially if seeds are sown too deep. Conversely, if seeds are sown too shallow then the soil surrounding the seed may be too dry and imbibition and germination will be delayed. This will also have a negative effect on the rate of emergence and early vigour.

Cultivars containing dwarfing genes have shorter coleoptiles (Whan, 1976b) which means that they are more susceptible to problems from deep sowing. A potential complication can arise due to the unpredictable nature of early winter rains in Mediterranean-type climates. The first rains for the season can sometimes be followed by weeks of dry weather (Richards, 1991) resulting in dry topsoil at sowing time. Under these conditions deeper sowing is necessary to place the seed in contact with moist soil but care must be taken not to place the seed too deep, especially with genotypes containing dwarfing genes. An alternative solution is to use press wheels or rollers to improve seed-soil contact so as to assist germination and ensure good vigour under drier conditions.

Coleoptile tiller production has been shown to affect early vigour in wheat through increased LAI and DM production (Liang and Richards, 1994)(see section 2.5.2.2.6). The seeding depth affects the production of coleoptile tillers (Hucl and Baker, 1990a): where increased sowing depth delays emergence and reduces the number of coleoptile tillers produced. Thus, by various mechanisms, sowing depth is of critical importance to plant establishment and early vigour.

2.5.2 Genetic potential for improving early vigour

2.5.2.1 Genetic variation

Any breeding population will express differences in early growth, the size of which will depend on the genetic diversity of the population. Large differences in early vigour occur between different species of temperate cereals (López-Castañeda and Richards, 1994a; López-Castañeda and Richards, 1994b; López-Castañeda *et al.*, 1995; López-Castañeda *et al.*, 1996). These vigour differences can be expressed through different traits and the role of genetic selection for vigour requires examination of the variation in these traits. The role of these attributes and their genetic diversity will be discussed later.

Positive correlations have been found between vegetative biomass and grain yield in wheat (Turner and Nicolas, 1987; Whan *et al.*, 1991) and barley (Acevedo, 1987; Acevedo *et al.*, 1991; Boukerrou and Rasmusson, 1990; Van Oosterom and Acevedo, 1992). In each case differences in early vigour were generated using diverse genetic backgrounds and in many cases greater vigour was evident in breeding lines than among the conventional lines. However, greater early vigour did not always result in increased grain yield (Clarke *et al.*, 1984; Regan *et al.*, 1992), but there was rarely a negative association with yield. This provides a positive stimulus for increasing grain yields in Mediterranean-type climates through breeding for early vigour.

Whan *et al.* (1991) found a significant genotype x environment x management interaction for early vigour. The wide variety of genotypes used in this experiment responded differently to the environments created through altering irrigation, sowing date and location. For example, plants expressing equal vigour (tillering DM) may partition DM into different plant organs, altering their yield components and the way they respond to stress. This interaction has caused some inconsistencies in the correlation of early vigour with grain yield. Turner and Nicolas (1987) found certain non-vigorous cultivars yielded well whilst Regan *et al.* (1992) found that some highly vigorous introductions had the wrong phenology and were not well adapted to Australian conditions, and consequently they yielded poorly.

Sometimes it can be hard to separate genetic effects from agronomic effects as different cultivars respond to management in different ways. An example of this is where Turner and Nicolas (1987) measured early vigour in terms of DM per plant. Larger plants at tillering produced more grain per plant at maturity. This is a rational finding but one which will be confounded by plant density due to the different responses of cultivars to plant population (Anderson, 1986; Anderson and Barclay, 1991).

The stage of development when vigour is assessed may affect the interpretation of genotypic differences in early vigour. Where vigour is measured as DM production and measurements are recorded at the same number of days after sowing, the rate of development of each cultivar may confound the vigour ranking. Early cultivars, with faster development patterns, will increase their biomass more quickly and earlier in the season than later cultivars despite having the same final biomass (Regan *et al.*, 1993). Where only one measurement of DM is taken, the accuracy of vigour estimation may therefore be compromised by maturity type, especially when the measurements are taken at late tillering. One way to avoid this error is to take DM measurements sufficiently early so as to avoid differential stages of development between the cultivars but late enough that the vigour difference between cultivars have been allowed to express themselves.

Previous vigour studies have used one DM measurement at the 5-6 leaf stage to define vigour (Regan *et al.*, 1992; Turner and Nicolas, 1987; Whan *et al.*, 1991) as this stage of development was viewed as the time when vigour differences are maximised and developmental differences are not too advanced. Care must be taken, however, to ensure very early cultivars have not already reached terminal spikelet by this stage. This may be more of a problem where a large range of genetic material is used with only one time of sampling.

Although there is a relationship between early vigour and grain yield, there is also a need to define early vigour more precisely than through the broad integrative measurements of DM, GAI and LI. These definitions may mask more subtle traits that influence yield and yield stability. Breeding strategies also require specific, measurable selection criteria and individual vigour traits may provide greater potential for genetic gain than integrated measurements. Careful observation of the differences between vigorous and non-vigorous species (López-Castañeda and Richards, 1994a) have led researchers to propose certain attributes as vigour traits. These include a large embryo, thin leaves, fast emergence, a high frequency of large coleoptile tillers and the absence of major dwarfing genes (Richards, 1988a; Richards, 1996; Richards and Condon, 1994; Richards *et al.*, 1996).

2.5.2.2 Traits which promote early vigour

2.5.2.2.1 Rate of emergence

The rate of emergence can have a large impact on seedling vigour and grain yield. Soentono and Donald (1980) found that barley plants which emerged 1 day earlier were 16% heavier at 17 DAS and produced 14% more grain. The same trial found that a 3 day delay in plant emergence reduced grain number by 43%. This is supported by Bulisani and Warner (1980) who found that field emergence and early vigour were highly correlated. Similarly, Knight (1983) found that individual plants which emerged 5 DAS yielded, on average, three times as much as plants which emerged 12 DAS. However, these results suffered from a high coefficient of variation.

Plant emergence is the combination of germination and coleoptile growth, and there is genetic variation for both traits. A distinction must be drawn between the rate of germination and the rate of emergence once germination has taken place. López-Castañeda *et al.* (1996) noted that the faster establishment and greater early vigour of barley over wheat was due to the fact that barley emerged earlier (due to faster imbibition) rather than having a faster rate of emergence. This is supported by Benjamin (1990) who found that the spread of emergence was just as important as the rate of emergence and it formed a major source of variation in mature plant weight. Boyd *et al.* (1971) also found a similar effect due to the speed of germination, where there was a three fold difference in time to 75% emergence in barley despite all cultivars having the same total percentage emergence and similar rates of emergence. The effects of these differences in time of emergence are especially evident when the plants are competing with one another, such as when seed is sown at high density or the plants have high relative growth rates.

Seed dormancy has a large impact on the rate of germination and subsequent plant vigour, and there is good variation for this trait in wheat (Odiemah and Atta, 1985). Dormancy can occur when the inner layer of the pericarp remains green and prevents development of the embryo as water becomes available (Wellington, 1966). This is broken down as the seed dries out, however, some cultivars also have the ability for the outer layer of the pericarp to restrict embryo growth after the effect of the inner layer has ceased, with negative effects on seedling vigour (Wellington, 1966). King and Richards (1984) found a two fold variation in water uptake between cultivars due to physiochemical (dormancy) effects within the grain. The age of the seed will affect percentage germination and seedling growth since the seed reaches maximum germination potential at or before physiological maturity (Rasyad *et al.*, 1990). This is when the embryo is most viable but is restrained by seed dormancy.

The rate of germination can be affected by the conditions during grain filling of the parent crop. Grass and Burris (1995) found germination was delayed 24-48 hours in seeds which matured under high temperatures as embryos had a low oxygen uptake. The subsequent seedling vigour was also retarded.

The percentage emergence is sometimes referred to as a measure of seed vigour (Copland and McDonald, 1995) and it can be highly correlated with grain yield (Das Gupta and Austenson, 1973) . This is especially so when seed is harvested under poor conditions and with low levels of germinable seed. If the percentage germination is similar we can test for seedling vigour by measuring the level of nucleotides or nucleotide sugars in the embryo of seeds germinating at low temperature (Standard *et al.*, 1983).

If the rate of germination is similar, the rate of emergence will depend on the rate of coleoptile growth. There is large genotypic variation in coleoptile growth (Whan, 1976a) and cultivars with short coleoptiles can take 2-3 days longer to emerge than those with long coleoptiles (Addae and Pearson, 1992). This is supported by Murray and Kuiper (1988) who found that emergence is positively correlated with coleoptile length and that emergence was greatly reduced in plants with coleoptiles less than 50mm. Dwarfing genes play a major role in coleoptile development (Allan, 1980), but seed size can also be used as a tool to select for coleoptile length between cultivars (Addae and Pearson, 1992).

The genetic variability that exists for traits affecting germination and coleoptile development provide a good basis for genetic improvement in plant emergence. Improvement in this area should provide increases in early vigour, or at the very least, we can select cultivars which are not penalised by slow emergence and subsequent growth.

2.5.2.2.2 Specific leaf area

Specific leaf area (SLA) is defined as the area (single side) per gram of leaf (cm^2/g) and is a measure of leaf thickness. The SLA has been shown to be positively correlated with early vigour (López-Castañeda and Richards, 1994b; López-Castañeda *et al.*, 1995; Rawson *et al.*, 1987; van den Boogaard *et al.*, 1996a) due to the leaf exhibiting a greater leaf area for the same investment in biomass.

Genetic variation in SLA can be most dramatically seen in comparisons between cereal species (López-Castañeda and Richards, 1994b; López-Castañeda *et al.*, 1995). Barley for example has a greater average SLA than wheat and this is thought to be a major reason for its greater early vigour and grain yield. Although the variation in SLA within a species is not as large as between species, it is still significant (López-Castañeda and Richards, 1994b; López-Castañeda *et al.*, 1995; Rawson *et al.*, 1987) and this represents the potential for further improvements in SLA through breeding. Rebetzke *et al.* (1996) found wide genetic variation in SLA amongst an international selection of genotypes, indicating an even more positive outlook for SLA improvement through breeding.

Rawson *et al* (1987) found that high light intensity reduced SLA by approximately 4 cm^2/g per $mol/m^2/d$ increase in PAR, producing smaller, thicker leaves. This should not be a major problem under Mediterranean-type conditions, however, as light levels are generally low over the wet winter period. Since SLA has been shown to positively influence early vigour and there is good genetic variation in SLA, then we can assume that there is a good chance for genetic advancement in early vigour through this trait.

2.5.2.2.3 Leaf angle and canopy architecture

Leaf angle can have both a positive and negative impact on early vigour depending on the way it is defined. If vigour is defined as light interception then prostrate types may be favoured, whereas if DM or GAI are use for the definition then erect types may be favoured. The leaf angle also strongly interacts with plant density as erect types will grow better than prostrate types at high density, where there is strong interplant competition. Conversely, increasing plant density may tend to influence the plants to produce more erect leaves. For this reason the leaf angle must be viewed in conjunction with plant arrangement for a truer assessment of ground cover and early vigour.

Prostrate types will provide greater ground cover early in the growing season but are more susceptible than erect-leaf types to problems with inter and intra plant competition for light (Donald, 1963). This is exacerbated at high densities (de Witt, 1965; Monteith, 1965) and so the early gains in vigour are offset by mutual shading of later leaves and early leaf senescence (Austin *et al.*, 1976). This can represent a loss of assimilates (Austin *et al.*, 1976), which is inefficient in terms of RUE. Plants types which change their habit from prostrate early in the season to erect as ground cover increases, should have high RUE.

Erect plant types allow greater light penetration into the canopy (Steven *et al.*, 1986) which increases the area of each leaf exposed to light. The effect is an increased photosynthetic output for a given leaf area and a higher RUE (Innes and Blackwell, 1983; Siddique *et al.*, 1989a; Yunusa *et al.*, 1993c). The greater rate of assimilate supply increases the relative growth rate, producing more leaf area and DM at anthesis. The greater transmission of light into erect canopies may also increase the amount of light reaching the soil surface. However, if plant density is increased so as to maintain light interception, E_{sc} will not increase, the water balance will not be affected and greater productivity will be possible through a more efficient use of light.

The delayed senescence of lower leaves (increased green area duration) in erect canopies (Austin *et al.*, 1976) prolongs the time that the crop can photosynthesise after anthesis and can directly benefit grain yield (Siddique *et al.*, 1989a). The greater contribution of lower leaves to net photosynthesis may also improve yields under drought conditions when fewer leaves are produced (Austin *et al.*, 1976), however, this may be more relevant to northern hemisphere growing conditions where heavier canopies are apparent.

Adaptation through empirical breeding methods has seen a trend towards erect canopy types. In a study of old and modern cultivars Siddique *et al.* (1989a) found that modern cultivars tended to have more erect canopies. These erect canopies allow a greater proportion of each leaf to be exposed to light and consequently modern cultivars have the potential to intercept a greater amount of light for a smaller investment in leaf area. This observation was supported by Yunusa *et al.* (1993c). The former study demonstrated that an erect leaf cultivar required an LAI of 2.3 to provide 95% light interception whereas a cultivar with more floppy leaves required an LAI of 4 to produce an equivalent LI. This was due to the mutual shading of the lower leaves. It must be noted, however, that shading of lower leaves will not be a problem early in the growing season. Thus it could be expected that prostrate and semi erect types should have a higher RUE in this early period.

The extinction coefficient of a particular cultivar may change throughout the growing season (Yunusa *et al.*, 1993c) and cultivars which express prostrate vegetative growth may have erect leaf angles after stem elongation (Acevedo, 1987). This situation would maximise RUE as early ground cover is maximised, but later competition for light is avoided. The problem with this scenario is that current cultivars which express this growth habit are longer seasoned types, not adapted to Mediterranean conditions. An alternative method of maximising RUE is to select erect genotypes and increase the sowing rate in line with the ideotype proposed by Donald (1968b; 1979).

Clearly there is a role for leaf angle in promoting early vigour and the genetic variation for this trait provides hope for future increases in RUE, WUE and yield. It is also evident, however, that we must take into account leaf number, plant density and leaf angle when measuring canopy architecture.

2.5.2.2.4 Leaf size

Leaf length and width are both correlated with leaf area (Rebetzke *et al.*, 1996; Richards, 1996) but they are largely independent of each other (Rebetzke *et al.*, 1996). If the rate of leaf appearance is held constant then plants which produce larger leaves will intercept more light as seedlings and therefore be more vigorous. Since leaves extend at roughly the same rate, plants with wider leaves will accumulate leaf area more quickly and be more vigorous (Gallagher, 1979). This is in agreement with Rebetzke *et al.* (1996) who found that leaf width was more highly correlated with leaf area than leaf length.

Modern cultivars produce fewer leaves than older cultivars but their leaves tend to have a greater leaf area (Siddique *et al.*, 1989a). This corresponds with the greater early vigour observed amongst modern semi-dwarf lines (Siddique *et al.*, 1989a) but is contradicted to some extent by the fact that dwarfing genes affect leaf length, producing shorter leaves (Bush and Evans, 1988; McCaig and Morgan, 1993). It was found that in dwarf lines the first two leaves were shorter but subsequent leaves were often wider (Bush and Evans, 1988). This will have a compensating effect on leaf area development. Another explanation for the greater vigour of modern cultivars is that the lines examined in the former trial were semi-dwarf types and not full dwarfs, and that they may have displayed the increased width characteristics without a reduction in leaf length.

The differences in early leaf area may be traced back to the embryo of the seed as the primordia for the first three leaves are present in the embryo at planting (Perry and Hillman, 1991). A larger embryo will produce larger leaves due to the greater number of leaf cells present (Moussavi-nik *et al.*, 1996), resulting in increased early leaf area. Since there is genetic and environmental variation for embryo size, there will also be genetic and environmental variation in leaf dimensions.

Leaf size is positively correlated with the rate of relative leaf expansion (Rawson *et al.*, 1987). Day length can affect leaf size through an increase in the relative leaf expansion rate (RLER) (Rawson, 1991). Longer days produce a faster RLER and although there is compensation once days become shorter again, if the period of long days is long enough, permanent increases in the RLER will result (Rawson, 1991). In this way, early sowing may enhance leaf size and early vigour through a higher RLER due to the longer days during autumn.

Leaf dimensions can be used as a selection technique when selecting for early vigour (Rebetzke *et al.*, 1996; Richards, 1996) due to the close relationship with total leaf area. Rebetzke *et al.* (1996) found the heritability of leaf width to be greater than for total leaf area or leaf length and they estimate that vigour selection amongst genotypes will be 15% more efficient when selecting for this trait. Another advantage is that measuring leaf width is non-destructive and far quicker than measuring leaf area. In this way, the genetic variation in leaf size directly affects early vigour and can also be used as an effective mechanism for vigour screening.

2.5.2.2.5 Phyllochron interval

It would seem logical that a faster rate of leaf appearance would increase early vigour, providing the leaf size could be maintained. There is genetic variation in the phyllochron interval (PI) and vigorous modern cultivars produce their leaves more quickly (Siddique *et al.*, 1989a). This may be due to their earlier maturity but it is hard to elucidate the cause and effect. Other studies have found similar results. For example López-Castañeda *et al.* (1995) found that barley had a 17% faster rate of leaf appearance than wheat, producing 0.5 leaves more than wheat and expressing double the leaf area by 22 days after sowing (DAS). However, the large difference in LA relative to the PI led the authors to speculate that the rate of leaf appearance was not directly involved. This was supported by Liang and Richards (1994) and Rebetzke *et al.* (1996) who found that the rate of leaf appearance is not related to increases in early vigour. The later authors made reference to the fact that plants don't necessarily need to reduce the PI to improve vigour.

While there is genetic variation in the PI (Baker *et al.*, 1986; Frank and Bauer, 1995), it is also heavily dependent on temperature and photoperiod. Leaves appear more quickly under higher temperatures and longer days (Slafer and Rawson, 1997) and there is a cultivar interaction for both responses (Kirby and Perry, 1987). In this way, the PI will have an effect on early vigour but the genotypic response will be largely confined to the interaction with the temperature and day length through the time of sowing. Due to this interaction, there is little evidence to suggest that early vigour will be enhanced by faster leaf appearance *per se*.

2.5.2.2.6 Tillering ability

There is large genetic variation in tillering ability of wheat (Duggan and Richards, 1996; Hucl and Baker, 1988; Sharma, 1995; Siddique *et al.*, 1989a) and this can play an important role in enhancing early vigour. The delayed nature of tillering (Skinner and Nelson, 1994) and the high tiller mortality usually associated with high tillering lines (Hucl and Baker, 1989; Sharma, 1995; Siddique *et al.*, 1989a) mean that tillers subtended from the leaf axils may not always be of benefit under Mediterranean-type conditions. However, tillers produced at the coleoptile node are highly correlated with early vigour (Lewis and Garcia, 1979; Liang and Richards, 1994; Rebetzke *et al.*, 1996) but the effect of coleoptile tillers on grain yield is not so well documented.

Coleoptile tillers (CTs) generally emerge before the first main stem tiller (Skinner and Nelson, 1994) and the total tiller production is dependent on CT production up to 30-35 DAS. Thereafter tillers are produced at regular intervals from the leaf axils and their production is related to the phyllochron interval (Skinner and Nelson, 1994). Liang and Richards (1994) found the early growth from CTs provided a 25-35% increase in the rate of leaf expansion and a 24-30% increase in DM production up to the 5th leaf (the duration of the trial). The result was a clear improvement in early vigour but there was only an implied link with grain yield.

The role of CTs in improving productivity must be questioned, however, due to their low direct contribution to grain yield. Rawson (1971) found that the CT contributed only 12% to grain yield yet the later formed second tiller after the main stem (T2) contributed 20% to yield. This is supported by Hucl and Baker (1989) who found that the CT only contributed 4%, whilst the T2 tiller contributed 19% to grain yield. In each case the main stem and T1 tiller formed the bulk of the yield. These results suggest that any possible advantage of CT production would be conferred through early ground cover reducing E_{sc} and improving WUE. The earlier formed heads on the CTs would also reduce the time to anthesis.

The tillering ability of wheat plants is not always positively related to grain yield. Siddique *et al.* (1989a) found that the earlier maturing modern cultivars produced roughly half the number of tillers of their older, later maturing counterparts, yet formed significantly greater yields. This was due to the greater percentage of tillers surviving to form heads (51% compared to 35%) and contributing to grain yield, however, it is possible that maturity had a large influence on tiller survival and HI. The tillers in modern cultivars also formed nodal roots and did not form sub-tillers of their own which were positive survival traits under conditions of terminal drought. Other authors also report large genetic variation in tiller mortality (Hucl and Baker, 1988; Hucl and Baker, 1989; Rawson, 1971; Sharma, 1995).

Tiller mortality in CTs is generally higher than in conventional tillers. Hucl and Baker (1989) found that only 51% of coleoptile tillers survived in comparison with the survival of the first main stem tiller (T1) of 98%, T2 (82%) and T3 (76%). Apart from their low survival, coleoptile tillers are not produced from each seedling. Improved production and survival of coleoptile tillers would therefore enhance early vigour and increase the contribution of CTs to grain yield. The scope for genetic improvement is positive according to Rawson (1971), who found good variability in CT production. Krenzer and Nipp (1991) also found high variability in CT production, however, in this instance it was within cultivars, making selection more difficult.

Early vigour can still be improved by conventional tiller production. Comparisons between wheat and barley (López-Castañeda and Richards, 1994b) have shown that barley produced substantially more tillers and that barley produced the tillers 35% faster (López-Castañeda *et al.*, 1995). The net result was greater LA and DM in barley but the effect was slightly delayed due to the lag before the onset of tillering.

Tillering is affected by environmental stresses (Klepper *et al.*, 1981) and agronomy (Darwinkel, 1978; Longnecker *et al.*, 1993). This is also true for CT production where low light intensity or high plant density will suppress CT emergence and survival (Peterson *et al.*, 1982). Increased seeding depth will also reduce the expression of CTs (Hucl and Baker, 1989). So any program aimed at improving early vigour through a high tillering strategy or through the use of CTs needs to consider other factors as well, and tailor the overall agronomy package. Clearly there is a role for tillering ability in producing greater LA and DM but subsequent tiller mortality may negate yield benefits. There may however, be a role for coleoptile tiller production if the expression and survival can be improved.

2.5.2.2.7 Dwarfing genes

Dwarf and semi-dwarf cultivars have been noted for their lack of vigour and low early leaf area (Bush and Evans, 1988; McCaig and Morgan, 1993; Richards, 1992b). This can be explained through shorter leaves (Bush and Evans, 1988; McCaig and Morgan, 1993) but is more likely to be linked to a slower rate of emergence (Bush and Evans, 1988; Richards, 1992b) as there may be no difference in relative growth rates after the second leaf (Richards, 1992a). Bush (1988) speculated that the rate of emergence might be related to seed size but results were inconsistent and it is more likely that the effects were related to coleoptile length. Whan (1976a) found a significant positive correlation between coleoptile length and plant height and this had a large influence on the emergence ability of tall and dwarf genotypes. Tall cultivars, with long coleoptiles emerged from much greater depths and through much stronger soil, leading to large differences in top growth.

Despite differences in early growth, the effect of dwarfing genes on yield has been mixed. There are several reports of dwarfing genes having positive (Austin *et al.*, 1980b; Fischer and Quail, 1990; Fischer and Stockman, 1986; Innes *et al.*, 1985; Richards, 1992a) and negative (Ehdaie and Waines, 1994; Innes *et al.*, 1985; Richards, 1992a) effects on grain yield. The trend is for short wheats to do better under higher rainfall conditions, whereas tall genotypes perform better under drier environments. This is consistent with current theory on the role of shading in reducing E_{sc} and the remobilisation of stem reserves during grain filling. Taller cultivars have faster growth rates and would provide greater early shade, while their greater stem DM provides a greater reservoir of assimilates for remobilisation, whereas shorter cultivars require higher rainfall conditions to cover the ground more quickly due to higher inputs and increased plant densities.

Dwarfing genes have a role to play in the yield potential of wheat crops but Richards (1992a) hypothesised that it was height *per* se rather than the specific *Rht* genes involved which had the largest effect on yield. Richards found there was a trade off between HI and biomass; HI decreased as plant height exceeded 65cm but biomass increased with height up to 100cm. This provided an optimum range of plant height between 70-100cm, irrespective which *Rht* genes controlled culm length.

The yield increases witnessed over the last decade are largely due to gains in HI from the use of *Rht1*, *Rht2* and *Rht3* dwarfing genes. However, there is also a penalty associated with slow early vigour. To fully exploit the benefits associated with vigour, the link between short plants and short coleoptiles must be broken (Richards and Condon, 1994). This is possible with the use of *Rht8* dwarfing gene, common in European and Chinese wheats, which combines reduced height with long coleoptiles (Richards *et al.*, 1996). In this way, early vigour should be maximised, along with HI and grain yield.

2.5.3 Parental seed source effects

2.5.3.1 Seed nutrient content

It is well established that increased nutrient levels improve vegetative growth. During very early establishment, prior to emergence, the plant has no photosynthetic area and relies totally on seed reserves for growth. High seed nutrient levels will increase early shoot growth. The amount of nutrients available to the growing embryo will depend on the storage available (seed size), the nutrient concentration and the nutrient mobility (from the storage organs to the embryo). The seed nutrient content will be even more important for plants growing in poor soils as the seed nutrients will have a greater impact as a starter fertiliser (Ascher *et al.*, 1994).

There are many reports that grain protein concentration and grain protein content increase seedling vigour (as measured by shoot DM at approximately 21 DAS) (Ayers *et al.*, 1976; Bulisani and Warner, 1980; Evans and Bhatt, 1977; Lowe *et al.*, 1972; Lowe and Ries, 1972; Millet and Zaccai, 1991; Ries *et al.*, 1976; Ries and Everson, 1973). In most of these examples the protein content was altered by fertiliser management of the parent crop but Millet and Zaccai (1991) demonstrated that genotypic differences in grain protein content are also possible. Their study also showed that wild wheats have a higher grain protein content and hypothesised that this was an adaptive trait due to their need for greater early vigour and competitive ability for survival. Bulisani and Warner (1980) showed that grain protein increased vigour but the effect could be removed if fertiliser nitrogen is added within the first 3 days after sowing.

Grain phosphorus (P) content has been shown to be positively correlated with plant vigour from soon after emergence (De Marco, 1990) up to tillering (Bolland and Baker, 1988; Riley *et al.*, 1993). De Marco (1990) also found that increasing either the grain P concentration or the applied P concentration increased the rate of emergence but gave similar final emergence percentages. This is disputed by Riley *et al.* (1993) who found no such effects of P concentration on emergence but the latter authors were reporting field based trials whilst the former author was using controlled conditions. Riley *et al.* (1993) also noted that the normal range of seed P concentration in Western Australia was above that which gave a response in their trial, meaning that a vigour response to seed P may not be noticeable.

It has been shown that seedling vigour in wheat is best related to zinc (Zn) and manganese (Mn) levels in the grain (Moussavi-nik *et al.*, 1998). Seedlings originating from seeds high in Zn or Mn produced more extensive root systems and more tillers than from low Zn or Mn grain (Longnecker *et al.*, 1991; Marcar and Graham, 1986; Rengel and Graham, 1995). Much of the nutrients are held in the seed coat and are not remobilised during germination or growth (Moussavi-nik *et al.*, 1996; Moussavi-nik *et al.*, 1997). Since the seed coat would not be expected to break down and release the nutrients during the first 8 DAS (the period during which the plant is dependent on seed nutrients) a large proportion of the nutrients are unavailable. Conversely, there is only a small proportion of the total Zn and Mn available for growth and this may be the reason for the vigour response to increased levels of Zn and Mn in the seed.

The large response in early vigour to seed nutrient content, combined with the genetic variation in seed size and seed nutrient concentration provide good potential for increasing vigour by this means. Farmers should carefully select their parental seed crops to fully exploit this effect.

2.5.3.2 Seed size

There are numerous reports in the literature illustrating the positive association of seed size with increased early growth (Boyd *et al.*, 1971; Bulisani and Warner, 1980; Burris *et al.*, 1973; Chastain *et al.*, 1995; Evans and Bhatt, 1977; Gan and Stobbe, 1996; Hadjichristodoulou *et al.*, 1977; Lafond and Baker, 1986a; Liang and Richards, 1994; Millet and Zaccai, 1991; Moussavi-nik *et al.*, 1996; Perry, 1980; Peterson *et al.*, 1989; Ries *et al.*, 1976; Ries and Everson, 1973; Salopelto and Peltonen, 1995). Mian and Nafziger (1994) pointed out that this effect is more pronounced under dry conditions. These studies generally measured early vigour as shoot DM in the period from 2-4 weeks after sowing. In trials where seed size was not correlated with early vigour (Regan *et al.*, 1992), vigour was measured as DM at the 5-6 leaf stage, by which time other environmental factors could have become more apparent. The positive effects of seed size on early vigour can be conferred either through a larger endosperm and seed reserves, or via a larger embryo. Commonly it is the combination of the two.

The direct effect of endosperm size is best described by Peterson *et al.* (1989). In studies where part of the endosperm was excised, the authors found that reducing the seed reserves increased the phyllochron of the first two leaves and reduced early leaf area. This affected subsequent development through a reduction in tillering and nodal root formation.

The primordia of the first three leaves are contained in the embryo of the seed (Perry and Hillman, 1991) and Moussavi-nik *et al.* (1996) found that embryo size was positively correlated with shoot and root DM at 21 and 42 DAS. The size of the embryo is also highly correlated with seed size and this work showed that there was good genetic variation for seed/embryo size, such that advances in vigour could be made simply by grading seed lots and only growing large seeds. This is supported by López-Castañeda *et al.* (1996) who found that barley embryos were 90% heavier than wheat embryos and that embryo size was correlated with seed size within species. Since embryo size accounted for 90% of the vigour differences between the two cereals, these authors also hypothesised that vigour could be improved by selection for large seed. Richards (1996) used this relationship to propose that the size of the first two leaves could be used as a direct selection tool for identifying genotypes with large embryos.

Grading out smaller seeds can affect early vigour through the positive relationship of seed size with coleoptile length (Cornish and Hindmarsh, 1988). Addae and Pearson (1992) showed that doubling the seed weight within a cultivar increased coleoptile length by 9%, although this is disputed by Chastain *et al.* (1995). A potential negative aspect of selecting larger seeds is that large seeded lots may reflect high seed moisture content or that dormancy may not be broken. Colder and wetter conditions during grain filling tend to produce larger seeds but may fail to adequately dry out the pericarp and induce seed dormancy (Salopelto and Peltonen, 1995). Also large seeds take longer to imbibe which may slow the rate of germination and subsequent emergence (Lafond and Baker, 1986b). Seed dormancy should rarely be a problem under Mediterranean-type conditions due to the hot dry finish and the low seed moisture content at harvest.

Seed size can play a role in early vigour through sowing husbandry. If plants are sown by seed number then early vigour can be improved by sowing larger seeds as larger plants will result (Bockus and Shroyer, 1996). However, if plants are sown by seed volume then smaller seeds produce greater early vigour due to a greater plant density.

Genetic control over seed size may be exerted through the selection for preferred grain filling positions within the spike. If the seeds are named according to their position within the spikelet, with 'a' being the first position and 'b' being the second position, etc., then seeds grown in the 'a' and 'b' florets of the 10 spikelets closest to the peduncle of each spike have greater early vigour. Seeds grown from the 'a' and 'b' florets above the 10th spikelet or from any 'c' or 'd' floret will be less vigorous (Ries *et al.*, 1976). In this way, the potential vigour of the seed lot may theoretically be enhanced by promoting longer spikes with fewer florets per spikelet (i.e. fewer 'c' and 'd' florets) (Rawson and Ruwali, 1972).

Thus, the embryo size and seed reserves can be maximised simply by grading seed lots to select larger seeds within cultivars or by selecting cultivars which express larger first or second leaves (and hence, larger embryos). In this way early vigour can be improved.

2.5.3.3 Stresses during parental seed maturation

The conditions under which the parental seed matures will have a bearing on the vigour of the progeny. The environmental conditions will affect the physical parameters of the seed such as high temperature reducing seed or embryo size (Tashiro and Wardlaw, 1990), but they will also affect the physiological performance of the seed. Grass and Burris (1995) noted that seeds grown under high temperature stress during grain filling had decreased shoot and root growth which could not be explained by seed size alone. Instead it was hypothesised that the temperature stress altered the physiology of the seed at the cellular level. Similarly, Dornbos *et al* (1989) found a small but significant reduction in germination percentage of seeds originating from soybean plants that were drought stressed during grain filling. As previously mentioned, the conditions during grain filling and ripening can also affect seed dormancy (Odiemah and Atta, 1985; Salopelto and Peltonen, 1995).

2.6 Screening techniques for early vigour

In order to undertake widespread screening for early vigour a rapid, non-destructive method of vigour assessment is required. In field trials, vigour is best measured in terms of LAI or DM per unit area (see section 2.3) however this involves destructive sampling which is laborious, time consuming, and sufficient plant material may not be available. These physical limitations may reduce the replication of sampling and affect the significance of results. Consequently, alternative methods for rapid, non-destructive sampling may be appropriate; which include visual scoring, remote sensing, measurement of light interception and the use of photography.

2.6.1 Scoring for early vigour

Visual scoring techniques have been successfully employed to estimate early vigour in cereals and good correlations of vigour score with LAI and DM have been achieved (Boukerrou and Rasmusson, 1990; Regan *et al.*, 1992; Turner and Nicolas, 1987). In other situations, vigour scores have been used to identify adaptive traits for harsh Mediterranean conditions (Acevedo *et al.*, 1991; Van Oosterom and Acevedo, 1992).

The accuracy of any scoring method will be influenced by external factors and care must be taken to outline the scoring criteria carefully. A score based on ground cover may provide a different result to a score based on individual plant performance. Regan *et al* (1992) found that although vigour was significantly correlated to LAI and DM, it was not correlated to ground cover (due to the effect of plant morphology). Turner and Nicolas (1987) found that high plant density favoured higher vigour scores causing some inaccuracy due to variation in plant stand from poor emergence. Care must also be taken to ensure early maturing types aren't mistakenly rated as being vigorous.

Whilst visual assessment is very quick, the subjective nature of visual assessment means that variation between assessors may be large and that assessment skills will need to be learned. In a comparison between objective green leaf area measurement and subjective scoring of herbicide injury to soybeans, Adcock *et al* (1990) found that there was a large variation between six assessors' subjective scores but a low variation between their (objective) radiometer measurements. Furthermore, the results showed that objective assessment gave a much greater coefficient of determination than visual scoring, highlighting the limitations of a visual score system. A possible method of enhancing scoring accuracy is to use check varieties for cross-reference between assessors. If however, all assessments are to be done by a single person, this variation will not affect the evaluation.

2.6.2 Photography

Early vigour can be measured by taking photos from directly above the crop canopy and overlaying the photos with a random grid. Percentage ground cover is estimated by counting the number of intercepts with leaf material and good correlations with DM and light interception have been achieved (Regan *et al.*, 1992; Steven *et al.*, 1986; Whan *et al.*, 1991). The photos provide a permanent record of canopy development and colour photos also provide some insight into the percentage of senescent leaf material present. However, the method is limited by the fact that it is very time consuming and accuracy is affected by the ambient light conditions.

2.6.3 Canopy reflectance

The spectral response of light reflected from plant canopies provides a convenient method of non-destructive vigour assessment. Red light is absorbed by chlorophyll whilst near infra-red (NIR) light is transmitted through leaves and scattered or reflected from lower leaves (Knipling, 1970; McCloy, 1983). By measuring the amount of light reflected in the red (650nm) and NIR (800nm) wavelengths, it is possible to measure the amount of vegetative biomass present (Pearson *et al.*, 1976). Since the advent of satellite remote sensing, much work has been done in developing ratios of these wavelengths for improved accuracy in biomass determination (see Tucker (1979)). The most widely used ratios of these wavelengths are the simple ratio (SR) (equation (3)) and the normalised difference vegetation index (NDVI) (equation (4)).

$$\mathrm{SR} = \mathrm{NIR} / \mathrm{Red} \tag{3}$$

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{Red}) / (\mathrm{NIR} + \mathrm{Red}) \tag{4}$$

The SR is positively correlated to biomass and LAI, whilst the NDVI is used to reduce the error between each measurement and is regarded as the more accurate of the two equations (Aase and Siddoway, 1980; Tucker *et al.*, 1981).

The 650nm and 800nm wavelengths were selected as they provided the most information of the four wavebands available in the early Landsat satellites. Recent technology has enabled a more thorough investigation of canopy reflectance over a continuous range in wavelengths from 450nm - 2500nm (Elliott and Regan, 1993; Smith *et al.*, 1992). The studies showed that the visible and the mid-IR provided a better sensitivity to ground cover than the NIR, however, many hand-held radiometers do not sample the mid-IR wavelengths. Resolution in the NIR wavelengths is more severely affected when biomass is low and the soils are highly reflective (Elliott and Regan, 1993; Smith *et al.*, 1992) but this effect can be reduced by selecting sites with a dark soil background (Bellairs *et al.*, 1996).

The relationship between LAI and NDVI is asymptotic as the NDVI approaches 1. This limits the use of reflectance measurements for estimating LAI to the initial (linear) portion of the response curve, which previous research has found to be in the region of LAI ≤ 3 (Gardner and Blad, 1986; Nageswara Rao *et al.*, 1992). This is supported by Belford *et al.* (1993) who found a linear response up to an LAI of 0.5 and Bellairs *et al.* (1996) and Araus (1996) who found a linear response in the region LAI < 2. Linear responses have been found for LAIs as high as 9 (Kanemasu *et al.*, 1985) but this was under irrigation. Similarly, Penuelas *et al.* (1997) reported linear responses in barley up to a shoot biomass of 1000g/m^2 at jointing.

Using radiometry, it is possible to determine vigour differences very early in the life cycle of the crop. Aase and Siddoway (1980) found it was possible to distinguish plant material from soil background as early as LAI = 0.06 (or 30g/m^2) enabling vigour assessment to be carried out from as early as the two leaf stage. When this is combined with the ability to resolve DM differences between cultivars of 5-7g/m^2 over a large range of genetic material (Smith *et al.*, 1993), reflectance measurements become a powerful tool for vigour assessment. It must be said however, that the resolution of 5 g/m^2 was achieved at the 4-7 leaf stage (when differences between cultivars are larger) and that the resolution will be determined by the range of biomass present in the study (Smith *et al.*, 1992). It must also be noted that the presence of any weeds will greatly affect the accuracy of LAI estimation since the spectral response of most weeds would be similar to wheat.

Reflectance measurements are influenced by incident radiation, solar zenith angle and row orientation (Jackson *et al.*, 1979; Tucker, 1979). Variable incident radiation will have a large influence on reflectance measurements (Milton, 1987) and radiometers which need re-calibration for changes in light intensity will be disadvantaged. Studies which have compared hand-held radiometers (Bellairs *et al.*, 1996; Smith *et al.*, 1993), favour the use of equipment that can measure incident radiation simultaneously to canopy reflectance as they are more accurate under variable light conditions and far more convenient for field use. To account for the effects of sun angle, measurements should be taken close to solar noon when the zenith angle is $<40^\circ$ (Baret, 1991). The effects of row orientation will be insignificant (within the trial) if the whole trial is sown in the one direction.

Spectral reflectance of plant canopies can be affected by plant turgor, canopy surface moisture and soil background reflectance. Reflectance increases as leaves dehydrate (Ehleringer, 1980; Knipling, 1970), with the mid-IR wavelengths being more sensitive to leaf turgor (Jacquemoud and Baret, 1990). Dew droplets on the canopy will also affect the spectral response by increasing the reflectance of visible light but decreasing the reflectance in mid-IR wavelengths (Pinter, 1986). Similarly, soil moisture conditions will have a large impact on the background soil colour with an increase in the NDVI under moist conditions (Major *et al.*, 1990).

The effect soil background has on canopy spectral response is a potential problem in Australia considering the sparse, open canopies which are common in Mediterranean cropping regions. For this reason, calibration curves relating reflectance to LAI and biomass are site specific (Curran, 1983). In order to reduce the effect of soil background, various modifications have been made to equations (3) and (4) (Baret *et al.*, 1989; Gardner and Blad, 1986; Huete, 1988; Major *et al.*, 1990), resulting in the transformed soil adjusted vegetation index (TSAVI) (equation (5)).

$$\mathrm{TSAVI} = [a(\mathrm{NIR} - a)(\mathrm{red} - b)] \,/\, [(\mathrm{red} + a)(\mathrm{NIR} - (a \,.\, b))] \qquad (5)$$

$$\mathrm{NIR} = a \,.\, \mathrm{red} + b \qquad (6)$$

The constants *a* and *b* are derived from the regression of NIR on red from bare soil (equation (6)). Using the TSAVI gave a significant improvement in reducing background soil 'noise' when moving across soil types but offered little improvement within a soil type (Bellairs *et al.*, 1996). The TSAVI has more relevance when using satellite data or comparing across sites but none-the-less, sites should be selected to reflect dark, uniform soil types (Bellairs *et al.*, 1996).

Plant morphology will affect reflectance patterns with prostrate types having a lower, and erect types having a higher biomass than would be predicted from calibration curves (Bellairs *et al.*, 1996). This has implications when screening breeding material with a wide range of morphologies. Measurements must be timed to ensure enough differentiation so as to give good separation in LAI and biomass, but not so much as to allow differential development patterns to cause errors. Thus, with early measurements in a weed-free environment, it would be possible to use a spectral radiometer for screening breeding lines for early vigour.

2.6.4 Light interception

The concept of early vigour improving crop water use efficiency (section 2.4.1) and competition with weeds (section 2.4.1.5) hinges on the early development of ground cover. It is possible to measure this directly by determining the amount of photosynthetically active radiation (PAR) reaching the soil surface using a quantum line sensor or ceptometer. The amount of ground cover will be proportional to the light interception as determined by the difference between incident and transmitted light through the canopy. Historically tube solarimeters were used for this purpose, however, they were fixed devices and consequently not suitable for screening purposes. The portable nature of the modern ceptometers enables rapid assessment of light interception (and early vigour) across large numbers of breeding plots.

The relationship between light interception and LAI is asymptotic and approaches a maximum value as the canopy reaches full closure. Light interception is highly correlated with DM (Gregory *et al.*, 1992a; Regan *et al.*, 1992), ground cover (Steven *et al.*, 1986), and LAI (Nageswara Rao *et al.*, 1992). In the latter case, light interception was linearly related to leaf area for LAI < 3. Despite the good correlations, the use of the ceptometer for ranking of breeding plots is limited. This is due to the narrow window of opportunity created by the low resolution at low biomass levels and the asymptotic nature of the response curve at high biomass. The plant canopy moves from low light interception to high light interception very quickly.

Steven *et al.* (1986) found that canopy shape affected light interception readings with the calibration under-predicting LAI in erect canopies and over predicting LAI in prostrate canopies. This would increase error in LAI estimation of breeding plots where there is a large range of plant morphologies, however, it will not be a problem if the definition of early vigour reflects actual ground cover and not LAI.

Since light interception is calculated on the difference between incident and intercepted PAR, the ceptometer must be used during periods of uniform light. This limits usage to cloud free days. The combination of sun zenith angle and row direction will also have a large influence on the readings due to the shadows falling within the canopy. Care must also be taken to avoid error caused by the regular light and dark patches which form before complete ground cover is achieved. A simple solution is to place the ceptometer in a perpendicular direction to the crop rows and use the same orientation for every reading. Thus it is possible to screen for early vigour using a ceptometer, providing the sources of error are properly addressed.

2.7 Summary

The yield potential of a given environment depends on the amount and the timing of rainfall. Under Mediterranean-type conditions this will vary considerably but the season will always end in terminal drought. To maximise yield under these highly seasonal and drought prone conditions we must employ one of three mechanisms; drought resistance, drought tolerance or drought avoidance (drought escape) (Jones *et al.*, 1981; McWilliam, 1989). The first two mechanisms refer to the plant growing through periodic drought, whereas the third mechanism refers to finishing the growth cycle before the onset of drought. Although periods of temporary moisture deficit are possible under Mediterranean-type climates it is usually through drought avoidance where the largest yield improvements can be achieved (Passioura *et al.*, 1993).

The seasonality of Mediterranean-type regions offer good growing conditions early in the season that can bring other problems such as waterlogging, low light intensities, frosts and cool growing conditions. Later in the season, crops tend to finish grain filling on stored soil moisture, under rapidly rising temperatures and increasing evaporative demand. This has the effect of reducing HI. The key to increasing yield under these conditions is to maximise the yield potential and begin grain filling as early as possible. To achieve this requires the combination of a high anthesis biomass, adequate spike density and a well timed anthesis date to avoid frost damage but provide a long grain filling period.

There are presently some very early maturing cultivars available for use under commercial conditions but these aren't favoured due to their lower yields. The reliability that they bring to the cropping system through early flowering is overshadowed by the fact that anthesis biomass is still lower than longer seasoned cultivars. The problem lies in raising the yield potential within a shorter growing period. This is where early vigour can make a contribution.

It has been shown that, with early vigour, it is possible to increase WUE without affecting ET because increases in T under high vigour systems are usually at the expense of E_{sc}. Thus, using early vigour to promote DM_{anth} in early maturing lines has the double benefit of improving WUE as well as HI. Since grain yield relies on ET, WUE and HI (equation (1)), increases in early vigour have the potential to provide significant yield benefits. Even in mid-maturing lines, greater partitioning of ET into T in vigorous genotypes could provide increases in DM_{anth} with a similar pre-anthesis water use, preserving soil moisture for grain filling.

The genetic variation in early vigour that has been documented in the literature could be a very important source of vigour improvement. It is possible that through careful genetic selection, ground cover may be improved (and hence WUE increased) without a commensurate increase in anthesis biomass. This would tend to promote soil moisture storage for use in grain filling and increase HI and grain yield. Alternatively, improved WUE and HI could also be possible through the combination of vigorous growth and early maturity.

Clearly there are benefits in identifying more vigorous cultivars and incorporating vigour selection into wheat breeding programs. Despite these benefits, the genetic variation in vigour presently available in the Roseworthy Wheat Breeding Program germplasm is unknown. If characteristics which promote early vigour could be detected, then they could be improved within the breeding program. Good parental material could also be identified.

Historically, the most successful breeding programs have followed an empirical approach to breeding. This produces smaller gains, with a lower risk of failure. One of the main drawbacks, however, is that change is relatively slow and there is also a risk of discarding important genetic material which has been influenced by other factors. The recent ability to identify and incorporate single genes into target material has the potential to speed up the breeding process and now affords breeders much greater control over addressing specific physiological problems (Snape, 1996). It is becoming easier to follow an ideotype approach to breeding and the identification of individual genetic traits has become very important (Whan *et al.*, 1993). The development of molecular markers allows breeders to screen material for quantitative trait loci and reduces the risk of discarding material containing the target genes. Therefore, identifying traits which promote early vigour, and the location of the genes which encode for them, is of paramount importance if early vigour is going to be readily adopted by breeders.

The problem associated with following an ideotype approach to breeding is that genetic diversity must be present and the breeder must be able to select for the trait. South Australian wheat breeding programs don't currently select for early vigour *per se*, despite the breeder's acknowledgment of the potential benefits attributed to good early ground cover (Hollamby and Bayraktar, 1996). The problem lies with the inability to accurately assess breeding plots for early vigour and thus provide the breeding program with information which could be used for selection. It could be argued that most breeders subconsciously score for early vigour but a more objective approach is required. Previous research has shown that remote sensing has significant potential in ranking plots for early vigour and could be of major benefit in breeding if the techniques and calibrations could be refined.

It has been demonstrated that early vigour has a role to play in improving the productivity of wheat production in southern Australia, however, the impact of increasing crop vigour is not well understood. The task is to show whether early vigour can provide benefits to crop productivity in these regions. It is also to improve our understanding of the best methods to employ in order to promote early vigour under local conditions.

The following chapters of this thesis detail experiments designed to test the hypothesis that the stimulation of early vigour in wheat through agronomic manipulation and genotypic selection will improve productivity under field conditions. This led to further genetic studies which focussed on identifying plant characters which promote early vigour and the genes responsible for their expression.

CHAPTER 3

3. General materials and methods

3.1 Introduction

The research conducted during this study included field experiments and glasshouse studies. In each case, field experimentation followed the same basic procedure, the common elements of which, shall be reported in this section. This includes site descriptions, climatic information, basic field agronomy, soil moisture monitoring and remote sensing techniques for biomass production. This chapter shall also report the calibration procedures for the measurement of soil moisture and light interception.

Information relating to the methods employed in glasshouse studies as well as variations to agronomic procedures (including specific information on plant densities, quadrat sizes, weed control and other techniques), will be covered in detail in the relevant experimental chapters.

3.2 Site descriptions

3.2.1 Soils

Table 3.1 Soil descriptions for the topsoil (0-10cm) from each trial site.

Site	**Texture**	**pH (H_2O)**	**pH ($CaCl_2$)**	**EC**	**OC**	**P (ppm)**	**K (ppm)**
Roseworthy E7	sandy loam over white calcrete	6.9	6.2	70	0.60	40	290
Roseworthy B7	sandy loam over red clay	7.5	7.2	153	1.45	42	
Roseworthy N2a	loam over sandy clay	7.5	6.9	130	1.73	61	502
Kapunda BCC	black cracking clay	7.9	7.3	162	1.87	22	
Kapunda RBE	loam over red clay	7.8	7.0	189	1.69	34	

The experiments were conducted at two sites - Roseworthy and Kapunda. The locations chosen are representative of medium and high rainfall cropping regions of South Australia. Soils at both sites show a strong alkaline trend down the profile with duplex or gradational texture changes to clay or a calcareous layer at depth. The description for the top 100mm at each site is given in Table 3.1.

3.2.2 Climate

Roseworthy has a lower annual average rainfall than Kapunda. Each of the years of experimentation experienced different rainfall patterns (Table 3.2), with 1993 having below average rainfall in the first half of the season and above average rainfall after anthesis. The conditions experienced in 1994 were extremely dry with a late autumn break, significantly less annual rainfall and significantly reduced grain yields. The season in 1995 was close to the long term average, however a dry period was experienced from late tillering until after anthesis. The beginning of 1996 experienced above average rainfall, where periodic waterlogging occurred. Grain filling was largely achieved on stored soil moisture.

Table 3.2 Average monthly rainfall statistics for Roseworthy and Kapunda trial sites, including the growing season (April-October) sub-total and long term averages.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	Apr-Oct	Total
Roseworthy														
1993	49.4	7.1	11.8	3.1	21.3	44.9	37.5	40.0	63.7	89.4	20.2	23.6	299.9	412.0
1994	28.4	12.4	0.0	10.8	17.2	75.1	31.8	11.1	8.8	24.3	33.5	6.6	179.1	260.0
1995	18.2	29.0	14.4	27.1	44.9	55.1	87.5	16.7	24.5	49.2	7.6	8.1	305.0	382.3
1996	65.7	28.4	18.3	20.1	5.0	72.2	85.9	81.0	72.2	26.4	12.2	15.8	362.8	503.2
Long Term Av.	21.3	19.1	20.4	37.4	46.7	52.8	49.9	52.8	46.4	43.0	27.6	22.8	329.0	440.2
Kapunda														
1994	19.0	15.0	0.0	1.0	25.0	92.0	42.0	10.0	27.0	31.0	52.0	7.0	228.0	321.0
1995	28.0	24.0	13.0	34.0	53.0	65.0	109.0	22.0	41.0	68.0	31.0	8.0	392.0	496.0
Long Term Av.	20.6	19.8	23.3	38.4	54.9	58.1	60.2	62.2	54.6	47.3	30.5	25.1	375.7	495.0

The two sites are approximately 30km apart and they experience similar temperature patterns. However, the greater elevation of the Kapunda site ensures that both maximum and minimum temperatures are generally slightly lower (Table 3.3).

Table 3.3 Average monthly maximum and minimum temperatures for Roseworthy and Kapunda trial sites.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Roseworthy	14.9	15.2	13.5	11.0	8.9	6.8	6.0	6.3	7.2	9.1	11.6	13.6
	29.8	29.7	27.3	22.8	18.8	15.7	15.0	16.1	18.7	22.0	25.3	27.9
Kapunda	14.6	14.6	12.7	10.1	7.9	6.2	5.3	5.8	6.9	8.8	11.2	13.2
	29.7	29.3	26.6	21.5	17.5	14.2	13.5	15.0	17.9	21.3	25.1	27.9

3.3 Agronomy

The field experiments were all sown using the same general method and layout. The method was the same as that used by the Roseworthy Wheat Breeding Program. Variations to the following routine are described in detail in the relevant sections, including specific and detailed information regarding timing of operations, sowing rates, quadrat sizes and weed control.

The trials were sown using a John Shearer cone seeder with spear points and press wheels. Basal fertiliser was applied with the seed as 100 kg/ha of 19:13:0, N:P:K (unless otherwise specified). The plots were 6 rows x 5m and the inter-row width was 180mm, with the neighbouring plots closely adjoining each other to ensure that there were no inter-plot spaces. In 1993 the experiment was sown using a Conner Shea combine seeder with 14 tynes set at 150mm row spacing.

Emergence counts were made by counting all of the emerged seedlings in four 50 cm sections of drill row at approximately 21 DAS. Early vigour was usually assessed at approximately 8 weeks after sowing when destructive harvests were made by lifting all of the plants in 4 x 50 cm sections of the central drill rows with their roots intact. Where leaf area measurements were taken, generally this was done on a sub-sample using a Paton Scientific (Adelaide, SA) electronic planimeter. Leaf areas included the lamina, separated at the collar region, and the green portion of the stem (unless otherwise specified). Specific leaf weight was calculated using the leaf lamina only. Dry matter was always estimated on an above ground basis, after plant parts had been dried in a forced draught oven at 80°C for at least 48 hours.

At mid-late tillering the pathway between plots were sprayed out using a knockdown herbicide applied with a shielded sprayer. A 1.8m pathway was sprayed out at the junction of the plots in a perpendicular direction to seeding, which reduced the plot length from 5m to 3.2m. All plots were sown in duplicate (paired plots) to allow adequate area for destructive plant sampling and an intact plot for machine harvest.

Plants were either hand harvested at maturity by lifting four adjacent 50cm sections of drill row (0.36m^2) for measurement of shoot DM and yield components, or the whole plot was machine harvested using a Wintersteiger plot harvester to determine grain yield. Hand harvesting involved pulling plants up with their roots intact so as to count plant numbers when assessing yield components. Yield components generally included the number of spikes, total above ground biomass, grain yield and thousand grain weight. Hand harvested samples were threshed using a rotary peg-drum thresher and grain samples were cleaned using a 1.9 mm sieve in an aspirated seed cleaner.

Destructive measurements at tillering and maturity were conducted for all treatments on the same day. Destructive harvests at anthesis were generally made as close as possible to the time of anthesis. Growth stage was recorded using the Zadoks Growth Scale (Zadoks *et al.*, 1974) and shall be reported in the form (Z##) in this thesis.

3.4 Data analysis

Experiments were usually analysed using analysis of variance (ANOVA) (unless otherwise specified) and trials were generally set up as randomised complete block designs (RCBD). All data was analysed using Genstat 5 statistical analysis software, release 3.1 for DEC Alpha © 1994 (Lawes Agricultural Trust, Rothamstead, UK).

3.5 Soil moisture monitoring

3.5.1 Method

The soil moisture was monitored with a model 503 DR hydroprobe (CPN Corporation, Martinez, California), also known as a neutron moisture meter (NMM).

Steel access tubes with sealed bases were inserted to a depth of 1.6m (1993) or 1.2m (1995). At each time of sampling, neutron counts were taken over a 16 second period for each depth. The tubes were inserted between the crop rows in the centre of each plot either before crop emergence (1995) or soon after emergence (1993). Care was taken to ensure minimal damage to the crop plants surrounding each tube.

The tops of each tube protruded from the ground surface by 100 mm and the open ends were covered to prevent moisture from entering the tubes. In 1993, counts were taken at depths 30, 45, 60, 75, 90, 110, 130, 150 cm below the ground surface. In 1995, counts were taken 15, 20, 40, 60, 80 cm below the ground surface.

3.5.2 Calibration

The NMM was calibrated for each site by inserting access tubes into representative areas of each trial site. Neutron counts and gravimetric soil moisture measurements were taken and an average of 5 counts for each depth at each site was recorded. Gravimetric soil moisture was calculated as the average moisture content of three soil samples from each depth, at depths corresponding to the NMM counts. The soil for gravimetric analysis was extracted using a 50 mm core and samples were placed in sealed containers to prevent moisture loss before weighing. Dry weights were measured after the soil had been oven dried at 105°C for at least 48 hours. The standard neutron count was taken using an access tube inserted in a 200 litre drum filled with water.

In order to get adequate spread in the calibration data points the entire procedure was conducted after maturity, when the soil moisture had been depleted, and again after the soil had been artificially wetted up to field capacity. The same locations were used in each case.

The calibration equations listed below (Table 3.4 and Table 3.5) refer to the linear regression equations where x is the count ratio and y is the soil moisture in mm/mm. The bulk density used in each calculation was measured from samples taken at each site. The calibration for Roseworthy E7 (1993), (Table 3.4) was only conducted to a depth of 75 cm, although readings were taken to 100cm, as the soil type below 75cm did not vary and the calibration is expected to remain unchanged.

Table 3.4 Calibration equations for the neutron moisture meter in Roseworthy paddock East 7, 1993

Depth	Equation	R^2
30cm	$y = 0.6275x - 0.0525$	0.99
45cm	$y = 0.466x - 0.0679$	0.99
60cm	$y = 0.6505x - 0.0711$	0.99
75cm	$y = 0.5573x - 0.0442$	0.93

Table 3.5 Calibration equations for the neutron moisture meter in Roseworthy paddock Buckby's 7, 1995

Depth	Equation	R^2
15cm	$y = 0.4435x + 0.0416$	0.99
20cm	$y = 0.6065x + 0.0206$	0.89
40cm	$y = 0.8977x - 0.117$	0.98
60cm	$y = 0.8405x - 0.0859$	0.99
80cm	$y = 0.9859x - 0.1317$	0.97

3.6 Remote sensing for vigour estimation

3.6.1 Multi-spectral radiometer

A multi-spectral radiometer (MSR) was used to estimate above ground biomass for rapid non-destructive assessment of early vigour. The radiometer used was a Cropscan® (Rochester, MN) model 100 MSR, which measured incoming radiation in eight spectral wavebands. Each waveband was approximately 25 nm wide, with centres at 460, 507, 558, 613, 661, 706, 760, 813 nm. The incident and reflected light were measured simultaneously and the measurements recorded as a percentage reflectance in each waveband.

The readings were converted to a normalised difference vegetation index (NDVI) (see equation 4) using the 661 nm (red) and 813 nm (near infra-red) reflectance values. The readings were always taken within 2 hours either side of solar noon to reduce the effect of azimuth angle (Jackson *et al.*, 1979).

Figure 3.1 shows the relationship between the NDVI and LAI achieved over a range of cultivars at different sampling times. The response of NDVI to increasing LAI was asymptotic above LAI 2 but good resolution was achieved for LAI < 1. It should be noted that two response curves for two different growing seasons have a similar slope but are separated by different intercepts due to different background soil reflectance. The high sensitivity of the MSR is ideal for providing early ranking measurements before canopy closure.

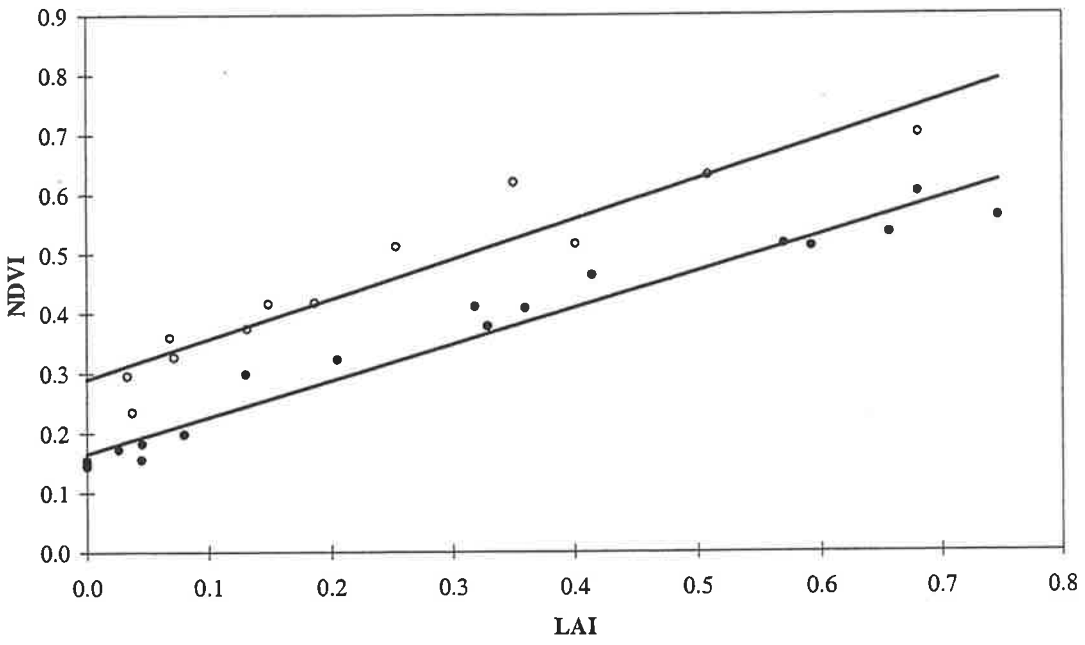

Figure 3.1 NDVI versus LAI for two radiometer calibrations; 1996 (O) y = 1.3425x - 0.3654 and 1997 (●) y = 1.5466x - 0.2573. Equations are highly significant ($P < 0.01$) with r values of 0.95 and 0.98 respectively.

3.6.2 Ceptometer

Readings were taken using a Decagon Sunfleck Ceptometer (Delta T Devices, Ltd. Cambridge, U.K.) which measured photosynthetically active radiation (PAR) in the 400-700 nm waveband. The instrument consisted of 80 sensors at 1 cm intervals, mounted on a wand with a logging head attached.

Measurements were taken by inserting the ceptometer along the soil surface under the canopy at an angle of approximately 45° to the direction of the drill row. Incident light was measured as an average of 5 readings taken above the canopy and measurements below the canopy were averaged from readings taken in three separate locations. Light interception was calculated as the percentage PAR reaching the soil surface below the canopy. Sampling times were restricted to the period from 10am to 2pm and cloudless, sunny days were preferred. In each case the ceptometer was held level and in the same orientation to the sun.

The ceptometer was calibrated by taking destructive samples for dry matter and leaf area assessment. Figure 3.2 illustrates the calibration curve between light interception and LAI, achieved by using a range of cultivars at various sampling times. Light interception was highly correlated to LAI and the relationship was asymptotic towards maximum light interception. The most sensitive region in the response curve was for (1 < LAI < 3) which meant that the ceptometer was best adapted for use in the period between tillering and anthesis.

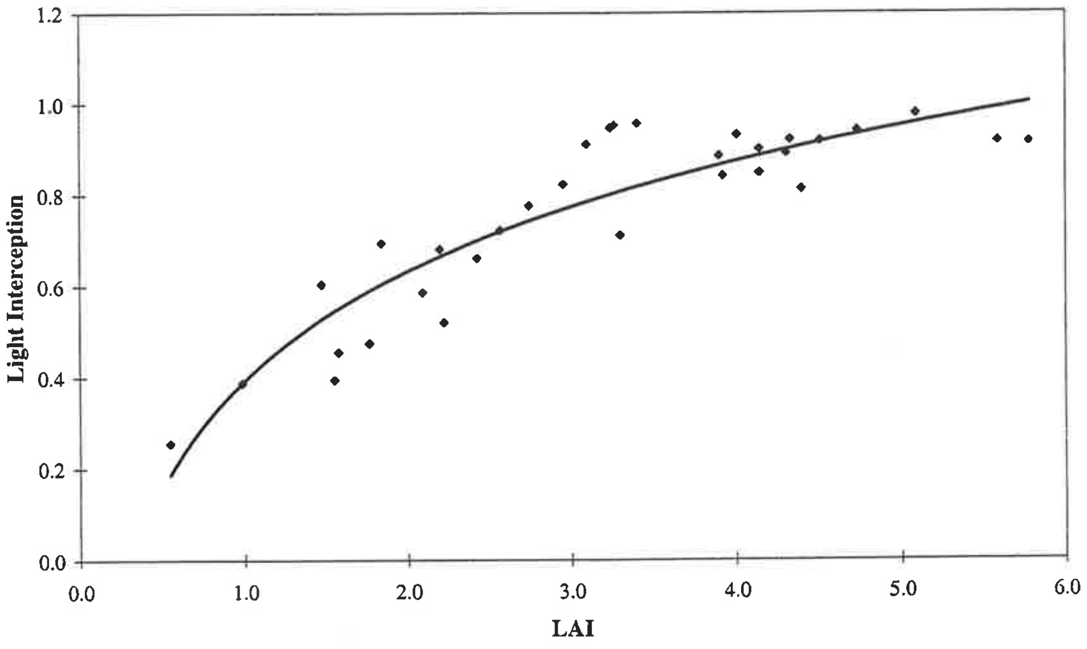

Figure 3.2 Ceptometer calibration for light interception versus LAI.
$Y = 0.3477\ln(x) + 0.3921$. $R = 0.91$ ($P < 0.01$)

CHAPTER 4

4. Promoting early vigour by agronomic means

4.1 Introduction

In Mediterranean-type climates, where up to a third of growing season rainfall can be lost to evaporation (French and Schultz, 1984), anything that can be done to reduce E_{sc} and increase transpiration should be of benefit to grain yield (Acevedo, 1987; Dakheel *et al.*, 1993; Loss and Siddique, 1994; Richards, 1991). Early vigour has been promoted as a desirable trait for wheat grown under such conditions as early ground cover can shade the soil and improve WUE by reducing evaporative loss (Acevedo and Ceccarelli, 1989). Highly vigorous crops are also likely to produce greater anthesis biomass which, providing HI can be maintained, will translate into greater yields.

Of the many agronomic variables able to promote early vigour (see section 2.5.1), plant density (Puckridge and Donald, 1967) and crop nutrition (Brown *et al.*, 1987b; Cooper *et al.*, 1987a; McDonald, 1992) have been shown to be highly effective in manipulating ground cover. Large differences in early growth can be generated using either of these variables and the combination of the two may result in large gains in early vigour.

Increased growth due to higher plant density and nitrogen supply can affect pre-anthesis water use, which is likely to alter the ratio of pre- and post-anthesis water use (van den Boogaard *et al.*, 1996b). It is possible that with high vigour systems, greater anthesis biomass could be generated without any increase in pre-anthesis water use due to reductions in E_{sc} (Tompkins *et al.*, 1991). Alternatively, pre-anthesis water use may be increased and HI reduced, but grain yield may still be increased due to greater anthesis biomass. (Turner *et al.*, 1987). The risk is, however, that HI will be reduced so much that yield is also reduced.

Given that the benefits to grain yield of increased early vigour under dryland Mediterranean-type climatic conditions may show strong interactions with seasonal conditions, the question still remains as to whether increasing early vigour using increased agronomic inputs will be a reliable method of improving grain yield in South Australia. If benefits can be derived from promoting early vigour, under what conditions will these benefits be most apparent? Much of the published work to date suggests that this is especially relevant to the post anthesis period which is so important for maintaining HI and increasing promoting yield.

To address these questions, a field experiment was conducted to examine the effect of agronomically increasing early vigour on grain yield under different post-anthesis environmental regimes. Vigour was promoted using increased plant density and nitrogen supply, and different environments were created in the post anthesis period using supplementary irrigation and rain out shelters. Further experiments were conducted at two locations with contrasting environments, over two seasons, to test the validity and consistency of the results found in Experiment 1.

4.2 The effect of increased sowing rate and nitrogen application on early vigour and grain yield

4.2.1 Materials and methods

4.2.1.1 Experiment 1: Roseworthy 1993

A split plot randomised complete block (RCBD) experiment with 4 replicates was sown at Roseworthy (Field E7) on 31 May 1993. The plots were 14 rows wide x 15m long (see section 3.3) and were laid out with the post-anthesis treatment (rain fed (RF), rain out (RO) or irrigated (Irrig)) as the main plot and the cultivar x vigour treatment as the sub-plots.

The experiment was sown into a cultivated seedbed with a Conner Shea combine seeder with conventional points and harrows. Two popular local cultivars (Machete and Trident) were used and seed was sown to a depth of 50mm. The low vigour treatment (LV) consisted of a sowing rate of 170 seeds/m^2 and 20 kg/ha nitrogen (N); the high vigour treatment (HV) consisted of a sowing rate of 260 seeds/m^2 and 70 kg/ha N. Nitrogen (20 kg/ha) was applied as 111 kg/ha DAP (18:20:0) N:P:K to all plots at sowing and a further 50 kg/ha N was applied as urea (46:0:0) N:P:K at mid tillering to the high vigour treatments.

The rainout shelters were erected at anthesis and consisted of a 3m x 2m wooden frame covered in clear plastic, suspended approximately 200mm above the crop canopy. The shelters were inclined at 10°C to facilitate run-off and gutters were dug around the shelters to facilitate drainage. The irrigated plots received eight irrigations, supplied at regular intervals in the period from 90 DAS to late grain filling. Water was applied by micro sprinklers designed to give an even coverage across the plots. Soil moisture was measured using a neutron moisture meter (see section 3.5) to a depth of 1m. Water use efficiency was calculated using the assumption that soil moisture was uniform across the plots at sowing, so that any soil moisture at maturity could be balanced against moisture supplied through the season to calculate ET_{total}.

Leaf area and shoot DM were measured 7 times between 24 DAS and anthesis by cutting the plants at ground level in 0.15m² quadrats. Anthesis measurements were conducted on a 0.45 m² quadrat and a hand harvest was conducted at maturity on a 1.2 m² quadrat.

4.2.1.2 Experiments 2 - 5: Roseworthy and Kapunda 1994, 1995

Four experiments were sown at Roseworthy (R) and Kapunda (K) in 1994 and 1995 using the method described in section 3.3. In each case the layout was a RCBD with four replicates and treatments were a factorial of two sowing rates (200, 400 seeds/m²), two fertiliser rates (20 kg/ha N and 80 kg/ha N) and three cultivars (Aroona, Machete and Trident). All plots were fertilised with 105 kg/ha (19:13:0) N:P:K at sowing and a further 60 kg/ha N was applied as ammonium nitrate (NH_4NO_3) where required, immediately after sowing.

Similar measurements were taken at each site, which included emergence counts and destructive sampling at mid tillering, anthesis and maturity (1995 only). Ground cover was scored using NDVI (section 3.6.1) and light interception (section 3.6.2) as indicated in Table 4.1. All plots were machine harvested for grain yield using a Wintersteiger plot harvester. Weed control was conducted as necessary.

Table 4.1 Timing of destructive harvests and remote sensing for early vigour estimation in Experiments 2 - 5.

Experiment	Site	Year	Sown	H1 (DAS)	LI (DAS)	NDVI (DAS)
2	Roseworthy	1994	3 Aug	48		37, 48
3	Kapunda	1994	27 July	58	58	58
4	Roseworthy	1995	6 June	56	66, 120	
5	Kapunda	1995	22 June	71	61	

4.2.2 Results

4.2.2.1 Experiment 1

4.2.2.1.1 Early vigour

The high vigour treatment caused a significant increase in dry matter and leaf area from as early as the 2.5 leaf stage (24 DAS) (Table 4.2). The differences were significant until late tillering (66 DAS) and were evident also at anthesis.

Table 4.2 Dry matter and leaf area measurements in the period from before the onset of tillering until anthesis.

			24 DAS	31 DAS	41 DAS	51 DAS	66 DAS	84 DAS	Anthesis
Dry Matter (g/m^2)	LV		1.61	3.49	8.31	18.6	59.9	140	895
	HV		2.34	4.77	10.46	24.5	62.8	153	1065
		LSD	0.33	0.80	1.41	3.2	7.3	14.3	56
		Sig.	***	**	**	***	ns	ns	***
	Machete		2.24	4.98	10.30	23.3	64.5	139	888
	Trident		1.72	3.29	8.47	19.8	58.2	154	1072
		LSD	0.33	0.80	1.41	3.2	7.3	14.3	56
		Sig.	**	***	*	*	ns	*	***
LAI	LV		0.04	0.06	0.15	0.37	1.06	1.54	2.32
	HV		0.05	0.08	0.19	0.45	1.13	1.65	3.55
		LSD	0.01	0.01	0.03	0.08	0.13	0.18	0.31
		Sig.	***	**	**	*	ns	ns	***
	Machete		0.05	0.08	0.19	0.45	1.22	1.58	2.67
	Trident		0.04	0.05	0.14	0.37	0.97	1.60	3.20
		LSD	0.01	0.01	0.03	0.08	0.13	0.18	0.31
		Sig.	**	***	***	*	***	ns	**

*** = $P < 0.001$; ** = $P < 0.01$; * = $P , 0.05$; ns = $P > 0.05$

Genotype also had a significant effect on early vigour with the cultivar Machete producing greater DM and LAI in the period up until 51 DAS (Table 4.2). The differences progressively decreased until 66 DAS, after which time Trident produced greater shoot growth.

There was an interaction of genotype with vigour treatment only at 24 DAS and anthesis. Machete responded to the high vigour treatment better than Trident at 24 DAS, however at anthesis this was reversed.

4.2.2.1.2 Moisture supply

Table 4.3 shows the differences in moisture supply between the 3 post-anthesis treatments created by using rainout shelters and irrigation. The rainfed and rain-out treatments received the same amount of pre-anthesis rainfall, as the rain-out shelters were erected after anthesis. The rain-out shelters were removed for one 42mm rainfall event that occurred 142 DAS. Irrigation was commenced 90 DAS and thus the irrigated treatment received greater pre-anthesis moisture.

Table 4.3 Pre and post-anthesis moisture supply (rainfall + irrigation) for plants grown under rain-out shelters, natural rainfall and supplementary irrigation. Rainfall was calculated between sowing and final harvest.

Post-anthesis treatment	Pre-anthesis (mm)	Post-anthesis (mm)	Total (mm)
Rain-out	165	42	206
Rainfed	165	120	285
Irrigated	250	174	424

4.2.2.1.3 Grain yield

There was a significant interaction between vigour treatment and post-anthesis treatment for grain yield and above ground biomass (Table 4.4). Where post-anthesis water availability was supplemented using irrigation, a large increase in grain yield due to the HV treatment was observed. However, when moisture was restricted using rainout shelters, no yield differences between LV and HV treatments were found. Under rainfed conditions, the trend was towards increased grain yield under the high vigour treatment, however the differences were not significant ($P > 0.05$).

The trend was for lower TGW with high early vigour. This was most notable under rainfed conditions, where the grain weight was reduced from 40 mg to 35 mg (Table 4.4). Harvest index was also marginally reduced across all three environments under the HV treatment. There were no differences in TGW or HI between cultivars.

WUE was strongly influenced by the moisture availability in the post-anthesis period, however, it was also positively affected by vigour treatment. The high vigour package significantly ($P = 0.017$) increased the amount of grain produced per mm of available water from 10.6 kg/mm/ha to 12.1 kg/mm/ha when the WUE was averaged across vigour treatments. However, the biggest gain in WUE due to the HV treatment was achieved under irrigation.

Table 4.4 Grain yield, dry matter, water use efficiency and yield components at maturity. Error terms are based on the interaction of vigour treatment with post-anthesis moisture availability.

	Yield$_{gr}$ g/m^2	Yield$_{gr}$ g/plant	DM g/m^2	Spikes m^{-2}	Spikes plant^{-1}	TGW mg	HI	Height cm	WUE[a] kg/mm/ha
LV-RO	149	1.30	454	204	1.79	39.3	0.33	57	14.92
LV-RF	171	1.43	533	238	1.98	40.0	0.32	58	10.24
LV Irrig	212	1.66	647	235	1.86	37.0	0.33	64	6.67
HV-RO	146	0.86	496	264	1.50	37.7	0.29	55	15.21
HV-RF	194	1.07	648	257	1.93	35.0	0.30	56	11.37
HV-Irrig	311	1.90	1017	382	2.33	34.4	0.31	69	9.77
LSD[b]	44	0.39	132	64	0.49	2.2	0.01	4	3.08
LSD[c]	36	0.28	102	54	0.47	2.4	0.02	3	2.09
Sig.	***	**	***	ns	ns	ns	ns	**	ns

*** = $P < 0.001$; ** = $P < 0.01$; * = P , 0.05; ns = $P > 0.05$

[a] WUE is a relative measure based on a root zone from 0-100cm and the assumption that the soil profile was initially dry.

[b] LSD for comparing means across vigour treatments and environments.

[c] LSD for comparing means within environments.

4.2.2.2 Experiments 2 - 5: Roseworthy and Kapunda 1994, 1995

4.2.2.2.1 Early vigour

Plant density had a strong influence on early vigour, as indicated by NDVI and light interception in the early vegetative period (Table 4.5). Doubling the sowing rate from 200 seeds/m² to 400 seeds/m² significantly increased early vigour (as estimated by the NDVI) at both Roseworthy and Kapunda. Light interception was increased 47% by increasing the sowing rate from 200 to 400 seeds/m² at Kapunda in 1995, however, no increase was detected in 1994 (Table 4.5).

The rate of nitrogen application had no effect on NDVI at either site in 1994 (Table 4.5). There was a corresponding lack of response to nitrogen in the amount of light intercepted at Kapunda in 1994. However, in 1995 significant increases in light interception at the higher nitrogen rate occurred at both Roseworthy and Kapunda, although the magnitude of the response was smaller than for plant density.

Table 4.5 The effect of plant density and nitrogen fertiliser on the normalised difference vegetation index (NDVI) and percent light interception as an estimate of early vigour for field experiments at Roseworthy and Kapunda in 1994 and 1995.

	NDVI			**% Light Interception**			
	R 94 37 DAS	**R 94 48 DAS**	**K 94 58 DAS**	**K 94 58 DAS**	**R 95 66 DAS**	**R 95 120 DAS**	**K 95 61 DAS**
200 seeds/m²	0.53	0.61	0.56	28.2	65.6	76.3	39.1
400 seeds/m²	0.58	0.64	0.61	29.6	77.4	78.8	57.5
LSD	0.02	0.02	0.02	3.5	3.5	2.7	3.4
Sig.	***	*	***	ns	***	ns	***
20 kg/ha N	0.55	0.62	0.58	29.3	69.4	76.0	45.4
80 kg/ha N	0.56	0.63	0.59	28.4	73.6	79.1	51.2
LSD	0.02	0.02	0.02	3.5	3.5	2.7	3.4
Sig.	ns	ns	ns	ns	*	*	**

*** = P < 0.001; ** = P < 0.01; * = P , 0.05; ns = P > 0.05

Table 4.6 The effect of high and low plant density and high and low nitrogen application on early vegetative biomass and final grain yield for plants grown in two locations in each of two years.

		Harvest 1		Maturity					
		DM g/m^2	LAI	Yield g/m^2	Spikes m^{-2}	HI	Grains m^{-2}	TGW mg	Protein %
Experiment 2	200 seeds/m^2	46.6	0.76	137	250		3902	35.6	15.3
Roseworthy	400 seeds/m^2	61.7	1.03	127	304		3820	33.5	15.1
1994	LSD	6.53	0.14	8.9	30		298	1.0	0.5
	Sig.	***	***	*	***		ns	***	ns
	20 kg/ha N	52.0	0.86	130	267		3842	34.3	15.1
	80 kg/ha N	56.3	0.93	133	288		3880	34.8	15.2
	LSD	6.53	0.14	8.9	30		298	1.0	0.5
	Sig.	ns	ns	ns	ns		ns	ns	ns
Experiment 3	200 seeds/m^2	39.0	0.73	122	255		3506	35.4	15.71
Kapunda	400 seeds/m^2	57.0	1.11	113	395		3343	34.2	15.62
1994	LSD	5.9	0.19	10.0	29		344	1.1	0.61
	Sig.	***	**	ns	***		ns	*	ns
	20 kg/ha N	46.5	0.93	121	336		3555	34.6	15.79
	80 kg/ha N	49.5	0.91	114	314		3294	35.0	15.54
	LSD	5.9	0.19	10.0	29		344	1.1	0.61
	Sig.	ns	ns	ns	ns		ns	ns	ns
Experiment 4	200 seeds/m^2	49.2	1.07	387	364	0.41	9037	43.0	13.6
Roseworthy	400 seeds/m^2	83.0	1.87	383	393	0.39	8983	42.7	13.9
1995	LSD	8.3	0.20	18	22	0.01	482	0.6	0.4
	Sig.	***	***	ns	*	***	ns	ns	ns
	20 kg/ha N	63.7	1.42	382	387	0.41	8898	43.0	13.3
	80 kg/ha N	68.4	1.52	388	371	0.40	9122	42.7	14.3
	LSD	8.3	0.20	17.7	22	0.01	482	0.6	0.4
	Sig.	ns	ns	ns	ns	ns	ns	ns	***
Experiment 5	200 seeds/m^2	101	1.80	475	485	0.43	11504	41.4	10.6
Kapunda	400 seeds/m^2	155	2.74	494	548	0.42	11887	41.8	10.0
1995	LSD	12.7	0.25	28	46	0.02	758	0.8	0.6
	Sig.	***	***	ns	**	ns	ns	ns	ns
	20 kg/ha N	119	2.11	454	471	0.42	10702	42.6	9.9
	80 kg/ha N	137	2.43	515	562	0.43	12690	40.6	10.7
	LSD	12.7	0.25	28	46	0.02	758	0.8	0.6
	Sig.	**	*	***	***	ns	***	***	*

*** = $P < 0.001$; ** = $P < 0.01$; * = P , 0.05; ns = $P > 0.05$

Doubling the plant density produced significant increases in DM and LAI during early tillering (Table 4.6). Consistent increases were achieved across the two sites in each of the two seasons and the increases in DM and LAI ranged from 32% for DM at Roseworthy in 1994, to 75% for LAI at Roseworthy in 1995. Generally DM and LAI were increased in the order of 50% as sowing rate was increased from 200 to 400 seeds/m^2.

Increasing nitrogen fertiliser rate generally produced small increases in DM and LAI production, however, the differences were only significant at Kapunda (a higher rainfall site) in 1995. The average magnitude of the increase in early vigour was lower for nitrogen (15%) than for sowing rate (50%). There were no interactions of plant density with nitrogen rate at any of the experimental sites.

There were significant genotypic differences in the expression of early vigour in each experiment, with Aroona and Machete generally being more vigorous than Trident. The differences between Aroona and Machete were not consistent across sites. There were no interactions of genotype with either sowing rate or nitrogen rate.

4.2.2.2.2 Grain yield

Grain yield was reduced by 8% at Roseworthy in 1994 as sowing rate increased from 200 to 400 seeds/m^2, and was unaffected by sowing rate at the other three sites. Increasing nitrogen supply produced an increase in grain yield at Kapunda in 1995 but no response in other experiments. Increasing nitrogen fertiliser did, however, produce an increase in grain protein at Roseworthy and Kapunda in 1995. The 13% increase in grain yield under increased nitrogen at Kapunda in 1995 corresponded with a 15% increase in tillering DM, however grain yield was not correlated with early vigour at the other sites.

The high vigour strategy of increasing sowing rate and nitrogen supply had the general effect of reducing grain size. Significant reductions in grain size occurred for the high sowing rate at both sites in 1994 and for high nitrogen at Kapunda in 1995. The K95 result corresponds to an increase in total grain numbers under high nitrogen but the R94 and K94 results showed no change (Table 4.6).

There were no significant interactions between nitrogen supply and sowing rate, however there were significant cultivar x nitrogen x sowing rate interactions at Kapunda in both 1994 and 1995 (Table 4.7). The dry conditions in 1994 produced no yield response to fertiliser. In 1995, Aroona produced a yield response to increased nitrogen at 200 plans/m^2 but not at 400 plants/m^2, whereas Machete and Trident responded to increased nitrogen at 400 plants/m^2 only. In 1994 the yield differences between combinations of lower (20 kg/ha N + 200 plants/m^2) and higher (80 kg/ha N + 400 plants/m^2) inputs did not affect grain yield. However, in 1995 the higher inputs significantly increased grain yield for Aroona and Trident. The three cultivars used in the experiments showed that genotype had a significant effect on grain yield. Machete yielded significantly lower at all sites, whilst Trident and Aroona produced similar yields.

Table 4.7 The interaction of high and low plant density with high and low nitrogen application on grain yield of wheat grown at Kapunda in 1994 and 1995.

	200 plants/m^2		**400 plants/m^2**	
	20 kg/ha N	**80 kg/ha N**	**20 kg/ha N**	**80 kg/ha N**
	g/m^2	g/m^2	g/m^2	g/m^2
Kapunda 1994				
Aroona	124	132	142	106
Machete	106	102	87	91
Trident	142	125	124	128
LSD ($P<0.05$)			24	
Kapunda 1995				
Aroona	445	557	474	532
Machete	432	484	409	492
Trident	491	441	476	581
LSD ($P<0.05$)			66	

4.2.3 Discussion

4.2.3.1 Experiment 1

The preliminary work in Experiment 1 demonstrated that early vigour could be significantly improved from as early as 24 DAS using a combination of increased plant density and nitrogen fertiliser. This experiment also showed that increased vigour under high input systems could provide yield benefits when post anthesis moisture was adequate, but even when post-anthesis moisture was restricted there was no reduction in grain yield.

Despite increases in LAI under the HV treatment, it is not likely that early vigour would have had any effect on evaporation from the soil surface. Maximum LAI was only 3.2, which was not achieved until anthesis. Whereas the LAI during the early vegetative period was generally <1 and was still less than 2 at 84 DAS (Table 4.6). According to Ritchie (1972), soil evaporation will not be affected when LAI is less than 2.5, suggesting the level of vigour achieved in this study may not have been high enough to reduce soil evaporation. This is supported by the fact that the vigour treatment produced no differences in WUE under rain-out shelters or rainfed conditions (Table 4.4).

The WUE reported in this experiment is somewhat lower than the potential WUE for this environment (French and Schultz, 1984). It is also likely that the WUE would be lower than those displayed in Table 4.4 as they were calculated on the assumption of an initially dry soil profile. Since there was pre-sowing rainfall, it would be expected that there would be some soil moisture present before sowing. The generally low WUE indicates that there may have been other factors influencing grain yield.

Genotypic differences were detected in early vigour from very early in the growing season (Table 4.5) and the magnitude of the differences was as large or larger than those generated by the vigour treatments. These differences were generated between two closely related cultivars from the same breeding program, which indicated that there is a potential role for genotype selection in enhancing early vigour. It was therefore decided to expand the range of genotypes in subsequent investigations into the vigour-yield relationship where vigour was stimulated with agronomic inputs.

The additional nitrogen applied to the HV treatments was not applied until mid-tillering. This would have reduced the response to nitrogen in early vigour measurements and increased the response to nitrogen in grain yield and grain protein (Anderson, 1985; Darwinkel, 1983). The nitrogen was supplied as surface spread urea which was applied immediately prior to a rainfall event to reduce volatilisation, however, losses may still have occurred (Glendenning, 1990). Thus it was decided to use ammonium nitrate (NH_4NO_3) in future work to reduce volatilisation and that application would be at the time of sowing to maximise the vigour response.

Clearly, there was an interaction between grain yield and the post-anthesis moisture treatments and as such, the results required further verification in other seasons and environments. It was also obvious that the biomass levels generated by the vigour treatments did not provide adequate differences in early ground cover and as such, the levels of inputs needed to be increased. One obvious limitation to the design of experiment 1 was that the HV and LV treatments were a high or low combination of sowing rate and nitrogen supply. This meant that the effect of plant density could not be separated from the effect of the fertiliser. Thus, subsequent experiments had a factorial design to isolate the impact of sowing rate and nitrogen supply on early vigour and grain yield.

4.2.3.2 Experiments 2-5

The 1994 and 1995 growing seasons experienced markedly different rainfall (Table 3.2) and the Kapunda site has a higher long term average rainfall than at Roseworthy. This provided a good range of seasonal responses, providing greater confidence in the different vigour treatments.

Large differences in early DM and LAI were achieved with the use of increased sowing rate and nitrogen supply. However, sowing rate had a much larger effect on vigour than nitrogen, producing significant responses in all four experiments (Table 4.6). The magnitude of the differences in DM and LAI was also greater for sowing rate than for nitrogen, reinforcing the benefits of plant density over nitrogen for promoting vegetative biomass and ground cover.

Early vigour was not correlated with grain yield in any of the four experiments. There was no general pattern in the yield response to either plant density or nitrogen supply across the different seasons. Even under the high rainfall conditions experienced at Kapunda in 1995, the high density treatment, which increased tillering DM by 50%, failed to increase grain yield. The only treatment that was able to increase grain yield at any site was an increase in nitrogen supply at Kapunda in 1995. This was largely due to increased tillering producing greater spike density and more grains/m² (Table 4.6), rather than an increase in early ground cover *per se*.

The early DM response to sowing rate is well documented (see section 2.5.1.1) and is not related to seasonal rainfall. However, the fact that a doubling of sowing rate produced only 32% more biomass at 48 DAS (Roseworthy 1995) (Table 4.6) indicates the presence of interplant competition, even at this early stage. This is hardly surprising given that 170 plants/m² was the recommended plant density for Roseworthy as a standard (conservative) farmer practice. The interplant competition experienced at 400 plants/m² could be largely responsible for the negative yield response and smaller grain weight observed in this experiment.

The response in early DM production and LAI to nitrogen was generally positive but was only significant at the highest rainfall site (Kapunda 1995). It would appear that growth is still constrained by available moisture in the vegetative period. Thus increases in N supply seem to be of little benefit to early vigour under lower rainfall conditions. It is also evident that where higher N levels promoted early vigour, they had a negative effect on TGW. One possible explanation is that the pre:post anthesis water use ratio was influenced towards greater water use in the pre-anthesis period under higher N levels, leaving less available moisture for grain filling. This could be due to 'haying off' (Dann, 1969; van Herwaarden, 1996) but is more likely to be due to source limitation caused by an increased sink size from increased grain numbers.

4.3 Genotypic responses to high and low combinations of sowing rate and nitrogen supply

Genotypes respond differently to nitrogen application (Anderson *et al.*, 1991) and plant density (Anderson and Barclay, 1991). Experiment 1 showed different genotypic responses to sowing rate and nitrogen supply, expressed as differences in early vigour. However, the effect of this genotypic response in early growth was unclear as the early growth advantage of Machete over Trident, was reversed by anthesis. This experiment also showed large genotypic differences in grain yield, however there was no interaction between post-anthesis environment and genotype.

It is therefore apparent that the genotypic differences may not have been large enough to provide a significant response.

When we consider that these differences were observed between two cultivars of similar genetic background, it was prudent to examine this effect across a wider and more varied range of genotypes. For this reason, an expanded range of 12 genotypes was included in experiments at Roseworthy and Kapunda to examine the genotypic response to altering early vigour by agronomic means. The high and low vigour treatments were similar to those used in previous experiments.

4.3.1 Materials and methods

4.3.1.1 Experiments 6 & 7

Similar experiments were sown at Roseworthy (Experiment 6) and Kapunda (Experiment 7) on 26 and 27 July 1994 respectively. The equipment and methodology were the same as that described in section 3.3. Treatments consisted of 12 cultivars and two vigour treatments and in each case the layout was an RCBD with four replicates. The low vigour (LV) treatment consisted of 20 kg/ha N and a sowing rate of 200 seeds/m²; the high vigour (HV) treatment consisted of 80 kg/ha N and a sowing rate of 400 seeds/m². All plots were fertilised with 105 kg/ha (19:13:0) N:P:K at sowing and a further 60 kg/ha N was applied as ammonium nitrate (NH_4NO_3) to the HV plots immediately after sowing.

Similar measurements were taken at each site, which included destructive sampling at growth stage Z22-Z24 and anthesis, and a mechanical harvest for grain yield at maturity. Ground cover was scored using NDVI (see section 3.6.1) at 37 DAS (Roseworthy) and 58 DAS (Kapunda) and light interception (see section 3.6.2) was measured at 58 DAS at Kapunda. Weed control was conducted as necessary.

4.3.2 Results

4.3.2.1 Experiments 6 & 7

4.3.2.1.1 Early vigour

The high vigour treatment significantly improved NDVI and LI in the early vegetative period (Table 4.8). A similar increase in NDVI for the HV treatment was noted across all genotypes at Roseworthy, however the response was not as clear cut at Kapunda. There was an interaction between genotype and vigour treatment for NDVI measured at Kapunda 58 DAS (Table 4.8) due to the fact that some genotypes failed to respond to the HV treatment.

Table 4.8 Estimates of early vigour using the normalised difference vegetation index and percent light interception for plants grown in field experiments at Roseworthy and Kapunda in 1994. Data represent the interaction of cultivar with high and low vigour treatment and the main treatment effect.

	Roseworthy 1994		**Kapunda 1994**			
	NDVI - 37 DAS		**NDVI - 58 DAS**		**% LI - 58 DAS**	
	LV	**HV**	**LV**	**HV**	**LV**	**HV**
Aroona	0.61	0.74	0.55	0.59	27.8	27.3
Corrigin	0.55	0.72	0.51	0.54	22.8	25.5
Excalibur	0.61	0.75	0.55	0.67	23.0	30.5
Kulin	0.58	0.71	0.50	0.60	21.5	23.0
Lowan	0.56	0.69	0.50	0.58	17.3	22.8
Maya 74	0.62	0.68	0.54	0.58	27.8	22.5
Machete	0.62	0.75	0.51	0.62	19.3	30.3
Oxley	0.62	0.73	0.45	0.64	27.0	33.3
RAC655	0.60	0.72	0.50	0.61	19.8	30.0
Rosella	0.64	0.73	0.57	0.57	23.8	27.5
Tatiara	0.62	0.73	0.56	0.64	23.5	29.0
Trident	0.60	0.73	0.52	0.64	27.3	34.5
Mean	0.60	0.72	0.52	0.61	23.4	28.0
LSD (Vigour)	0.01		0.02		3.1	
Sig.	***		***		**	
LSD (CVxVigour)	0.04		0.06		10.6	
Sig.	ns		***		ns	

*** = $P < 0.001$; ** = $P < 0.01$; * = P , 0.05; ns = $P > 0.05$

When vigour was estimated using light interception (Table 4.8), the overall effect was a significant improvement in LI for the HV treatment. The NDVI and LI measurements taken at Kapunda are not as highly correlated as would be expected for measurements taken on the same day, however, it should be noted that the canopies were sparse due to late time of sowing and cold, dry growing conditions. This may have adversely affected the ceptometer more than the spectral radiometer as the LSD for NDVI was relatively small compared to the corresponding LSD for LI (Table 4.8).

Table 4.9 Vegetative biomass and leaf area at mid tillering for plants grown in field experiments at Roseworthy and Kapunda in 1994. Data represent the interaction of cultivar with vigour treatment as well as the main vigour treatment effects.

	Roseworthy 1994 - 48 DAS				**Kapunda 1994 - 58 DAS**			
	Dry Matter (g/m^2)		**LAI**		**Dry Matter (g/m^2)**		**LAI**	
	LV	**HV**	**LV**	**HV**	**LV**	**HV**	**LV**	**HV**
Aroona	12.1	22.8	0.65	1.23	38.2	55.1	0.70	1.08
Corrigin	10.0	20.0	0.56	1.24	33.0	45.5	0.63	0.90
Excalibur	8.6	20.5	0.50	1.08	32.6	50.5	0.67	0.76
Kulin	12.5	21.6	0.62	1.23	28.5	38.7	0.53	0.87
Lowan	11.3	16.4	0.55	0.99	29.3	47.0	0.59	0.96
Maya 74	12.6	21.0	0.63	1.09	37.0	57.7	0.72	1.06
Machete	11.4	20.7	0.68	1.11	47.0	67.2	0.96	1.27
Oxley	12.4	17.1	0.58	1.06	30.3	55.2	0.50	0.96
RAC655	13.6	22.5	0.73	1.06	32.7	58.7	0.58	1.12
Rosella	12.0	21.1	0.65	1.15	28.5	54.5	0.52	1.18
Tatiara	13.5	24.1	0.69	1.17	41.0	63.7	0.84	1.25
Trident	12.9	21.1	0.57	1.16	33.5	59.2	0.74	1.09
Mean	11.9	20.7	0.62	1.13	34.3	54.4	0.66	1.04
LSD (Vigour)	0.9		0.08		4.3		0.12	
Sig.	***		***		***		***	
LSD (CVxVig)	3.1		0.27		15.1		0.43	
Sig.	ns		ns		ns		ns	

*** = P < 0.001; ** = P < 0.01; * = P , 0.05; ns = P > 0.05

All genotypes responded in a similar fashion to the vigour treatment with large increases in DM and LAI under the HV treatment. Dry matter was increased by 74% and LAI by 82% under the HV treatment at Roseworthy and approximately 58% for each variable at Kapunda. This represents a very large response to the higher levels of inputs, irrespective of genotype and is in agreement with the NDVI data at Roseworthy.

4.3.2.1.2 Grain yield

Grain yield was significantly reduced under the HV treatment at both sites (Table 4.10). There was a genotypic interaction with vigour treatment for grain yield at Kapunda that was not present at Roseworthy. Despite the general trend for grain yield to decrease under the HV treatment, both experiments contained many cultivars that maintained yield under the HV treatment. Where significant differences were present, grain yield was always reduced under higher inputs.

Table 4.10 Grain yield and thousand grain weight for plants grown in field experiments at Roseworthy and Kapunda in 1994. Data represent the interaction of cultivar with vigour treatment as well as the main vigour treatment effects.

	Roseworthy 1994				**Kapunda 1994**			
	Grain Yield (g/m^2)		**TGW** (mg)		**Grain Yield** (g/m^2)		**TGW** (mg)	
	LV	**HV**	**LV**	**HV**	**LV**	**HV**	**LV**	**HV**
Aroona	189	143	34.8	28.9	124	106	36.4	33.8
Corrigin	156	139	26.1	22.9	122	112	27.8	25.4
Excalibur	161	126	31.5	31.2	145	121	35.2	32.4
Kulin	156	136	31.6	29.0	110	130	36.0	32.9
Lowan	140	146	28.7	28.4	96	89	31.9	30.6
Maya 74	142	145	36.2	36.1	106	91	37.2	36.3
Machete	146	108	35.2	32.7	78	31	39.4	37.9
Oxley	140	109	30.2	31.3	98	110	30.0	29.1
RAC655	169	146	38.7	37.2	118	95	39.5	36.1
Rosella	79	69	33.7	33.8	60	47	30.4	28.7
Tatiara	137	119	31.2	33.0	130	91	32.2	29.0
Trident	138	94	30.1	30.3	142	128	33.7	32.5
Mean	146	123	32.3	31.2	111	96	34.1	32.1
LSD (Vigour)	8.4		0.6		7.5		0.5	
Sig.	***		***		***		***	
LSD (CVxVig)	29.1		2.2		26.1		1.7	
Sig.	ns		***		*		ns	

*** = $P < 0.001$; ** = $P < 0.01$; * = P , 0.05; ns = $P > 0.05$

Thousand grain weight was also reduced significantly by the HV treatment, although there was an interaction with genotype for TGW at Roseworthy. This interaction showed that certain cultivars had similar grain size for both the LV and HV treatments, but other cultivars had reduced grain size under the HV treatment. Grain size was never significantly increased under the HV treatment.

4.3.3 Discussion

The estimated vigour measurements (NDVI & LI) were highly correlated with the destructive vigour measurements (LAI & DM) at both sites. All cultivars at Roseworthy behaved in a similar manner, with increased ground cover under the HV treatment. At Kapunda, early vigour (both estimated and actual) was either increased or not affected by the HV treatment. The variable response produced an interaction between NDVI and genotype at Kapunda (Table 4.8) but no interaction for LI, DM or LAI. Closer examination reveals that the trends are similar for LI, DM and LAI, however, the error is too large to produce an interaction at this site. This could be a function of the dry conditions combined with the heavy soil (see Table 3.1) which would tend to increase variability.

No genotypes were adversely affected by the HV treatment. This is not unexpected, as increasing the agronomic inputs will simply allow the plants to reach the biologically determined maximum biomass more quickly (Donald and Hamblin, 1976).

It appears the NDVI measurements at Kapunda were more sensitive than the LI measurements. This was probably due to the small amount of ground cover and low LI readings, meaning the ceptometer found it difficult to resolve differences. The lower variability in NDVI reading using the spectral radiometer enabled comparisons to be drawn between vigour treatments within cultivars and was the reason for the significant interaction. This also suggests that the spectral radiometer is a useful indicator of early vigour as it had a better resolution than for destructive measurements.

The reduction in grain yield at both sites under the high vigour treatment is likely to be due to increased inter-plant competition, exacerbated by the dry conditions. The heavier soil at the Kapunda site meant that this experiment actually produced a lower mean grain yield than at Roseworthy (Table 4.10), despite having a greater seasonal rainfall.

Interplant competition may have produced the genotypic interaction with vigour treatment, as the plants were under greater moisture stress which would tend to magnify any adaptive traits such as larger root biomass or greater grain filling ability. Cultivars were either unaffected or were negatively affected (Machete, RAC655 and Tatiara) by the higher inputs. There were no genotypes that had a significant positive yield response to the high HV treatment.

Phenology plays a crucial role in the adaptation of cultivars to the local environment, particularly in dry years under later times of sowing (Regan *et al.*, 1997). The effect of early maturity is to increase the ratio of post:pre anthesis water use (Siddique *et al.*, 1990b). This could be of benefit as the HV treatment may have increased pre-anthesis moisture usage at the expense of post-anthesis moisture availability (Passioura, 1977). Using these two assumptions, it could reasonably be expected that earlier maturing cultivars (Aroona, Kulin and Maya 74) might be more responsive to the HV treatment. Maya 74 is an extremely early maturing variety and should have been most able to utilise the higher inputs, however the failure of even this cultivar to respond to the HV treatment, highlights the fact that the high input system experienced too much inter-plant competition for moisture.

4.4 General discussion

4.4.1 Early vigour

The series of experiments reported in this chapter have consistently shown that increasing sowing rate and nitrogen supply can enhance early vigour. When the two variables were combined as a package in Experiment 1 (1993) and Experiments 6 and 7 (1994), large increases in vegetative DM of up to 74% were achieved (Figure 4.3).

Sowing rate had a much larger effect on early biomass than nitrogen supply. Average increases in vegetative DM ranging between 32 - 69% were observed when sowing rate was increased from 200 - 400 plants/m² (Figure 4.3). This was compared to increases in tillering biomass of between 6 - 15% when nitrogen fertiliser was increased from 20 kg/ha to 80 kg/ha. It is also clear from Figure 4.3 that there was a large variation in the expression of early vigour between experiments, when sowing rate was doubled.

The increase in sowing rate from 170 / 240 seeds/m² in Experiment 1, to 200 / 400 seeds/m² in subsequent experiments, produced larger growth differences between the density treatments. This meant that LAI went from a level too low to affect E_{sc} in 1993, to a situation where the higher sowing rate in 1995 approached levels where soil evaporation could reasonably be expected to be reduced (Ritchie, 1972). However, the maximum LAI was still below the required level of LAI = 3 suggested by Fischer and Kohn (1966).

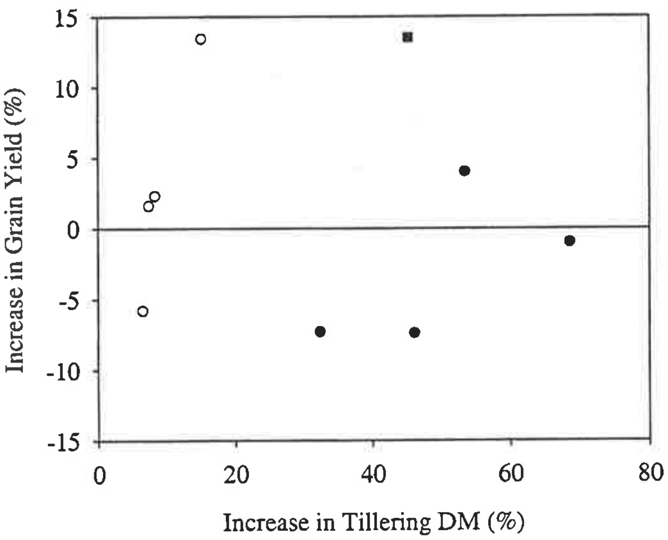

Figure 4.3 Percentage increase in tillering DM and grain yield due to the HV treatment growing under rainfed conditions in 1993 (■); or sowing rate (●) and nitrogen (O) at Roseworthy and Kapunda in 1994 and 1995.

The largest differences in ground cover occur when moving from low to moderate density (TeKrony and Egli, 1991), whereas the low sowing rate of 200 plants/m² was the recommended rate for the Roseworthy environment (Taylor *et al.*, 1991). The increases in early vigour would have therefore been larger if, for example, sowing rates of 100 plants/m² and 300 plants/m² were used. However, since the LAI at 400 plants/m² was only just approaching the target levels, it is anticipated that reducing the sowing rate below 200 plants/m² would have no impact on E_{sc} at all and as such, could not provide any benefit in WUE.

The variability in maximum LAI between the different seasons illustrates one major drawback in using plant density as a tool for increasing early vigour in this environment. The fact that only one season in three produced adequate biomass to possibly reduce E_{sc} would indicate that this strategy might not be worth pursuing in this environment.

4.4.2 Grain yield

It is evident from Figure 4.3 that there was a highly variable relationship between early vigour achieved through agronomic manipulation and grain yield. Grain yield was more variable when vigour was increased using higher sowing rates, compared to when vigour was increased using higher fertiliser N rates.

The yield-vigour relationship was dependent on growing season rainfall as can be seen from the positive yield response to the HV treatment under irrigation in 1993 and a similar response to high nitrogen at the highest rainfall site (K95). The low rainfall in 1994 showed that negative associations between early vigour and grain yield were possible, despite the absence of such a relationship under rainout shelters in Experiment 1. Two possible reasons for this include the fact that inputs were increased in 1994 compared to 1993; and that anthesis biomass was lower in 1994 due to the late sowing, drier pre-anthesis period and heavier soil type.

In trials where increased sowing rates have been successful in improving grain yield under similar rainfall conditions, plant density has been increased from less than 100 plants/m² to 200 plants/m² (Anderson, 1992) or 340 plants/m² (Tompkins *et al.*, 1991). While some reduction in E_{sc} in these trials was acknowledged, it was an increase in anthesis biomass and timely rainfall which generally promoted grain yield. This supports the variable results found in Experiments 1-5 and reinforces the yield risk associated with increasing early vigour via plant density.

4.4.3 Genotypic effects

The fact that all genotypes responded in a similar fashion to the high density-fertiliser package with increased vegetative biomass in both trials, yet only certain genotypes suffered a yield reduction under conditions of moisture stress, indicates a genotype x environment interaction. Some genotypes could provide a greater yield potential (anthesis DM) under higher inputs and could maintain production under adverse conditions. Therefore, it would appear that genotype has a role to play in agronomic vigour packages.

The cultivar which consistently yielded well (Trident) did not display the greatest vigour. This may mean that either early vigour was not important for grain yield in these experiments or that if vigour could be improved in Trident, then yield may be further increased. Given the dry conditions in 1994 (see Table 3.2), it is more likely that early vigour was not as important as other drought response mechanisms for grain yield in that particular growing season.

The late sowing date and extremely dry conditions experienced at both sites in 1994 are likely to have reduced the genotypic differences in DM production. While a genotypic response to the high and low vigour packages would be expected under normal circumstances, the short growing season reduced the total biomass so percentage differences were smaller. This had the effect of increasing the variability and made it difficult to resolve any common genotypic response to the vigour treatments. Under more typical rainfall patterns the early maturing genotypes may have provided a greater response to the HV treatment.

4.4.4 Viability of promoting early vigour agronomically

Pursuing high input agronomic strategies for increasing early vigour will only be of benefit to grain yield if there is adequate post-anthesis moisture available. The fact that the most reliable rainfall occurs early in the season but that E_{sc} is unlikely to be reduced means that the crop still relies to some extent on stored soil moisture. This work has shown that the variable post anthesis rainfall makes yield increases under this system less reliable.

The use of early maturing genotypes would reduce pre-anthesis water use (Siddique *et al.*, 1990b) and could possibly alleviate the competition effects that were evident under the high input treatments. There was some evidence of this in Experiments 6 and 7 but the extremely dry conditions experienced in that year meant that the results were inconclusive. Given the small differences in maturity date, it is likely that other genotypic differences such as root growth / activity may have also had an effect.

The fact that only two levels of each variable were investigated is a drawback of this investigation, since it is not possible to ascertain the vigour response to either density or nitrogen supply with only two data points. However, given that the highest levels of N and plant density were only marginal in their anticipated impact on E_{sc}, yet these levels were able to elicit negative yield responses, demonstrates that greater levels of ground cover were required but that they are likely to negatively affect grain yield.

Given the fact that there is little evidence to suggest that we can reduce E_{sc}, using plant density or nitrogen application alone, anthesis DM and partitioning of water use become the driving force in the yield equation. While it is true that improving early vigour may be of benefit to grain yield in some circumstances (Richards, 1991), it is evident that yield can also be negatively affected by competition for resources, principally moisture. The recommended sowing rate (180 plants/m² for Roseworthy) takes a more conservative approach to yield formation which may produce lower yield variability. Thus, improving early vigour above current levels cannot be generally regarded as desirable with the use of current genotypes at recommended sowing rates in this region.

4.5 Conclusions

The promotion of early vigour using increased inputs did not consistently result in higher grain yields. This was presumably due to increased inter-plant competition. The greatest increases in grain yield were achieved either when irrigation was supplied in the post anthesis period or when there was significant and timely rainfall during grain filling.

Increasing plant density was shown to be a powerful tool for improving early vigour, however benefits were limited by inter-plant competition affecting moisture availability. All genotypes responded similarly to increased sowing rate and nitrogen supply, and the use of early maturing genotypes could not reduce post-anthesis moisture stress. Unless E_{sc} or inter-plant competition for moisture can be reduced, the erratic rainfall experienced in southern Australia would limit the effectiveness of this agronomic early vigour strategy.

CHAPTER 5

5. The effect of plant density on early vigour and grain yield in high and low tillering genotypes.

5.1 Introduction

Experiments described in Chapter 4 showed that increasing sowing rate and nitrogen supply increased early vigour but produced variable responses in grain yield. Two reasons for these inconsistent responses to early vigour were suggested: firstly, there was insufficient ground cover to reduce E_{sc} and secondly, interplant competition for moisture was increased in the post anthesis period, which reduced HI.

It may be possible to increase ground cover to a level where E_{sc} is reduced by using more vigorous plant types. While the experiments in Chapter 4 did not reveal any genotypic interaction with sowing rate for LAI at 57 DAS, the genotypes used were all commercial cultivars and were morphologically quite similar. If vigorous genotypes were selected from a wider range of experimental and breeding lines, then it may be possible to elicit larger improvements in early vigour through genotype x density interactions.

In previous work conducted to identify vigorous genotypes, two different plant morphologies emerged as being vigorous; namely genotypes that produce large leaves on few tillers or genotypes that produce smaller leaves on many tillers (Regan *et al.*, 1992). High tillering ability has been identified as a vigour trait in crop-weed competition studies (Lemerle *et al.*, 1996a) and comparisons between wheat and barley (a highly vigorous crop) have also revealed large differences in tillering ability (López-Castañeda and Richards, 1994b).

The characters of large leaves and limited tillering are displayed in gigas wheats (Atsmon and Jacobs, 1977). However, since gigas wheats have been largely used under high fertility situations, little information is available on their potential to improve early vigour. No studies have specifically compared the genotypic variation in early vigour between gigas types and high tillering lines.

Genotypic selection could also be used to overcome the second problem with the high density vigour strategy identified in Chapter 4; namely, the reduction in interplant competition for moisture and other resources. Donald (1968a) proposed an ideotype for communal planting at high density which had short stature, limited tillering, short erect leaves and a large spike. It was hypothesised that a single culm with a large spike would create a high HI, and reduced tiller mortality would help maintain HI under stress. The gigas genotypes possess the essential features of this ideotype, but also possess broad leaves that may increase early vigour. It remains to be seen if this plant type can improve the partitioning of water use and enhance grain yield.

The two contrasting plant morphologies (low tillering and large leaves; high tillering and small leaves) would make it difficult to incorporate selection for early vigour into wheat breeding programs based on morphology. However, the availability of high and low tillering experimental lines offers the opportunity to investigate the role of these contrasting morphological traits in promoting early vigour. The inclusion of a range of sowing rates also enabled the comparison of genotypic and agronomic vigour effects, and examination of the relationship between early vigour and grain yield under local dryland conditions. Data are presented separately from Experiment 1 and Experiment 2, followed by a combined discussion of the results.

5.2 Experiment 1: Plant density x tillering ability

Early vigour can be promoted in commercial cultivars by increasing plant density or by using high tillering, competitive genotypes. Since tillering ability is reduced at high plant density, the two strategies for increasing early vigour would appear to be mutually exclusive. To examine this relationship two low tillering gigas type wheats, derived from crosses made by C.M. Donald which were subsequently selected by the Roseworthy Wheat Breeding Program, and two high tillering breeding lines from the Roseworthy Wheat Breeding program were sown at 4 densities in a field experiment at Roseworthy. In addition, 4 commercial cultivars, including 2 low tillering, semi-dwarf types (Excalibur and Kulin), and two freely tillering, taller wheats (Frame and Halberd) were included.

5.2.1 Materials and methods

Four breeding lines and four commercial cultivars (Table 5.1) were sown at densities of 100, 200, 300 and 400 plants/m^2 in a factorial experiment with 3 replicates. The trial was sown at Roseworthy (Field N2a) on 12 June 1996 using a 6 row cone seeder with spear points and press wheels (see section 3.3). The seed bed had been cultivated and cross-harrowed, with the herbicide Glean® (20 g/ha) applied and incorporated before sowing. The seeds were sown at a depth of 40mm into good soil moisture and 130 kg/ha of 19:13:0 N:P:K fertiliser was applied with the seed. Paired plots were sown of which one was used for destructive sampling and the other harvested at maturity. The experiment was laid out in a randomised complete block design.

Table 5.1 Morphology and origin of experimental lines and commercial cultivars used in field experiments.

Cultivar	Tillering Ability	Height	Origin
92SR3-415[1]	low	short	C.M. Donald (expt)
92SR4-419[1]	low	short	C.M. Donald (expt)
RAC416-1[2]	high	short semi-dwarf	Roseworthy (breed)
92SR10-413[1]	high	moderate	Roseworthy (breed)
Excalibur	moderate	semi-dwarf	Roseworthy (1991)
Kulin	low	semi-dwarf	WA Ag. (1985)
Frame	high	tall semi-dwarf	Waite (1995)
Halberd	high	tall	Roseworthy (1969)

[1] Refers to accession number in the Roseworthy Plant Breeding Unit

[2] Refers to advanced selection number in the Roseworthy Plant Breeding Unit

Coleoptiles were first observed 9 DAS and the mean date of emergence was 10 DAS. Emergence counts were conducted 27 DAS (Z12) by counting the number of plants in 50 cm sections of two drill rows in each plot. The trial site was kept free of weeds with the application of Starane® (1000 ml/ha), MCPA LVE (500 ml/ha) and Lontrel® (200 ml/ha) on 28 July. The fungicide Folicur® 430 SC was applied at 290 ml/ha on 3 October to control stripe rust (*Puccinia striiformis*).

Ground cover was estimated at 40, 54 and 60 DAS using a Cropscan multispectral radiometer; and 59 and 98 DAS using a Decagon Sunfleck Ceptometer. The methods followed those outlined in section 3.4.1. The green leaf area at 142 DAS was estimated in the field by visual assessment and expressed as a percentage of the total leaf area present (i.e. the percentage of leaf area that had not senesced).

Destructive harvests were taken at 57 DAS (Z22-25), anthesis (Z65) and maturity by removing 50 cm of drill row from the centre 4 rows of each plot. Vegetative measurements included DM, leaf area, SLW, plant number and tiller number. Anthesis and maturity measurements were similar to vegetative measurements with the exception of leaf area and SLW. Maturity measurements included yield components (spike number, grain number, thousand grain weight) and HI. A mechanical grain harvest for yield comparison was conducted on the intact plots on 17 December using a Wintersteiger plot harvester.

Results were statistically analysed using Genstat 5. There was some transient waterlogging of the trial site, however, this was restricted to the first replicate. For this reason, analysis for Harvest 1 was conducted on the data from replicates two and three only. The layout of the RCBD was able to account for this effect.

5.2.2 Results

5.2.2.1 Early Vigour

A good, even plant establishment was achieved for each density treatment, with average plant populations of 112, 221, 317 and 414 plants/m² at 27 DAS. There were no differences in plant emergence or establishment between genotypes. Radiometer reflectance measurements (NDVI) revealed significant differences in ground cover at 40 DAS (Figure 5.1). Plant density had a highly significant effect on the NDVI but there was no interaction with genotype. The largest difference in NDVI was between densities of 100 and 200 plants/m². Plant density was positively correlated with ground cover up until 300 plants/m² (Figure 5.1 (a)). By 60 DAS the differences between 200, 300 and 400 plants/m² were not detectable using NDVI (Figure 5.1 (b)) or LI (Figure 5.2 (a)). There was good general agreement between plant density effects measured using the radiometer and ceptometer and similar differences in LI were still detectable at 98 DAS (Figure 5.2 (b)).

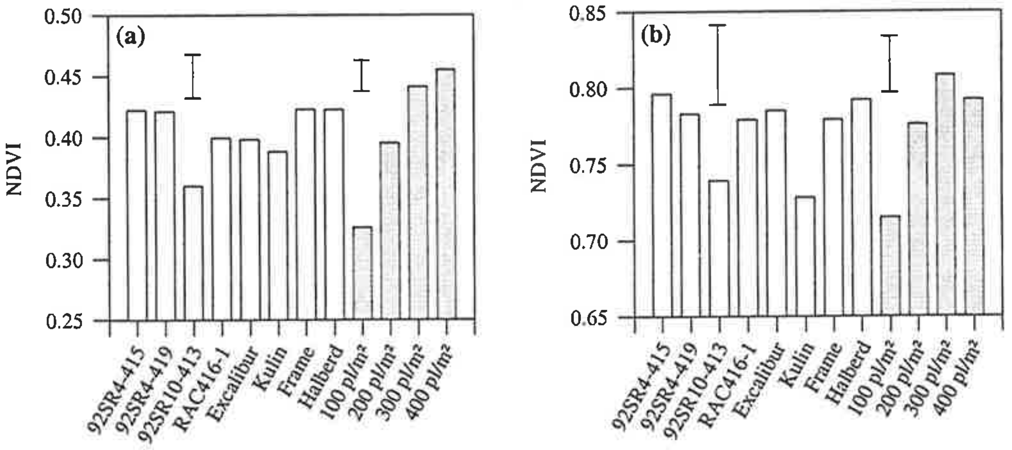

Figure 5.1 Normalised difference vegetation index (NDVI) at (a) 40 DAS and (b) 60 DAS for genotype and density treatment averages. Error bars indicate LSD.

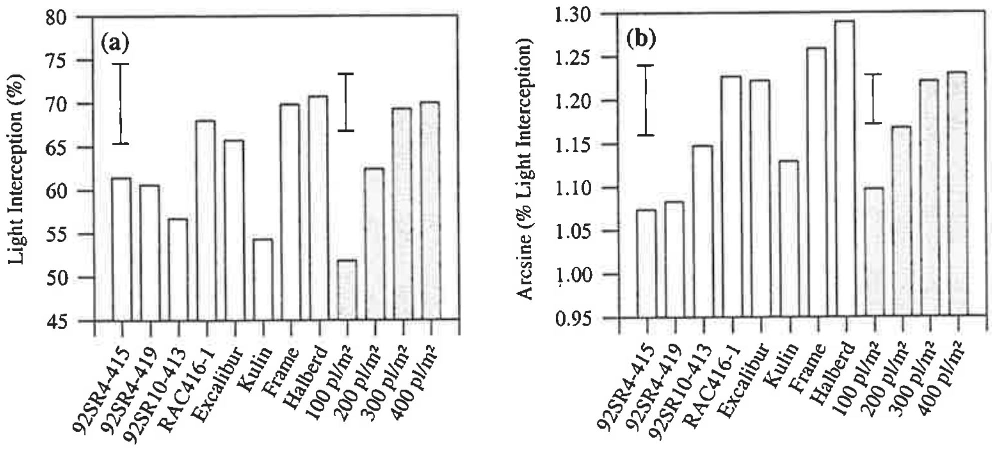

Figure 5.2 Percent light interception at (a) 59 DAS and (b) 98 DAS. Light interception values in (b) have been arcsine transformed to remove skew in the data. Error bars indicate LSD.

Genotype had a significant effect on ground cover (NDVI) at 40 DAS, with the low tillering lines (92SR4-415 and 92SR4-419) producing significantly greater ground cover than the high tillering line 92SR10-413 but similar ground cover to RAC416-1. There were no significant differences in ground cover between the commercial cultivars at 40 DAS, however the taller lines (Frame and Halberd) showed slightly greater NDVI.

There were still genotypic differences in NDVI between the experimental lines at 60 DAS (Figure 5.1 (b)) however they were not significant. In contrast, significant genotypic differences in LI were detected using the ceptometer 59 DAS (Figure 5.2 (a)). Kulin, a shorter, low tillering cultivar, displayed significantly less light interception than the other commercial cultivars.

Comparison of NDVI and LI for estimating ground cover show slightly different rankings across genotypes. The low tillering lines 92SR3-415 and 92SR4-419 were ranked as having equivalent ground cover to the taller cultivars Frame and Halberd using NDVI at 60 DAS (Figure 5.1 (b)) but as having less ground cover when measured using light interception at 59 DAS (Figure 5.2 (a)). The two methods were however, consistent in determining the least vigorous genotypes 92SR10-413 and Kulin.

When plant growth was measured destructively at 57 DAS, all genotypes showed a linear increase in early vigour with increasing plant density (Figure 5.3). Similar relationships were observed with LAI (Figure 5.4) and there were no genotypic differences for either variable. Despite the general linear relationships, there were indications in the high tillering lines (92SR10-413 and RAC416-1) of an asymptotic relationship which may suggest the beginning of interplant competition at high density. Average leaf area indices were relatively low at 57 DAS and were approaching 2, with the highest individual measurement being almost 2.5.

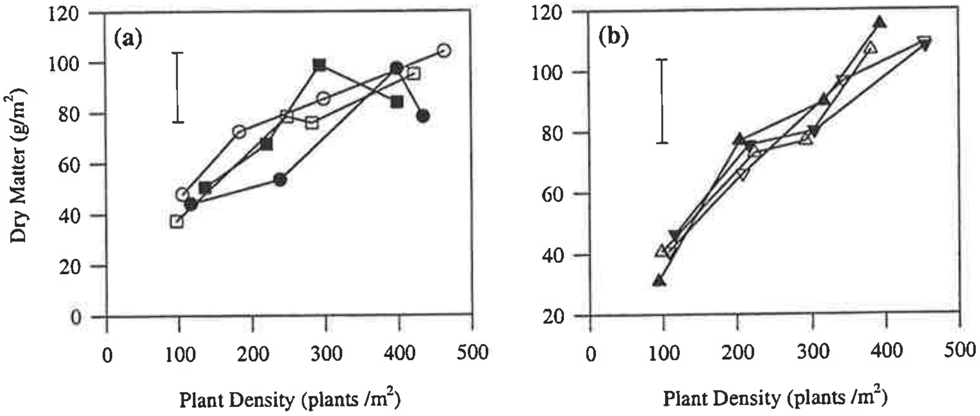

Figure 5.3 Dry matter versus plant density at 57 DAS for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

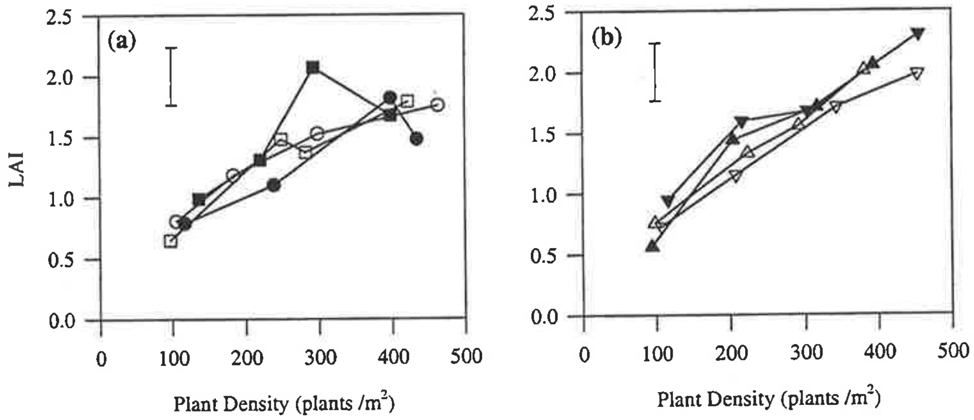

Figure 5.4 Leaf area index 57 DAS versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

Table 5.2 Correlations between different estimates of early vigour

	Plant Density	**NDVI 40 DAS**	**NDVI 60 DAS**	**LI 59 DAS**	**LI 98 DAS**	**DM 57 DAS**	**LAI 57 DAS**
NDVI 40 DAS	***						
NDVI 60 DAS	**	***					
LI 59 DAS	***	***	***				
LI 98 DAS	**	**	*	**			
DM 57 DAS	***	***	***	***	**		
LAI 57 DAS	***	***	***	***	***	***	
Tiller No. 57DAS	(***)	(***)	ns	ns	ns	(***)	(**)

*** = P < 0.001; ** = P < 0.01; * = P , 0.05; ns = P > 0.05
Values in parentheses () indicate negative correlations

The four methods of estimating early vigour (NDVI, LI, DM and LAI) were all highly correlated with each other (Table 5.2). The greater range in vigour due to plant density, relative to genotypic differences, meant there was good general agreement between all methods of vigour estimation, despite some inconsistency in genotypic vigour rankings. The negative correlation between DM and tiller number (Table 5.2) was not a function of genotypic differences in tillering, but a function of plant density, where high density increased biomass but reduced tillers per plant.

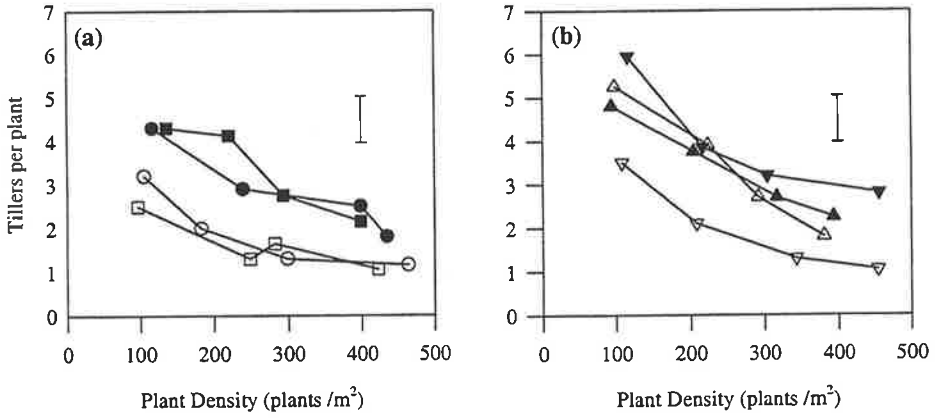

Figure 5.5 Tiller number per plant at 57 DAS for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

Tiller number per plant declined with increasing plant density (Figure 5.5). The high tillering lines produced almost twice as many tillers as the low tillering lines at any given density. The low tillering lines did produce some tillers, however, this was only at 100 plants/m². At a density of 400 plants/m² these lines only produced one (mainstem) tiller per plant, whereas the lines 92SR10-413 and RAC416-1 still produced about 2 tillers per plant.

With the exception of Kulin, the high tillering experimental lines produced fewer tillers than the commercial cultivars. Excalibur was selected as a higher tillering cultivar, however this line produced many small tillers which senesced soon after they appeared. The most freely tillering cultivar was Halberd with almost 6 tillers per plant at 100 plants/m², almost 2.5 times that of 92SR4-419. Even at 400 plants/m² Halberd produced over 3 tillers per plant for a total tiller density in excess of 1200 tillers/m², whereas Kulin produced only mainstems at density greater than 300 plants/m². The size of individual plants decreased with increasing plant density (Figure 5.6), which is consistent with the reduction in tillering at high density observed in Figure 5.5.

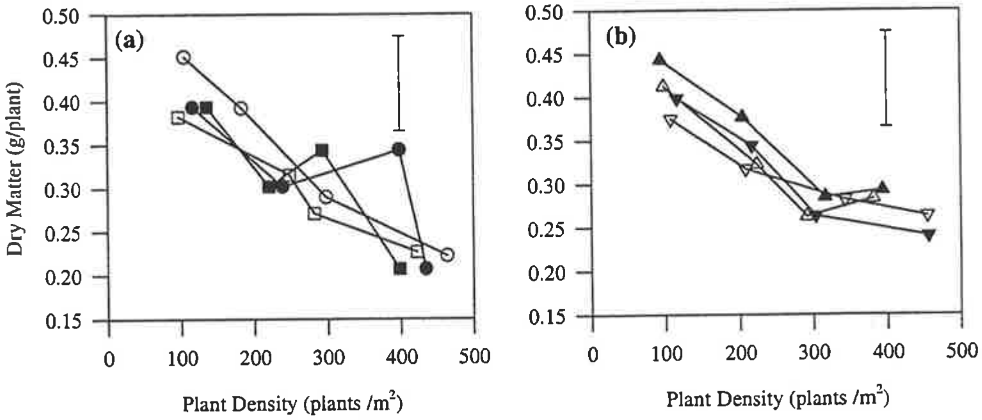

Figure 5.6 Dry matter per plant 57 DAS versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

The results clearly show that increasing plant density promotes early vigour irrespective of the tillering capacity. However, the data also show that the size of the response will depend on the time of measurement, as displayed by the fact that there were significant differences between 200 and 300 plants/m² at 40 DAS but not at 60 DAS. It was also evident that a plant density of 400 plants/m² did not significantly increase early vigour over a density of 300 plants/m² when measured at 57 DAS.

5.2.2.2 Leaf senescence

Leaf senescence was estimated as the percentage green leaf calculated from visual assessment during early grain filling and showed large genotypic and density effects (Figure 5.7). The later flowering commercial cultivars (Frame and Halberd) had relatively uniform percentage green leaf across the range of density treatments, whereas the early maturing line Kulin displayed a sharp decrease in percentage green leaf as density increased from 100 to 300 plants/m².

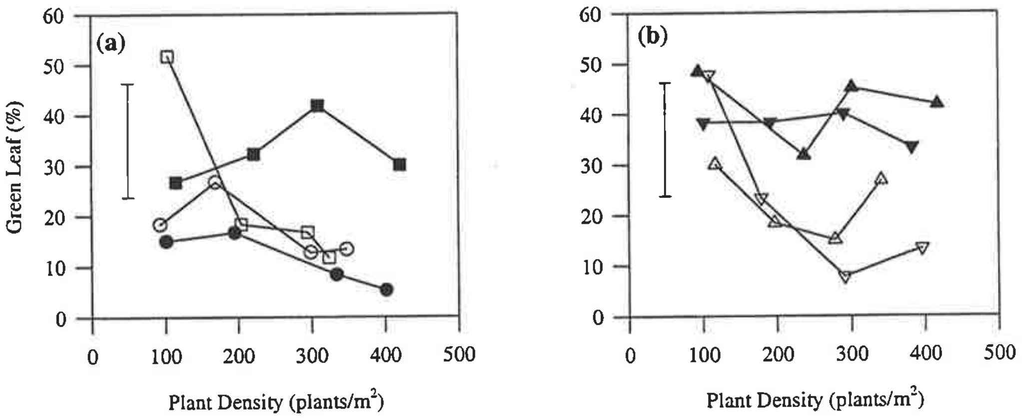

Figure 5.7 Estimated percentage of leaf area which was green 142 DAS for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

The percentage green leaf area in the low tillering line 92SR4-419 was highly affected by plant density, whereas the high tillering line RAC416-1 was not. The very low levels of green leaf area at density >300 plants/m² compared to the commercial cultivars (RAC416-1 excepted), indicates higher levels of stress during grain filling and poor adaptation in these genotypes.

5.2.2.3 Grain Yield

Significant genotypic differences in grain yield were observed, with the commercial cultivars generally out yielding the experimental lines (Figure 5.8). Kulin had the highest yield whilst the low tillering line 92SR4-419 had the lowest yield. Of the experimental lines, the locally adapted senior breeding line RAC416-1 produced the highest yield, which approached the yields of the commercial cultivars.

Neither early vigour or tillering ability were significantly correlated with grain yield (Table 5.3). Harvest index and TGW were highly correlated with each other and were the strongest determinants of grain yield (Table 5.3). Thus it would appear that all treatments were able to produce enough grains to fulfil the yield potential for this environment, although this will be discussed later in more detail. There was a negative correlation between grain yield and anthesis date, where earlier flowering genotypes produced greater grain yield (Table 5.3).

Table 5.3 Correlation between early vigour and grain yield

	Plant Density	**DM 57DAS**	**LAI 57DAS**	**Tiller No. 57DAS**	**DM Anth.**	**Anth. Date**	**TGW**	**Grain Yield**
DM 57 DAS	***							
LAI 57 DAS	***	***						
Tiller No. 57DAS	(***)	(***)	(**)					
DM Anthesis	ns	*	**	ns				
Anthesis Date	ns	ns	ns	ns	ns			
TGW	ns	ns	ns	ns	ns	ns		
Grain Yield	ns	ns	ns	ns	ns	(*)	***	
HI	(**)	(*)	(**)	ns	ns	*	***	***

*** = P < 0.001; ** = P < 0.01; * = P , 0.05; ns = P > 0.05
Values in parentheses () indicate negative correlations

Plant density had no effect on the grain yield of all of the genotypes investigated (Figure 5.8) and grain yield per plant decreased exponentially as density increased (Figure 5.9). The largest reduction occurred between 100 and 200 plants/m^2 and at the lowest density the commercial cultivars had generally better yield per plant than the experimental lines. At the highest density there was no difference in yield per plant between any of the genotypes. Notably, there was no difference in yield per plant between high and low tillering types at any density (Figure 5.9 (a)). The low tillering lines failed to maintain yield per plant as density increased, indicating that inter-plant competition had a similar effect on all lines.

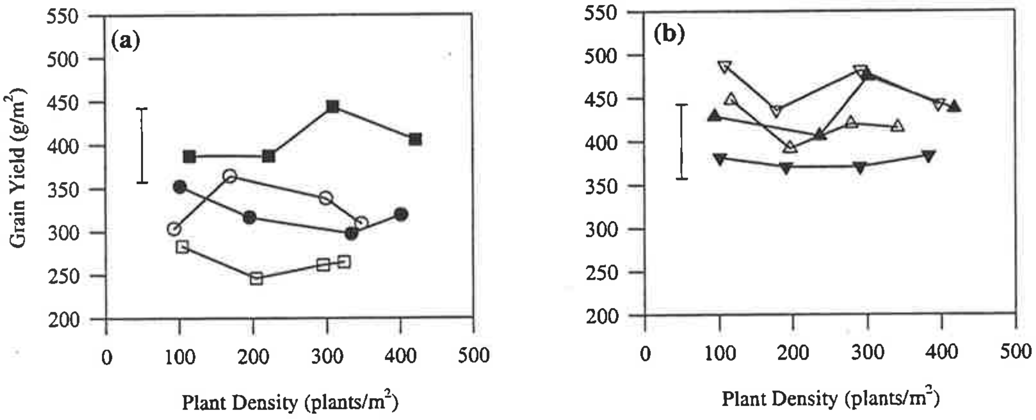

Figure 5.8 Grain yield versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

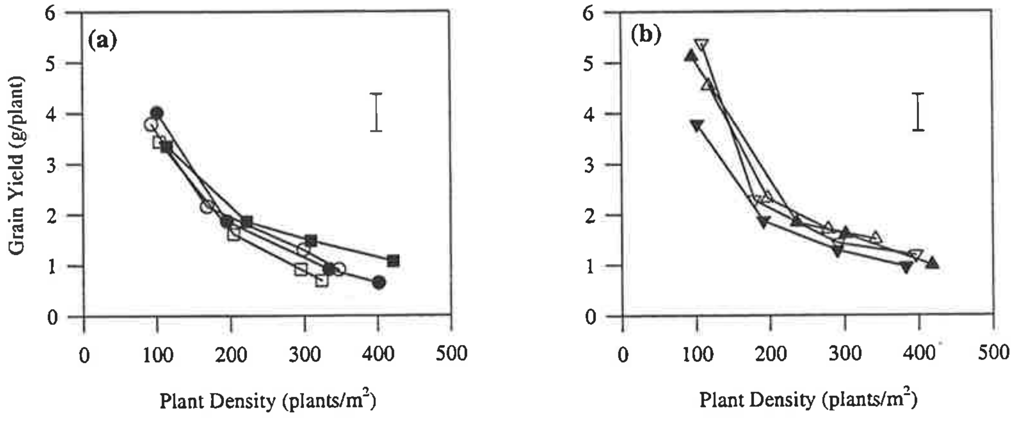

Figure 5.9 Grain yield per plant versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

The relative differences in biomass at anthesis between sowing rates were much smaller than sowing rate differences in biomass during early vegetative growth. This may reflect greater interplant competition at higher densities and compensatory growth at lower densities. The high tillering experimental lines generally produced greater anthesis biomass and grain yield than the low tillering experimental lines (Figure 5.10 (a)). The high tillering commercial cultivars also produced generally greater anthesis biomass than the lower tillering commercial cultivars, however there were no differences in grain yield.

The commercial cultivars produced adequate biomass to achieve maximum grain yield at all densities. This is in contrast to the trend towards a positive correlation between grain yield and anthesis biomass in the experimental lines (Figure 5.10). This suggests that anthesis biomass may have been sub-optimal in the experimental lines.

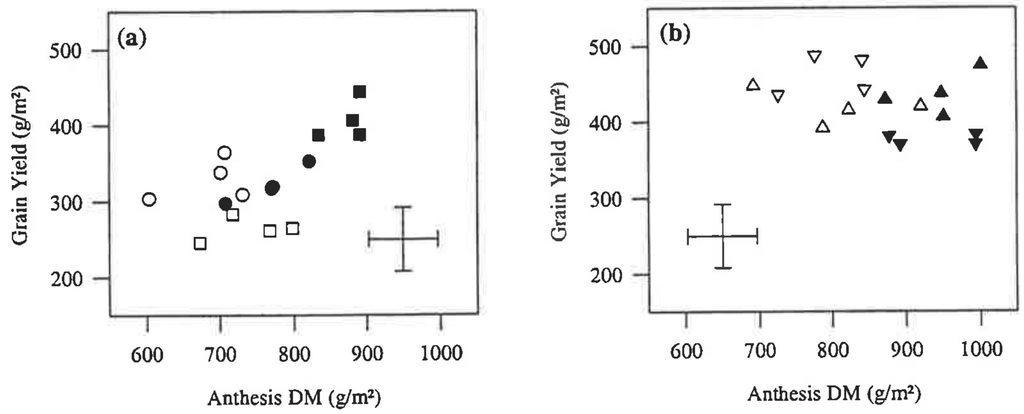

Figure 5.10 Grain yield versus above ground dry matter at anthesis for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (○); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼).

Plant density had a significant effect on the time of anthesis of some genotypes, however, the effect was generally small, with the high density treatments flowering 1 day earlier on average. In contrast, the genotypic differences in phenology produced up to 20 days difference in flowering time (Figure 5.11). The large range in phenology had a significant effect on grain yield with the early flowering lines producing the greatest yields (Figure 5.11). The earliest flowering line Kulin, showed a 5 day delay in anthesis at 100 plants/m² compared to 400 plants/m² which was associated with a reduction in grain yield of almost 10%. In comparison 92SR4-419, which reached anthesis last, showed a slight increase in grain yield at 100 plants/m² despite taking almost 4 days longer to reach anthesis than at 400 plants/m².

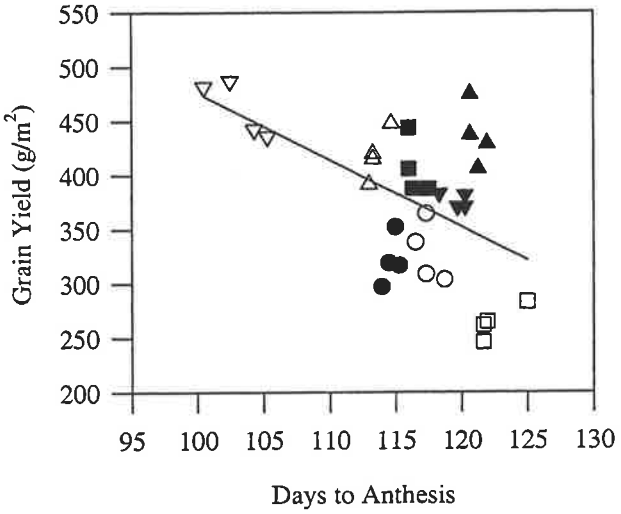

Figure 5.11 Grain yield versus time to anthesis. The four data points for each cultivar represent averages for densities of 100, 200, 300 and 400 plants/m². Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). r = 0.541 (P < 0.01).

5.2.2.4 Harvest index (HI)

There were genotypic differences in HI (Figure 5.12), however there was no genotype x sowing rate interaction. The low tillering lines generally had greater HI than the higher tillering lines, with the exception of the late maturing line 92SR4-419. Harvest index was negatively correlated with sowing rate and the response was similar for all genotypes.

Plant density had a larger effect on HI where differences in green area duration were also evident. This was reflected in the late maturing line 92SR4-419, where HI fell from 0.43 to 0.27 as density increased to 400 plants/m². In lines that were scored as having a high percentage of green leaf area during grain filling (RAC416-1, Frame and Halberd) the HI was relatively little affected by density. This could be due to the fact that these lines were able to photosynthesise and maintain grain filling for longer.

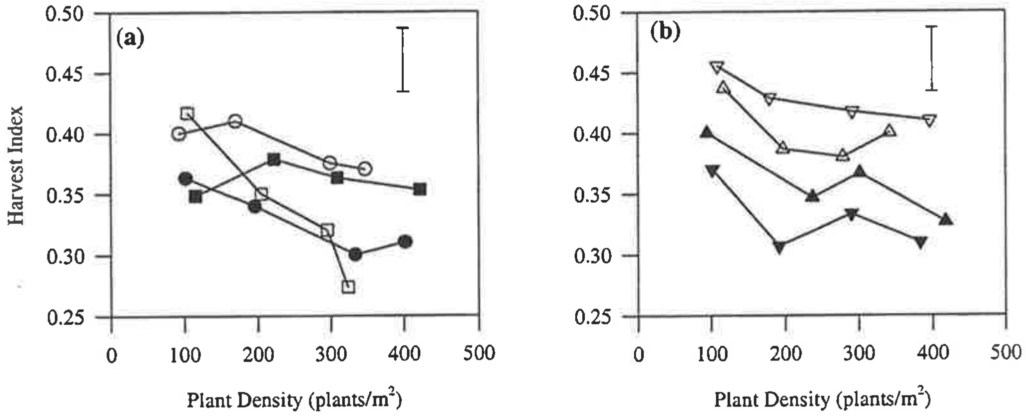

Figure 5.12 Harvest index versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

5.2.2.5 Tiller mortality

The inter-plant competition in each genotype is reflected in the loss of tillers from 57 DAS to anthesis (Figure 5.13). This is especially evident when comparing the tiller mortality of the commercial cultivars, where the lower tillering, semi-dwarf types (Kulin and Excalibur) produced fewer tillers at high plant density and consequently, fewer were aborted. It should be noted that Excalibur did produce many tillers at 100 plants/m^2 (Figure 5.5) and the corresponding tiller mortality was high. However, the sharp decrease in tiller production as density increased led to an increase in tiller survival.

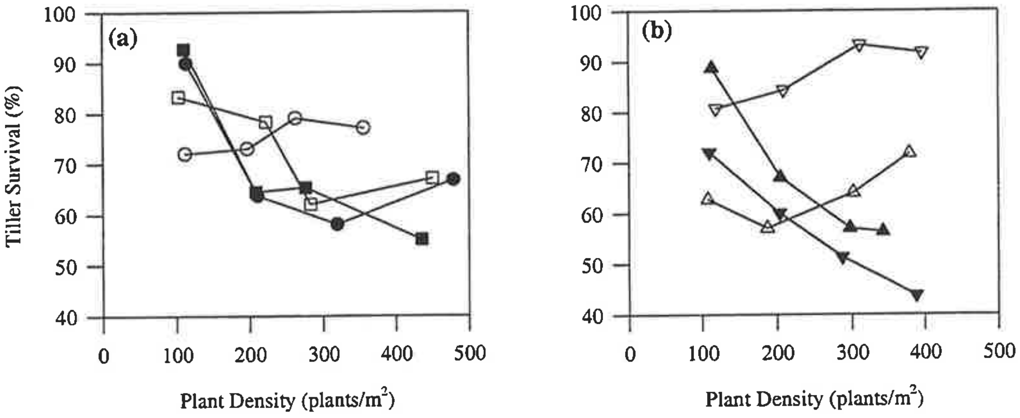

Figure 5.13 Percentage of tillers present at 57 DAS which formed spikes at anthesis for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

The more freely tillering cultivars Frame and Halberd still produced a number of tillers at high plant density and as a result more than 40% were aborted. The interaction of tillering ability with plant density for tiller survival (Figure 5.13), indicates the importance of matching tillering capacity with plant density to maximise HI.

5.2.2.6 Yield Components

Examination of the yield components (Figure 5.14) demonstrates both genotypic and plant density effects. There are large genotypic differences in the total number of spikes at maturity, with the high tillering experimental lines producing more, and the low tillering experimental lines producing fewer, spikes/m² than the commercial cultivars. Whilst the gigas type wheats had generally superior tiller survival, they experienced greater plant mortality at high plant density. Density fell from over 400 plants/m² at tillering to less than 350 plants/m² at maturity, reducing the total spike numbers. This phenomenon was not evident in these lines at lower plant densities or in the high tillering lines.

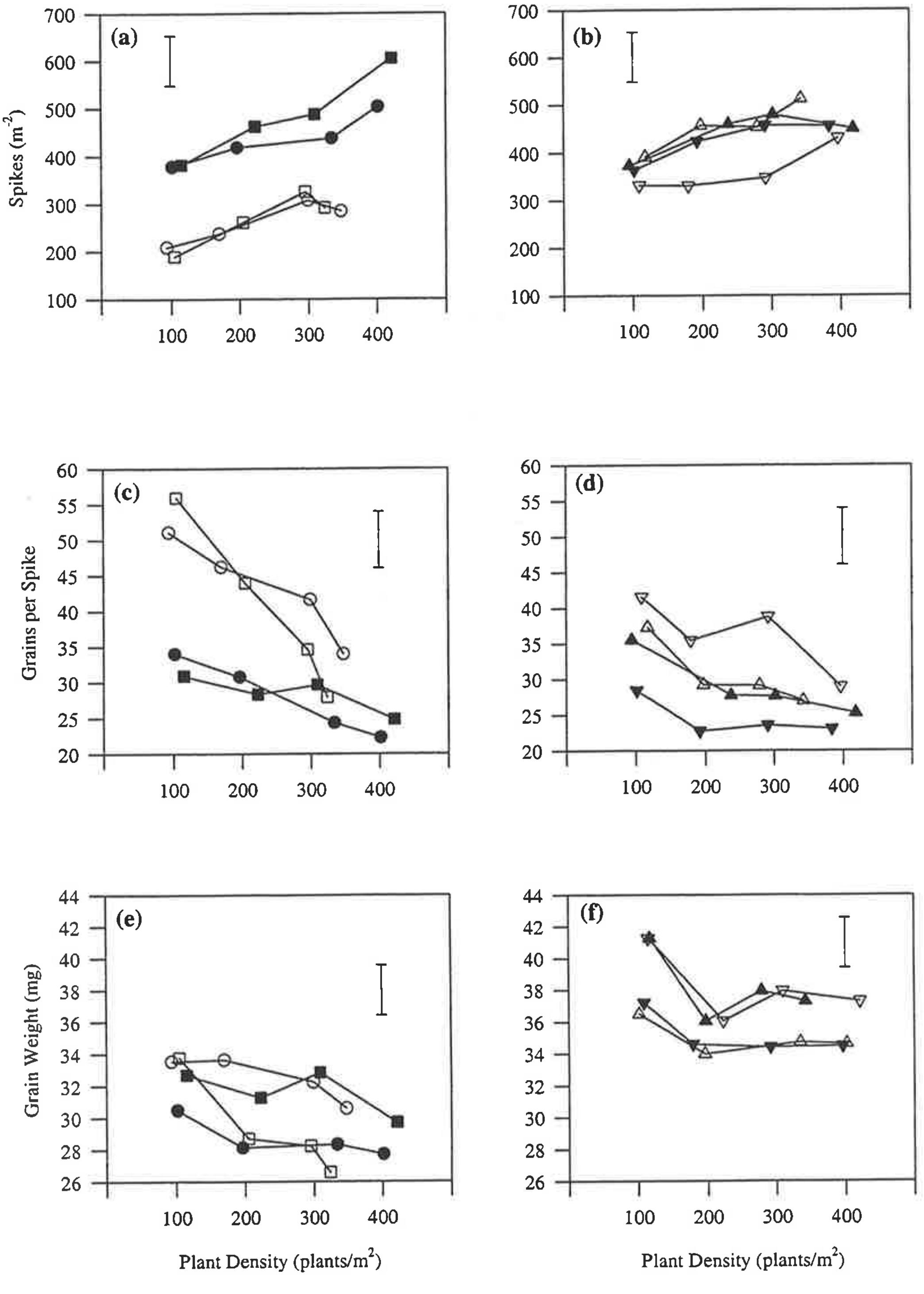

Figure 5.14 Spikes per m^2 versus plant density for experimental lines (a) and commercial cultivars (b); grains per spike versus plant density for experimental lines (c) and commercial cultivars (d); and grain weight versus plant density for experimental lines (e) and commercial cultivars (f). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

The commercial cultivars produced larger grains than the experimental genotypes (Figure 5.14 (e) & (f)), which given the large overlap in total grain number (Figure 5.15), would largely account for the general yield differences between the commercial and experimental lines. Grain weight followed a very similar trend to HI in response to plant density and could be used a an indicator of plant stress. It is evident that most genotypes produced a higher TGW at 100 plants/m² than at 200, 300 or 400 plants/m², and this would indicate lower interplant competition at this density.

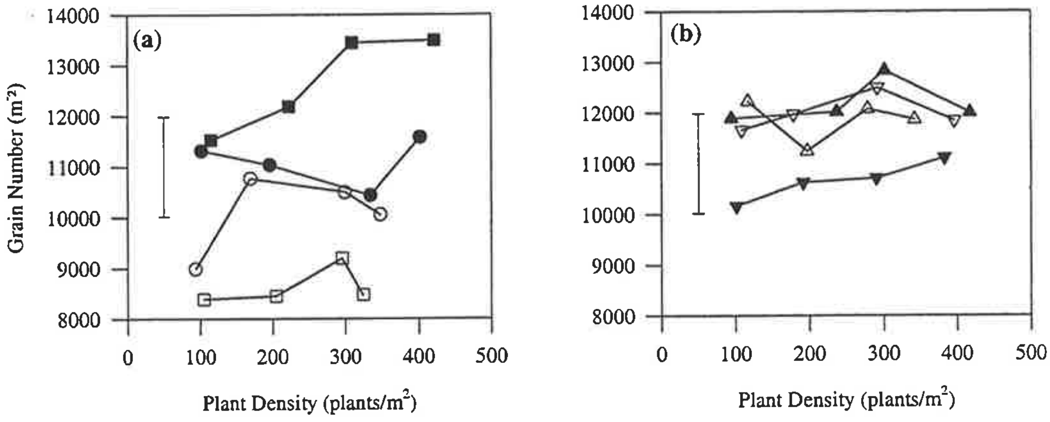

Figure 5.15 Number of grains per m² versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

The combination of high tillering and small spike size or low tillering and large spike size generally nullified any differences in total grain numbers due to plant density (Figure 5.15). The low grain numbers in the gigas type lines 92SR3-415 and 92SR4-419 (Figure 5.15) was due to the production of many sterile florets. The gigas lines produced more potential grain filling sites than the other genotypes, despite having a lower spike density. However, floret sterility meant that the number of grains per spike, while still greater than the other lines, was not large enough to compensate for the lower spike density and these lines produced fewer total grains.

The number of small grains (screenings) below accepted commercial standards (width < 1.9 mm) was not affected by plant density, however there were genotypic differences (Figure 5.16). The better adaptation of the commercial cultivars is clearly evident from the very low levels of screenings compared to those produced by the experimental lines.

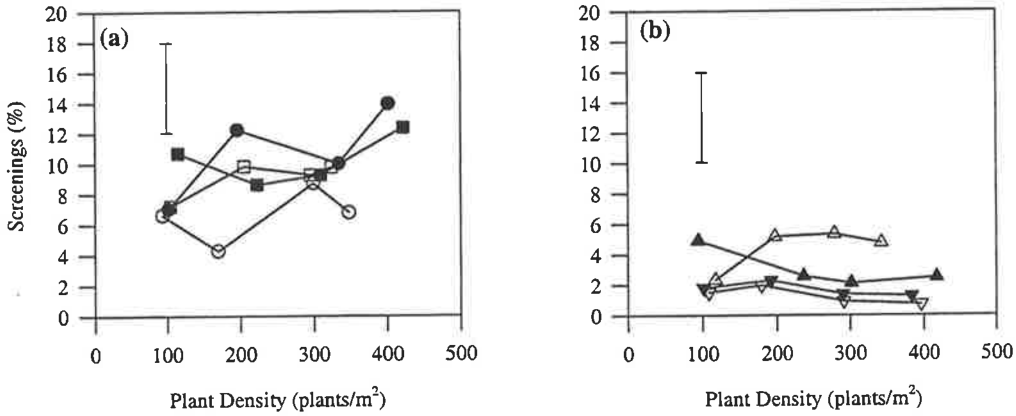

Figure 5.16 Percent screenings (grain width < 1.9 mm) versus plant density for experimental lines (a) and commercial cultivars (b). Symbols represent 92SR3-415 (O); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Kulin (∇); Frame (▲); Halberd (▼). Error bars indicate LSD.

5.3 Experiment 2: Glasshouse vigour studies

Experiment 1 showed that significant genotypic differences in early vigour (NDVI and LI) could be detected during early vegetative growth, but that these differences were not due to tillering ability. Since tillering capacity did not affect early vigour when plants were sown at rates of 100 - 400 plants/m², there must have been other intrinsic differences in plant morphology affecting early ground cover. Genotypic differences existed at 40 DAS (the earliest time of measurement) so it is likely that they existed before this time. Indeed, the vigour differences between barley (high) and wheat (low) have been shown to occur in the period from sowing to the 2 leaf stage (López-Castañeda *et al.*, 1995). Therefore it was considered necessary to investigate the increase in leaf area in the period from emergence until the onset of tillering to fully characterise early vigour in the genotypes studied.

5.3.1 Materials and methods

The 4 experimental lines and 2 commercial cultivars (Excalibur and Halberd) used in experiment 1 were grown in an evaporatively cooled glasshouse at Roseworthy with day / night temperatures in the order of 19 / 9°C. The experiment was sown on 24 May 1997 and laid out as an RCBD with 4 replicates and duplicate pots were sown for each of the two harvests.

The seed was pre-weighed to reflect the thousand grain weight (+/- 5%) and sown into unlined 150 mm diameter black plastic pots which were filled with a modified lucerne/medic mix (see Appendix A). Six seeds were sown into every pot at a depth of 35 mm and the pots were then watered to field capacity. Temperature was monitored at seed depth in three pots in representative locations inside the glasshouse.

Emergence was recorded as the number of coleoptiles in each pot which had emerged every 6 hours after the first coleoptile appeared. Time to 50% emergence was calculated by fitting sigmoidal curves to the emergence data and the percentage emergence was calculated using the final number of plants which emerged in each pot. After all plants had emerged (11 DAS) the plants were thinned to 4 plants per pot.

A destructive harvest was made 15 DAS (221 °Cd) when the plants were at the 1.5 leaf stage (Z 11.5). All four plants in each pot were cut at ground level and the material separated into leaf and stem by cutting the lamina at the collar region of each leaf. Images were recorded by placing the fully opened leaves between clear acetate sheets and photocopying them at a scale of 1:1. Leaf length and width measurements were made using the photocopied images and leaf area was recorded by scanning the images into a personal computer using a flat-bed scanner and Sci Scan image analysis software (Kirchof and Pender, 1993). Dry matter was recorded after drying the leaf material in a drying oven at 80°C for 48 hours.

The remaining (duplicate) pots were re-randomised after the first harvest and watered as necessary to ensure moisture was non-limiting. Aquasol® liquid fertiliser (see Appendix B) was applied periodically to ensure nutrients were also non-limiting.

A second harvest was made 29 DAS (405 °Cd), which was after the third leaf had fully expanded in all lines. The plants were cut in a similar fashion to Harvest 1 and the components were separated into 1st, 2nd and 3rd leaves with the remaining leaf and stem being bulked as a fourth sample. Leaf dimensions were recorded by measuring each leaf with a ruler (using the same method as for Harvest 1). However, the leaves were too large to fit between acetate sheets for photocopying and scanning (as per the method for Harvest 1) and so leaf area was measured using a Paton Scientific (Adelaide, SA) electronic planimeter. The plant parts were dried in an oven at 80°C for 48 hours and weighed.

After each harvest, the roots of all four plants (i.e. after the plants had been cut at ground level) were washed from each pot and collected by gently hosing the soil from the root mass over a plastic sieve. The operation was conducted carefully to ensure that minimal damage was done to the roots and the entire root system remained intact. The root systems from all four plants in each pot were bulked together and the roots were then oven dried at 80°C and weighed.

The data were analysed using Genstat 5 and means compared using ANOVA. Thermal time was calculated in °Cd to the nearest hour using daily maxima and minima.

5.3.2 Results

The experimental lines displayed significant differences in early dry matter production, leaf area and root weight (Table 5.4). The high tillering line RAC416-1 had the shortest time to 50% emergence and was more vigorous than all other lines except 92SR3-415, at both times of sampling. The other high tillering line 92SR10-413 had the poorest DM and LA production, while the remaining lines and cultivars were not significantly different from each other. The rankings for DM and LA were similar at both harvests.

The differences in time to 50% emergence (T50) were small and constituted less than one day. Consequently, T50 was not highly correlated with growth measurements such as leaf area or biomass.

Table 5.4 Time to 50% emergence, leaf DM and root growth up to the 3 leaf stage for high and low tillering genotypes grown in the glasshouse.

	T50[a]	Harvest 1 - 221 °Cd				Harvest 2 - 405 °Cd				RGR	RGR
	°Cd	DM mg/plant	LA cm^2/plant	Roots mg/plant	R:S Ratio	DM mg/plant	LA cm^2/plant	Roots mg/plant	R:S Ratio	Shoot g/g/°Cd x 10^3	Root g/g/°Cd x 10^3
92SR3-415	108.8	19.16	0.71	12.27	0.64	103.5	29.55	33.20	0.32	9.11	5.39
92SR4-419	111.8	18.40	0.63	10.52	0.57	99.7	28.23	35.20	0.35	9.12	6.70
92SR10-413	114.1	16.56	0.57	12.52	0.76	81.1	24.25	29.90	0.37	8.58	4.74
RAC416-1	104.9	20.71	0.73	12.09	0.58	109.4	30.90	38.00	0.35	9.00	6.85
Excalibur	105.0	17.91	0.63	10.01	0.56	95.7	27.00	27.20	0.28	9.07	5.39
Halberd	105.5	17.33	0.60	8.55	0.50	95.0	27.36	27.17	0.28	9.23	6.88
LSD	6.3	1.72	0.07	4.00	0.19	11.9	3.53	6.58	0.07	0.78	2.20
Significance	*	**	**	ns	ns	**	*	*	ns	ns	ns

*** = $P < 0.001$; ** = $P < 0.01$; * = P , 0.05; ns = $P > 0.05$

[a] Time to 50% emergence

The line RAC416-1 had the greatest root growth at 29 DAS which mirrored its good top growth. This line produced significantly greater root DM than the other high tillering line 92SR10-413 and the commercial cultivars, however the differences were generally small and were not well correlated with other vigour measurements. There were no differences in the root:shoot ratio or the relative growth rates of shoots or roots.

Table 5.5 Dimensions of the first three leaves for high and low tillering genotypes.

	Leaf length (mm)			Leaf width (mm)		
	1st	2nd	3rd	1st	2nd	3rd
92SR3-415	101.9	190.3	230.5	4.74	5.50	8.82
92SR4-419	111.3	190.6	224.0	4.76	5.34	8.76
92SR10-413	104.8	184.8	200.6	4.60	5.19	7.60
RAC416-1	104.0	182.0	241.9	4.58	4.94	6.49
Excalibur	98.8	164.5	225.9	4.04	4.59	6.04
Halberd	119.6	198.6	260.1	4.09	4.22	5.93
LSD	8.6	11.8	16.1	0.22	0.47	0.88
Significance	**	***	***	***	***	***

*** = $P < 0.001$; ** = $P < 0.01$; * = P , 0.05; ns = $P > 0.05$

There was significant variation in leaf length and leaf width among the lines examined, however the range was small (Table 5.5). Halberd produced long, narrow leaves whereas the low tillering lines produced shorter, wider leaves. The range in leaf dimensions increased with subsequent leaves and leaf width was more highly correlated with leaf area than leaf length (Table 5.6).

Table 5.6 Correlation coefficients between leaf dimensions and leaf area of the first 3 leaves at Harvest 2.

	Leaf 1	**Leaf 2**	**Leaf 3**
Length 1st	0.57		
Width 1st	0.60		
Length 2nd		0.66	
Width 2nd		0.86	
Length 3rd			0.43
Width 3rd			0.72

Significance: $r = 0.40$ ($P < 0.05$); $r = 0.52$ ($P < 0.01$)

The greater leaf area of RAC416-1, despite its relatively narrow leaves, can be explained when we consider that this line had a greater cumulative leaf length than the low tillering lines due to the greater length of the fourth leaf. This is evident in Figure 5.17 where there were 5 days difference amongst the material examined in the time taken to reach three fully expanded leaves. RAC416-1 produced an average of 3.5 leaves by the time 92SR3-415 and 93SR4-419 had produced three. The commercial cultivars (Excalibur and Halberd) and the advanced breeding line RAC416-1 produced more leaves than the experimental lines (92SR3-415, 92SR4-419 and 92SR4-413) despite having a similar rate of leaf appearance (Figure 5.17). Differences in leaf number must have occurred soon after emergence as the average leaf number varied at the first time of measurement (18 DAS) and the rates of leaf appearance were similar.

The lower total leaf area of Excalibur in comparison to RAC416-1 can be explained by the fact that it had narrower leaves, despite having similar cumulative leaf length (Table 5.5). The low tillering lines (92SR3-415 and 92SR4-419) were already beginning to show signs of the gigas characters (short stature, wide leaves) which were evident in the field.

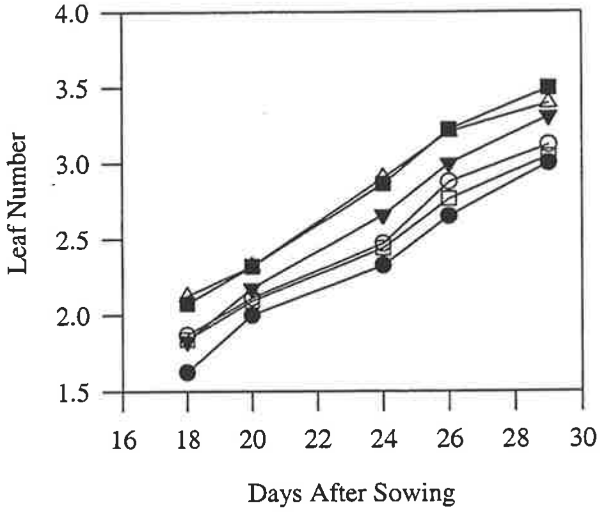

Figure 5.17 Average number of leaves per plant versus time. Symbols represent 92SR3-415 (○); 92SR4-419 (□), 92SR10-413 (●); RAC416-1 (■), Excalibur (Δ); Halberd (▼).

5.4 General Discussion

5.4.1 Early vigour

5.4.1.1 Measurement of early vigour

Despite the significant correlations between the different methods of early vigour measurement (Table 5.2), slight variation was encountered between the ranking achieved by each method (NDVI, LI, DM, LAI). However each method was able to discriminate between the least and the most vigorous lines included in this study.

Rapid screening methods using NDVI (40 DAS) and LI (59 DAS) could detect genotypic differences in early vigour, whereas DM and LAI (57 DAS) could not. It was apparent that, despite having similar amounts of leaf area, different cultivars could intercept different amounts of light. This could be due to genotypic differences in plant morphology giving rise to differences in the light extinction coefficient (k) (Yunusa *et al.*, 1993c). Since (k) should be relatively stable within a cultivar for the whole of the vegetative period (Thorne *et al.*, 1988) the remotely sensed vigour measurements should also be relatively stable over this period.

5.4.1.2 Genotypic vigour differences

Small genotypic differences in early vigour were detected using NDVI (40 DAS) (Figure 5.1(a)) and LI (60 DAS) (Figure 5.2 (a)) but apart from Kulin and 92SR4-413, which showed relatively low early vigour, there was little difference between other genotypes in early seedling vigour.

The range of genotypes used in Experiment 1 established significant differences in tiller number at 57 DAS (Table 5.5), however tillering ability was not correlated with early vigour. Duggan and Richards (1996) found a similar response to high and low tillering genotypes, where tillering had no effect on leaf area in the period up to 40 DAS in growth studies using wheat and barley lines which were near-isogenic except for tillering ability.

Due to small genotypic variation in early vigour and the absence of any effect of tillering, vigour differences are best explained through the detailed measurements taken in the period before the onset of tillering. Experiment 2 showed that significant differences in early vigour were detectable as early as 15 DAS (Table 5.4). However, by 29 DAS the only difference was that line 92SR4-413 had lower leaf area than the other lines. This is in close agreement with the field observations in Experiment 1.

The genotypic differences in early vigour identified in Experiment 2 were largely attributed to leaf width (Table 5.6) and the average number of leaves that had appeared by Harvest 2 (Figure 5.17). This concurs with the findings of Rebetzke *et al.* (1996) who found that leaf width was very important for early leaf area development. However these authors also stated that the most vigorous lines did not have the highest leaf number at the time of sampling.

The data for both experiments show that the early vigour of the experimental lines was not significantly greater than the commercial cultivars, despite being selected for morphological dissimilarity. This is in general agreement with Regan *et al.* (1992) who found equal plant vigour in genotypes of divergent morphology. However, other studies (Turner and Nicolas, 1987; Whan *et al.*, 1991) have found superior early vigour than commercial cultivars using a larger range of genotypes. It is therefore suggested that future work should encompass a wider range of genotypes to properly characterise genotypic differences in early vigour.

5.4.1.3 Agronomy versus genotype

Plant density had a large effect on early vigour, with a linear response between DM production at 57 DAS and sowing rate. Plant density had a much larger effect on early vigour than genotype and there was no genotype x density interaction. This is not surprising given the small genotypic differences in early vigour (Section 5.4.1.1) and the large vigour differences due to plant density (Figure 5.3). McDonald (1987) found a similar response in high and low tillering barley lines, where vegetative biomass was related to plant density and all genotypes responded in a similar manner.

The similarity in all vigour measurements (NDVI, LI, DM & LAI) between plants sown at 300 plants/m^2 and 400 plants/m^2 indicates the presence of interplant competition at this early growth stage. The hyperbolic shape of the density-LAI relationship and the fact that the largest increases occur when moving from low to moderate densities (TeKrony and Egli, 1991) it is likely that earlier measurement would have produced a significant increase in LAI at 400 plants/m^2 (Puckridge and Donald, 1967). Considering that 3 of the 4 treatments have a density in excess of 180 plants/m^2, which is recommended for this environment (Taylor *et al.*, 1991), the lack of a density-LAI response is understandable.

5.4.2 Relationship of early vigour with grain yield

Growing season rainfall experienced during 1996 was slightly above the long term average but was highly variable during the different phases of crop growth and development. The June - September (pre-anthesis) rainfall was 154% of the long term average, whilst the October - November (post-anthesis) rainfall was only 55% of the long term average (Table 3.2). This meant that the soil surface was moist for most of the early vegetative period which would have promoted E_{sc} and the dry spring would have increased the dependence on stored soil moisture for grain filling. These conditions would tend to enhance any advantage in WUE early vigour may have bestowed (see section 2.4.1.1) and the agronomic and genotypic vigour effects shall be discussed in this context.

5.4.2.1 Agronomic effects

Despite a large effect on early vigour, plant density had no effect on grain yield. Consequently, the agronomic promotion of early vigour was not correlated with grain yield (Table 5.3). The plots sown at high density produced greater anthesis biomass, however the higher yield potential was never realised. It was apparent that when plant density was increased from 100 plants/m² to 400 plants/m² LI at 59 DAS was increased from approximately 50% to 70% (Figure 5.2(a)), however the LAI measurements show (max LAI = 2.2 (Figure 5.4)) that this was possibly insufficient to reduce E_{sc} (Ritchie, 1972). It is hypothesised that the dry post-anthesis period would have placed greater dependence on stored soil moisture for grain filling and that plants sown at increased density would have been disadvantaged as they were not able to derive adequate benefits in conserving early rainfall (Passioura *et al.*, 1993).

It is significant, however, that even under such seasonal moisture conditions, that the yield – density response was not negative. Fukai *et al.* (1990) found similar responses in barley where plants that underwent moisture stress early in grain filling gave a flat response to increases in plant density, whereas plants sown at high density that experienced favourable conditions during grain filling, produced greater grain yield. Other authors who have noted a lack of negative yield effects at very high density are McDonald (1990) and Darwinkel (1978) who both found that grain yield was similar at 400 plants/m² compared to 800 plants/m² in barley and wheat.

The absence of a yield response to plant density may be a function of the range of plant densities used in the experiment. Darwinkel (1978) found that grain yield did not increase beyond a density of 100 plants/m² . This is supported by Anderson and Barclay (1991) who also found the density-yield response occurred below a density of 100 plants/m². The fact that this experiment used nominal plant densities in the range 100-400 plants/m² may have reduced any density-yield response. The results from the latter authors were produced under similar Mediterranean growing conditions and achieved similar yields to those experienced in this experiment.

TGW was significantly reduced as density increased, however, there were no significant differences between the two intermediate densities of 200 and 300 plants/m². This overall response, however, is consistent with other reports that grain weight is reduced with increasing sowing density (Darwinkel, 1978; Darwinkel, 1979; Hucl and Baker, 1990b; McDonald, 1990). It should be noted that McDonald, (1990) found a variable response, where in some genotypes grain size was not affected by plant density.

5.4.2.2 Genotypic effects

There were large genotypic differences in grain yield however these were not related to early vigour or tillering ability (Table 5.3). The lack of a yield response to tillering ability is supported by other authors who have found similar results in wheat (Fischer *et al.*, 1976; Whan *et al.*, 1988) and barley (McDonald, 1990). Where experiments between high and low tillering lines have shown a response, the results have been both positive (Donald, 1979; Islam and Sedgley, 1981) and negative (Borojevic and Kraljevic Balalic, 1980).

The main genotypic yield advantage was attributed to phenology, where earlier flowering genotypes produced greater yield (Figure 5.11). This would have been enhanced by the seasonality of rainfall and small amount of rain during the grain filling period (Table 3.2).

The large difference in grain yield between the two latest flowering genotypes (Frame and 92SR4-413), despite similar maturity and HI, can be attributed to superior anthesis biomass. The greater maintenance of green leaf area and more stable HI at high density also tends to indicate the presence of other adaptive traits such as superior root growth or the ability to maintain growth under higher moisture stress. This would enable Frame to remain photosynthetically active for a longer period and is reflected in the larger TGW in Frame compared to 92SR4-413 (Figure 5.14 (e) & (f)).

The low tillering experimental lines 92SR3-415 and 92SR4-419 experienced greater plant mortality at 400 plants/m² than other genotypes, with the plant population falling from 433 and 420 plants/m^2 at 57 DAS to 349 and 324 plants/m^2 (respectively) at maturity. The mortality was almost solely confined to the high density treatments and is in agreement with Donald (1979) who found this phenomenon to be predominant in low tillering lines at high density. In the case of lines 92SR3-415 and 92SR4-419 the spike density was actually (but not significantly) reduced at a plant density of 400 seeds/m^2 compared to 300 seeds/m^2 (Figure 5.14 (a)). The mortality in the experimental lines is likely to be caused by moisture stress, which is indicated by the very low levels of green leaf area during grain filling (Figure 5.7).

The low tillering (gigas) types were not well adapted to the local environment as can be seen from the relatively poor yields. Plasticity in spike size and grain set with changes in density (Figure 5.14 (c)) combined with low spike number (Figure 5.14 (a)) resulted in lower grain number in these lines (Figure 5.15). This phenomenon seems to be a feature of low tillering lines (Atsmon and Jacobs, 1977; Whan *et al.*, 1988) which makes the interaction with plant density much more apparent. These had more potential grain filling sites however, many of the florets were sterile and consequently, grain yield was not highly correlated with anthesis biomass in these lines (Figure 5.10 (a)).

The low tillering lines reached anthesis at 115 - 120 DAS. If maturity was altered in these low tillering genotypes to reduce the time to anthesis, this would increase the length of the grain filling period and should reduce the VPD during grain filling. This may reduce the amount of floret abortion and could be an integral component in the use of these lines (especially when sown at high density). Evidence of this is given in the comparison of the two low tillering experimental lines. The earlier maturing line 92SR3-415 had less variability in the number of grains per spike as plant density increased, which enabled more grains to be produced and TGW to be maintained. If time to anthesis can be further reduced, then these low tillering lines may have a role to play in raising grain yield in southern Australia as they have a combination of naturally high HI (Figure 5.12) and good early vigour.

5.4.2.3 Genotype x density effects

The absence of density x genotype interactions for early vigour (section 5.4.1.3) or grain yield confirm that early vigour was not related to grain yield in this season. It was apparent from Figure 5.4 that no genotype x density combination was able to generate enough LAI during early vegetative growth (57 DAS) to have had a positive influence on WUE through reduced E_{sc} (Ritchie, 1972).

The absence of any genotype x density interaction for grain yield could possibly be due to the fact that plants sown at 100 plants/m² were still able to produce adequate anthesis biomass to achieve the potential yield for this season. This was evident from the fact that the commercial cultivars produced similar biomass at all densities (Figure 5.10 (b)). It was also evident that all genotypes (except for the low tillering experimental lines) were able to achieve close to 400 spikes/m² (Figure 5.14 (a) & (b)), which is considered optimal for this environment (Taylor *et al.*, 1991).

Since all genotypes achieved a similar yield potential irrespective of density, and no treatment derived any benefit in WUE, grain yield was more closely related to the traits which maintained HI. Since the dry post-anthesis environment tended to reduced HI at higher plant densities, the main benefits were largely due to genotypic differences in HI which were closely related to phenology.

The stress encountered by the low tillering line 92SR4-419 is evident considering this line had fewer spikes and fewer grains per spike at 400 plants/m² compared to 300 plants/m², yet there was still a reduction in grain weight. This is unusual as it would be expected that the grain weight would be maintained or increased where fewer grains/m² are produced (Voltas *et al.*, 1997). Moisture increased leaf senescence at high density (Figure 5.7 (a)) which reduced the availability of photosynthates for grain filling. This line had the latest time of flowering and was clearly unadapted to the conditions, as can be seen in the uniformly low grain yield at all densities.

There were large genotypic and density effects on tiller survival (Figure 5.13) and high tiller mortality has often been regarded as wasteful of plant resources (Donald, 1968a). Closer examination reveals that tiller mortality increased with plant density, however spike density at maturity or grain yield were unaffected. Darwinkel (1978) found a similar response and this leads to the conclusion that tiller mortality did not affect DM partitioning into grain forming organs or was wasteful of resources.

Field observations in Experiment 1 revealed that the later leaves in the gigas lines 92SR3-415 and 92SR4-419 were much wider than the corresponding leaves on the commercial cultivars, culminating in the flag leaf being almost double the width of the other lines. Marshall and Boyd (1985) found that gigas types actually produced greater leaf area from the 5th mainstem leaf onwards, when compared with commercial Australian cultivars in a similar environment.

This meant that, while the lines displaying the gigas characters (92SR3-415 and 92SR4-419) did not display any increase in vigour, neither did they show any sign of reduced inter-plant competition which would enable these lines to respond positively to increases in high plant density. These low tillering lines diverged somewhat from the Donald (1968b) ideotype of producing limited leaf area and would have been more competitive than their limited tillering would suggest. This is consistent with Richards (1988b) who found similar vigour in gigas type wheats and would help to explain why the limited tillering lines did not yield well at high density.

It is apparent that the rainfall pattern can interact with plant density and genotype to produce differing yield responses. As such, the results from this study are limited by the fact that they refer to one site in one season. Whan *et al.* (1988) found a seasonal interaction for plant density. In one season there was no yield response to density in either high or low tillering lines, but in a second season, with higher rainfall, there was a positive yield response to density for all genotypes. Similarly Hucl and Baker (1990b) found the optimum density for both high and low tillering types was 320 plants/m² in one season and 640 plants/m² in another. For this reason, the results gained from this experiment should be treated with caution when viewed in a wider context.

The strategy of reduced tillering and early maturity of Kulin was clearly suitable in this season for producing high yield in this environment. However, Kulin would not be classed as a vigorous variety. This raises two points; one is that early vigour may not be of any benefit in this environment. The second is that, assuming early vigour is beneficial, then improving vigour in a line with early maturity and reduced tillering (i.e. high HI) would further raise grain yield. This was outlined by Sedgley and Seaton (1987) who proposed a wheat ideotype for similar climatic conditions in Western Australia that included early flowering, restricted tillering, short stature and early terminal spikelet formation. High sowing density would ensure high biomass at anthesis and early maturity would ensure high HI.

5.5 Conclusions

Genotypic differences in early vigour were detected but these were generally small and not related to tillering ability. Detailed observations revealed that genotypic differences in vigour may exist from very early in the vegetative period and that these are likely to be caused by leaf dimensions and the rate of leaf appearance, however, further work is required to confirm these results. Further genotypic vigour studies would benefit from the availability of a larger range of genotypes which display greater variation in early vigour.

Plant density clearly has a much larger effect on early vigour than the use of high or low tillering genotypes. Generally the low tillering genotypes had greater HI, however, this was largely dependent on phenology. Inter-plant competition in the low tillering genotypes was similar to that experienced in the high tillering lines and consequently there was no tillering ability x density interaction for grain yield.

Despite growing conditions that were conducive to favourable yield responses in more vigorous genotype x density combinations, there was no correlation between early vigour and grain yield. It is likely that this was caused by insufficient ground cover to reduce E_{sc} and greater pre:post anthesis water use which limited the fulfilment of greater yield potential in more vigorous treatments. While there were no negative yield effects due to plant density, it was apparent that increasing plant density provided no yield benefit due to early vigour. This confirms earlier findings.

CHAPTER 6

6. Genetic variability in early vigour: Field studies

6.1 Introduction

There are large differences in early vigour between cereals and these have been associated with differences in grain yield (López-Castañeda and Richards, 1994b). Considerable variation in early vigour has also been detected within cereal species and greater early vigour has been reported as a yield positive trait in Mediterranean-type climates (Acevedo, 1987; Boukerrou and Rasmusson, 1990; Van Oosterom and Acevedo, 1992).

Studies conducted in Western Australia (WA) have shown there is genetic diversity for early vigour in wheat (Whan *et al.*, 1991) and that high early vigour can be a yield positive trait (Turner and Nicolas, 1987). The latter authors demonstrated that genotypes which produce large plants at tillering produce high yield at maturity, but they failed to provide more specific information as to which attributes contributed to plant vigour and could be used in plant breeding programs.

Turner and Nicolas (1987) also found that plant density had a confounding effect on detecting genotypic differences in early vigour and may also have influenced grain yield. When we consider that the range in plant densities in their trial was lower than is recommended for the South Australian cropping regions, this raises questions as to the specific applicability of their results to the current investigation.

When diverse germplasm collections have been explored to identify vigorous genotypes (Rebetzke *et al.*, 1996; Regan *et al.*, 1992), it has been shown that highly vigorous introductions may not be locally adapted and may fail to yield well without further genetic manipulation. If vigorous lines could be identified from within local breeding programs then overcoming the hurdle of poor local adaptation might be easier. Experiments conducted in Chapter 5 identified genotypic differences in early vigour but the range of genotypes studied was limited and only small differences in vigour were detected. Therefore, it is necessary to examine genetic variation in early vigour present in local wheat breeding programs and the role that early vigour plays in yield formation.

In order to assess genetic variation for early vigour and its contribution to grain yield, a two-stage investigation was undertaken. A set of 348 lines of early generation breeding material was chosen from the Roseworthy Plant Breeding (RPB) program and screened for differences in early growth. The germplasm represented the widest range of genetic variation within the program and contained lines with widely diverging morphology, growth rates and maturities. Selections from this set were then used to undertake a more detailed field based study in 1996 to verify the yield-vigour relationship and identify plant traits related to early vigour.

6.2 Initial screening of Roseworthy breeding lines for early vigour

Detailed vigour studies could not be undertaken on all 348 genotypes, so an initial experiment was conducted to quantify the level of vigour present in the RPB program, and to select a representative subset of these genotypes for further evaluation. F5 lines were chosen for screening as they were the earliest generation breeding material grown in whole plots and the material covered the large range of genetic variation for early vigour present in the RPB germplasm. Whilst earlier generations were available, whole plots were necessary to allow vigour to be estimated from canopy measurements using PAR interception and to permit destructive sampling. Vigour was estimated by measuring PAR interception (LI) at approximately growth stage Z15.5.

6.2.1 Materials and methods

An unreplicated field trial consisting of 348 randomly selected F5 breeding lines and 8 cultivars (check varieties) was planted at Roseworthy (Field B7) on 8 June, 1995. These lines were a subset of the total F5 population and were likely to represent the full range of vigour expression within the RPB program.

The plots were sown using the equipment and method outlined in section 3.3. Plots were sown at a nominal rate of 70 kg/ha, however the seed was measured out on a volume basis and some variation in plant density due to seed size did occur. A good even seedling emergence was achieved and weed control was conducted as necessary.

Light interception readings were taken 66 DAS, when the plants were at growth stage Z30-33. Destructive measurements were also taken at this time by cutting the plants at ground level in 2 x 50cm sections of drill row (0.18 m^2) from the centre rows of each plot and plant density was recorded for all plots. Anthesis dates were recorded as the time when 50% of the spikes in each plot had exposed anthers. Plots were harvested at maturity using a Wintersteiger plot harvester.

6.2.1.1 Data analysis

The experimental layout consisted of 12 bays, each containing 37 plots. To account for site variation, 8 check varieties (Excalibur, Frame, Halberd, Janz, Machete, Meering, Molineux and Trident) were randomly sown in every bay and analysis was done using TwoD nearest neighbour analysis (Gilmour, 1992). The spatial analysis was able to account for site variation and the analysis of light interception was further improved with the use of plant density as a covariate. The use of plant density as a covariate did not improve yield results and no covariate analysis was used.

6.2.2 Results

There were good genotypic differences in early vigour with light interception at 66 DAS ranging from 11% to 81% (Figure 6.1). There were also a large differences in grain yield, which ranged from 200 g/m^2 to 495 g/m^2. The average unadjusted LI for the check varieties ranged from 0.40 (Janz) to 0.52 (Excalibur), and average yields ranged from 321 g/m^2 (Trident) to 377 g/m^2 (Excalibur) (Figure 6.1). This demonstrates that the range for both attributes was greatly exceeded by the breeding lines.

There was variation in plant density due to the genotypic differences in seed size and the fact that the experiment was sown on a volume basis. The plant density ranged from 67 plants/m² to 322 plants/m² (Table C.1), with an average of 171 plants/m². Light interception was improved with higher density and this effect was accounted for by including plant density as a covariate in the TwoD data analysis. No covariate analysis for plant density was required for analysis of grain yield.

When the external influences were excluded using TwoD nearest neighbour analysis, the genotypic differences in light interception were reduced to a range of between 27% and 60% and the range in grain yield was reduced to 225 g/m² and 430 g/m² (Figure 6.2). Nearest neighbour analysis used the check varieties to remove environmental variation and the yield for these check varieties is presented as a single average value for all check plots. Figure 6.2 indicates that there are many genotypes with higher or lower LI and grain yield than the average of the check varieties. This again demonstrates the large variation in early vigour and grain yield present within the local breeding program.

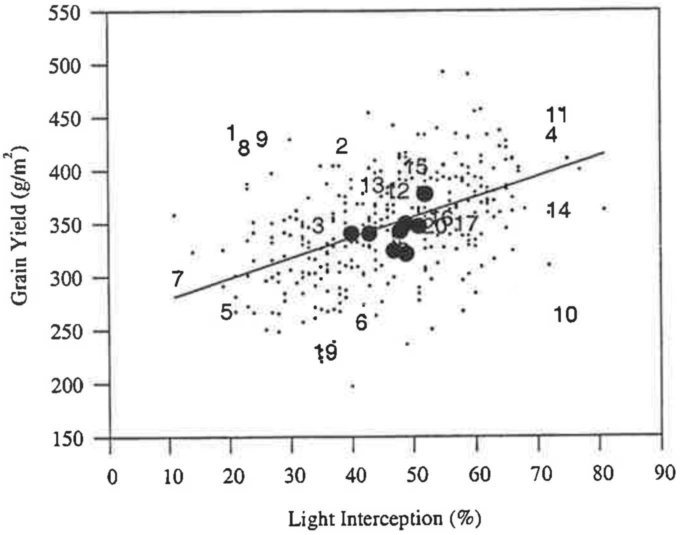

Figure 6.1 Grain yield versus light interception (66 DAS) for raw data. Breeding lines are represented by (.), check varieties are indicated by (•) and lines selected for further study are indicated by numbers (see Table 6.7). (r = 0.48, P < 0.01)

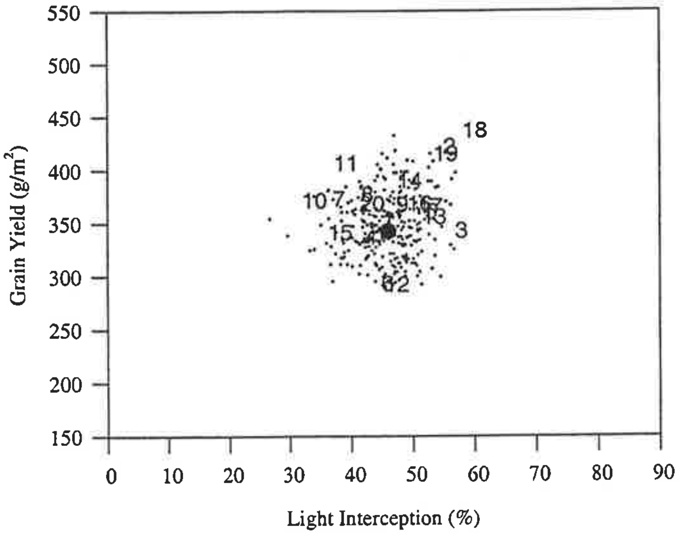

Figure 6.2 Grain yield versus light interception for data adjusted using TwoD nearest neighbour analysis with plant density as a covariate for light interception. Breeding lines are indicated by (.), average of check varieties are indicated by (•) and lines selected for further study are indicated by numbers (see Table 6.7). (r = 0.11, ns)

Light interception at 66 DAS was significantly correlated ($P < 0.01$) with grain yield for the raw data (Figure 6.1). However, the reduction in the range of response variables after the TwoD analysis reduced the significance of the correlation to non-significant levels (Figure 6.2). It is apparent, however, that the highest yielding genotype after nearest neighbour analysis (line #18) is also the most vigorous.

The TwoD analysis made large changes to the ranking for both light interception and grain yield (Appendix C - Table C.1). The changes in rank were generally larger for the LI measurements than for grain yield and there were few lines which displayed similar rank for both raw and TwoD adjusted data sets. Given the large changes in rank and the reduction in range of LI and grain yield after adjustment by TwoD analysis, results for both raw and TwoD adjusted data sets are presented.

The large changes in LI and yield ranking after adjustment by TwoD analysis (Appendix C, Table C.1) caused some concern as to the risk of omitting valuable genetic material in the second experiment. Since the trial was unreplicated and the variability reasonably high, it was decided to take field observations using breeders notes into account, as well as both the raw and adjusted data in the selection process. It was therefore decided to conduct parallel selection for high and low vigour lines using both raw and TwoD adjusted data sets.

The selection process involved making selections comprising of lines from the groups displaying high vigour - high yield (VY); high vigour - low yield (Vy); low vigour - high yield (vY); and low vigour - low yield (vy). Figure 6.1 illustrates the vigour and yield characteristics of the selected lines based on raw data. Figure 6.2 represents the same data set which has been adjusted using TwoD spatial analysis. The selections are identified by a number which corresponds to a crossing number and pedigree listed in Table 6.7.

Table 6.7 Crossing numbers and pedigrees of selected vigorous and non-vigorous breeding lines. Pedigrees identified as in Purdy *et al* (1966).

No.	CROSS No.	PEDIGREE
1	CO4191-401	RAC595,CO2084-203,BAYONET/3/75IRN217,/,CO2477-445,VS/3*177
2	CO4196-403	RAC520-4,MDN/4*RAC177,/,CO2477-536,VS/3*177
3	CO4196-412	RAC520-4,MDN/4*RAC177,/,CO2477-536,VS/3*177
4	CO4197-404	CRANBROOK/,CO2477-536,VS/3*177
5	CO4201-402	C3/3WI111/3WT211/7//,CO2477-536,VS/3*177
6	CO4202-402	RAC571,14IBSWN189,/,CO2477-437,VS/3*177
7	CO4203-401	CO1218-219,76ECN-43/COOK,/,RAC608,VS/3*177//SPR
8	CO4204-402	CO1284-209,75IRN-193/RAC88,/,CO2477-437,VS/3*177
9	CO4212-401	RAC416-1,CONDOR/PETITROJO,/,F84.3532,KT/242//KT/242
10	CO4226-401	CO3040/4/RAC430-6/RVN//9IBWSN180/3/CO2767/Sr26/6*177-6010S
11	CO4254-401	RAC549/RAC569
12	CO4259-401	HAHN'S'2/PRL'S'//,CO2498-406,RAC416/Sr21/3*CDO
13	CO4289-401	MACHETE/ISR493
14	CO4289-402	MACHETE/ISR493
15	CO4323-403	7923,3Ag14/5*CDO,82ECN-175,//,RAVEN/(LNC/ISR493//RAC177SR26),
16	CO4330-401	AUS17886,AIFENO#3,/,RAVEN/(LNC/ISR493//RAC177+SR26),CO1657-4
17	CO4372-402	RAC416-1/CDO
18	CO4372-403	RAC416-1/CDO
19	CO4382-406	RAC592/3/CO1982-405,((WExCNO-NO66/ZBZ)JAR'S')//RAC98/ARGIX
20	CO4418-401	CIII/4*RAC416,DT56862,//C3/4*RAC416:DT56874

Table 6.7 lists the lines selected to cover the full range in the yield-vigour relationship. Each breeding line was allocated a number for easy identification and reference in future experiments. Of the 20 lines selected for further study, there were

three pairs of selections from identical crosses and 14 selections from separate crosses.

Lines #2 and #11 displayed consistently above average, and line #6 displayed consistently below average, grain yield in both the raw and adjusted data sets. Only line #7 showed consistently low LI and there were no lines which displayed consistently high LI in both data sets.

6.2.3 Discussion

The screening process demonstrated that there is a large range in early vigour currently available in the germplasm of the Roseworthy Plant Breeding Unit. It also demonstrated that many of the lines are more vigorous than the current cultivars with approximately half of the material tested having greater light interception (Figure 6.2). This provides the scope for further increases in early vigour without having to introduce unadapted lines and risk incorporating negative traits into the breeding program.

Since the raw LI values were not adjusted for differences in plant population, the significant correlation between early vigour and grain yield in the raw data (Figure 6.1) may have been influenced by plant density. Since the effect of plant density on LI is large (see Chapter 4), it is likely that the range of LI values would have been larger than for genotypic differences alone. Variation in plant density is also likely to have increased the range of genotypic yield response (Anderson, 1986). The combination of an increase in the range of both variables would have contributed to the significant correlation observed in Figure 6.1. This is supported by the absence of such a correlation when the effect of density on LI was removed using covariate analysis (Figure 6.2). The independence of early vigour (as estimated by LI) and grain yield, suggests that there are other factors which are more important for grain yield in this environment. These may include phenology.

The use of light interception for vigour estimation may have reduced the error associated with the time of sampling and maturity type. The vigour measurements were taken when some lines had already reached stem elongation (Z31 - Z34) and as such they would have been rapidly increasing biomass without commensurate increases in ground cover. However, there is little change in the extinction coefficient of a genotype before ear emergence (Thorne *et al.*, 1988) and as such, LI would not be greatly effected.

The timing of the screening process was well suited to the use of the ceptometer as the raw light interception measurements fell within the range 10% to 90%. This corresponds to the most sensitive portion of the LI / LAI relationship (Figure 3.2). Possibly greater accuracy in screening could have been achieved with the use of a spectral radiometer as the resolution would allow measurements to be taken before the start of stem elongation, however a radiometer was unavailable.

There is a trade-off in statistical significance between screening early generation material in unreplicated trials, where material covers a wider range of plant characteristics, and later generation material in replicated trials, where material has undergone more rigorous selection, resulting in a narrower range. The choice is between greater repetition and genetic diversity. In either case, the material should be sown to achieve a target plant density to ensure a uniform comparison and thus improve the accuracy of screening. This factor may have implications for breeding programs where plant density may have a confounding effect on plant growth and yield.

The number of days from sowing to anthesis ranged from 103 to 134 across all lines in the trial (Table C.1). Of the selected material, the number of days from sowing to anthesis ranged from 112 to 131 which compares to the mean time to anthesis for the locally adapted cultivars of 114 DAS for Machete, 115 DAS for Trident and 119 DAS for Excalibur. The timing of anthesis is critical under rainfed Mediterranean-type conditions and is known to limit grain yield of late maturing cultivars (Loss *et al.*, 1990). However, fifteen of the twenty selections reached anthesis in 118 days or less and time to anthesis was not correlated with grain yield. The 6 selections which reached anthesis in greater than 118 days (lines #1, #9, #12, #16, #19) tended to be less vigorous in raw observations (Figure 6.1), but there was no apparent trend after adjustment by TwoD analysis (Figure 6.2).

The selections were based on lines which covered the full range of vigour expression from highly vigorous to non-vigorous lines. The lines were also selected to reflect a range of grain yields for both high and low vigour types. The resulting selections cover the VY, Vy, vY and vy vigour-yield combinations and should provide good genotypic diversity for vigour traits in subsequent experiments.

6.3 Field vigour studies of selected breeding lines

6.3.1 Introduction

The selection of vigorous and non-vigorous lines with high and low yield potential (section 6.2) provides the opportunity to explore the vigour-yield relationship in greater detail. Whilst Experiment 1 demonstrated a large range in early vigour present in the germplasm of the RPB program, it did not provide any indication of why one genotype was more vigorous than another. Furthermore, when spatial analysis was applied to Experiment 1, it showed that early vigour and grain yield were not well correlated with each other within the genotypes examined.

In order to identify vigour traits and confirm how strongly early vigour influences grain yield, a replicated field trial was conducted at Roseworthy in 1996 using the progeny from lines selected in 1995. The aim was to identify specific traits which promote vigour and examine the relationship of these vigour traits with grain yield. The inclusion of the Vy and vY types should facilitate better understanding of traits required to promote a yield x vigour response.

6.3.2 Method

The field trial was conducted at Roseworthy (Field N2a) in 1996. Twenty breeding lines selected from material grown at Roseworthy in 1995 (Table 6.7) and eight named cultivars (Aroona, Excalibur, Frame, Janz, Kulin, Machete, Spear and Trident) were sown as checks. The trial was sown on 12 June and was laid out in a randomised complete block design with three replicates. Each line was sown at a seeding rate of 200 seeds/m^2 using the method outlined in section 3.3. Weed control was conducted as necessary to ensure the experimental site was free of weeds.

A spectral radiometer was used to measure NDVI at 36, 40 & 60 DAS and a ceptometer was used to measure LI at 60, 79, 97 & 113 DAS to evaluate genotypes for early vigour. Plant vigour and leaf angle were also scored by visual assessment 48 DAS (growth stage Z15-25) as a subjective comparison, using a vigour scale of 1 (low) to 5 (high) and leaf angle scale of 1 (erect) to 3 (floppy). Above ground biomass samples from 4 rows x 50cm (0.36m^2) for growth analysis were collected on 8 August (57 DAS), 2-28 October (anthesis) and 16 December (maturity). Leaf area analysis was conducted at the first time of sampling. Tiller mortality was expressed as the percentage of vegetative tillers at 57 DAS which failed to produce a grain bearing spike at maturity.

Anthesis dates were recorded as the time when the anthers were exposed in 50% of the spikes of each plot and canopy height was measured during grain filling. The fungicide Folicur® 430 SC was applied at 290 ml/ha on 3 October to control stripe rust (*Puccinia striiformis*). The trial was harvested on 17 December using a Wintersteiger plot harvester.

6.3.2.1 Data analysis

The 1996 growing season experienced above average rainfall, with the first 50 DAS being continuously cool and wet. As a result, a portion of the trial site underwent transitory waterlogging, however, the affected area was restricted to a single replicate. The waterlogging caused reduced shoot growth during the early vegetative period but compensatory growth reduced the site variation by maturity. The boundary of the affected area coincided with the boundary between replicates, aiding the effectiveness of the RCBD in accounting for the site variation. The analysis of variance (ANOVA) showed significant differences between replicates but was still able to identify genotypic effects. Comparisons between ANOVA and spatial analysis techniques using AS-REML nearest neighbour analysis (Gleeson and Cullis, 1987) revealed that ANOVA adequately accounted for the site variation. Since the rankings were not significantly different from the spatial analysis, ANOVA was selected for examination of the data.

6.3.3 Results

6.3.3.1 Early vigour

Significant differences in early vigour were detectable from as early as 40 DAS using a spectral radiometer to measure the NDVI (Table 6.8). Although the results were not significant at the first time of sampling, the rankings remained largely unchanged for those lines which had high or low vigour. When vigour was ranked using the NDVI scores, line #16 performed very strongly from early tillering until stem elongation. Line #13 and the cultivar Kulin also displayed good early vigour, however, none of these lines corresponded with vigorous lines observed in Experiment 1. Lines #6, #8 and #15 were consistently the least vigorous across all sampling times during tillering and stem elongation. There was some consistency between these observations and those in Experiment 1, with line #8 having poor raw LI and line #15 having poor TwoD adjusted LI.

Table 6.8 Vigour rankings in the period from tillering to anthesis based on measurements with a spectral radiometer (NDVI), ceptometer (LI), and destructive sampling. 1 = most vigorous, 28 = least vigorous.

	Radiometer (NDVI)			Ceptometer (LI %)				DM (g/m^2)	LAI	DM (g/m^2)
	36 DAS	40 DAS	60 DAS	60 DAS	79 DAS	97 DAS	113 DAS	57 DAS	57 DAS	Anthesis
1-CO4191-401	10	5	2	2	1	3	1	1	4	15
2-CO4196-403	23	19	24	24	20	19	24	18	20	22
3-CO4196-412	22	22	26	23	23	16	14	25	26	23
4-CO4197-404	25	21	13	7	7	1	7	19	24	3
5-CO4201-402	13	8	10	13	11	17	21	17	13	21
6-CO4202-402	28	27	22	25	21	15	8	26	25	16
7-CO4203-401	4	7	11	14	4	6	6	14	12	13
8-CO4204-402	27	28	28	27	28	26	16	28	28	19
9-CO4212-401	15	11	3	4	10	20	17	4	8	1
10-CO4226-401	20	23	23	26	26	18	20	22	19	10
11-CO4254-401	24	24	18	6	16	14	12	7	3	4
12-CO4259-401	18	20	6	8	3	11	5	24	22	14
13-CO4289-401	7	3	17	18	19	13	26	6	5	17
14-CO4289-402	8	4	19	19	14	10	13	5	2	11
15-CO4323-403	26	26	27	28	27	28	27	27	27	28
16-CO4330-401	1	2	1	1	2	4	4	2	1	2
17-CO4372-402	3	14	20	22	25	25	19	20	10	26
18-CO4372-403	14	9	12	12	9	2	3	11	17	6
19-CO4382-406	12	16	16	16	15	22	10	16	14	8
20-CO4418-401	9	10	8	11	12	23	25	9	9	12
Aroona	19	15	25	21	22	7	18	10	6	18
Excalibur	21	25	21	17	24	27	28	23	18	24
Frame	6	12	7	3	5	8	9	15	23	5
Janz	11	13	15	15	17	5	2	21	16	20
Kulin	2	1	9	20	18	21	15	8	15	27
Machete	16	17	5	10	13	12	23	12	11	25
Spear	17	18	14	9	8	9	11	3	7	9
Trident	5	6	4	5	6	24	22	13	21	7
Min Value	0.29	0.31	0.57	0.42	0.78	0.83	0.79	26	0.40	675
Max Value	0.38	0.43	0.80	0.73	0.96	0.91	0.92	59	1.06	989
Significance	ns	*	*	*	***	*	ns	ns	ns	***

*** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; ns = $P > 0.05$

* The shaded regions indicate the lines with the highest and lowest average vigour ranking.

Table 6.9 Growth measurements and yield components for 20 breeding lines and 8 named cultivars grown at Roseworthy in 1996.

	Tillering					Anthesis			Maturity								
	DM (g/m^2)	Tillers /plant	LAI	SLW (g/m^2)	CT[a] (m^2)	DM (g/m^2)	RGR[b] (x10^{-2}) (g/g/m^2/day)	Days to Anthesis	Height (cm)	Spikes (m^2)	Spikes /plant	TGW[c] (g)	Grains /spike	Tiller Survival[d] (%)	Harvest Index	Yield (g/m^2)
1-CO4191-401	59.1	3.53	1.01	48.5	53.7	870	4.52	119	90	425	2.24	32.65	32.1	65	0.35	409
2-CO4196-403	44.5	2.70	0.71	45.4	9.3	732	4.94	114	93	382	2.01	37.47	30.3	77	0.38	452
3-CO4196-412	40.2	2.73	0.58	54.3	9.3	729	5.02	117	85	408	1.65	38.06	36.3	61	0.40	442
4-CO4197-404	44.4	2.50	0.63	50.2	5.6	967	5.21	117	99	369	1.75	33.80	32.1	70	0.34	403
5-CO4201-402	45.6	2.87	0.83	41.2	7.4	758	5.06	115	92	356	1.90	38.67	26.4	67	0.32	409
6-CO4202-402	39.1	2.60	0.61	44.9	7.4	870	5.49	114	109	358	1.69	37.68	25.9	54	0.30	357
7-CO4203-401	47.7	2.83	0.85	48.4	5.6	874	4.87	121	96	366	1.71	36.01	28.5	61	0.33	420
8-CO4204-402	26.5	2.97	0.40	51.3	17.6	807	5.44	120	83	428	2.12	34.84	33.9	74	0.39	440
9-CO4212-401	53.9	3.13	0.92	59.3	43.5	989	5.01	120	83	468	2.17	36.25	22.6	76	0.34	390
10-CO4226-401	42.2	4.00	0.72	48.3	44.4	902	4.48	126	98	442	2.44	37.73	22.7	61	0.32	414
11-CO4254-401	52.1	3.47	1.04	37.3	0.0	947	4.35	126	83	406	2.18	33.48	30.3	66	0.34	413
12-CO4259-401	40.3	4.47	0.69	47.2	27.8	873	5.05	120	108	360	1.93	40.27	17.0	44	0.25	408
13-CO4289-401	52.8	3.10	0.98	41.3	28.7	814	4.77	116	86	435	1.86	39.94	25.8	60	0.38	473
14-CO4289-402	53.8	3.90	1.05	36.0	15.7	902	4.94	115	88	498	2.40	37.70	27.5	63	0.38	433
15-CO4323-403	31.8	3.00	0.57	48.2	9.3	675	4.29	130	85	319	1.69	38.78	26.1	58	0.34	341
16-CO4330-401	57.9	3.17	1.06	41.3	3.7	975	5.21	113	100	440	2.13	43.62	24.1	66	0.34	399
17-CO4372-402	44.3	3.07	0.89	32.9	11.1	709	4.76	118	86	517	2.49	33.90	28.4	83	0.40	475
18-CO4372-403	49.4	3.03	0.74	50.2	33.3	919	5.15	116	76	483	2.20	35.28	27.6	64	0.38	504
19-CO4382-406	46.5	2.70	0.82	43.3	1.9	911	5.09	117	88	369	1.97	40.76	33.6	62	0.40	423
20-CO4418-401	50.1	3.23	0.90	44.5	9.3	887	4.73	120	90	451	2.13	39.06	24.4	66	0.34	463
Aroona	49.4	3.10	0.93	37.7	11.1	808	5.66	107	86	499	2.60	38.57	26.3	86	0.40	440
Excalibur	40.5	3.33	0.74	49.1	10.2	726	5.30	114	80	368	1.86	39.55	32.8	56	0.43	435
Frame	47.1	3.50	0.67	57.1	15.7	934	4.88	121	88	436	1.83	38.86	23.2	49	0.33	466
Janz	44.0	3.00	0.80	51.9	5.6	798	5.52	113	89	504	2.59	34.55	34.3	86	0.41	481
Kulin	51.7	1.60	0.80	41.8	3.7	706	5.83	103	92	362	1.57	43.54	33.1	89	0.42	515
Machete	49.1	3.57	0.86	45.1	22.2	719	4.80	115	89	484	2.31	39.86	25.3	66	0.39	471
Spear	56.7	3.33	0.93	47.5	32.4	910	4.74	119	87	457	2.17	38.45	28.5	65	0.38	476
Trident	49.1	3.03	0.69	53.6	14.8	919	5.08	117	87	480	2.19	39.27	26.6	72	0.38	492
Mean	46.8	3.12	0.80	46.4	16.4	844	5.01	117	90	424	2.06	37.81	28.1	67	0.36	437
LSD (P<0.05)	17.6	0.92	0.39	15.8	24.2	156	0.68	2.5	11	88	0.59	3.49	5.8	32	0.05	73
Significance	ns	***	ns	ns	***	***	**	***	***	***	***	***	***	*	***	***

*** = P < 0.001; ** = P < 0.01; * = P < 0.05; ns = P > 0.05

(a) CT = coleoptile tillers

(b) RGR = relative growth rate (shoot DM growth between 57 DAS and anthesis)

(c) % Tiller survival = tillers at maturity as a percentage of tillers at 57 DAS

(d) TGW = thousand grain weight

Coleoptile tiller (CT) development was not important for early vigour in any of the lines studied. Table 6.9 shows that the greatest density of coleoptile tillers was 54 CT/m² in line #1, which equates to 0.26 CT/plant or approximately 1 coleoptile tiller in every 4 plants. When coleoptile tillers were expressed as a percentage of total vegetative tillers, the largest ratio was 7% of total tiller production (lines #1 and #9). Coleoptile tiller production was not significantly correlated with LAI (57 DAS) and the results indicate there was little genotypic variation amongst the lines studied or that CT production was important for early vigour.

There was some change in the rankings (compared to NDVI) when varieties were ranked according to anthesis biomass (Table 6.8), however, the highest and lowest vigour lines remained largely unchanged. The most vigorous lines were #1, #16 and Spear, while the least vigorous lines were #6, #8 and #15. The three methods of early vigour assessment (DM, NDVI and LI) were well correlated and were all capable of identifying high and low vigour material (Table 6.10). This table also shows that early vigour, scored visually on a 1 to 5 scale, was significantly correlated with other, objective vigour assessment techniques.

Table 6.10 Correlations between methods of early vigour measurement.

	Vigour Score 48 DAS	DM 57 DAS	DM g/plant 57 DAS	LAI 57 DAS	SLW 57 DAS	NDVI 36 DAS	NDVI 40 DAS	NDVI 60 DAS	LI 60 DAS
DM 57 DAS	*								
DM per plant	**	***							
LAI 57 DAS	ns	***	***						
SLW 57 DAS	ns	ns	ns	(**)					
NDVI 36 DAS	*	***	***	***	ns				
NDVI 40 DAS	**	***	***	***	ns	***			
NDVI 60 DAS	*	***	***	***	ns	***	***		
LI 60 DAS	*	***	***	***	ns	**	***	***	
LI 79 DAS	*	***	***	**	ns	**	***	***	***

*** = P < 0.001; ** = P < 0.01; * = P < 0.05; ns = P > 0.05

6.3.3.2 Grain yield

Figure 6.3 shows that there was a positive trend between early DM production (57 DAS) and grain yield. The relationship was even stronger when early vigour was measured as NDVI at 40 DAS (Figure 6.4). Since genotypes were selected to cover the full range of the vigour-yield response (VY, Vy, vY, vy), it is not surprising that lines #8 and #16 were identified as outliers. If these outliers are removed, the regression for Figure 6.4 becomes more statistically significant ($r = 0.61$, $P < 0.01$). If the same two lines are removed in Figure 6.3 the correlation is also improved, however, it is still highly influenced by line #1, which produced the greatest DM at 57 DAS.

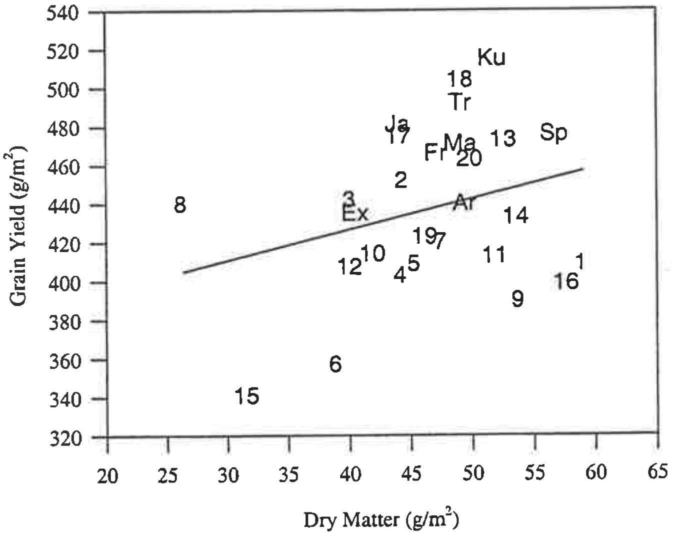

Figure 6.3 Dry matter (57 DAS) versus grain yield. Plots are averages listed by line number or CV name (Table 6.7). ($r = 0.28$, $P > 0.05$). However, the regression equation becomes highly significant ($r = 0.52$, $P < 0.01$) if lines 1, 8, and 16 are removed.

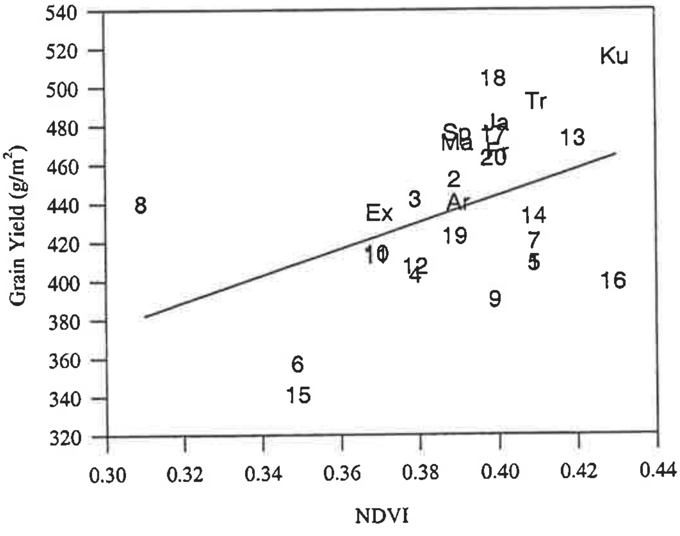

Figure 6.4 Early vigour measured as NDVI using a spectral radiometer (40 DAS) versus grain yield. ($r = 0.42$, $P < 0.05$). Regression equation becomes highly significant ($r = 0.61$, $P < 0.01$) if lines 8 and 16 are removed.

The named cultivars generally out-yielded the breeding lines, with Kulin being the most vigorous (measured using NDVI) as well as the highest yielding (Figure 6.4). Conversely, the lowest yielding lines #6 and #15 were among the least vigorous. For genotypes displaying similar early vigour, the named cultivars out-yielded the breeding lines in almost every case. Once again this is largely attributed to the generally superior HI in the named cultivars.

Phenology of the experimental lines did not have a large effect on grain yield. While phenology and grain yield were significantly correlated, this was largely due to the influence of the very early and very late lines. If the earliest (Kulin) and the latest (#15) lines were removed then the relationship between flowering time and yield is not significant. Closer examination revealed that 23 of the 28 genotypes flowered between 110 and 122 DAS (Table 6.9), and there was large yield variation between lines flowering on the same day. The above average growing season rainfall would also reduce the effect of phenology and provide adequate moisture for grain filling in all but the very late flowering lines.

There was no relationship between anthesis DM and grain yield (Figure 6.5). Many of the breeding lines produced greater anthesis biomass than the commercial cultivars, however the commercial cultivars generally produced greater grain yield. The poor correlation between anthesis DM and grain yield can be explained through the large variation in HI. Figure 6.6 illustrates the significant relationship between grain yield and HI in this environment and only a few of the breeding lines displayed HI comparable to the commercial cultivars.

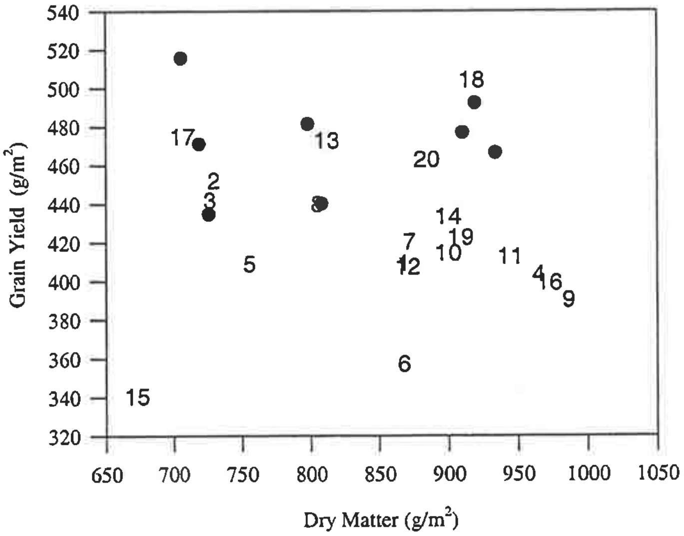

Figure 6.5 Anthesis dry matter versus grain yield. The symbols (●) represent named cultivars.

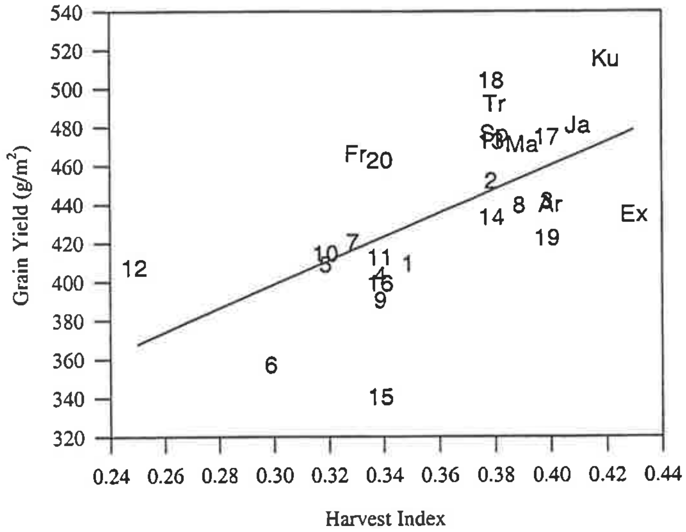

Figure 6.6 Harvest index versus grain yield. ($r = 0.60$, $P < 0.01$)

Harvest index was affected by phenology (Figure 6.7), tiller mortality and plant height (Figure 6.8). Kulin and Aroona flowered earlier than the other genotypes and had a greater HI, whereas, lines #10, #11 and #15 flowered later than the majority of genotypes and displayed lower HI's. Line #12 had a moderate flowering time (120

DAS) but had a very low HI. An explanation for this anomaly could be the high tiller mortality of line #12 combined with its tall stature (Figure 6.8).

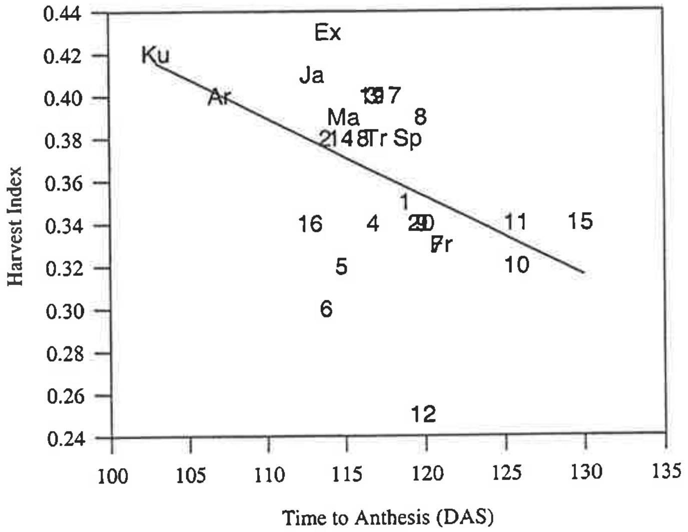

Figure 6.7 Time to anthesis versus harvest index. (r = 0.49, P < 0.01)

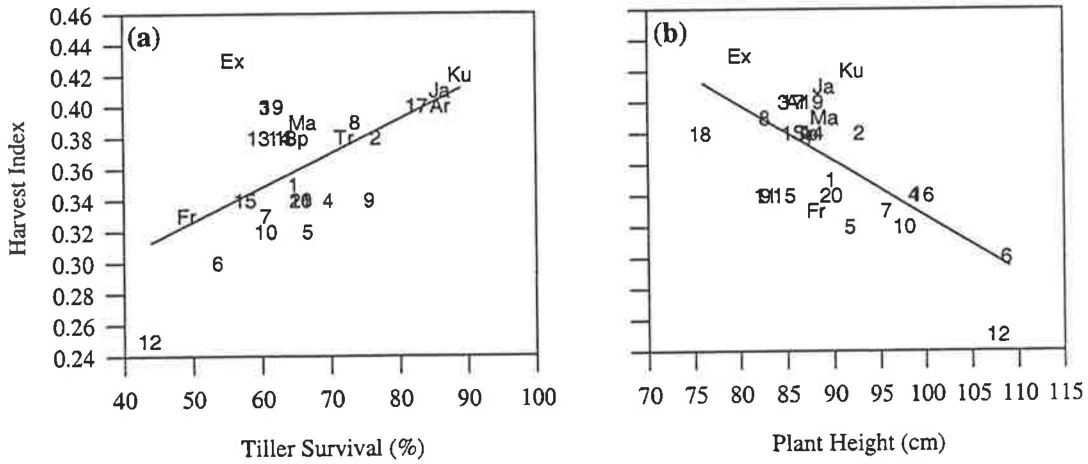

Figure 6.8 Harvest index versus percentage (a) tiller survival (57 DAS - maturity), (b) plant height. Correlations for (a) r = 0.58 (P < 0.01), (b) r = 0.67 (P < 0.01).

The HI was positively correlated with tiller survival (Figure 6.8 (a)), and tiller survival was negatively correlated with tiller numbers during vegetative growth (r = -0.52, P < 0.01). Excalibur was a notable exception, with poor tiller survival and high harvest index, but generally, the low tillering lines which had low tiller mortality had a yield advantage over the higher tillering lines with poor tiller retention. Harvest index was also strongly correlated with plant height (Figure 6.8 (b)), where shorter plants had higher HI.

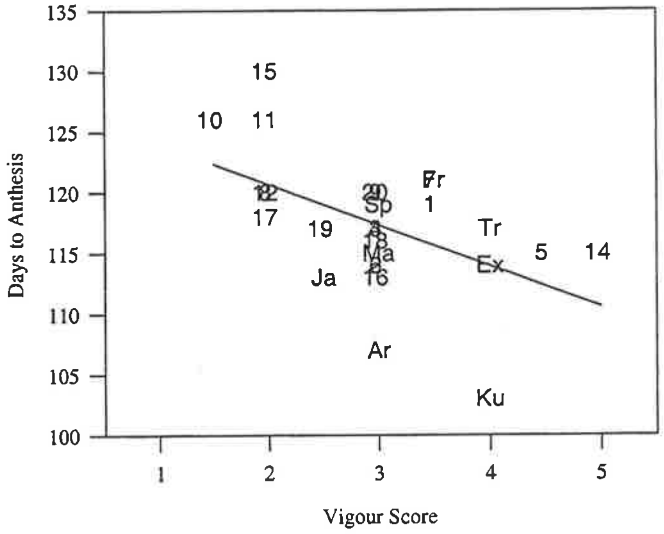

Figure 6.9 Vigour score (48 DAS) versus time to anthesis. (r = -0.51, P < 0.01)

When early vigour was assessed using an objective visual score, the average vigour score was correlated with flowering time. Thus, it was likely that the subjective vigour measurement was being influenced by the rate of plant development.

6.3.3.3 Comparison of 1995 / 1996 results

There was a reasonable correlation (P < 0.10) between LI (66 DAS - 1995) and LI (60 DAS - 1996) across the two seasons (Figure 6.10). Lines #8, #10 and #15 were consistently non-vigorous across the two years, however there was less consistency in vigorous genotypes. The variation in rank for the remainder of the lines could be attributed to seasonal interactions and background noise. Light interception (66 DAS) in 1995 was more highly correlated with NDVI (40 DAS) in 1996 (r = 0.44, P < 0.05) than with LI (60 DAS) in 1996 (Figure 6.10).

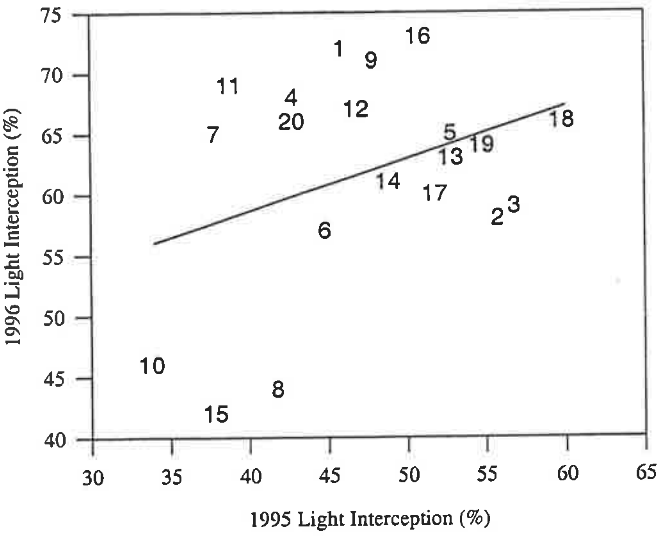

Figure 6.10 Comparison of TwoD adjusted LI (66 DAS) in 1995 versus LI (60 DAS) in 1996. ($r = 0.35$, $P < 0.10$).

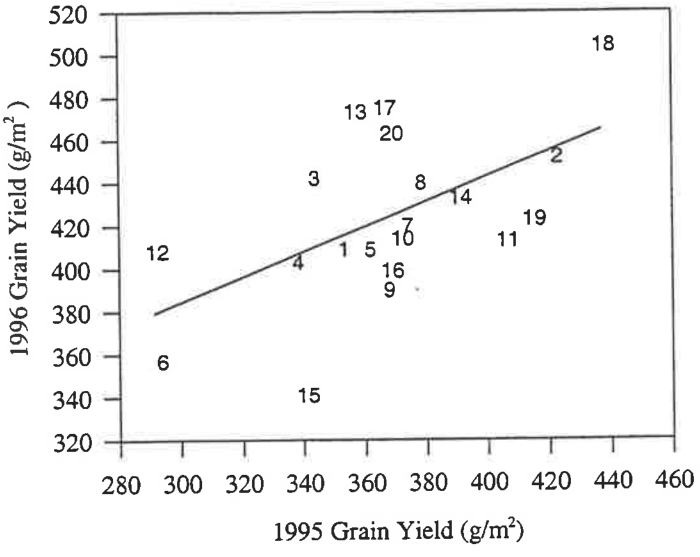

Figure 6.11 Comparison of grain yields between 1995 TwoD adjusted data and 1996 averages. ($r = 0.56$, $P < 0.01$)

The yield stability across both years of the study was very high and as a result, the yield results in 1995 were a good indicator of the yield in 1996. Line #18 was consistently the highest yielding of all the selected breeding lines (Figure 6.11).

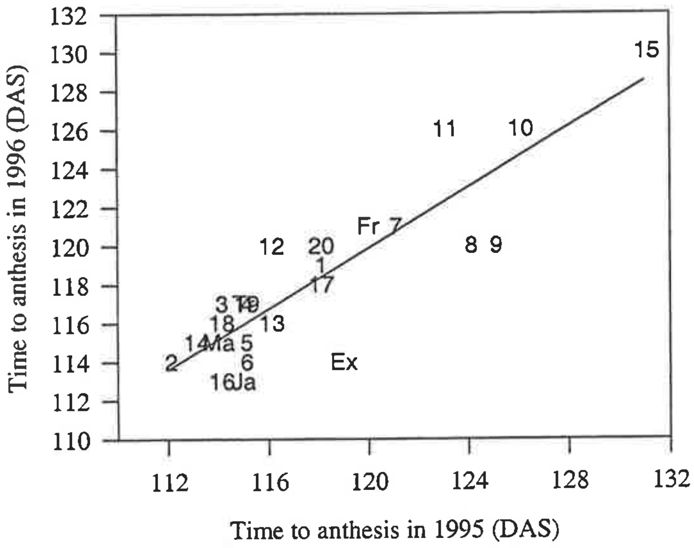

Figure 6.12 Comparison of the number of days from sowing to anthesis for cultivars grown in 1995 and 1996. ($r = 0.87$, $P < 0.01$)

The phenology was consistent across years with the time from sowing to maturity being similar within each line for 1995 and 1996 (Figure 6.12). In 1996, the time to flowering was not significantly different from the locally adapted, mid-seasoned cultivar Spear (Table 6.9) for all but three breeding lines. Those lines which were significantly later than Spear (lines #10, #11, & #15) generally showed poor early vigour which may suggest that early vigour is closely associated with early penological development.

6.4 Discussion

6.4.1.1 Early vigour

This experiment confirmed that there was good genotypic variation for early vigour within the germplasm of the Roseworthy Wheat Breeding Program (Table 6.9) and that many of the breeding lines are more vigorous than the current commercial cultivars. These results are consistent with other vigour studies which have also shown good variation in early vigour within wheat genotypes grown in a similar climate (Regan *et al.*, 1992; Turner and Nicolas, 1987; Whan *et al.*, 1991). This experiment found that Kulin had superior early vigour compared to other commercial cultivars (Table 6.8), which was in general agreement with other vigour studies (Karimi and Siddique, 1992; Whan *et al.*, 1991).

Comparison of vigour measurements between 1995 and 1996 (Figure 6.10) showed good correlation, where vigorous genotypes in 1995 were also more vigorous in 1996, despite different growing conditions and different methods of measurement. The ability to identify variation in early vigour using NDVI and LI should enable adoption of these techniques by plant breeding programs.

One of the mechanisms which produced genotypic differences in LAI at 57 DAS, was SLW (Table 6.10). There was a negative correlation between SLW and LAI, where genotypes with thinner leaves produced greater LAI. Comparisons between wheat and barley have shown that barley derives a vigour advantage in this way (López-Castañeda and Richards, 1994b), however, there were no significant genotypic differences in SLW in this experiment, despite the significant correlation with LAI.

6.4.1.2 Early vigour x grain yield

The use of breeding lines selected for high and low early vigour has shown that there was a significant relationship between early vigour and grain yield (Figure 6.3 and Figure 6.4), however, there is also yield variation for any given level of early DM production. The presence of some outliers (eg. #8 and #16 (Figure 6.4)) is not unexpected, given the selection procedure which incorporated vY and Vy genotypes, but even with the inclusion of these points, early vigour could be regarded as a yield positive trait in this environment. These outliers do clearly indicate, however, that other traits are also necessary for high yield. Figure 6.6 shows that HI is strongly correlated with grain yield and as such, the highest yielding vigorous types will be those genotypes which can maintain high HI.

Turner and Nicolas (1987) found a positive relationship between early vigour and grain yield. While these authors defined early vigour and grain yield on a per-plant basis rather than on an area basis (as in this study), these results support their finding that vigorous genotypes will generally produce greater yield (all other things being equal). Turner and Nicolas (1987) also found outliers in their study (low yielding vigorous types and high yielding non-vigorous types) which supports the results in this study and verifies that there may be other traits more closely associated with grain yield under Mediterranean-type conditions.

The significant vigour - yield relationship in Experiment 2 could be explained by the more even plant density and greater replication in 1996, which would have provided more accurate LI and grain yield measurements and improved the significance of the relationships between different crop attributes. This is evident in the poor correlation between LI measured in each experiment (Figure 6.10).

Given that the most vigorous genotypes were only able to generate a maximum LAI at 57 DAS of 1.1, early vigour is highly unlikely to have had any influence on reducing E_{sc} (Ritchie, 1972). Thus, the differences in HI were probably not due to improved WUE through soil shading. It is possible, however, that early vigour was correlated with phenology (Figure 6.9), which in turn was influencing WUE through earlier flowering and better partitioning of water use pre:post anthesis (Siddique *et al.*, 1990b).

While there may be many reasons for the genotypic variation in HI displayed in this experiment (eg root morphology, transpiration efficiency, etc), HI was correlated with tiller survival and plant height (Figure 6.8). The effect of plant height on HI has been well documented (Miralles and Slafer, 1995; Richards, 1992a; Siddique *et al.*, 1989b) and Richards (1992a) found that the relationship was negative and linear for plant height above 65cm. Since the shortest genotypes in this trial had an average height > 80cm, the significant correlation is not surprising.

The effect of tiller mortality is not so clear. It is possible that high tiller mortality and senescence was a wasteful use of plant resources (Palta and Fillery, 1993a), however, it may also be possible that high tillering had a delaying effect on mean anthesis date (Turner *et al.*, 1994) which contributed to high tiller mortality. Since the plants did not suffer any moisture stress before anthesis it is presumed that the tiller mortality was due to inherent genotypic differences.

Given the close correlation between HI and time to anthesis (Figure 6.7) and the link between tillering and delayed anthesis (Turner *et al.*, 1994), it is likely that flowering time would influence HI due to better partitioning of water use into the post-anthesis period (Siddique *et al.*, 1990b). The early flowering lines (Kulin and Aroona) would also have undergone grain filling during lower VPD (Richards, 1991) which would tend to reduce moisture stress and improve grain yield. Thus, it appears that early maturity, limited tillering and low tiller mortality are yield positive traits due to their positive influence on HI in this environment.

Selection for early vigour should therefore be biased towards lines with high rates of tiller survival or lines which express increased leaf area through means other than increased tillering. This is supported by Siddique *et al.* (1989a) who found that tiller survival was positively correlated with grain yield in a similar environment to this study. Regan *et al.* (1992) found high tillering was a valid means of increasing leaf area and early vigour but early vigour gained in this way was not correlated with grain yield. The vigour increases due to CT production reported by Liang and Richards (1994) were not evident in this study due to the low numbers of coleoptile tillers present (Table 6.9).

The yield of vigorous lines may depend on the agronomic practices used to grow the crop and there may be genotypic responses to plant density. Anderson and Barclay (1991) found that different genotypes may have different optimum densities, which vary according to environment. Since the lines were all grown at a single plant population and achieved similar plant establishment, it is possible that some bias may have been introduced into the experiment, but this is unlikely because such responses are likely to be more noticeable at lower plant densities (< 100 plants/m^2) (Darwinkel, 1978).

The interaction of plant density with early vigour and grain yield can be observed through the initial high vigour ranking of Kulin using NDVI at 36 & 40 DAS which was reduced to 9th (NDVI) or 20th (LI) some three weeks later. It is hypothesised that this vigour advantage would have created even larger yield gains if Kulin was sown at an increased density so as to achieve higher spike densities at anthesis. The tiller mortality in Kulin was also the lowest of all the lines sown and it was the earliest maturing genotype with high HI. The good performance of Kulin is consistent with the results of Siddique *et al.* (1990b) who also found that it produces a vigorous seedling and high yields.

6.4.1.3 Genotype x environment

While this experiment showed a positive relationship between early vigour and grain yield, it was also heavily influenced by factors which affect HI. Since HI is closely associated with the partitioning of water use (Siddique and Sedgley, 1987), which in turn is heavily influenced by a combination of phenology and the environment (Loss and Siddique, 1994), it could reasonably be expected that the genotypic vigour-yield response would be dependent on the environment.

As the growing season becomes shorter, the influence of phenology becomes stronger (Loss *et al.*, 1990). However, the variation in flowering time for the majority of genotypes was not significant (Table 6.9), which would tend to reduce this effect. If the genotypic variation in HI is influenced by other environmentally-dependent factors, which influence the partitioning of water use (pre:post anthesis), then changes in HI could still cause a genotype x environment interaction which affects early vigour and grain yield.

When early vigour and grain yield were compared between 1995 and 1996 (Figure 6.10 and Figure 6.11) there was a good general agreement. Genotypes produced larger differences in ranking for early vigour than for grain yield and the most consistent results were at the extremes. Despite the variability, these comparisons were able to identify consistently vigorous (#18, #19) and non-vigorous (#8, #10 & #15) lines; and consistently high (#18) and low (#6) yielding lines.

Whan *et al.* (1991) found that the vigour rankings between commercial cultivars and introduced lines changed between locations in the same year and between years in the same location. However, their results showed that even the cultivars at the extremes of rank (i.e. most and least vigorous or highest and lowest yielding) changed in different environments. When larger vigour and yield differences were encountered (as with comparisons between species) the results were highly consistent between environments (López-Castañeda and Richards, 1994b). The good consistency in vigour rankings between Experiment 1 and Experiment 2 would therefore tend to indicate good genotypic variability in early vigour.

6.4.1.4 Methods of early vigour assessment

There is a clear trend between high early vigour and high grain yield (Figure 6.3 & Figure 6.4). Therefore, the ability to identify high vigour lines could provide wheat breeders with another selection criterion to breed for higher grain yield. While there was some variation within the yield-vigour relationship, selection made on the basis of good early vigour would retain more high yielding lines than would be discarded. It is true that some high yielding material may also be discarded along with the non-vigorous lines, however, the net effect would be positive. Thus, early vigour could be a useful selection tool for wheat breeders.

The better relationship between NDVI and grain yield (Figure 6.4) compared to early DM production and grain yield (Figure 6.3) would be due to the fact the NDVI integrates many canopy attributes. DM measurements do not account for canopy architecture, leaf size and shape, and ground cover. Whereas the NDVI measurement not only provides an estimate of the leaf area present but integrates this with percentage ground cover and effectiveness of light interception. The amount of light reflected will also be directly proportional to the amount of light reaching the soil surface and through it, E_{sc}. Since NDVI is a rapid measurement to make, it could be an excellent tool for ranking wheat lines for early vigour.

The visual scoring system has two major drawbacks. First, it is subjective; there will be differences between assessors in the allocation of scores and their ability to detect subtle changes. Second, the scale is limited and only allows for basic differences in vigour to be recorded rather than subtle changes. Generally, there was good agreement between all methods of early vigour measurement, however, the visual assessment was the least reliable when ranked against DM at tillering. This is supported by Adcock *et al.* (1990) who also found that radiometer measurements provided more accurate ranking than visual assessment.

Despite the statistically significant results obtained, the variation encountered within the experiment was large. This was due to a combination of the site variation and limited replication (due to limited seed availability). Since many of the differences between breeding lines are often small, they require minimal background variation and a high degree of agreement between replicates to resolve differences between mid-ranked genotypes.

6.5 Conclusions

The selection process employed in this study was able to identify a set of genotypes displaying a wide range of early vigour and associated grain yield responses. Closer examination revealed significant variation in early vigour within the Roseworthy Wheat Breeding Program and three methods of rapid vigour determination were all able to consistently determine high and low vigour lines. The selected lines demonstrated that early vigour is positively correlated with grain yield under rain-fed Mediterranean-type growing conditions.

The results also show that there is some yield variation at any given level of vigour which strongly indicates that, while early vigour is a yield positive trait in this environment, there are other factors associated with grain yield. Maintaining high HI is crucial in this environment and HI is influenced by factors such as tiller mortality, plant height and anthesis date. Lines expressing early vigour must maintain HI either through early maturity, reduced tillering, or reduced height. If these traits can be combined then adaptation to the environment will be improved and grain yield will be maximised.

Clearly there is a role for vigorous cultivars in South Australian wheat cropping systems, however further work is required to identify vigorous traits which could be incorporated into well adapted lines.

CHAPTER 7

7. Plant characteristics which promote early vigour: Glasshouse studies

7.1 Introduction

Field studies have shown that the germplasm of the Roseworthy Wheat Breeding program contains considerable genetic variation for early vigour and that plant vigour is positively related to grain yield (Chapter 6). Despite determining differences in vigour and gross morphology, it was not feasible to identify traits promoting vigour during very early growth.

Evidence suggests that differences in early vigour occur very early in the vegetative period (López-Castañeda *et al.*, 1996) and are often related to factors such as embryo size (Moussavi-nik *et al.*, 1996) and rate of emergence (Soetono and Donald, 1980). It is not clear however, as to whether initial size or subsequent growth rate is more important in promoting early vigour. The literature also indicates that early vigour is influenced by morphological features of the seedling such as SLW and the width of the seedling leaves (Rebetzke and Richards, 1996; Rebetzke and Richards, 1999).

Much of the genetic comparison between high and low vigour genotypes has been done between vigorous and non-vigorous species, such as between wheat and barley (López-Castañeda and Richards, 1994b), or using limited numbers of lines. López-Castañeda and Richards (1994b) identified large differences in early vigour between wheat and barley, and demonstrated a link between plant vigour and grain yield. Moreover, they identified many characters that promote early vigour, which are present during very early growth. The question remains as to whether the same characters are responsible for promoting early vigour within a species, and is there enough variation in these traits to be useful in wheat breeding?

The selection of high and low vigour wheat genotypes from within the Roseworthy Wheat Breeding Program provided the opportunity to investigate the vigour differences during early growth between different wheat genotypes. The aim of these experiments was to examine the vigour differences between wheat lines, identify traits which promote early vigour and determine the relationship between these traits and early vigour. Continuity with previous work has been provided with the inclusion of experimental lines developed to reflect the positive vigour characteristics of barley (Rebetzke and Richards, 1996).

7.2 Experiment 1: Traits which promote early vigour

The set of 20 breeding lines selected in 1995 to examine vigour and yield differences in the field, were grown in the glasshouse to quantify early vigour differences in the period from sowing to the onset of tillering. Vigour was assessed by detailed measurements and observations in the period from sowing to the full expansion of the third seedling leaf. Destructive measurements were taken twice in the experimental period to estimate relative growth rates and leaf dimensions.

In addition to the breeding lines selected in 1995, the experiment included two experimental lines bred for early vigour by Dr Richard Richards (CSIRO Division of Plant Industry, Canberra) and consisted of a high vigour parent (Vig 18) and the most vigorous selection (S/2/1.19) from a cross between Vig 18 and Stiletto. The parental line (Vig 18) is derived from a cross between a Chinese wheat (Jing Hong) and an Indian wheat (Kharchia), and was bred to increase seedling leaf area through wider, longer leaves and reduced specific leaf weight (Rebetzke and Richards, 1996). Stiletto, developed by the Roseworthy Wheat Breeding Program, is a locally adapted cultivar and was also included in the study.

Two glasshouse studies were conducted. The first experiment was designed to fully characterise the leaf attributes and determine which plant characters promote early vigour. The second study was designed to verify the results of the first study and to measure root growth.

7.2.1 Materials and methods

7.2.1.1 Pot experiment

Twenty breeding lines used in previous field experiments (see Table 5.1), two experimental high vigour lines (Vigour 18 and S/2/1.19) and nine named cultivars were sown into 150 mm diameter unlined, black plastic pots on 21 November 1996. The experiment was conducted in an evaporatively cooled glasshouse at Roseworthy, with day / night temperatures in the order 24 / 11°C.

The trial was laid out as an RCBD with 10 replicates, to allow two harvests of 5 replicates each. The pots were filled with a University of California potting mix (Appendix A) and pressed with a template consisting of protruding dowel rods to provide even seed spacings and sowing depth. Seeds were individually selected to ensure uniform seed size within each cultivar. Six seeds were sown into every pot at a depth of 35 mm and the pots were then watered to field capacity. Temperature was monitored at seed depth in three pots in representative locations inside the glasshouse. Light intensity was measured on the eastern and western sides of the glasshouse.

Emergence was recorded as the number of coleoptiles in each pot which had emerged every 6 hours after the first coleoptile appeared. The time to 50% and 75% emergence (T50 and T75) was calculated by fitting sigmoidal curves to the emergence data using Genstat 5 and the percentage emergence was calculated using the final number of plants which emerged in each pot. The plants were thinned to 4 plants per pot after all plants had emerged (11 DAS).

A destructive harvest was made 12 DAS (207 °Cd) when the plants were at growth stage Z11.5. The plants were cut at ground level and the material separated into leaf and stem by cutting the lamina at the collar region of each leaf. Images were recorded by placing the fully opened leaves between clear acetate sheets and photocopying them at a scale of 1:1. Leaf length and width measurements were made using the photocopied images and leaf area was recorded by scanning the images into a personal computer using a flat-bed scanner and Sci Scan image analysis software (Kirchof and Pender, 1993). Dry matter was recorded after drying the leaf material in a drying oven at 80°C for 48 hrs.

The pots were re-randomised after the first harvest and watered as necessary to ensure moisture was non-limiting. The second harvest was made 23 DAS (400 °Cd), which was after the third leaf had fully expanded in all lines (Z13.0 - Z14.1). The harvest was made by cutting the plants at ground level and separating each of the leaves from the stem by cutting the lamina at the collar region. The plants were separated into 1st, 2nd and 3rd leaves with the remaining leaf and stem bulked as a fourth sample. Leaf dimensions were recorded by measuring each leaf with a ruler (using the same method as for Harvest 1). The leaves were, however, too large to fit between acetate sheets for photocopying and scanning (as per the method for Harvest 1), so leaf area was measured using a Paton Scientific (Adelaide, SA) electronic planimeter. The plant parts were dried in an oven at 80°C for 48 hrs and weighed.

7.2.1.2 Embryo size

Embryo size was measured by selecting 10 pre-weighed seeds of the same weight as those used in the glasshouse studies for each cultivar. The seeds were placed on two sheets of 90mm diameter Whatman No.1 filter paper in glass petri dishes. The paper was pre-wetted with approximately 2.5 ml of reverse osmosis (RO) water per petri dish, so that the papers were damp but not wet. The seeds were held at 2°C and allowed to imbibe for at least 24 hours.

Seed length was measured along the long axis and the embryos were then excised using a scalpel under a microscope. The method involved peeling back the testa and pericarp covering the base of each seed and separating the embryo from the scutellum. The seeds and embryos were then dried at 60°C for 48 h and weighed. Seed and embryo lengths were measured to 0.01 mm using a digital vernier calliper. The trial was analysed as a RCBD with 10 replicates. Statistical analysis (ANOVA) was calculated using Genstat 5, however statistical comparison for mean embryo weight was unable to be performed due to the fact that embryos from all 10 replicates of each genotype were bulked and weighed together.

7.2.1.3 Coleoptile length

Coleoptile lengths were measured by selecting 10 pre-weighed seeds of the same weight as those used in the glasshouse studies for each cultivar and growing them on Ekwip® filter paper (460 x 320 mm). The same 31 lines used in the glasshouse studies were selected, along with one extra line (Halberd), which allowed 8 lines to be grown on each of 4 papers to form 1 replicate. The lines were randomised within each of 10 replicates. Two seeds each from 2 check varieties (Oxley and Halberd) were also included to bring the total number of seeds on each paper to 12.

A line was ruled at the halfway point of the long axis of each paper and marks were made every 25 mm along this line. The paper was then thoroughly wetted in RO water and allowed to drain for approximately 5 minutes. The seeds were placed on their respective marks with the embryos facing the bottom of the paper and the papers were rolled, ensuring the seeds did not move. Each filter paper was wrapped in aluminium foil to exclude light and prevent the papers from dying out, before being placed with the embryos facing downwards in an incubator at 15°C.

After 14 days, coleoptile growth had ceased (as determined using extra filter papers containing check varieties). Coleoptile and root length were measured using a ruler. The trial was analysed as a randomised complete block design with 10 replicates.

7.2.1.4 Analysis

All data were analysed using Genstat 5 and means compared using ANOVA. Thermal time for the glasshouse study was calculated in °Cd to the nearest hour using daily maxima and minima. This accounted for differences in emergence and harvest time.

7.2.2 Results

There were significant genotypic differences in seed and embryo length (Table 7.1). The cultivar Trident had the longest embryo and the closely related cultivar Spear had the longest embryo as a proportion of seed length. There was also good variation in average embryo weight (Table 7.1), where the cultivar Aroona had the heaviest embryo and Stiletto had the largest embryo as a proportion of seed weight. Very large variation in coleoptile length was observed and the coleoptile of line S/2/1.19 was more than double that of line #6 (Table 7.1).

There were significant differences in the average time to 50% emergence (T50), with the high vigour line S/2/1.19 being the quickest and line #5 being the slowest to emerge (Table 7.2). There was a 13% range in T50 and a 15% range in T75 from the time of the earliest emerging cultivar. Coleoptile length was significantly correlated with T50, where genotypes with long coleoptiles emerged more quickly (Figure 7.1).

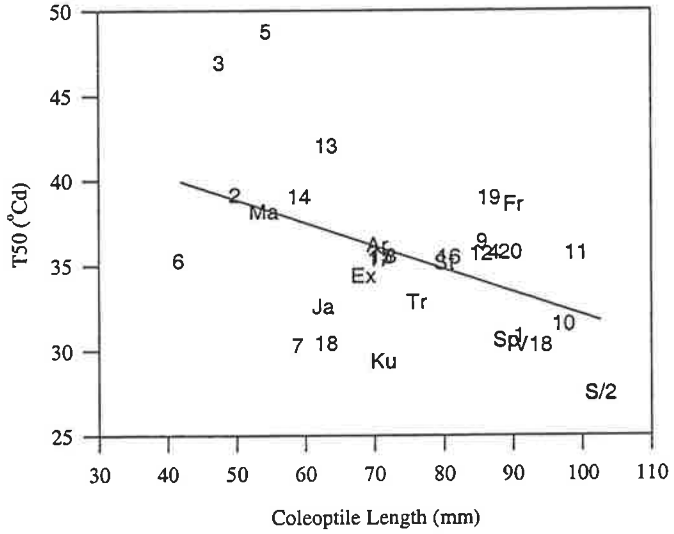

Figure 7.1 Coleoptile length versus time to 50% emergence ($r = 0.47$, $P < 0.05$).

Significant differences in DM and LA were detected at Harvest 1 (H1) (Table 7.2) with lines #15, #18 and S/2/1.19 producing the greatest DM and leaf area. Line #14 was the least vigorous line at this stage, however, there were many other lines which had a LA not significantly different from that of #14.

Table 7.1 Seed , embryo and coleoptile measurements for seed used in Experiment 1 and Experiment 2

Cultivar	Seed Length (mm)	Embryo Length (mm)	Embryo Length Ratio[a]	Embryo Wt (mg)	Emb Wt as % of Seed Wt	Coleoptile Length (mm)
1-CO4191-401	6.59	1.86	0.283	0.40	1.16	91.3
2-CO4196-403	6.69	2.03	0.303	0.47	1.22	50.2
3-CO4196-412	6.26	1.81	0.289	0.39	1.01	48.0
4-CO4197-404	6.71	2.03	0.303	0.40	1.18	87.7
5-CO4201-402	6.64	1.79	0.270	0.32	0.84	54.8
6-CO4202-402	6.47	1.81	0.279	0.32	0.91	42.0
7-CO4203-401	6.42	1.92	0.300	0.43	1.15	59.3
8-CO4204-402	6.64	1.88	0.283	0.41	1.08	72.8
9-CO4212-401	7.19	2.03	0.283	0.39	1.03	85.9
10-CO4226-401	6.45	1.87	0.291	0.30	0.78	97.7
11-CO4254-401	6.54	1.93	0.296	0.34	1.04	99.6
12-CO4259-401	6.72	1.87	0.279	0.30	0.86	85.8
13-CO4289-401	6.83	1.89	0.277	0.42	1.05	63.5
14-CO4289-402	6.72	1.94	0.289	0.47	1.23	59.5
15-CO4323-403	6.61	1.90	0.288	0.44	1.26	71.4
16-CO4330-401	6.60	2.01	0.304	0.50	1.24	81.1
17-CO4372-402	6.30	2.08	0.331	0.37	1.23	71.1
18-CO4372-403	6.70	2.19	0.327	0.49	1.28	63.4
19-CO4382-406	7.07	2.05	0.291	0.40	1.15	87.0
20-CO4418-401	6.66	2.18	0.327	0.43	1.03	90.1
S/2/1.19	7.56	2.09	0.276	0.41	1.15	102.6
Vig 18	7.35	1.98	0.270	0.47	1.22	92.9
Aroona	6.77	1.93	0.285	0.52	1.22	70.4
Excalibur	7.06	2.03	0.288	0.41	1.02	68.4
Frame	6.58	2.17	0.330	0.46	1.19	90.1
Janz	6.77	1.90	0.280	0.30	0.79	62.6
Kulin	6.71	2.05	0.306	n/a	n/a	71.3
Machete	6.87	2.17	0.316	0.50	1.22	54.0
Spear	6.81	2.34	0.344	0.50	1.19	89.0
Stiletto	6.49	1.97	0.305	0.49	1.42	80.0
Trident	6.80	2.22	0.326	0.45	1.14	76.1
Mean	6.73	2.00	0.297	0.42	1.07	74.8
LSD ($P < 0.05$)	0.23	0.11	0.002	n/a	n/a	15.4
Significance	***	***	***	n/a	n/a	***

*** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; ns = $P > 0.05$

(a) Embryo length ratio = embryo length / seed length

The leaf area and DM at Harvest 2 (H2) (Table 7.2) showed that the high vigour line S/2/1.19 had maintained its vigour advantage, producing the greatest LA and DM. Line #20 was the least vigorous line at this time (Table 7.3). The relative growth rate (RGR) and relative leaf expansion rate (RLER) were calculated using equations 7 and 8; where T_1 and T_2 are at Harvest 1 and Harvest 2 respectively.

$$\text{RGR} = (\ln DM_2 - \ln DM_1) / (T_2 - T_1) \tag{7}$$

$$\text{RLER} = (\ln LA_2 - \ln LA_1) / (T_2 - T_1) \tag{8}$$

Table 7.2 Emergence and growth results for breeding lines and named cultivars at Harvest 1 (207 °Cd) and Harvest 2 (400 °Cd) from Experiment 1 and root growth from Experiment 2.

Cultivar	**Emergence**		**Harvest 1**		**Harvest 2**				**Experiment 2**	
	T50 °Cd	T75 °Cd	DM (mg)	LA (cm²)	DM (mg)	LA (cm²)	RGR (mg/mg/°Cd)x10^{-3}	RLER (cm²/cm²/°Cd)x10^{-3}	Rt DM(a) (mg)	Rt:Sht Ratio(b)
1-CO4191-401	109.3	114.2	21.7	7.43	174.9	38.1	1.18	9.29	25.47	0.34
2-CO4196-403	114.4	121.1	19.7	6.17	163.6	33.3	1.21	9.71	38.45	0.48
3-CO4196-412	119.7	123.3	19.6	6.60	147.6	31.1	1.15	8.83	31.38	0.41
4-CO4197-404	112.5	116.4	18.9	7.11	150.5	30.8	1.19	8.45	33.67	0.44
5-CO4201-402	121.1	128.0	21.6	6.98	148.7	30.9	1.10	8.46	34.64	0.52
6-CO4202-402	111.8	115.7	19.7	6.80	150.9	33.0	1.17	9.06	22.38	0.35
7-CO4203-401	108.7	114.1	22.4	7.49	180.3	35.9	1.20	8.97	29.89	0.35
8-CO4204-402	112.5	117.0	22.3	7.68	170.8	35.8	1.16	8.83	30.92	0.37
9-CO4212-401	112.5	116.4	21.0	6.79	146.4	30.1	1.10	8.54	31.52	0.38
10-CO4226-401	109.9	113.8	19.1	6.55	143.5	30.9	1.14	8.87	34.77	0.44
11-CO4254-401	112.5	115.7	17.7	6.61	144.2	29.4	1.20	8.55	37.79	0.55
12-CO4259-401	112.5	115.7	18.8	6.67	137.5	28.3	1.13	8.23	29.10	0.41
13-CO4289-401	116.4	121.8	19.0	6.64	171.4	37.4	1.25	9.84	32.03	0.37
14-CO4289-402	114.4	119.7	18.5	6.13	162.9	33.2	1.23	9.55	31.23	0.37
15-CO4323-403	112.5	116.4	21.3	7.93	165.5	36.3	1.16	8.75	42.61	0.47
16-CO4330-401	111.8	115.7	22.6	7.14	167.0	37.0	1.14	9.36	38.33	0.42
17-CO4372-402	111.8	116.4	17.9	6.24	147.3	28.9	1.19	8.70	35.08	0.41
18-CO4372-403	108.7	112.8	22.9	8.40	171.7	37.5	1.15	8.59	33.40	0.44
19-CO4382-406	114.4	119.1	20.7	7.30	175.9	37.4	1.19	9.19	35.99	0.42
20-CO4418-401	112.5	116.4	20.7	7.16	128.2	24.8	1.04	7.10	25.74	0.36
S/2/1.19	106.8	111.2	23.3	8.30	197.1	41.3	1.20	9.04	31.88	0.35
Vig 18	108.7	112.4	21.5	7.98	174.9	36.2	1.18	8.64	51.19	0.50
Aroona	112.5	117.0	21.0	7.20	167.5	35.8	1.18	9.16	43.36	0.46
Excalibur	111.2	116.4	20.8	6.85	168.1	36.0	1.19	9.44	31.45	0.38
Frame	114.4	119.7	22.4	7.36	157.6	29.7	1.11	7.96	31.61	0.39
Janz	110.6	115.0	18.4	6.52	150.1	30.4	1.18	8.74	26.43	0.32
Kulin	108.0	111.2	19.6	6.76	158.0	29.1	1.18	8.26	30.09	0.37
Machete	113.7	120.4	18.9	6.25	163.2	34.0	1.22	9.57	31.28	0.38
Spear	109.3	113.3	21.8	7.57	160.1	31.9	1.13	8.14	34.69	0.40
Stiletto	111.8	115.7	18.5	6.67	151.1	28.6	1.19	8.30	25.11	0.36
Trident	110.6	114.0	19.4	7.04	173.0	35.5	1.23	9.13	31.06	0.36
Mean	112.2	116.6	20.4	7.04	160.3	33.2	1.17	8.81	33.00	0.41
LSD ($P < 0.05$)	4.6	6.1	2.5	0.92	24.9	5.7	0.11	1.30	9.89	0.09
Significance	***	***	***	***	***	***	ns	*	*	ns

*** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; ns = $P > 0.05$

(a) Root weight measured in Experiment 2 (405 °Cd)

(b) Rt:Sht ratio = Root : Shoot ratio (Experiment 2 - 405 °Cd)

There was a significant relationship between the time to 50% emergence and total leaf area up to 6 DAS (Figure 7.2a). Genotypes which emerged earlier produced greater leaf area at Harvest 1 but this relationship was no longer significant at Harvest 2 (Figure 7.2b). There was no observable effect of rate of emergence on DM (Figure 7.3).

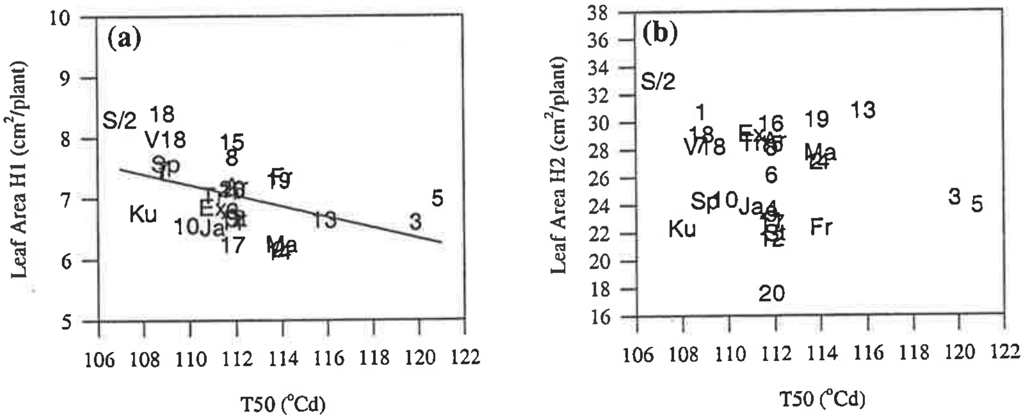

Figure 7.2 Thermal time to 50% emergence versus total leaf area at H1 (a) and H2 (b). Correlation for (a) r = 0.44 ($P < 0.05$), (b) is ns ($P > 0.05$).

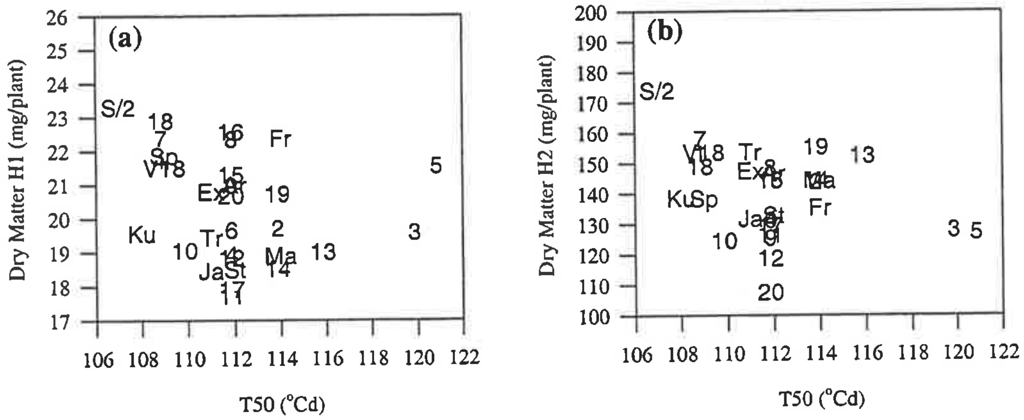

Figure 7.3 Thermal time to 50% emergence versus total DM at H1 (a) and H2 (b). Correlations are not significant ($P > 0.05$).

Embryo weight was correlated with shoot DM and LA at 400°Cd in Experiment 1 (Figure 7.4), where genotypes with large embryos produced greater biomass and LA. Despite having reasonable embryo weight, Line #20 was less vigorous than its embryo size would suggest. Embryo weight was more strongly correlated with DM than LA, and the correlations between embryo size and vigour measurements (DM and LA) were greater at H2 than H1. Embryo weight as a proportion of total seed weight was also well correlated with early growth measurements but embryo length was not.

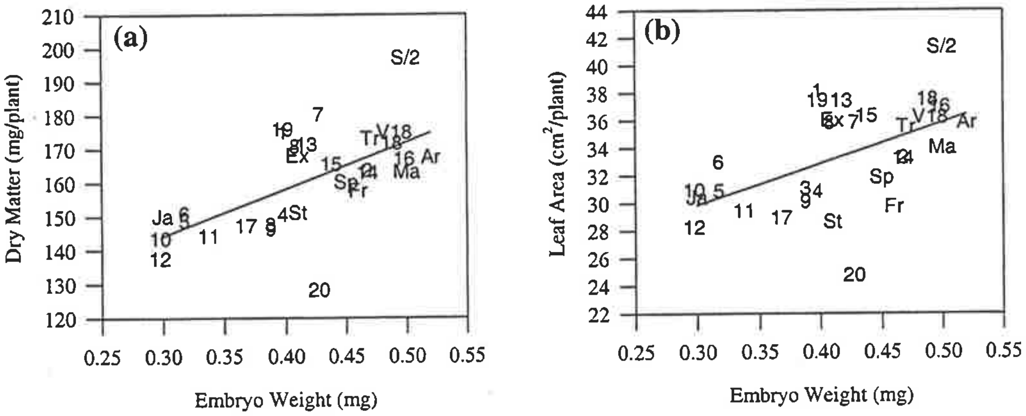

Figure 7.4 Embryo weight versus (a) shoot DM at H2; (b) leaf area at H2. Correlation for (a) $r = 0.62$ ($P < 0.01$), (b) $r = 0.52$ ($P < 0.01$).

Figure 7.5 (a) illustrates the growth rate (DM / °Cd) from emergence - H1 (GR1) and H1 - H2 (GR2) and Figure 7.5 (b) illustrates the leaf expansion rate (LER) over the same period. The positive relationship between GR1 v GR2 and LER v LER 2 indicates that larger plants at Harvest 1 were also larger at Harvest 2. However, due to differences in SLW, the genotypic ranking is different for comparisons of GR and LER.

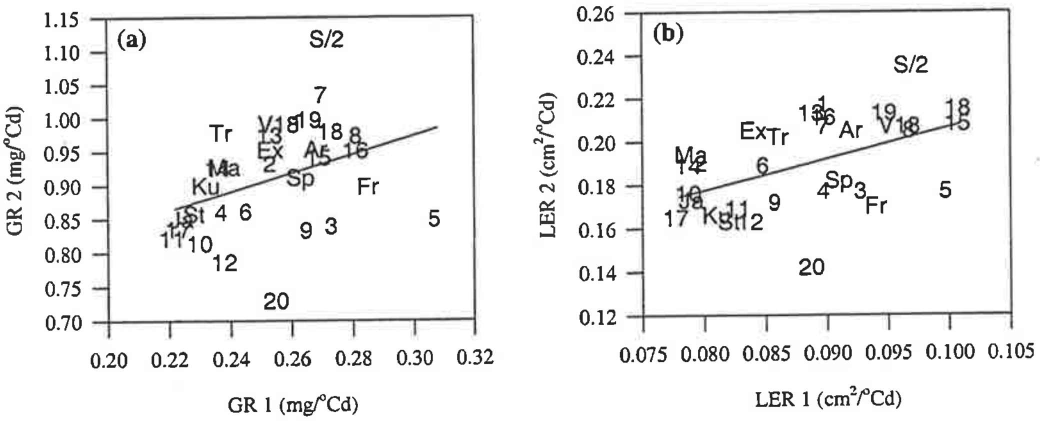

Figure 7.5 Growth rate comparisons for (a) shoot growth rate (GR 1) from emergence-H1 versus GR 2 from H1-H2; (b) leaf expansion rate (LER 1) from emergence-H1 versus LER 2 from H1-H2. Correlation for (a) r = 0.36 (P < 0.05), (b) r = 0.48 (P < 0.01).

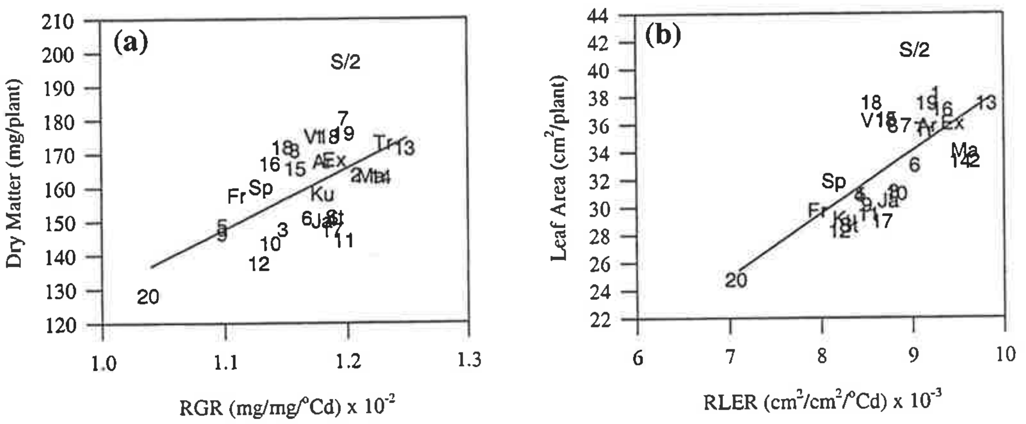

Figure 7.6 Relative growth rate comparisons for (a) RGR versus DM at 400 °Cd; (b) RLER versus LA at 400 °Cd. Correlation for (a) r = 0.55 (P < 0.01), (b) r = 0.69 (P < 0.01).

Total DM and LA at the second harvest were strongly correlated with relative growth rate (r = 0.55) and relative leaf expansion rate (r = 0.69) (Figure 7.6). It is interesting to note that the most vigorous line S/2/1.19, does not have the highest RGR and RLER at H2. However, this can be explained by the fact that this line did not have a significantly different (P > 0.05) RGR or RLER from the majority of the other lines, despite the strong correlation.

Table 7.3 Specific leaf weight and leaf dimensions. Leaf length and width were measured using a ruler, where leaves 1-3 were fully expanded and leaf 4 was taken at 400 °Cd.

Cultivar	Specific Leaf Weight			Leaf Dimensions (mm)							
	Leaf 1	Leaf 2	Leaf 3	Leaf 1		Leaf 2		Leaf 3		Leaf 4	
	(g/m^2)	(g/m^2)	(g/m^2)	Length	Width	Length	Width	Length	Width	Length	Width
1-CO4191-401	41.0	42.7	35.9	107	4.51	205	5.40	275	8.02	109	7.54
2-CO4196-403	46.6	44.0	38.8	117	4.54	214	5.32	268	8.42	112	8.19
3-CO4196-412	48.7	43.5	35.2	117	4.33	204	5.18	258	8.64	89	7.48
4-CO4197-404	51.8	46.2	35.5	134	4.21	253	5.19	279	8.83	88	7.24
5-CO4201-402	42.0	43.3	35.1	144	5.07	230	6.28	233	9.65	29	n/a
6-CO4202-402	42.0	41.8	37.2	115	4.68	219	5.37	286	8.58	74	7.66
7-CO4203-401	47.2	46.9	39.2	131	4.22	235	5.10	329	7.25	168	7.02
8-CO4204-402	44.2	46.8	38.7	119	4.57	208	5.26	279	7.98	118	7.34
9-CO4212-401	47.2	45.4	37.6	112	4.74	222	5.30	282	8.09	60	6.18
10-CO4226-401	45.8	44.7	40.5	98	4.13	187	4.55	257	6.24	185	7.68
11-CO4254-401	49.9	47.2	38.7	115	4.38	207	4.83	278	6.79	131	6.59
12-CO4259-401	55.9	46.4	41.8	105	4.31	200	4.62	265	6.14	157	6.80
13CO4289-401	45.8	42.9	36.5	113	4.49	207	5.38	280	8.21	109	8.10
14-CO4289-402	43.5	43.4	39.8	106	4.34	206	5.18	276	7.92	107	8.39
15CO4323-403	46.7	42.2	36.2	102	4.59	233	5.35	284	8.52	126	9.00
16-CO4330-401	46.5	43.7	36.6	125	4.54	234	5.25	318	7.99	131	8.34
17-CO4372-402	55.1	51.4	42.4	120	3.88	220	4.11	290	5.83	161	7.36
18-CO4372-403	51.3	42.3	40.9	117	4.46	213	4.95	275	6.66	221	8.85
19-CO4382-406	45.8	44.8	37.1	119	4.41	220	5.44	302	8.73	120	8.38
20-CO4418-401	47.4	49.9	41.1	114	4.10	198	4.38	298	6.03	129	6.44
S/2/1.19	43.9	38.0	36.5	152	4.88	255	5.63	308	9.29	111	7.85
Vig 18	44.1	42.4	34.6	165	4.77	266	6.10	273	9.68	70	6.51
Aroona	41.5	48.9	40.2	117	4.32	203	4.69	261	6.01	219	7.90
Excalibur	47.3	41.0	41.5	102	4.28	188	4.77	265	6.51	210	8.08
Frame	52.6	48.2	40.0	115	4.31	199	4.69	298	6.44	163	7.08
Janz	52.2	52.0	43.5	105	3.82	198	4.25	268	6.10	203	7.86
Kulin	48.7	53.0	41.3	121	4.40	210	5.04	258	7.46	114	6.63
Machete	51.4	44.9	36.2	102	4.17	194	5.15	272	7.89	117	7.58
Spear	50.4	50.1	40.5	116	4.13	208	4.61	291	6.26	187	7.07
Stiletto	61.5	54.5	40.8	120	4.19	209	4.51	292	6.82	144	7.40
Trident	47.6	46.5	40.9	115	4.34	204	4.84	282	6.70	198	7.97
Mean	47.9	45.8	38.7	118	4.39	214	5.05	280	7.54	134	7.55
LSD (P<0.05)	9.6	6.5	4.3	7.5	0.27	12.8	0.29	18.8	0.46	28.8	1.22
Significance	*	***	***	***	***	***	***	***	***	***	***

*** = P < 0.001; ** = P < 0.01; * = P < 0.05; ns = P > 0.05

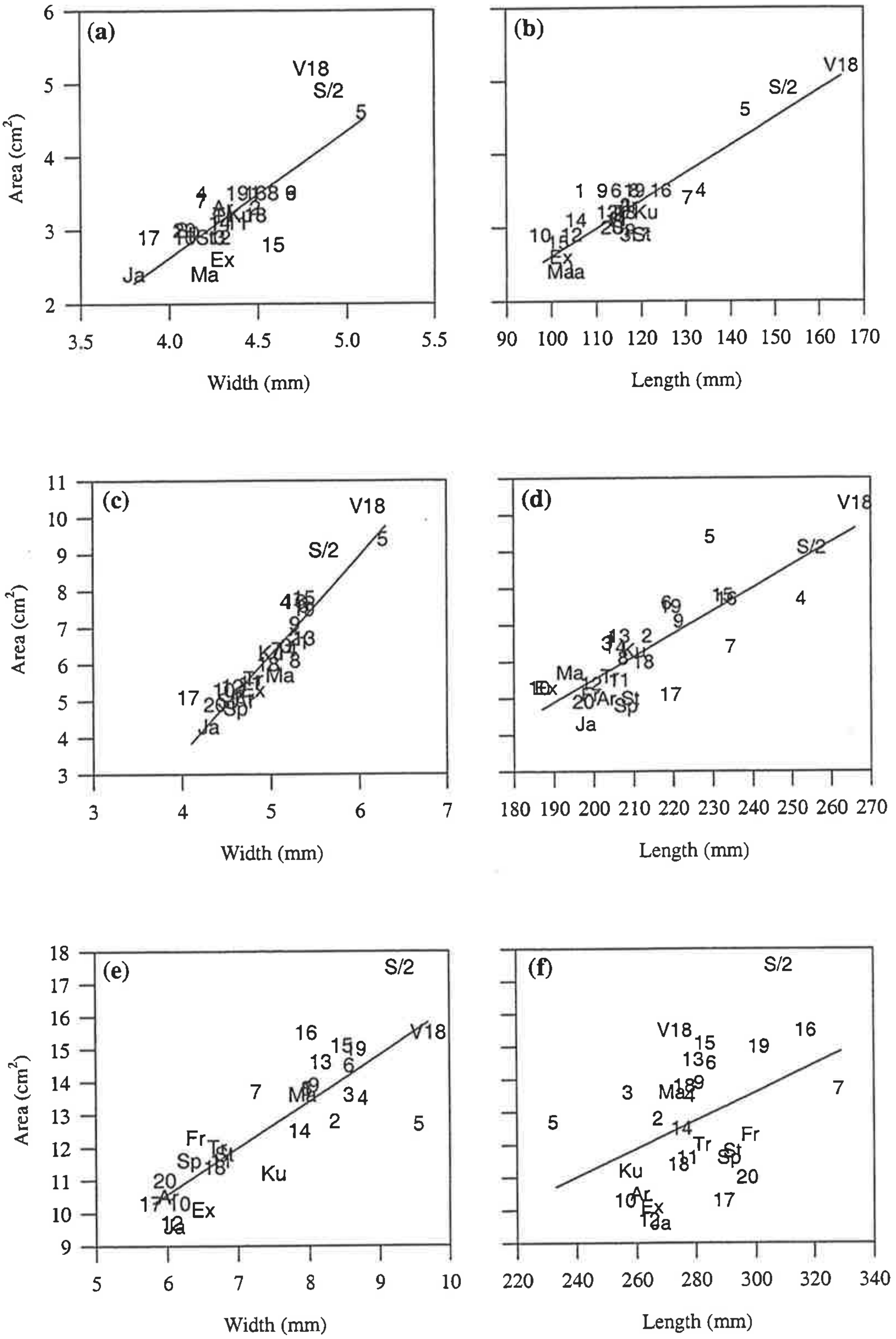

Figure 7.7 Leaf width versus LA at 400 °Cd for (a) leaf 1; (c) leaf 2; (e) leaf 3. Leaf length versus LA at 400 °Cd for (b) leaf 1; (d) leaf 2; (f) leaf 3. Correlations for (a) r = 0.77; (b) r = 0.89; (c) r = 0.92; (d) r = 0.83; (e) r = 0.84; (f) r = 0.42. Significance for (a), (b), (c), (d), (e) is ($P < 0.01$); (f) is ($P < 0.05$).

Leaf area of the first leaf was highly correlated with leaf length and leaf width, (Figure 7.7a, b) however, width accounted for more LA variation in subsequent leaves (Figure 7.7e). There was a narrow range in the dimensions of the first leaf amongst the lines studied, except for lines #5, S/2/1.19, and Vigour 18, which expressed greater leaf length and width (Figure 7.7 a, b). The variation in leaf dimensions between lines increased with later leaves, although the high vigour lines continued to produce the widest leaves. Since the later leaves have a larger influence on the total leaf area, leaf width becomes an important tool for increasing early leaf area and hence early vigour.

To better assess the importance of leaf dimensions, the length and width of each leaf was summed to give a cumulative total length and cumulative total width for all leaves on the plant. Figure 7.8 illustrates the cumulative effect of leaf dimensions on total LA at harvest 2. It can be clearly seen that leaf width had a far greater effect on total leaf area than leaf length. It is evident that S/2/1.19 had greater cumulative leaf length than #18 despite the fourth leaf of the latter line being twice as long (Table 7.3).

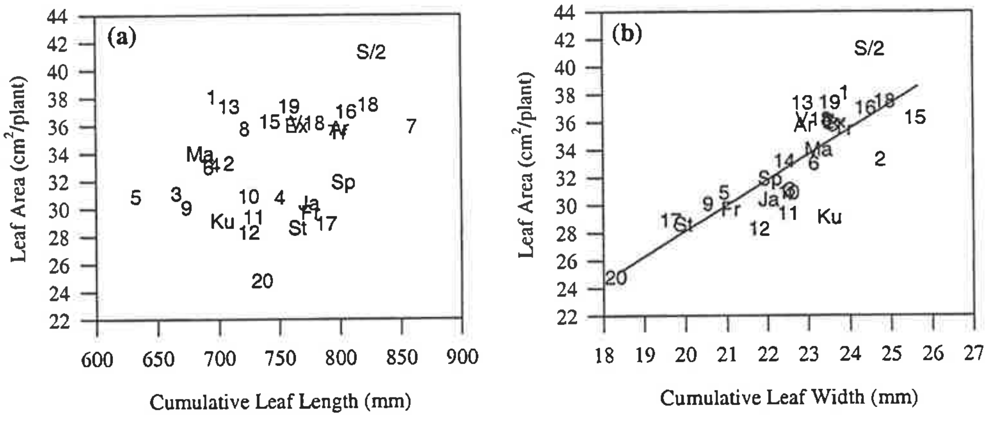

Figure 7.8 The effect of (a) cumulative leaf length and (b) cumulative leaf width on LA at harvest 2. Correlation for (a) ns (P > 0.05); (b) r = 0.79 (P < 0.01).

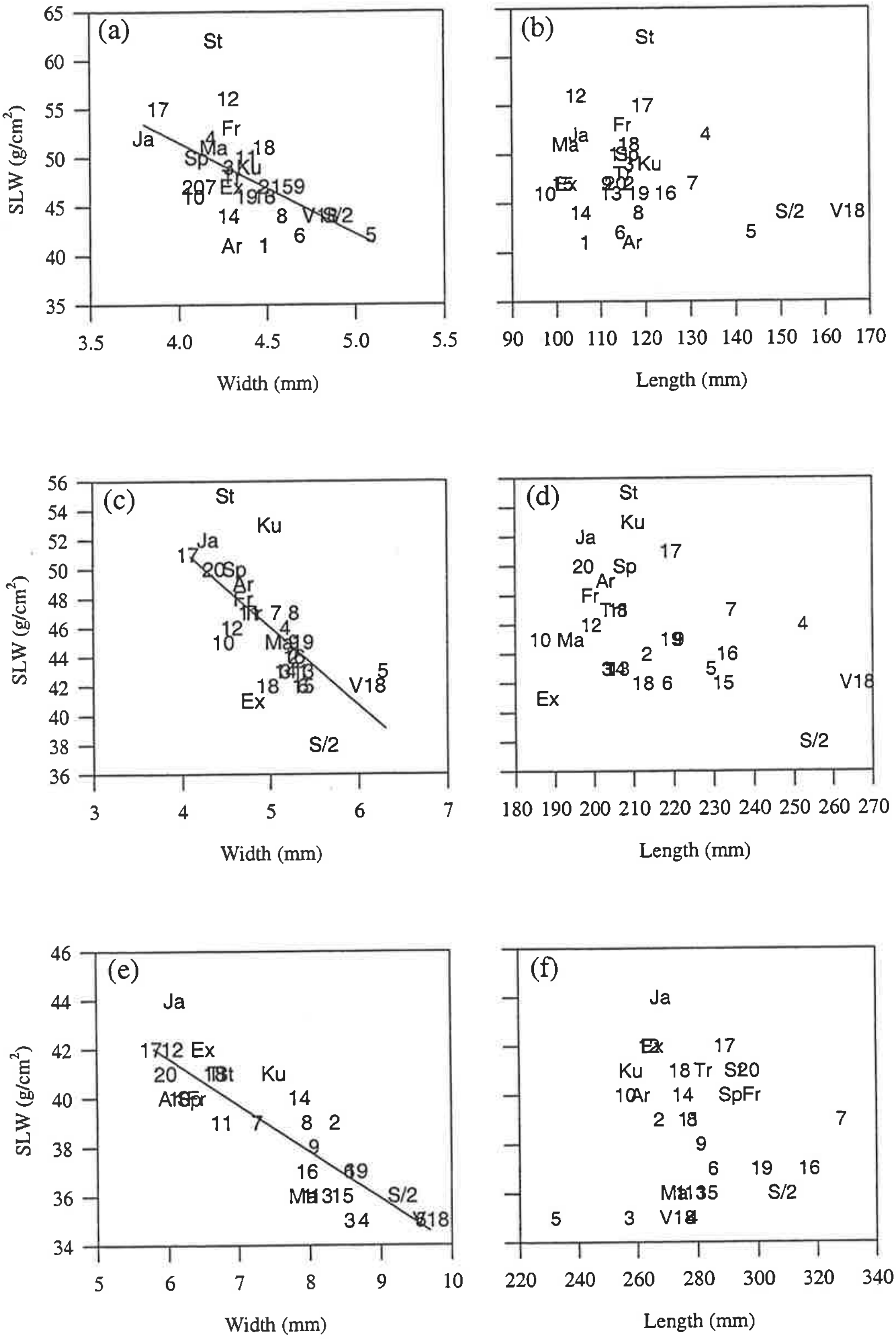

Figure 7.9 Leaf width versus SLW at 400 °Cd for (a) leaf 1; (c) leaf 2; (e) leaf 3. Leaf length versus SLW at 400 °Cd for (b) leaf 1; (d) leaf 2; (f) leaf 3. Correlations for (a) r = 0.56; (c) r = 0.68, (e) r = 0.87. Significance for (a), (c) and (e) is ($P < 0.01$); (b), (d) and (f) are ns ($P > 0.05$).

The area of individual leaves was more strongly correlated with leaf width than leaf length (Figure 7.7) and leaf width was also significantly correlated with SLW (Figure 7.9), particularly amongst later leaves, whereas leaf length was not correlated with SLW for any of the first 3 leaves (Figure 7.9). Thus, increases in leaf width will not only increase leaf area and early vigour, but also have the effect of reducing SLW.

There were genotypic differences in the phyllocron interval ($P < 0.001$) which meant that by Harvest 2 some lines (Aroona, Excalibur and #18) had produced 4.1 leaves, whilst other lines (#5) had only produced 3 (Figure 7.10). Differences in total leaf number were present at the first time of measurement (11 DAS) but the phyllocron interval was not correlated with T50 or LA at either harvest ($P > 0.05$).

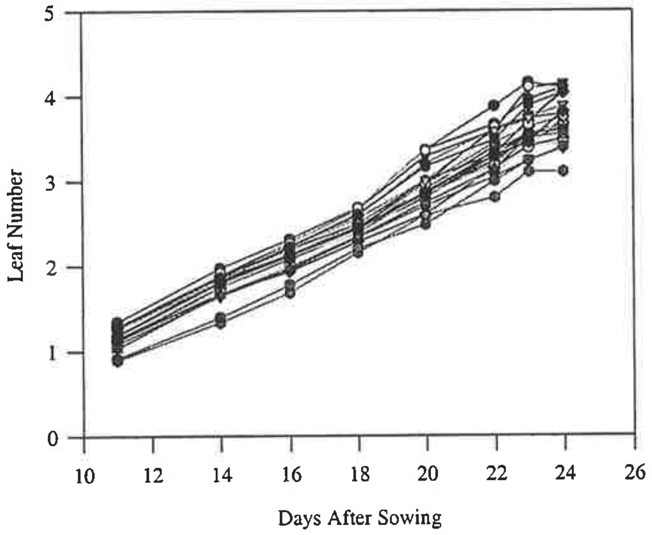

Figure 7.10 Leaf number versus days after sowing.

7.3 Experiment 2: Root growth

7.3.1 Materials and methods

The 22 breeding lines and 9 named cultivars used in experiment 1 were also used in a second glasshouse trial sown at Roseworthy on 24 May 1997. The methodology was identical to that employed in Experiment 1 except that only one destructive harvest was made 29 DAS (405 °Cd), after the third leaf had fully expanded in all lines. The same seed source was used as for Experiment 1 and the method remained the same in terms of potting-up, sowing and general husbandry. To enable root measurement, the potting mix was changed to a modified lucerne/medic mix (Appendix A) which was pH stabilised and the nutrient concentration increased to match the potting mix used in the first experiment.

The roots were washed out by gently hosing the soil from the root mass over a plastic sieve. The operation was conducted carefully to ensure that minimal damage was done to the roots and the entire root system remained intact. The root systems from all four plants in each pot were bulked together and the roots were then oven dried at 80°C and weighed. The data were analysed as a RCBD with 4 replicates using Genstat 5 and the means compared using ANOVA.

7.3.2 Results

There were significant differences in root biomass, with the high vigour line Vigour 18 being the most vigorous genotype and line #6 the least vigorous both above and below the ground (Figure 7.11). Line #11 had the highest root:shoot ratio whilst Janz had the lowest.

Figure 7.11 demonstrates the close relationship between shoot DM and root DM at the 3.5 leaf stage (405 °Cd); plants that displayed good shoot growth also produced larger root biomass. The same relationship held true for root DM and LA, where plants with larger root systems had a greater total leaf area.

It is interesting to note the large improvement in shoot DM in S/2/1.19 over the parent cultivar Stiletto, which was similar to Experiment 1. The improvement in shoot growth of S/2/1.19 was greater than for root growth and consequently the root shoot ratio of this line is very low. The root:shoot ratio was not correlated to DM or LA and thus had no bearing on early vigour in pot culture.

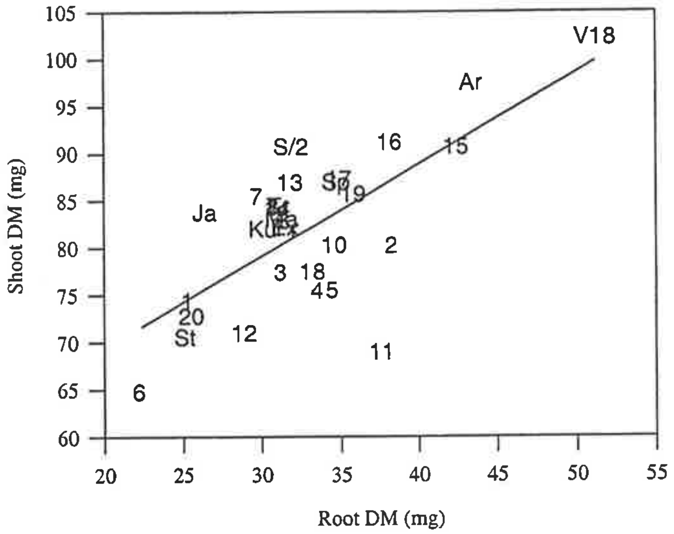

Figure 7.11 Root DM versus shoot DM 405 °Cd. ($r = 0.69$, $P < 0.01$)

7.4 Comparison of vigour experiments

Experiment 1 was sown on 21 November 1996 and Experiment 2 was sown on 24 May 1997. Shade netting was used in Experiment 1 to reduce the incident light intensity from around 2000 μmol/m²/s photons of PAR to approximately 500 μmol/m²/s. This was comparable to the 400 μmol/m²/s PAR experienced in Experiment 2. The shade netting also enabled the evaporative cooling to reduce temperatures within the glasshouse, however, greater thermal time was still accumulated during the first experiment (Table 7.4).

Day length was different between the two experiments. Experiment 1 experienced increasing day lengths, in the order of 13-14 hours per day, whilst experiment 2 experienced decreasing day lengths in the order of 9.5-10 hours per day. When this was combined with the greater incident radiation in Experiment 1, the net effect was a much greater incidence of PAR and twice the average daily accumulated light energy in the first experiment (Table 7.4). This had the effect of producing greater dry matter and SLW in the summer experiment. Given that it took 400°Cd and 405°Cd to reach growth stage Z13.5 in each experiment, it would appear that differences in day length did not have any effect on the rate of plant development.

Table 7.4 Glasshouse environmental conditions. Figures are averages for each experiment.

	Max Temp (°C)	Min Temp (°C)	Day Degrees (°Cd/day)	Day Length (Hours)	Average PAR (mol/m²/day)
Experiment 1	24.8	10.9	17.9	13.5	12
Experiment 2	18.9	9.1	14.0	10.0	6

The differences in the accumulation of thermal time meant that the ligule of third leaf had fully appeared in all genotypes by 23 DAS in Experiment 1 but took until 29 DAS in Experiment 2. Figure 7.12 shows that the area of the first two leaves were very similar between the two experiments, and the high vigour experimental lines, Vigour 18 and S/2/1.19, produced greater LA for the first two leaves than all other lines except for line #5 (Figure 7.12).

The leaves in Experiment 1 (summer experiment) had greater SLW compared to Experiment 2 (winter experiment) (Figure 7.12). The SLW of leaves 2 and 3 were correlated between experiments indicating that there was some genetic control.

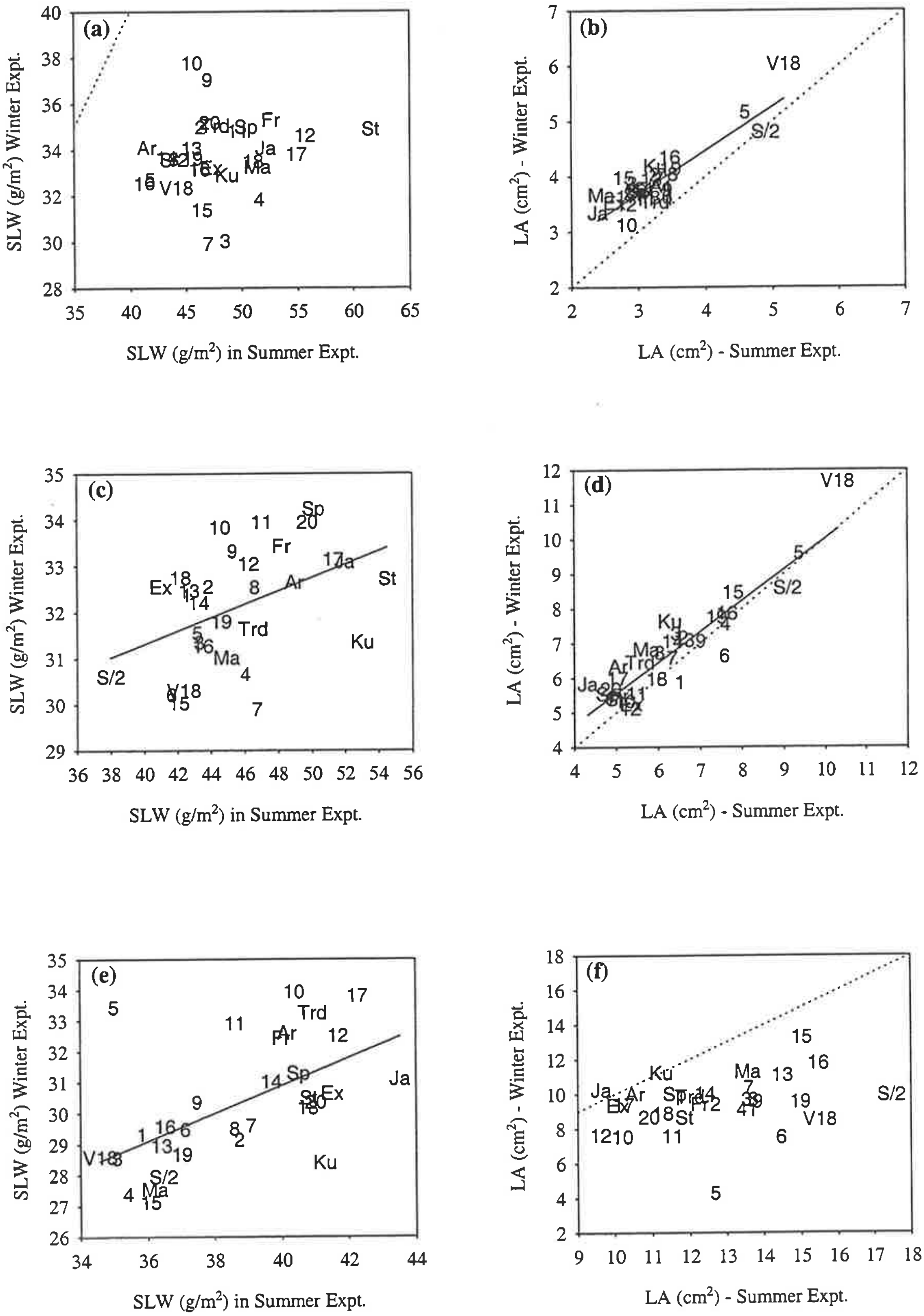

Figure 7.12 Comparison of SLW and leaf area between the 1996 and 1997 glasshouse experiments, (a) SLW leaf 1; (b) LA leaf 1; (c) SLW leaf 2; (d) LA leaf 2; (e) SLW leaf 3; (f) LA leaf 3. Correlations for (a) ns; (b) r = 0.87, (c) r = 0.44, (d) r = 0.91, (e) r = 0.56, (f) ns. Significance level for (b), (d) and (e) is (P < 0.01); (c) is (P < 0.05); (a) and (f) are ns (P > 0.05). Dotted line (….) indicates 1:1.

7.5 Discussion

7.5.1 Differences in early vigour

The results show that significant differences in early growth could be detected between wheat genotypes from as early as 6 days after emergence (207 °Cd from sowing) and there was good correlation between vigour measurements taken at Harvest 1 and Harvest 2 (Table 7.5). This compares favourably with López-Castañeda *et al.* (1994b) who detected significant differences in growth between cereal species from approximately 150 °Cd. Whilst the differentiation between genotypes was not as large in this (current) study, this is to be expected due to the fact that the López-Castañeda *et al.* (1994b) study examined differences between species whereas this study measured differences within a species.

The difference in time to 50% emergence from the earliest line to the latest line was 14.3 °Cd, or 21 hours. The significant correlation between T50 and LA at Harvest 1 (Figure 7.2) is supported by López-Castañeda *et al.* (1996), who found that a 10 °Cd difference in T50 between wheat and barley gave a significant difference in DM and LA at the 2 leaf stage. These results can be further extrapolated to a field situation where emergence often takes as long as 10-14 days, compared to 6 days in the glasshouse. Thus, the 1 day difference in T50 in the glasshouse translates to a 2 day difference under field conditions. Thus, the earlier emerging plants under field conditions would accumulate greater solar radiation and experience greater growth than earlier emerging plants in the glasshouse.

The most vigorous lines followed different strategies of leaf area accumulation. At Harvest 1, the first leaf accounted for approximately 81% of the total leaf area in the high vigour line S/2/1.19, whereas the first leaf accounted for only 61% of the total area in line #15 and only 57% in line #18. The total leaf length at Harvest 1 in these three lines was very similar (214, 214 and 229 mm for lines S/2/1.19, #15 and #18 respectively).

The data suggest that there was compensation between the rate of leaf appearance and leaf size. Lines S/2/1.19 and #5 formed large leaves more slowly whereas lines #15 and #18 formed small leaves more quickly. Plants with a shorter phyllochron generate a greater proportion of their LA from later formed leaves and since later formed leaves are wider than earlier leaves (Table 7.3), these genotypes may have a greater rate of leaf area accumulation. This would tend to favour lines with very short phyllochron interval. Despite the significant differences, variations in phyllochron interval were small (Figure 7.10), so it is possible that at some time after Harvest 2, the line S/2/1.19 could produce significantly greater LA due to greater leaf width.

7.5.2 Traits which promote early vigour

The correlation matrix (Table 7.5) shows that early vigour (defined as either DM or LA at Harvest 2) is significantly correlated with embryo weight, SLW, leaf dimensions and relative growth rates (RGR and RLER).

Table 7.5 Correlation matrix between early vigour (DM and LA), and quantitative growth traits.

	TGW	Em Wt[a]	Clpt[b]	T50	SLW	LW[c]	LL[d]	Pi[e]	DM H1	LA H1	RGR	RLER	DM H2
Embryo Wt	*												
Coleoptile	ns	ns											
T50	ns	ns	(**)										
Av SLW	ns	ns	ns	ns									
Leaf Width	ns	ns	ns	ns	(***)								
Leaf Length	ns	*	ns	ns	ns	**							
Phyllochron	**	ns	ns	ns	ns	ns	ns						
DM (H1)	ns	**	ns	ns	(*)	ns	**	ns					
LA (H1)	ns	*	*	(*)	ns	ns	**	ns	***				
RGR	ns	ns	ns	ns	ns	ns	ns	ns	(*)	ns			
RLER	ns	ns	(*)	ns	(**)	ns	ns	ns	ns	ns	***		
DM (H2)	ns	***	ns	ns	(**)	*	**	ns	***	**	**	***	
LA (H2)	ns	**	ns	ns	(***)	**	*	ns	**	**	***	***	***

*** = P < 0.001; ** = P < 0.01; * = P < 0.05; ns = P > 0.05

Values in parentheses () indicate negative correlations

[a] = Embryo weight

[b] = Coleoptile length

[c] = Cumulative width of leaves 1-3

[d] = Cumulative length of leaves 1-3

[e] = Phyllochron interval

This study found that embryo size was closely related to seed size (TGW) (Table 7.5) and early vigour (Figure 7.4), however, TGW was not directly correlated with early vigour (Table 7.5). Embryo size has been previously identified as being important for early vigour (see Section 2.5.3.2) and seed size was found to be closely related to embryo size within lines (López-Castañeda *et al.*, 1996; Moussavi-nik *et al.*, 1996).

Thus TGW was not a good measure for direct vigour selection. This is presumably due to genotypic differences in the size of the embryo as a proportion of seed size (see embryo length ratio (Table 7.1)). It also suggests that the vigour advantage is conferred through greater initial number of plant cells in the embryo, rather than greater seed reserves, common in seeds with large endosperm (Peterson *et al.*, 1989).

There was significant genotypic variation for embryo size within the genotypes studied, however, there were no breeding lines which had larger embryos than the commercial cultivars (Table 7.1). All cultivars (except Janz) had embryo weights greater than the mean, which could mean that the commercial cultivars have already been (albeit subconsciously) selected for large embryo size.

It has been suggested that the width of the first seedling leaf could be used as a surrogate measure to estimate embryo size (Richards, 1996), but this was not supported by these results. There was no correlation between embryo weight and the width of any of the first three leaves ($r_1 = 0.15$, $r_2 = 0.18$, $r_3 = 0.14$), however, embryo weight as a proportion of seed weight was correlated with leaf length ($r_1 = 0.36$, $r_2 = 0.45$, $r_3 = 0.41$).

Specific leaf weight was highly correlated with early vigour (Table 7.5) and this was due to increased leaf width (Figure 7.9). Plants with wider leaves had lower SLW, which indicates greater light interception for the same investment in biomass. The relationship between SLW and leaf width was more strongly correlated in later leaves (Figure 7.9), which could possibly be a function of greater variation in leaf width. The contribution of SLW to early vigour has been well documented (see section 2.5.2.2.2) and most authors have noted the strong relationship between SLW and leaf width (eg. Rebetzke and Richards (1996)).

Leaf length and leaf width were both highly correlated with leaf area (Figure 7.7), however, cumulative totals for the first 3 leaves show that leaf width is more important for promoting early vigour (Figure 7.8). Good genotypic variation was found for both length and width, and many experimental lines had dimensions that were significantly greater than for commercial cultivars. This is in close agreement with Rebetzke and Richards (1996) who found a similar relationship between LA and leaf length and width, however, their study found greater genotypic variability in width of the first leaf.

Rebetzke and Richards (1999) found that for every 1mm increase in average leaf width of leaves 1 & 2, there was a 7.9 cm^2 increase in leaf area. This compares with an increase of approximately 2 cm^2 for every mm increase in leaf width in this experiment (Figure 7.7) and illustrates the greater genotypic range in LA and leaf width in their genotypes. Indeed, two of the three lines with the largest first leaves identified in this study (Vigour 18 and S/2/1.19) were progeny from crosses made by R.A. Richards.

The RGR and RLER were both highly correlated with early vigour (Table 7.5), despite there being no significant differences identified for RGR and only small differences were detectable in RLER (Table 7.2). López-Castañeda *et al.* (1995) had similar results, where there were differences in early vigour between wheat and barley, yet no differences in relative growth rates. It is possible that, had greater genotypic variation in relative growth rates been present, then greater commensurate increases in early vigour could have resulted. However, this is unlikely given the large vigour differences between wheat and barley.

Long coleoptile length has been associated with good early vigour through faster rate of emergence (Richards, 1992a). While genotypic differences in coleoptile length were present (Table 7.1) and were correlated with T50, the differences in T50 were not large enough to affect LA or DM at Harvest 2. It is possible that this could be a function of the shallow sowing depth (35 mm), friable potting mix and well watered conditions which allowed fast emergence in the glasshouse and a relatively small variation in T50. It is therefore quite possible that long coleoptile length may be a vigour trait for plants grown in field conditions where seeds are sown deeper and take longer to emerge (Richards, 1992b).

7.5.3 Initial size versus rate of growth

It is clear that both embryo size and relative rates of growth (RGR and RLER) have a role to play in enhancing early vigour, despite the relatively small variation in each trait within the genotypes examined. It is also likely that time of measurement will influence the relative expression of each trait. Plants with similar RGR but different embryo weight should display larger vigour differences during early vegetative growth (eg. López-Castañeda *et al.* (1996)), whereas, plants with similar embryo size but differences in RGR may take longer before differences in vigour become detectable (eg. Karimi and Siddique (1991a)).

It is interesting to note that RGR was correlated with early vigour, despite the fact that there were no observable differences within the genotypes studied. If genotypic variation in the RGR could be identified, then it is likely that greater differences in early vigour could be generated. The fact that RGR and embryo size are independent of each other (Table 7.5) means that it should be possible to select for genotypes expressing superiority for each trait. However, since the genotypes used in these experiments were not selected for either RGR or embryo size, it is difficult to make comparisons. Given that wider genotypic variation should exist for these traits (Karimi and Siddique, 1991a; Moussavi-nik, 1997), it should be possible to promote early vigour through genetic selection for large embryos and high relative growth rates.

7.5.4 Genotype x environment interaction

Experiment 1 was repeated using the same seed source some 6 months later, which meant that the only major differences between experiments were temperature, day length and solar radiation. These different environments provided the opportunity to examine the environmental interaction with the expression of vigour traits. Since the two experiments took approximately the same time to reach similar growth stages (400°Cd and 405°Cd), it is unlikely that differences in day length affected growth.

Figure 7.12 shows that the main differences were in SLW, as the plants grown during the summer (Experiment 1) produced thicker leaves than plants grown during the winter. This is in agreement with Rawson *et al.* (1987) who found that SLW was increased by high light intensity by approximately 0.25g/cm^2 per mol/m^2/d. The experimental high vigour lines (S/2/1.19 and Vig 18) had a higher ranking for DM and LA under the summer conditions. This may be due to the higher growth rates experienced in Experiment 1, or to better adaptation to warm, high fertility conditions due to their Indian parentage.

The LA of the first two leaves are highly significantly correlated and the regression line sits close to 1:1. This demonstrates the genetic control of the leaf area of the first two leaves despite the DM (and hence SLW) differences. It is interesting to note that plants sown during warmer conditions produced slightly smaller first leaves which concurs with the findings of Rebetzke and Richards (1999). These authors also found that environmental differences in the first two leaves were small in comparison with genotypic differences.

The environmental effects on the leaf area of the third seedling leaf are quite evident as the LA is not correlated between experiments. It seems likely that the size of the first two leaves is pre-determined by the number of cells in the embryo (Moussavi-nik *et al.*, 1996), whilst the size of the third leaf is determined environmentally through a genotype x environment interaction.

The most vigorous genotypes in the glasshouse experiments (Experiments 1 and 2) were not the most vigorous genotypes in the field experiment (Chapter 6). This could be due to a number of factors. Firstly, the comparisons were made at different stages of growth; which may affect the relative rankings over time. Secondly, the comparisons were made in vastly different environments, which may affect a number of morphological traits through a genotype x environment interaction. Thirdly, the most vigorous genotypes in the glasshouse experiments (Vigour 18 and S/2/1.19) were not included in the field experiment as they were not available in 1996.

7.6 Conclusions

Observation of high and low vigour lines selected from early generation material within the Roseworthy Wheat Breeding Program was able to identify several plant traits which promote LA and DM in the period up to growth stage Z13.0. These vigour traits include large embryo, low SLW, wide leaves and high RGR and RLER, and there is reasonable genotypic variation for most traits. Since the lines were not selected on the basis of these traits, and given the superior vigour of lines which were selected on the basis of some of these traits (i.e. Vigour 18 and S/2/1.19), it should be possible to make further gains in early vigour using these traits as selection criteria.

The results also showed that the morphology of the first two seedling leaves was genetically controlled, whereas the morphology of the third seedling leaf was influenced by a genotype x environment interaction. These experiments were not able to separate the importance of large starting size (i.e. embryo size) from high relative growth rates in the promotion of early vigour.

CHAPTER 8

8. Identifying quantitative trait loci (QTLs) for traits which promote early vigour

Detailed observations of high and low vigour lines (Chapter 7) revealed a number of traits which promote early vigour, such as embryo size, SLW and seedling leaf morphology. In order for these vigour traits to be incorporated into wheat breeding programs, genetic variation must be identified, which in turn requires good selection techniques. Selection must be able to not only identify good parental source material but also distinguish which progeny are genetically superior. While there is evidence to suggest that selection for large embryo and low SLW could be achieved through measurement of the width of the first seedling leaf (López-Castañeda *et al.*, 1996), this is at best a correlative technique.

Recent advances in molecular genetics using molecular markers has enabled accurate mapping of chromosomes and the locations of genes coding for specific traits. If these markers are well correlated with quantitative phenotypic traits (such as vigour traits), then quantitative trait loci (QTLs) can be determined for those traits. Breeders can then see which combinations of traits are likely to be contained within the segregating progeny of each cross. In this way, breeding material can be screened to assess the likelihood of expressing specific phenotypes using marker assisted selection (MAS) techniques.

In a review on the use of molecular markers in plant breeding Paterson *et al.* (1991) list the potential advantages of using QTLs in marker assisted breeding programs. These include: knowledge of where genes are located and the number of genes that influence specific traits, the contribution of each gene to the trait in question; the effect of gene mutation; knowledge of pleiotropic effects; environmental sensitivity of each gene; and epistatic effects.

Doubled haploid (DH) lines of wheat, whereby half the complement of chromosomes (n = 21) (i.e. the chromosomes from one gamete) are doubled to give the full compliment of chromosomes (n = 42), are very useful for the identification of QTLs. These lines contain large phenotypic variation compared to the parent lines (due to transgressive segregation) and they are homozygous, which allows greater selection efficiency and the absence of dominance effects of major genes (Snape, 1989).

The discovery by Laurie and Bennett (1988) that chromosome elimination could be exploited by using an intergeneric cross with maize pollen, enabled large populations of doubled haploid lines to be produced at a reasonable cost. This technique was used by the ARC Special Research Centre for Basic and Applied Plant Molecular Research (Adelaide, SA) to generate various doubled haploid populations, one of which (Cranbrook x Halberd) showed large variation for various morphological traits. While the work is ongoing, the wheat genome has been well characterised using molecular markers.

Given the potential advantages of identifying QTLs for traits which promote early vigour and the availability of a suitable doubled haploid population, it was decided to undertake an experiment to identify QTLs for the vigour traits identified in Chapter 7 (i.e. leaf width, leaf length, SLW and kernel weight / embryo size). If QTLs for these traits could be identified, it might assist the adoption of early vigour as an objective of breeding programs which in turn could lead to increases in grain yield in Mediterranean-type growing conditions.

8.1 Screening of a doubled haploid population

An experiment was conducted at Roseworthy in 1997 to identify QTLs for early vigour traits. A Cranbrook x Halberd doubled haploid population was used in this study as it displayed good variation for vigour traits. This population has been well characterised, with 479 molecular markers identified, consisting of 180 RFLP markers, 252 AFLP markers and 47 microsatellites.

8.1.1 Materials and methods

8.1.1.1 Glasshouse experiment

A population of 168 doubled haploid lines derived from a Cranbrook x Halberd cross, along with the two parental lines, were sown into 150mm black plastic pots in a temperature controlled glasshouse at Roseworthy. The experiment was laid out in two replicates and was sown on 4 June 1997. The pots were filled to a pre-determined level with a modified lucerne/medic mix (Appendix A) which was pH stabilised and fertilised with Nitrophoska® (Appendix B). The sowing configuration was marked using a template and six seeds were sown to a depth of 35 mm in each pot. The pots were watered to field capacity immediately after sowing and kept well watered for the duration of the experiment. Temperature was monitored at seed depth in 3 control pots and light intensity was monitored on the eastern and western sides of the glasshouse.

Aquasol® liquid fertiliser (see Appendix B) was applied on a regular basis, with 5 doses being applied over the course of the trial. The seedlings were thinned to 4 plants per pot 18 DAS by removing the smallest and weakest seedlings in each pot.

The plants were harvested at 34 DAS (412°Cd) which was when the third leaf had fully expanded in all lines. The harvest was made by cutting the plants at soil level and the shoots were separated into 1st, 2nd and 3rd leaves by cutting the lamina at the collar region of each leaf. The remainder was bulked as a fourth sample. The leaves were then laid flat between two acetate (overhead transparency) sheets and photocopied at a scale of 1:1. Leaf length and width measurements were made using the photocopied images and leaf area was recorded by scanning the images into a personal computer using a flatbed scanner and Sci Scan image analysis software (Kirchof and Pender, 1993). Dry matter was recorded after drying the leaf material in a drying oven at 80°C for 48 hrs.

The roots were washed out by hosing the soil from the root mass over a plastic sieve. The operation was conducted gently to ensure that minimal damage was done to the roots and the entire root system remained intact. The root systems from all four plants in each pot were bulked together and the roots were then oven dried at 80°C and weighed.

The data was analysed using QGENE software (Nelson, 1997) to locate quantitative trait loci (QTLs) for plant vigour traits, using the Cranbrook x Halberd linkage map. The map consisted of 486 markers with 27 linkage groups of which 427 markers have been positively mapped to chromosomes. The analysis involved interval and regression analysis using the means of the doubled haploid lines. The threshold for significance for the log-likelihood of difference (LOD) score was above 3.0.

8.1.2 Results

Doubled haploid lines derived from a Cranbrook x Halberd cross showed good morphological variability (Table 8.1) and a comparison of mean phenotypic expression between DH and parental lines showed that transgressive segregation had occurred (i.e. the range of values in the progeny was always greater than for the parents). Table 8.1 shows that QTLs were identified for all vigour traits except leaf width and root biomass.

Table 8.1 Range in response variables illustrating the amount of segregation, number of QTLs and explained variance for each trait.

	Cranbrook	**Halberd**	**Minimum for DH lines**	**Maximum for DH lines**	**QTLs detected**	**Explained Variance %**
Leaf Area (cm²)						
1st leaf	3.8	4.5	2.6	5.7	1	13
2nd leaf	6.6	6.8	4.5	10.2	1	17
Leaf width (mm)						
1st leaf	4.2	4.3	3.5	5.0	0	
2nd leaf	4.7	4.8	4.0	5.7	0	
Leaf length (mm)						
1st leaf	9.5	11.2	8.7	13.6	2	28
2nd leaf	17.5	18.2	14.0	23.3	2	27
SLW.(g/m²)						
1st leaf	37.8	33.4	29.6	41.7	1	20
2nd leaf	37.8	32.2	22.0	41.2	1	10
Kernel Weight (mg)	48.5	48.7	32.4	56.4	2	30
Root Wt (mg)	51.3	40.3	20.0	75.0	0	

Since the environment was shown to influence the morphology of the third seedling leaf (Chapter 7), data analysis was conducted on leaves 1 and 2 only. In this way, environmental effects should be minimised and genotypic correlations enhanced.

8.1.2.1 Leaf area

There was large transgressive segregation for leaf area, especially for the second leaf. The range in leaf area between the parents was 0.2 for leaf 2 and 5.7 for the DH progeny. This segregation represented more than a two-fold range in values and produced a good correlation between leaf area of leaves 1 and 2, and molecular markers which have been mapped to chromosome 2D (Figure 8.1). The same marker (CDO366) was most strongly correlated with leaf area of each leaf.

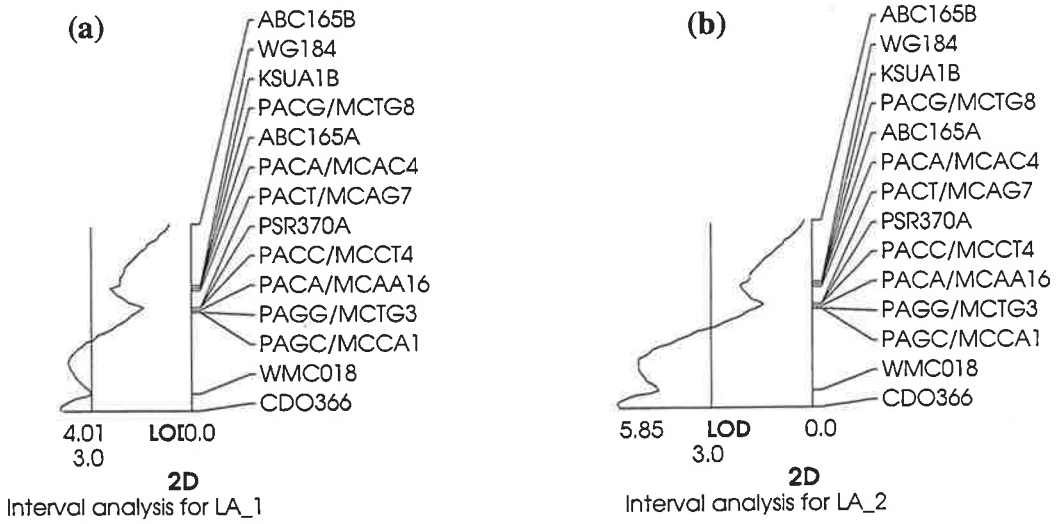

Figure 8.1 LOD plots for markers correlated with area of (a) 1st leaf and (b) 2nd leaf. The markers are mapping to chromosome 2D in each case.

8.1.2.2 Leaf width

The range in leaf width within this set of DH lines was small, and whilst it was comparable with earlier glasshouse experiments (eg, Chapter 7), it was not large enough to provide a significant correlation with any molecular markers. Consequently, no QTL for leaf width was established using this DH population.

8.1.2.3 Leaf length

The relatively large difference in leaf length between Cranbrook and Halberd meant that there was a large variation in leaf length in this DH population. The same QTL, which mapped to chromosome 2D (Figure 8.2), was strongly associated with the length of both 1st and 2nd leaf; and a second, more weakly correlated QTL was also located for each leaf (Figure 8.3). The second QTLs mapped to different chromosomes in each case (chromosome 7A - leaf 1 and chromosome 6B - leaf 2) (Figure 8.3).

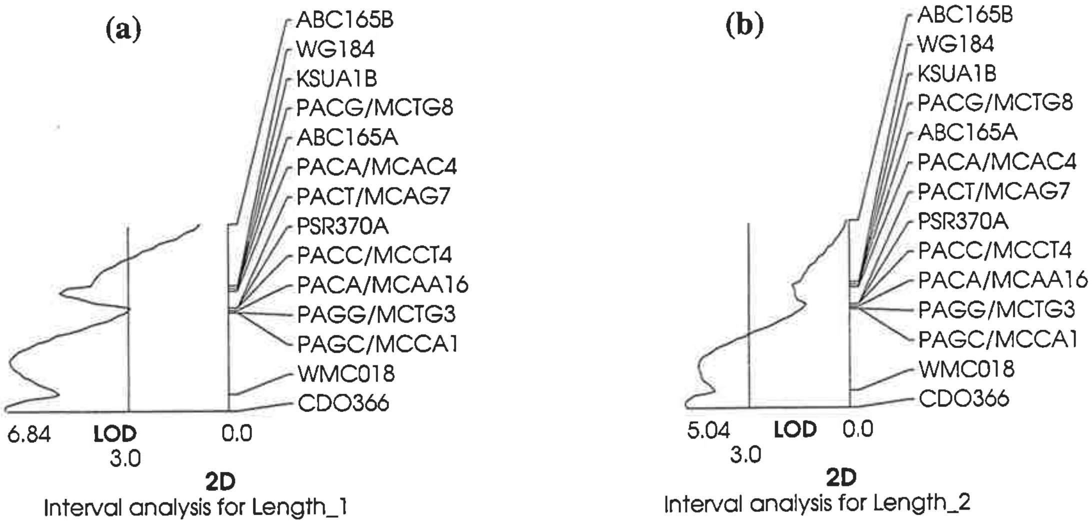

Figure 8.2 LOD plots for markers correlated with length of (a) 1st leaf and (b) 2nd leaf. The markers are mapping to chromosome 2D in each case.

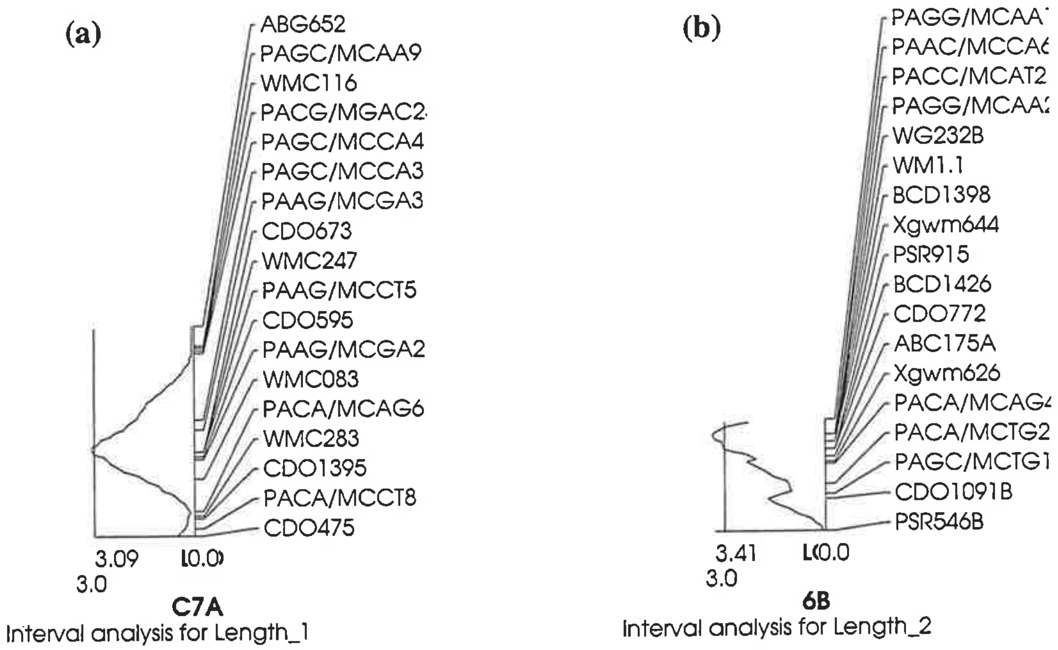

Figure 8.3 LOD plots for markers mapping to (a) chromosome 7A which are correlated with the length of leaf 1; and (b) chromosome 6B which are correlated with the length of leaf 2.

8.1.2.4 Specific leaf weight

The parental lines showed reasonable and consistent differences in SLW for each of the first two leaves (Table 8.1). Consequently there was very good segregation for SLW in the DH progeny. Figure 8.4 shows that SLW was highly correlated with a number of molecular markers from the same linkage group. The correlation was stronger with SLW of the 1st leaf.

The linkage group which contains the markers has not yet been positively mapped to a specific chromosome. However, it is considered likely that these markers will eventually be traced to chromosome 1.

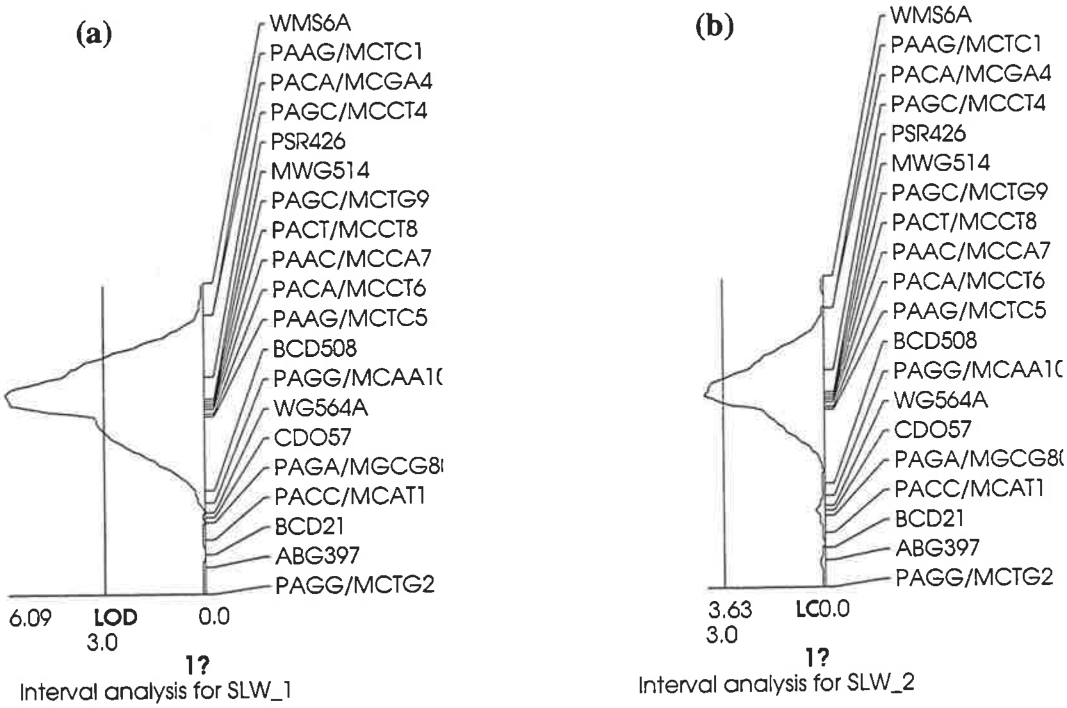

Figure 8.4 LOD plots for markers correlated with SLW of (a) 1st leaf and (b) 2nd leaf. The markers are possibly mapping to chromosome 1 but this requires confirmation.

8.1.2.5 Kernel weight

It was not practical to measure embryo size on such a large number of lines and so kernel weight was used as surrogate measurement for this vigour trait, due to its high correlation with embryo size (Chapter 7). Kernel weight was determined for each line by dividing the weight of approximately 100 seeds by the actual seed number. The kernel weights varied from 32.4g to 56.4g providing good quantitative variation for this trait. Two QTLs for kernel weight were identified and the markers are associated with different linkage groups (Figure 8.5). While the linkage groups have not been positively mapped to chromosomes, it is likely that there are at least two genes controlling kernel weight and it is possible that they are on different chromosomes.

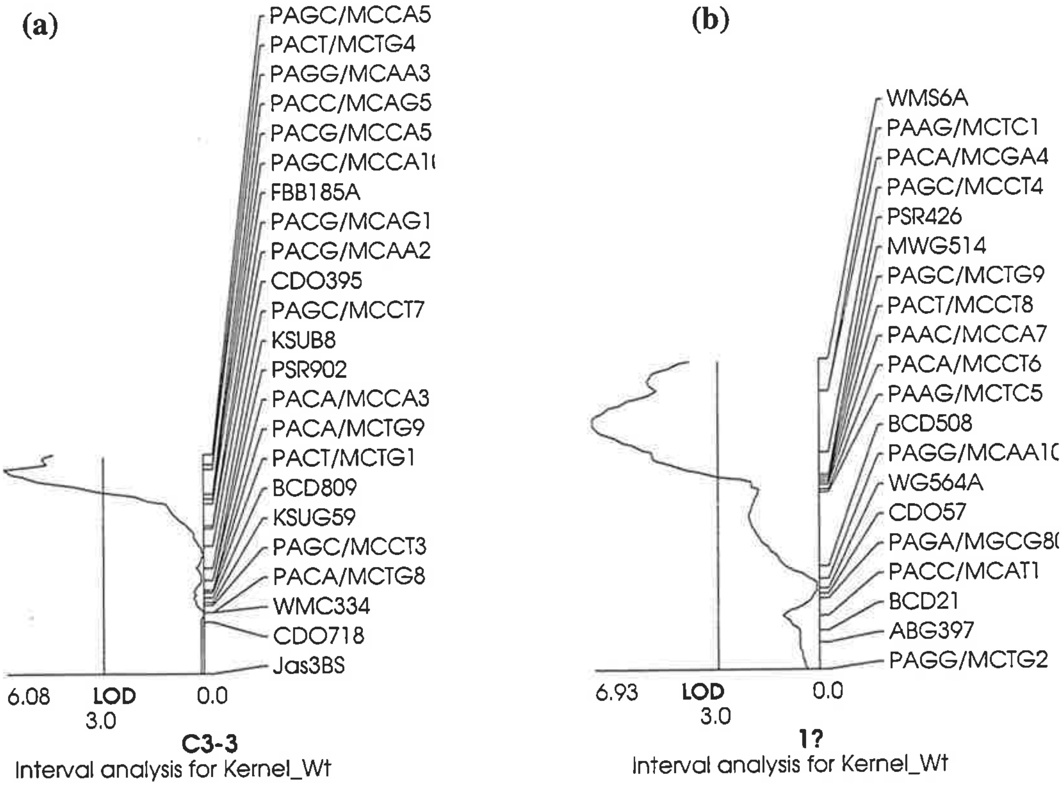

Figure 8.5 LOD plots for markers correlated with kernel weight. Markers are mapping to (a) chromosome 3 and (b) chromosome 1, however these chromosome locations require verification.

8.1.2.6 Root weight

The root weight varied from 20 - 75 mg per plant, indicating good segregation for root weight within the population. However, root weight was not significantly correlated with any molecular markers, which is probably a function of the complexity of this trait.

8.2 Discussion

8.2.1 Early vigour traits

Given the high correlation between leaf length and leaf area of the first two leaves (Figure 7.7) it is not surprising that the same QTLs were identified for each trait. The RFLP marker CDO366 was highly correlated with length and LA of the first two leaves, however, Figure 8.1 and Figure 8.2 show that there are relatively few markers in this region of chromosome 2D. If this part of the chromosome was more closely mapped, then it is possible that a better marker could be found for the length of the first two leaves.

The QTL for leaf area of leaves 1 and 2 explains 13% and 17% of the genetic variation respectively, whereas, the same QTL explains 28% and 27% of the genetic variation for leaf length. While the level of explained variance is low in each case, the relatively lower value for leaf area could be due to the fact that it is a more complex trait.

The second QTL identified for the length of leaf 1 was different to the second QTL identified for the length of leaf 2 (Figure 8.3), which suggests that different genes were involved in each case. This apparent contradiction reduces confidence in the ability of these QTLs to identify genotypes with longer leaves. Confidence is further reduced by the barely significant LOD scores in each case (Figure 8.3).

Gill and Coleman (1999) identified two QTLs for the length of the second leaf using the same Cranbrook x Halberd population. These QTLs mapped to chromosome 1A and 2D which strengthens confidence in the fact that at least one gene coding for leaf length is contained on chromosome 2D. This chromosome also contained QTLs for other morphological traits such as height and flag leaf area (Gill and Coleman, 1999). These authors also failed to find any QTLs for leaf width in this population, which supports the results of this experiment and suggests that this doubled haploid population does not contain large enough variation for leaf width.

The same markers were correlated with the SLW of each leaf (Figure 8.4), which provides greater confidence in the value of this QTL in plant breeding. The single QTL identified for this trait also indicates that SLW may be controlled by a single gene. However, the low level of variance accounted for (20% and 10% for the 1st and 2nd leaf respectively) suggests that there are probably other (as yet unidentified) QTLs coding for SLW. The linkage group containing the markers for this QTL is not yet mapped to a specific chromosome.

The two QTLs identified for kernel weight accounted for 30% of the genetic variation (Table 8.1), which suggests that this trait could be reasonably well characterised using QTLs. The highly significant LOD scores (Figure 8.5), also suggests that the molecular markers are in very close proximity to the genes coding for kernel weight. While the linkage groups have not been positively mapped to chromosomes at this stage, it is thought that at least one group is located on chromosome 3. When we consider homoeologous chromosomes in other species (Snape *et al.*, 1996), we find this corresponds with the findings of Backes *et al.* (1995) who detected two QTLs for kernel weight in barley, one on chromosome 2 and one on chromosome 3.

Once identified, QTLs can be used to reduce selection error due to the influence of genotype x environment interactions on phenotype (Paterson *et al.*, 1991). However, QTLs can also be influenced by environment and so the identification of loci needs to be verified in other environments (Paterson *et al.*, 1991). For this reason, further work is required to confirm the locations and the value of the QTLs identified in this experiment.

The use of QTLs and MAS in plant breeding is still evolving and one of the limitations is that very large DH populations (> 500 lines) are required if characters controlled by more than 3 genes are to be accurately mapped (Langridge, 1994). This may explain the relatively low values of explained variance for the QTLs identified (Table 8.1). However, the development of microspore culture may reduce the cost of developing DH lines and allow the widespread use of DH systems in plant breeding (Snape, 1996). Thus, the use of MAS in wheat breeding should increase, the likelihood of the use of these QTLs for selecting vigorous genotypes.

8.2.2 Benefits to plant breeding

The plant breeding process is dependent on identifying genetic variation, making crosses and obtaining recombination, and the accurate selection of desired progeny. The use of QTLs can assist this breeding process at every stage (Paterson *et al.*, 1991). Therefore, the identification of QTLs for traits which promote early vigour should increase the opportunities for breeders to improve early vigour in wheat breeding programs.

Using MAS in combination with DH populations could allow large reductions in breeding time due to greater homozygosity and use of earlier generation material for field based selection (Moreau *et al.*, 1999). Indeed, breeders could predict the likelihood of whether a genotype will be vigorous or non-vigorous based on the presence or absence of the markers depicting QTLs for vigour traits. This could lead to greater confidence in the prediction of the phenotype (Paterson *et al.*, 1991). It has also been shown that MAS can be used effectively in unreplicated field trials if appropriate spatial analysis is conducted (Moreau *et al.*, 1999).

Fewer selections can be made with greater reliability ensuring that the desired trait is being passed onto the next generation (Paterson *et al.*, 1991). This has the potential to reduce the cost of breeding, including selection for increased early vigour. Breeders can use MAS to reduce the effect of environment which can allow selection in non-target environments (eg. glasshouses or out of season nurseries) (Paterson *et al.*, 1991). This can further increase accuracy and could reduce the time and cost of generating new high vigour varieties.

The review of literature (section 2.4) indicated that increased early vigour will be of most benefit in specific (Mediterranean-type) environments. The identification of QTLs for vigour traits combined with the ability to insert specific genes through genetic engineering (Snape, 1998), may provide the opportunity to effect physiological breeding and tailor specific crop types to specific regions (eg Hay (1993) and Richards *et al.* (1997)). This technology could allow QTLs for beneficial traits to be pyramided together to further refine the crop for the target environment.

The use of QTLs in plant breeding will be most beneficial for traits which are either difficult or time consuming to identify. Embryo size is one trait which was well correlated with early vigour but is very time consuming to measure. While it was not investigated in this current study, the identification of QTLs correlated with embryo size should greatly benefit breeding for improved early vigour.

8.3 Conclusions

A doubled haploid population from a Cranbrook x Halberd cross was used to identify QTLs for traits which promote early vigour. This population displayed good variation for LA, leaf length, SLW, kernel weight and root weight, but there was less variation for leaf width. QTLs were identified for LA, leaf length, SLW and kernel weight, and there was good agreement between the QTLs identified for the 1st and 2nd leaves. This population was either not large enough or did not contain adequate variation for leaf width to identify a QTL for this trait.

This investigation clearly showed that it is possible to identify QTLs for traits which promote early vigour. Whilst some of the QTLs did not explain enough genetic variation to be useful at this stage, work is ongoing and it is likely that more markers will be identified to give greater coverage of each chromosome. This should benefit future efforts to locate QTLs for different plant traits and may improve the significance of the QTLs already established. The use of a different doubled haploid population, formed from parents with even greater differences in early vigour traits, may also benefit future work.

CHAPTER 9

9. General Discussion

The experiments outlined in this thesis showed that early vigour could be promoted using increased plant density, increased nitrogen fertiliser application, or through the selection of more vigorous genotypes. Increased plant density provided the most dramatic increase in early DM and LA production, however both agronomic methods of vigour improvement had variable responses in grain yield. These variable responses were largely due to increased interplant competition and caused an increase in the reliance on post anthesis rainfall to realise gains in grain yield. Strategies to reduce interplant competition using limited tillering lines (Donald, 1968a) were unsuccessful due to poor adaptation of these lines to the experimental conditions.

Good variation for early vigour was found within the Roseworthy Wheat Breeding Program and it was shown that early vigour was positively associated with grain yield, however, there was still some variation in grain yield at any given level of early vigour. Thus, it was found that, whilst early vigour is a yield positive trait, the maintenance of HI is of paramount importance in this environment. This could be achieved through reduced plant height, a reduction in tillering and earlier flowering (lower pre:post anthesis ratio of water use).

To facilitate incorporation of improved early vigour into wheat breeding programs, plant vigour traits were identified and QTLs for some of these traits were found. Since mapping of the wheat genome is incomplete, the location of QTLs for vigour traits is very promising and should form the basis for further work. This study also showed that screening techniques exist for the rapid identification of vigorous cultivars in field grown wheat. So the combination of identification tools for conventional breeding techniques, combined with QTLs for MAS, should allow improvements in early vigour and gains in productivity of wheat grown in South Australia.

9.1 Improving early vigour

Increasing the agronomic inputs of plant density and nitrogen nutrition provided increases in early vigour which were in keeping with previous reports in the literature. The reason for the failure of this strategy to consistently improve grain yield was likely to have been caused by insufficient early ground cover to have had a large impact on E_{sc} (Ritchie, 1972). As a result of insufficient ground cover in the first experiment, plant density was increased from a high rate of 260 plants/m^2 to 400 plants/m^2 (Chapter 4). However, even this increase in plant density did not provide an increase in LAI to a level that might provide consistent benefits in WUE through soil shading. Consequently, it was hypothesised that unless there was an increase in total water use, plants at high density would be more prone to moisture stress due to greater pre-anthesis water use, meaning that grain yield was highly reliant on post-anthesis moisture supply. This is supported by the experiment where irrigation water was applied in the post-anthesis phase and resulted in large yield gains in the high input treatments (Table 4.4).

Despite a reduction in HI under high inputs in some experiments, in most cases there was no reduction in grain yield or grain quality. This was largely due to greater anthesis biomass. The changes in HI were generally small and the phenomenon of haying-off (van Herwaarden, 1996) did not occur. None the less, the costs of inputs would be increased and gross margins may have been reduced. Thus, farmers' reluctance to increase agronomic inputs in this environment is well founded, based on grain yield alone. However, there is good evidence to suggest that using plant density to improve early vigour will provide increased competition with weeds (eg. Zaicou and Gill (1992); Radford *et al.* (1980)). If there are other tangible benefits such as improved weed control, then there may still be a role for improving early vigour using agronomic inputs.

Experiments conducted in Chapter 6, indicated that good genetic variation for early vigour was available, but unlike previous studies (Turner and Nicolas, 1987; Whan *et al.*, 1991), this selection process was performed on a much larger set of genotypes and characterised the range of early vigour within an entire local wheat breeding program. Many genotypes had superior early vigour to current cultivars and it was shown that within this population, early vigour was positively correlated with grain yield. This investigation also proved that genotypes which produced greater vegetative biomass and intercepted more light, produced higher grain yield per unit area. This is in agreement with Turner and Nicolas (1987) but should be more applicable to commercial practice than the per plant based measurements of these authors.

The results of these genotypic studies confirmed that whilst early vigour is a yield positive trait, the maintenance of HI is perhaps more critical in this environment. This confirms earlier agronomic studies where HI was reduced under high plant density and nitrogen supply and supports the findings of Whan *et al.* (1991) who found that some high vigour lines had unsuitable phenology and low grain yield.

None of the high vigour genotypes selected in Chapter 6 were able to generate LAI > 1.5 at the early tillering stage (57 DAS) (Table 6.4). Therefore, it is unlikely that these lines had the potential to reduce E_{sc} and increase total water use. It is more likely, however, that early vigour simply improved anthesis biomass, which when combined with high HI, produced high grain yield. While, selection of lines based purely on early vigour should have a positive effect within wheat breeding programs, yield improvement would be increased considerably if selection is based on lines displaying high early vigour and high HI (Regan *et al.*, 1997). This includes lines with appropriate phenology, short stature and limited tillering (Siddique *et al.*, 1990b).

9.2 Plant traits which promote early vigour

Given that early vigour is a desirable trait for wheat grown in Mediterranean-type cropping conditions it is appropriate to identify traits conferring early vigour. The good range in early vigour which was observed within the Roseworthy Wheat Breeding Program allowed several plant vigour traits to be identified. These included large embryo, low SLW, wide leaves and high RGR.

This study differs from previous studies (eg. López-Castañeda *et al.*, 1995) in that plant vigour traits have been identified from comparisons between vigorous and non-vigorous wheat genotypes, not vigorous and non-vigorous cereal species (i.e. barley versus wheat). Notwithstanding the different methodologies, the vigour traits identified bear remarkable similarity.

While there is a good agreement between this work and previous studies conducted by López-Castañeda *et al.* (1996), showing that large embryo size, low SLW and wide leaves are highly correlated with early vigour, there is disagreement over the role of RGR. Experiments in Chapter 7 show that RGR and RGLER are well correlated with early vigour between wheat genotypes, however, López-Castañeda *et al.* (1995) found no evidence for this relationship between species. Since the genotypes used in this study showed a small range in RGR and RLER, this relationship requires further investigation using a more appropriate range of genotypes.

López-Castañeda *et al.* (1996) found that time of emergence had a large effect on early vigour between species. However, the current study found that differences in time of emergence between genotypes were too small to evaluate the influence of rate of seedling emergence on early vigour.

9.3 Selection tools for early vigour

It has been shown that the best avenue for early vigour to improve productivity of wheat production in South Australia is through genetic enhancement and wheat breeding. For this to happen, appropriate selection tools are required to enable breeders to select more vigorous genotypes *per se*, or genotypes containing vigorous traits. This study has identified selection tools which should benefit traditional breeding methods and MAS techniques.

One of the drawbacks for physiological breeding using traditional empirical techniques, is the ability to screen large numbers of genotypes for the trait being selected. For breeders to realistically select for early vigour, fast and accurate screening techniques are required.

While it was not a core aim of this investigation, this study has verified that it is possible to use both near infrared reflectance (using a spectral radiometer) and PAR interception (using a ceptometer) as rapid selection tools for identifying vigorous plant canopies. These methods were used extensively throughout this study and were found to be accurate and reliable when compared to destructive measurements and more accurate than subjective visual assessments.

Recent advances in molecular genetics have allowed breeding programs to incorporate marker assisted selection using QTLs for desirable plant traits. This is particularly useful for traits which are not easily measured or are too time consuming to be practical. While rapid screening techniques have been proposed for early vigour selection based on the width of the first seedling leaf (López-Castañeda *et al.*, 1996), this is a correlative technique and cannot provide the benefits of MAS.

This study has shown that it is possible to identify QTLs for plant vigour traits. While only a relatively small amount of genetic variation was accounted for, these results were in good agreement with other published data (Gill and Coleman, 1999) and should form the basis for further investigation. Since embryo size has been shown to be highly correlated with early vigour but is time consuming to measure, locating a QTL for embryo size may provide major dividends in MAS for early vigour. The good correlation of kernel weight with embryo size, combined with the successful location of two QTLs for kernel weight, provides some incentive for further work.

Leaf width was also shown to be a major determinant of LA and early vigour, however this study failed to locate any QTL for leaf width. It is possible that this was a function of the variation for leaf width in the DH population used and so further investigations to identify QTLs for vigour traits may benefit from using a different DH population with greater variation for vigour traits. Increasing the size of the DH population will almost certainly increase the ability to identify QTLs (Langridge, 1994) and improve results.

9.4 Conclusions

The findings of this study shall be reported against the aims of the investigation.

1. It has been clearly shown that early vigour can be promoted via increased plant density and nitrogen supply, however, agronomic promotion of early vigour had an extremely variable effect on grain yield.

2. Genotypic variation in early vigour was positively correlated with grain yield and there was good genetic variation for early vigour within the germplasm of the Roseworthy Wheat Breeding Program which may provide the opportunity for yield enhancement through the breeding of more vigorous genotypes.

3. Large embryo, wide leaves and low SLW were identified as traits which promote early vigour.

4. QTLs were identified for SLW, leaf length and kernel weight, which would enable the use of MAS to enhance early vigour in wheat genotypes in wheat breeding programs. Rapid screening tools, in particular the use of remote sensing, were found to be reliable and promising and could be used to improve selection for early vigour in wheat breeding programs.

10. References

Aase, J. K. (1978). Relationship between leaf area and dry matter in winter wheats. *Agronomy Journal* **70**, 563-565.

Aase, J. K., and Siddoway, F. H. (1980). Determining winter wheat stand densities using spectral reflectance measurements. *Agronomy Journal* **72**, 149-152.

Acevedo, E. (1987). Assessing crop and plant attributes for cereal improvement in water-limited Mediterranean environments. *In* "Drought Tolerance in Winter Cereals" (J. P. Srivastava, E. Porceddu, E. Acevedo and S. Varma, eds.), pp. 303-319. John Wiley & Sons Ltd, Chichester, U.K.

Acevedo, E., and Ceccarelli, S. (1989). Role of the physiologist-breeder in a breeding program for drought resistance conditions. *In* "Drought resistance in cereals" (F. W. G. Baker, ed.), pp. 117-139. C.A.B. International, Wallingford, U.K.

Acevedo, E., Craufurd, P. Q., Austin, R. B., and Perez-Marco, P. (1991). Traits associated with high yield barley in low rainfall environments. *Journal of Agricultural Science, Cambridge* **116**, 23-36.

Adcock, T. E., Nutter, F. W., Jr., and Banks, P. A. (1990). Measuring herbicide injury to soybeans (*Glycine max*) using a radiometer. *Weed Science* **38**, 625-627.

Addae, P. C., and Pearson, C. J. (1992). Variability in seedling elongation of wheat, and some factors associated with it. *Australian Journal of Experimental Agriculture* **32**, 377-382.

Allan, R. E. (1980). Influence of semidwarfism and genetic background on stand establishment of wheat. *Crop Science* **20**, 634-638.

Anderson, W. (1989). Increased returns from agronomic inputs in early sown cereal crops. *Western Australian Journal of Agriculture*, 30-31.

Anderson, W. K. (1985). Grain yield responses of barley and durum wheat to split nitrogen applications under rainfed conditions in a Mediterranean environment. *Field Crops Research* **12**, 191-202.

Anderson, W. K. (1986). Some relationships between plant population, yield components and grain yield of wheat in a Mediterranean environment. *Australian Journal of Agricultural Research* **37**, 219-233.

Anderson, W. K. (1992). Increasing grain yield and water use of wheat in a rainfed Mediterranean type environment. *Australian Journal of Agricultural Research* **43**, 1-17.

Anderson, W. K., and Barclay, J. (1991). Evidence for differences between three wheat cultivars in yield response to plant population. *Australian Journal of Agricultural Research* **42**, 701-713.

Anderson, W. K., Seymour, M., and MF, D. A. (1991). Evidence for differences between cultivars in responsiveness of wheat to applied nitrogen. *Australian Journal of Agricultural Research* **42**, 363-377.

Araus, J. L. (1996). Integrative physiological criteria associated with yield potential. *In* “Increasing yield potential in wheat: Breaking the barriers . Proceedings of a workshop held in Obregón, Sonora, Mexico” (M. P. Reynolds, S. Rajaram and A. McNab, eds.), pp. 150-166. CIMMYT, Mexico.

Armstrong, L. G., Abrecht, D. G., Anderson, W. K., and Belford, R. K. (1996). The effect of non-lethal water deficits during establishment on the growth of wheat crops. *In* “Eighth Australian Agronomy Conference” (M. Asghar, ed.), pp. 80-83. The Australian Society of Agronomy, Toowoomba, Queensland.

Ascher, J. S., Graham, R. D., Elliott, D. E., Scott, J. M., and Jessop, R. S. (1994). Agronomic value of seed with high nutrient content. *In* “Wheat in heat-stressed environments: Irrigated, dry areas and rice-wheat farming systems” (D. A. Saunders and G. P. Hettle, eds.). CIMMYT, Mexico.

Aschmann, H. (1973). Distribution and peculiarity of Mediterranean ecosystems. *In* “Mediterranean type ecosystem: Origin and structure” (F. di Castri and D. Mooney, eds.), pp. 11-19. Springer-Verlag, New York.

Aspinall, D. (1961). The control of tillering in barley plants. I. The pattern of tillering and it's relationship to nutrient supply. *Australian Journal of Biological Sciences* **14**, 493-505.

Atsmon, D., and Jacobs, E. (1977). A newly bred 'Gigas' form of bread wheat (*Triticum aestivum* L.): Morphological features and thermo-periodic responses. *Crop Science* **17**, 31-35.

Auld, B. A., Kemp, D. R., and Medd, R. W. (1983). The influence of spatial arrangement on grain yield in wheat. *Australian Journal of Agricultural Research* **34**, 99-108.

Austin, R. B., Bingham, J., Blackwell, R. D., Evans, L. T., Ford, M. A., Morgan, C. L., and Taylor, M. (1980a). Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *Journal of Agricultural Science, Cambridge* **94**, 675-689.

Austin, R. B., Edrich, J. A., Ford, M. A., and Blackwell, R. D. (1977). The fate of dry matter, carbohydrates and ^{14}C lost from the leaves and stems of wheat during grain filling. *Annals of Botany* **41**, 1309-1321.

Austin, R. B., Ford, M. A., Edrich, J. A., and Hooper, B. E. (1976). Some effects of leaf posture on photosynthesis and yield in wheat. *Annals of Applied Biology* **83**, 425-446.

Austin, R. B., Ford, M. A., and Morgan, C. L. (1989). Genetic improvement in the yield of winter wheat: A further evaluation. *Journal of Agricultural Science* **112**, 295-301.

Austin, R. B., Morgan, C. L., Ford, M. A., and Blackwell, R. D. (1980b). Contributions to grain yield from pre-anthesis assimilation in tall and dwarf barley phenotypes in two contrasting seasons. *Annals of Botany* **45**, 309-319.

Ayers, G. S., Wert, V. F., and Ries, S. K. (1976). The relationship of protein fractions and individual proteins to seedling vigour in wheat. *Annals of Botany* **40**, 563-570.

Backes, G., Graner, A., Foroughi-Wehr, B., Fishbeck, G., Wenzel, G., and Jahoor, A. (1995). Localization and quantitative trait loci (QTL) for agronomic important characters by the use of a RFLP map in barley (*Hordeum vulgare* L.). *Theoretical and Applied Genetics* **90**, 294-302.

Baker, J. T., Pinter, P. J., Jr., Reginato, R. J., and Kanemasu, E. T. (1986). Effects of temperature on leaf appearance in spring and winter wheat cultivars. *Agronomy Journal* **78**, 605-613.

Balyan, R. S., Malik, R. K., Panwar, R. S., and Singh, S. (1991). Competitive ability of winter wheat cultivars with wild oat (*Avena ludoviciana*). *Weed Science* **39**, 154-158.

Baret, F. (1991). Vegetation canopy reflectance: factors of variation and application for agriculture. *In* "Remote sensing and geographical information systems for resource management in developing countries" (A. S. Belward, ed.), Vol. 1, pp. 145-167. Kluwer Academic Publishers, Dordrecht, Netherlands.

Baret, F., Guyot, G., and Major, D. M. (1989). TSAVI: a new vegetation index which minimises soil brightness effects on LAI and APAR estimation. *In* "Quantitative remote sensing: An economic tool for the nineties, IGARSS 89. Proceedings of the 12th Canadian Symposium on Remote Sensing.", Vancouver, Canada.

Belford, R., Dracup, M., and Tennant, D. (1990). Waterlogging limits crop growth on duplex soils. *Western Australian Journal of Agriculture* **31**, 62-65.

Belford, R. K., Harvey, E. R., and Di Prinzio, P. (1993). Remote sensing of crop biomass with a hand held multispectral radiometer. *In* "Seventh Australian Agronomy Conference" (G. K. McDonald and W. D. Bellotti, eds.), pp. 392. The Australian Society of Agronomy, Adelaide, South Australia.

Bellairs, S. M., Turner, N. C., Hick, P. T., and Smith, R. C. G. (1996). Plant and soil influences on estimating biomass of wheat in plant breeding plots using field spectral radiometers. *Australian Journal of Agricultural Research* **47**, 1017-1034.

Benbi, D. K. (1994). Prediction of leaf area indices and yields of wheat. *Journal of Agricultural Science* **122**, 13-20.

Benjamin, L. R. (1990). Variation in time of seedling emergence within populations: A feature that determines individual growth and development. *Advances in Agronomy* **44**, 1-25.

Bidinger, F., Musgrave, R. B., and Fischer, R. A. (1977). Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley. *Nature* **270**, 431-433.

Blackshaw, R. E. (1994). Differential competitive ability of winter wheat cultivars against downy brome. *Agronomy Journal* **86**, 649-654.

Blum, A., Mayer, J., and Golan, G. (1988). The effect of grain number per ear (sink size) on source activity and its water-relations in wheat. *Journal of Experimental Botany* **39**, 106-114.

Blum, A., and Pnuel, Y. (1990). Physiological attributes associated with drought resistance of wheat cultivars in a Mediterranean environment. *Australian Journal of Agricultural Research* **41**, 799-810.

Bockus, W. W., and Shroyer, J. P. (1996). Effect of seed size on seedling vigor and forage production of winter wheat. *Canadian Journal of Plant Science* **76**, 101-105.

Bolland, M. D. A., and Baker, M. J. (1988). High phosphorus concentrations in seed of wheat and annual medic are related to higher rates of dry matter production of seedlings and plants. *Australian Journal of Experimental Agriculture* **28**, 765-770.

Borojevic, S., and Kraljevic Balalic, M. (1980). Productivity of single-culm and multi-culm plants of winter wheat cultivars in field conditions. *Euphytica* **29**, 705-713.

Boukerrou, L., and Rasmusson, D. D. (1990). Breeding for high biomass yield in spring barley. *Crop Science* **30**, 31-35.

Boyd, W. J. R., Gordon, A. G., and LaCroix, L. J. (1971). Seed size, germination resistance and seedling vigour in barley. *Canadian Journal of Plant Science* **51**, 93-99.

Brown, S. C., Gregory, P. J., and Wahbi, A. (1987a). Root characteristics and water use in Mediterranean environments. *In* "Drought Tolerance in Winter Cereals" (J. P. Srivastava, E. Porceddu, E. Acevedo and S. Varma, eds.), pp. 275-83. John Wiley & Sons Ltd, Chichester, U.K.

Brown, S. C., Keatinge, J. D. H., Gregory, P. J., and Cooper, P. J. M. (1987b). Effects of fertilizer, variety and location on barley production under rainfed conditions in northern Syria. 1. Root and shoot growth. *Field Crops Research* **16**, 53-66.

Bulisani, E. A., and Warner, R. L. (1980). Seed protein and nitrogen effects upon seedling vigor in wheat. *Agronomy Journal* **72**, 657-662.

Burris, J. S., Edje, O. T., and Wahab, A. H. (1973). Effects of seed size on seedling performance in soybeans: 2. Seedling growth and photosynthesis and field performance. *Crop Science* **13**, 207-210.

Bush, M. G., and Evans, L. T. (1988). Growth and development in tall and dwarf isogenic lines of spring wheat. *Field Crops Research* **18**, 243-270.

Calderini, D. F., Dreccer, M. F., and Slafer, G. A. (1995). Genetic improvement in wheat yield and associated traits - a re-examination of previous results and the latest trends. *Plant Breeding Zeitschrift fur Pflanzenzuchtung* **114**, 108-112.

Chastain, T. G., Ward, K. J., and Wysocki, D. J. (1995). Stand establishment responses of soft white winter wheat to seedbed residue and seed size. *Crop Science* **35**, 213-218.

Christensen, S. (1995). Weed suppression ability of spring barley varieties. *Weed Research Oxford* **35**, 241-247.

Clarke, J. M., Townley Smith, T. F., McCaig, T. N., and Green, D. G. (1984). Growth analysis of spring wheat cultivars of varying drought resistance. *Crop Science* **24**, 537-541.

Condon, A. G., and Richards, R. A. (1993). Exploiting genetic variation in transpiration efficiency in wheat: An agronomic view. *In* "Stable isotopes and plant carbon/water relations" (J. R. Ehlringer, A. E. Hall and G. D. Farquar, eds.), pp. 434-450. Academic Press, Inc., San Diego, California.

Condon, A. G., Richards, R. A., and Farquhar, G. D. (1992). The effect of variation in soil water availability, vapour pressure deficit and nitrogen nutrition on carbon isotope discrimination in wheat. *Australian Journal of Agricultural Research* **43**, 935-947.

Conner, D. J., Theiveyanathan, S., and Rimmington, G. M. (1992). Development, growth, water-use and yield of a spring and a winter wheat in response to time of sowing. *Australian Journal of Agricultural Research* **43**, 493-516.

Cooper, P. J. M., Gregory, P. J., Keatinge, J. D. H., and Brown, S. C. (1987a). Effects of fertilizer, variety and location on barley production under rainfed conditions in northern Syria. 2. Soil water dynamics and crop water use. *Field Crops Research* **16**, 67-84.

Cooper, P. J. M., Gregory, P. J., Keatinge, J. D. H., and Harris, H. C. (1987b). Improving the water use efficiency of annual crops in the rain fed farming systems of West Asia and North Africa. *Experimental Agriculture* **23**, 113-158.

Cooper, P. J. M., Keatinge, J. D. H., and Hughes, G. (1983). Crop evapotranspiration - A technique for calculation of its components by field measurements. *Field Crops Research* **7**, 299-312.

Copland, L. O., and McDonald, M. B. (1995). Seed vigour and vigour tests. *In* "Principles of seed science and technology", pp. 153-180. Chapman & Hall, New York.

Cornish, E. A. (1950). The influence of rainfall on yield of wheat in South Australia. *Australian Journal of Scientific Research, Series B. Biological Sciences* **3**, 178-218.

Cornish, P. S., and Hindmarsh, S. (1988). Seed size influences the coleoptile length of wheat. *Australian Journal of Experimental Agriculture* **28**, 521-523.

Cornish, P. S., and Lymbery, J. R. (1987). Reduced early growth of direct drilled wheat in southern New South Wales: causes and consequences. *Australian Journal of Experimental Agriculture* **27**, 869-880.

Cousens, R. (1985). A simple model relating yield loss to weed density. *Annals of Applied Biology* **107**, 239-252.

Cousens, R. D. (1996). Comparative growth of wheat, barley, and annual ryegrass (*Lolium rigidum*) in monoculture and mixture. *Australian Journal of Agricultural Research* **47**, 449-464.

Coventry, D. R., Reeves, T. G., Brooke, H. D., and Cann, D. K. (1993). Influence of genotype, sowing date, and seeding rate on wheat development and yield. *Australian Journal of Experimental Agriculture* **33**, 751-757.

Cox, J., and McFarlane, D. (1990). The causes of waterlogging. *Western Australian Journal of Agriculture* **31**, 58-61.

Cox, T. S., Shroyer, J. P., Liu, B. H., Sears, R. G., and Martin, T. J. (1988). Genetic improvement in agronomic traits of hard red winter wheat cultivars from 1919 to 1987. *Crop Science* **28**, 756-760.

Curran, P. J. (1983). Multispectral remote sensing for the estimation of green leaf area index. *Philosophical Transactions of the Royal Society of London. A* **309**, 257-270.

Dakheel, A. J., Naji, I., Mahalakshmi, V., and Peacock, J. M. (1993). Morphophysiological traits associated with adaptation of durum wheat to harsh Mediterranean environments. *Aspects of Applied Biology* **34**, 297-307.

Dann, P. R. (1969). Response by wheat to phosphorous and nitrogen with particular reference to 'haying-off' *Australian Journal of Experimental Agriculture and Animal Husbandry* **9**, 625-629.

Darwinkel, A. (1978). Patterns of tillering and grain production of winter wheat at a wide range of plant densities. *Netherlands Journal of Agricultural Science* **26**, 383-398.

Darwinkel, A. (1979). Ear size in relation to tiller emergence and crop density. *In* "Crop physiology and cereal breeding" (J. H. J. Spiertz and T. Kramer, eds.), pp. 10-15. Centre for Agricultural Publication and Documentation, Wageningen; Netherlands.

Darwinkel, A. (1983). Ear formation and grain yield of winter wheat as affected by time of nitrogen supply. *Netherlands Journal of Agricultural Science* **31**, 211-225.

Darwinkel, A., Hag, B. A. t., and Kuizenga, J. (1977). Effect of sowing date and seed rate on crop development and grain production of winter wheat. *Netherlands Journal of Agricultural Science* **25**, 83-94.

Das Gupta, P. R., and Austenson, H. M. (1973). Analysis of interrelationships among seedling vigor, field emergence, and yield in wheat. *Agronomy Journal* **65**, 417-422.

De Marco, D. G. (1990). Effect of seed weight and seed phosphorous and nitrogen concentrations on the early growth of wheat seedlings. *Australian Journal of Experimental Agriculture* **30**, 545-549.

de Witt, C. T. (1965). "Photosynthesis of leaf canopies," Rep. No. 663. PUDOC, Wageningen.

Donald, C. M. (1963). Competition among crop and pasture plants. *Advances in Agronomy* **15**, 1-118.

Donald, C. M. (1968a). The breeding of crop ideotypes. *Euphytica* **17**, 385-403.

Donald, C. M. (1968b). Design of a wheat ideotype. *In* "Third International Wheat Genetics Symposium" (K. W. Finlay and K. W. Shepherd, eds.), pp. 377-387. Butterworths, Australian Academy of Science, Canberra.

Donald, C. M. (1979). A barley breeding programme based on an ideotype. *Journal of Agricultural Science, Cambridge* **93**, 261-269.

Donald, C. M., and Hamblin, J. (1976). The biological yield and harvest index of cereals as agronomic and plant breeding criteria. *Advances in Agronomy* **28**, 361-405.

Dornbos, D. L., Mullen, R. F., and Shibles, R. M. (1989). Drought stress effects during seed fill on soybean seed germination and vigour. *Crop Science* **29**, 476-480.

Doyle, A. D., and Fischer, R. A. (1979). Dry matter accumulation and water use relationships in wheat crops. *Australian Journal of Agricultural Research* **30**, 815-829.

Dracup, M., Belford, R. K., and Gregory, P. J. (1992). Constraints to crop growth of wheat and lupin crops in duplex soils. *Australian Journal of Experimental Agriculture* **32**, 947-61.

Duggan, B. L., and Richards, R. A. (1996). Effect of tiller inhibition genes on growth and partitioning in wheat and barley. *In* "Eighth Assembly of the Wheat Breeding Society of Australia" (R. A. Richards, C. W. Wrigley, H. M. Rawson, G. J. Rebetzke, J. L. Davidson and R. I. S. Brettle, eds.), pp. 163-167. The Wheat Breeding Society of Australia, Canberra, ACT.

Ehdaie, B., and Waines, J. G. (1994). Growth and transpiration efficiency of near-isogenic lines for height in a spring wheat. *Crop Science* **34**, 1443-1451.

Ehleringer, J. (1980). Leaf morphology and reflectance in relation to water and temperature stress. *In* "Adaptation of plants to water and high temperature stress" (N. C. Turner and P. J. Kramer, eds.), pp. 295-308. John Wiley & Sons, New York.

Elliott, G. A., and Regan, K. L. (1993). Use of reflectance measurements to estimate early cereal biomass production on sandplain soils. *Australian Journal of Experimental Agriculture* **33**, 179-183.

Evans, L. E., and Bhatt, G. M. (1977). Influence of seed size, protein content and cultivar on early seedling vigor in wheat. *Canadian Journal of Plant Science* **57**, 929-935.

Fathi, G., McDonald, G. K., and Lance, R. C. M. (1997). Effects of post-anthesis water stress on the yield and grain protein concentration of barley grown at two levels of nitrogen. *Australian Journal of Agricultural Research* **48**, 67-80.

Fischer, R. A. (1975). Yield potential in dwarf spring wheat and the effect of shading. *Crop Science* **15**, 607-613.

Fischer, R. A. (1980). Influence of water stress on crop yield in semiarid regions. *In* "Adaptation of plants to water and high temperature stress" (N. C. Turner and P. J. Kramer, eds.), pp. 323-339. John Wiley & Sons, New York.

Fischer, R. A., Aguilar, M. I., Maurer, O. R., and Rivas, A. S. (1976). Density and row spacing effects on irrigated short wheats at low latitude. *Journal of Agricultural Science, UK* **87**, 137-147.

Fischer, R. A., and Hille Ris Lambers, D. (1978). Effect of environment and cultivar on source limitation to grain weight in wheat. *Australian Journal of Agricultural Research* **29**, 443-458.

Fischer, R. A., and Kertesz, Z. (1976). Harvest index in spaced populations and grain weight in microplots as indicators of yielding ability in spring wheat. *Crop Science* **16**, 55-59.

Fischer, R. A., and Kohn, G. D. (1966). The relationship between evapotranspiration and growth in the wheat crop. *Australian Journal of Agricultural Research* **17**, 255-267.

Fischer, R. A., and Laing, D. R. (1976). Yield potential in a dwarf spring wheat and response to crop thinning. *Journal of Agricultural Science, UK* **87**, 113-122.

Fischer, R. A., and Miles, R. E. (1973). The role of spatial pattern in the competition between crop plants and weeds. A theoretical analysis. *Mathematical Biosciences* **18**, 3-4.

Fischer, R. A., and Quail, K. J. (1990). The effect of major dwarfing genes on yield potential in spring wheats. *Euphytica* **46**, 51-56.

Fischer, R. A., and Stockman, Y. M. (1986). Increased kernel number in Norin 10-derived dwarf wheat: Evaluation of the cause. *Australian Journal of Plant Physiology* **13**, 767-784.

Fischer, R. A., and Turner, N. C. (1978). Plant productivity in the arid and semiarid zones. *Annual Review of Plant Physiology* **29**, 277-317.

Frank, A. B., and Bauer, A. (1995). Phyllochron differences in wheat, barley, and forage grasses. *Crop Science* **35**, 19-23.

French, R. J., and Schultz, J. E. (1984). Water use efficiency of wheat in a Mediterranean-type environment. I Water use and climate. *Australian Journal of Agricultural Research* **35**, 743-764.

Fukai, S., Searle, C., Baiquni, H., Choenthong, S., and Kwye, M. (1990). Growth and grain yield of contrasting barley cultivars under different plant densities. *Field Crops Research* **23**, 239-254.

Gallagher, J. N. (1979). Field studies of cereal leaf growth. II The relation between auxanometer and dissection measurements of leaf extension and their relation to crop leaf expansion. *Journal of Experimental Botany* **30**, 637-643.

Gan, Y., and Stobbe, E. H. (1996). Seedling vigor and grain yield of 'Roblin' wheat affected by seed size. *Agronomy Journal* **88**, 456-460.

Gardner, B. R., and Blad, B. L. (1986). Evaluation of spectral reflectance models to estimate corn leaf area while minimising the influence of soil background effects. *Remote Sensing of Environment* **20**, 183-193.

Garrity, D. P., Movillon, M., and Moody, K. (1992). Differential weed suppression ability in upland rice cultivars. *Agronomy Journal* **84**, 586-591.

Gill, G., and Coleman, R. (1999). The use of a doubled haploid population to investigate the relationship between crop morphological traits and competitiveness with weeds. *In* "12th Australian Weeds Conference" (A. C. Bishop, M. Boersma and C. D. Barnes, eds.), pp. 501-505. Tasmanian Weeds Society Inc., Hobart, Tasmania.

Gilmour, A. R. (1992). "TwoD. A program to fit a mixed linear model with two dimensional spatial adjustment for local trend," NSW Agriculture, Tamworth, Australia.

Gleeson, A. G., and Cullis, B. R. (1987). Residual maximum likelihood (REML) estimation of a neighbour model for field experiments. *Biometrics* **43**, 277-288.

Glendenning, J. S. E. (1990). "Fertilizer Handbook," Incitec Pty. Ltd., Morningside, Qld.

Gooding, M. J., and Davies, W. P. (1997). "Wheat production and utilization. Systems, quality and the environment," CAB International, Wallingford, U.K.

Grass, L., and Burris, J. S. (1995). Effect of heat stress during seed development and maturation on wheat (*Triticum durum*) seed quality .1. Seed germination and seedling vigor. *Canadian Journal of Plant Science* **75**, 821-829.

Greacen, E. L., and Hignett, C. T. (1976). "A water balance model and supply index for wheat in South Australia,".

Gregory, P. J. (1984). Water availability and crop growth in arid regions. *Outlook on Agriculture* **13**, 208-215.

Gregory, P. J., Tennant, D., and Belford, R. K. (1992a). Root and shoot growth, and water and light use efficiency of barley and wheat crops grown on a shallow duplex soil in a Mediterranean-type environment. *Australian Journal of Agricultural Research* **43**, 555-573.

Gregory, P. J., Tennant, D., Hamblin, A. P., and Eastham, J. (1992b). Components of the water balance on duplex soils in Western Australia. *Australian Journal of Experimental Agriculture* **32**, 845-855.

Hadjichristodoulou, A., Della, A., and Photiades, J. (1977). Effect of sowing depth on plant establishment, tillering capacity and other agronomic characters of cereals. *Journal of Agricultural Science, UK* **89**, 161-167.

Hamblin, A. P., and Tennant, D. (1987). Root length density and water uptake in cereals and grain legumes: How well are they correlated? *Australian Journal of Agricultural Research* **38**, 513-527.

Hay, R. K. M. (1993). The contribution of physiology to breeding progress. *Aspects of Applied Biology* **34**, 17-24.

Hollamby, G., and Bayraktar, A. (1996). Breeding objectives, philosophies and methods in South Australia. *In* "Increasing yield potential in wheat: Breaking the barriers . Proceedings of a workshop held in Obregón, Sonora, Mexico" (M. P. Reynolds, S. Rajaram and A. McNab, eds.), pp. 52-65. CIMMYT, Mexico.

Hucl, P., and Baker, R. J. (1988). An evaluation of common spring wheat germplasm for tillering. *Canadian Journal of Plant Science* **68**, 1119-1123.

Hucl, P., and Baker, R. J. (1989). Tiller phenology and yield of spring wheat in a semiarid environment. *Crop Science* **29**, 631-635.

Hucl, P., and Baker, R. J. (1990a). Effect of seeding depth and temperature on tillering characteristics of four spring wheat cultivars. *Canadian Journal of Plant Science* **70**, 409-417.

Hucl, P., and Baker, R. J. (1990b). Seeding rate effects on low-tillering spring wheats in a semiarid environment. *Canadian Journal of Plant Science* **70**, 9-17.

Huete, A. R. (1988). A soil adjusted vegetation index (SAVI). *International Journal of Remote Sensing* **9**, 295-309.

Innes, P., and Blackwell, R. D. (1983). Some effects of leaf posture on the yield and water economy of winter wheat. *Journal of Agricultural Science, Cambridge* **101**, 367-376.

Innes, P., Hoogendoorn, J., and Blackwell, R. D. (1985). Effects of differences in date of ear emergence and height on yield of winter wheat. *Journal of Agricultural Science, Cambridge* **105**, 543-549.

Ishag, H. M., and Taha, M. B. (1974). Production and survival of tillers of wheat and their contribution to yield. *Journal of Agricultural Science, UK* **83**, 117-124.

Islam, T. M. T., and Sedgley, R. H. (1981). Evidence for a "uniculm effect" in spring wheat (*Triticum aestivum* L.) in a Mediterranean environment. *Euphytica* **30**, 277-282.

Jackson, R. D., Pinter, P. J., Jnr, Idso, S. B., and Reginato, R. J. (1979). Wheat spectral reflectance: interactions between crop configuration, sun elevation, and azimuth angle. *Applied Optics* **18**, 3730-3732.

Jacquemoud, S., and Baret, F. (1990). PROSPECT: A model of leaf optical properties spectra. *Remote Sensing of Environment* **34**, 75-91.

Jones, M. M., Turner, N. C., and Osmond, C. B. (1981). Mechanisms of drought resistance. *In* “The physiology and biochemistry of drought resistance in plants” (L. G. Paleg and D. Aspinall, eds.), pp. 15-37. Academic Press Australia.

Jordan, N. (1993). Prospects for weed control through crop interference. *Ecological Applications* **3**, 84-91.

Kanemasu, E. T., Ransom, J., Saunders, D., Killeen, J., and Yoshida, M. (1985). Use of spectral data to assess wheat response to soil water. *Field Crops Research* **12**, 105-113.

Karimi, M. M., and Siddique, K. H. M. (1991a). Crop growth and relative growth rates of old and modern wheat cultivars. *Australian Journal of Agricultural Research* **42**, 13-20.

Karimi, M. M., and Siddique, K. H. M. (1991b). “Rainfall distribution and grain yield of spring wheat in Western Australia,” Rep. No. 29. Department of Agriculture, W.A., Perth, W.A.

Karimi, M. M., and Siddique, K. H. M. (1992). The relationships between grain yield of spring wheat and rainfall distribution in Western Australia using regression models. *Iran Agricultural Research* **11**, 1-23.

Kemp, D. R., Auld, B. A., and Medd, R. W. (1983). Does optimizing plant arrangements reduce interference or improve the utilization of space? *Agricultural Systems* **12**, 31-36.

Kerr, N., and Arbrecht, D. (1992). Opportunity knocks - Sowing wheat early in the north eastern wheatbelt. *Western Australian Journal of Agriculture* **33**, 32-35.

Kerr, N. J., Siddique, K. H. M., and Delane, R. J. (1992). Early sowing with wheat cultivars of suitable maturity increases grain yield of spring wheat in a short season environment. *Australian Journal of Experimental Agriculture* **32**, 717-723.

Khah, E. M., Ellis, R. H., and Roberts, E. H. (1986). Effects of laboratory germination, soil temperature and moisture content on the emergence of spring wheat. *Journal of Agricultural Science, Cambridge* **107**, 431-438.

King, R. W., and Richards, R. A. (1984). Water uptake in relation to pre-harvest sprouting damage in wheat: Grain characteristics. *Australian Journal of Agricultural Research* **35**, 337-345.

Kirby, E. J. M. (1993). Effect of sowing depth on seedling emergence, growth and development in barley and wheat. *Field Crops Research* **35**, 101-111.

Kirby, E. J. M., and Perry, M. W. (1987). Leaf emergence rates of wheat in a Mediterranean environment. *Australian Journal of Agricultural Research* **38**, 455-464.

Kirby, E. J. M., Siddique, K. H. M., Perry, M. W., Kaesehagen, D., and Stern, W. R. (1989). Variation in spikelet initiation and ear development of old and modern Australian wheat varieties. *Field Crops Research* **20**, 113-128.

Kirchof, G., and Pender, C. (1993). Sci-Scan agricultural engineering image analysis system. .

Klepper, B., Belford, R. K., and Rickman, R. W. (1984). Root and shoot development in winter wheat. *Agronomy Journal* **76**, 117-122.

Klepper, B., Rickman, R. W., and Peterson, C. M. (1981). Quantitative characterisation of seedling development in small cereal grains. *Agronomy Abstracts. 73rd annual meeting, American Society of Agronomy*, 107-108.

Knight, R. (1983). Some factors causing variation in the yield of individual plants of wheat. *Australian Journal of Agricultural Research* **4**, 219-228.

Knipling, E. B. (1970). Physical and physiological basis for the reflectance of visible and near infrared radiation from vegetation. *Remote Sensing of Environment* **1**, 155-159.

Krenzer, E. G., Jnr, and Nipp, T. L. (1991). Mainstem leaf development and tiller formation in wheat cultivars. *Agronomy Journal* **83**, 667-670.

Lafond, G. P., and Baker, R. J. (1986a). Effects of genotype and seed size on speed of emergence and seedling vigor in nine spring wheat cultivars. *Crop Science* **26**, 341-346.

Lafond, G. P., and Baker, R. J. (1986b). Effects of temperature, moisture stress, and seed size on germination of nine spring wheat cultivars. *Crop Science* **26**, 563-567.

Lafond, G. P., and Derksen, D. A. (1996). Row spacing and seeding rate effects in wheat and barley under a conventional fallow management system. *Canadian Journal of Plant Science* **76**, 791-793.

Lange, O. L., Lösch, R., Schulze, E.-D., and Krappen, L. (1971). Responses of stomata to changes in humidity. *Planta* **100**, 76-86.

Langridge, P. (1994). Molecular markers in wheat breeding and research. *In* "Seventh Australian Wheat Breeding Assembly" (J. Paull, I. S. Dundas, K. J. Shepherd and G. J. Hollamby, eds.), pp. 137-140. Wheat Breeding Society of Australia, Adelaide, South Australia.

Lanning, S. P., Talbert, L. E., Martin, J. M., Blake, T. K., and Bruckner, P. L. (1997). Genotype of wheat and barley affects light penetration and wild oat growth. *Agronomy Journal* **89**, 100-103.

Laurie, D. A., and Bennett, M. D. (1988). The production of haploid wheat plants from maize wheat crosses. *Theoretical and Applied Genetics* **70**, 100-105.

Lemerle, D., Cousens, R. D., Verbeek, B., and Fisher, J. A. (1994). The potential to breed more competitive wheat cultivars. *In* "Seventh Australian Wheat Breeding Assembly" (J. Paul, I. S. Dundas, K. J. Shepherd and G. J. Hollamby, eds.), pp. 19-21. Wheat Breeding Society of Australia, Adelaide, South Australia.

Lemerle, D., Michael, P. W., and Sutton, B. G. (1979). The competitive abilities of wheat and triticale against different densities of *Lolium rigidum*. *In* "Seventh Asian-Pacific Weed Science Conference", pp. 447-450, Sydney, NSW.

Lemerle, D., Verbeek, B., and Coombes, N. (1995). Losses in grain yield of winter crops from *Lolium rigidum* competition depend on crop species, cultivar and season. *Weed Research Oxford* **35**, 503-509.

Lemerle, D., Verbeek, B., Cousens, R. D., and Coombes, N. E. (1996a). The potential for selecting wheat varieties strongly competitive against weeds. *Weed Research* **36**, 505-513.

Lemerle, D., Verbeek, B., and Martin, P. (1996b). Breeding wheat cultivars more competitive against weeds. *In* "Second International Weed Control Congress", pp. 1323-1324, Copenhagen.

Leuning, R., Condon, A. G., Dunin, F. X., Zegelin, S., and Denmead, O. T. (1994). Rainfall interception and evaporation from soil below a wheat canopy. *Agricultural and Forest Meteorology* **67**, 221-238.

Lewis, E. J., and Garcia, J. A. (1979). The effect of seed weight and coleoptile tiller development on seedling vigour in Tall Fescue, *Festuca arundinaceae*. *Euphytica* **28**, 393-402.

Liang, Y. L., and Richards, R. A. (1994). Coleoptile tiller development is associated with fast early vigour in wheat. *Euphytica* **80**, 119-124.

Longnecker, N., Kirby, E. J. M., and Robson, A. (1993). Leaf emergence, tiller growth, and apical development of nitrogen-deficient spring wheat. *Crop Science* **33**, 154-160.

Longnecker, N. E., Marcar, N. E., and Graham, R. D. (1991). Increased manganese content of barley seeds can increase grain yield in manganese deficient conditions. *Australian Journal of Agricultural Research* **42**, 1065-1074.

Lopez-Bellido, L. (1992). Mediterranean cropping systems. *In* "Ecosystems of the world" (C. J. Pearson, ed.), pp. 311-356. Elsevier, Amsterdam.

López-Castañeda, C. (1992). A comparison of growth and water use efficiency in temperate cereal crops. PhD, Australian National University, Canberra.

López-Castañeda, C., and Richards, R. A. (1990). Traits to increase the early vigour of wheat: learning from barley. *In* "Sixth Australian Wheat Breeding Assembly" (L. O'Brien, F. W. Ellison, R. A. Hare and M. C. Mackay, eds.), pp. 61-65. Wheat Breeding Society of Australia, Tamworth, NSW.

López-Castañeda, C., and Richards, R. A. (1994a). Variation in temperate cereals in rainfed environments. I. Grain yield, biomass and agronomic characteristics. *Field Crops Research* **37**, 51-62.

López-Castañeda, C., and Richards, R. A. (1994b). Variation in temperate cereals in rainfed environments. II. Phasic development and growth. *Field Crops Research* **37**, 63-75.

López-Castañeda, C., and Richards, R. A. (1994c). Variation in temperate cereals in rainfed environments. III. Water use and water-use efficiency. *Field Crops Research* **39**, 85-98.

López-Castañeda, C., Richards, R. A., and Farquhar, G. D. (1995). Variation in early vigor between wheat and barley. *Crop Science* **35**, 472-479.

López-Castañeda, C., Richards, R. A., Farquhar, G. D., and Williamson, R. E. (1996). Seed and seedling characteristics contributing to variation in early vigor among temperate cereals. *Crop Science* **36**, 1257-1266.

Loss, S. P., Kirby, E. J. M., Siddique, K. H. M., and Perry, M. W. (1989). Grain growth and development of old and modern Australian wheats. *Field Crops Research* **21**, 131-146.

Loss, S. P., Perry, M. W., and Anderson, W. K. (1990). Flowering times of wheats in south-western Australia: A modelling approach. *Australian Journal of Agricultural Research* **41**, 213-223.

Loss, S. P., and Siddique, K. H. M. (1994). Morphological and physiological traits associated with wheat yield increases in Mediterranean environments. *Advances in Agronomy* **52**, 229-277.

Lowe, L. B., Ayers, G. S., and Ries, S. K. (1972). Relationship of seed protein and amino acid composition to seedling vigor and yield of wheat. *Agronomy Journal* **64**, 608-611.

Lowe, L. B., and Ries, S. K. (1972). Effects of environment on the relation between seed protein and seedling vigour in wheat. *Canadian Journal of Plant Science* **52**, 157-164.

Ludlow, M. M. (1980). Adaptive significance of stomatal responses to water stress. *In* "Adaptation of plants to water and high temperature stress" (N. C. Turner and P. J. Kramer, eds.), pp. 123-138. John Wiley & Sons, New York, USA.

Ludlow, M. M., and Muchow, R. C. (1990). A critical evaluation of traits for improving crop yields in water-limited environments. *Advances in Agronomy* **43**, 107-153.

Major, D. J., Baret, F., and Guyot, G. (1990). A ratio vegetation index adjusted for soil brightness. *International Journal of Remote Sensing* **11**, 727-740.

Marcar, N. E., and Graham, R. D. (1986). Effect of seed manganese content on the growth of wheat (*Triticum aestivum*) under manganese deficiency. *Plant and Soil* **96**, 165-174.

Marshall, C., and Boyd, W. J. R. (1985). A comparison of the growth and development of biculm wheat lines with freely tillering cultivars. *Journal of Agricultural Science, Cambridge* **104**, 163-171.

McCaig, T. N., and Morgan, J. A. (1993). Root and shoot dry matter partitioning in near-isogenic wheat lines differing in height. *Canadian Journal of Plant Science* **73**, 679-689.

McCloy, K. (1983). Principles of remote sensing II. Characteristics of surface reflectance. *Department of Agriculture, NSW, Advisory Note* **26/83**.

McDonald, G. K. (1987). The response of uniculm and tillered barley to high seeding rates. *In* "Fourth Australian Agronomy Conference", pp. 341, Melbourne, Vic.

McDonald, G. K. (1989). The contribution of nitrogen fertiliser to the nitrogen nutrition of rainfed wheat crops in Australia: A review. *Australian Journal of Experimental Agriculture* **29**, 455-481.

McDonald, G. K. (1990). The growth and yield of uniculm and tillered barley over a range of sowing rates. *Australian Journal of Agricultural Research* **41**, 449-461.

McDonald, G. K. (1992). Effects of nitrogenous fertilizer on the growth, grain yield and grain protein concentration of wheat. *Australian Journal of Agricultural Research* **43**, 949-967.

McDonald, G. K., and Gardner, W. K. (1987). Effect of waterlogging on the grain yield response of wheat to sowing date in south-western Victoria. *Australian Journal of Experimental Agriculture* **27**, 661-670.

McDonald, M. B. (1980). Vigour test subcommittee report. *Association of Official Seed Analysts Newsletter* **54**, 37-40.

McWilliam, J. R. (1989). Dimensions of drought. *In* "Drought resistance in cereals" (F. W. G. Baker, ed.), pp. 1-11. CAB International, Wallingford; UK.

Medd, R. W., Auld, B. A., Kemp, D. R., and Murison, R. D. (1985). The influence of wheat density and spatial arrangement on annual ryegrass, *Lolium rigidum* Gaudin, competition. *Australian Journal of Agricultural Research* **36**, 361-371.

Meyers, L. F., and Lipsett, J. (1958). Competition between skeleton weed (*Chondrilla juncea* L.) and cereals in relation to nitrogen supply. *Australian Journal of Agricultural Research* **9**, 1-12.

Mian, A. R., and Nafziger, E. D. (1994). Seed size and water potential effects on germination and seedling growth of winter wheat. *Crop Science* **34**, 169-171.

Millet, E., and Zaccai, M. (1991). Effects of genotypically and environmentally induced differences in seed protein content on seedling vigor in wheat. *Journal of Genetics and Breeding* **45**, 45-49.

Milton, E. J. (1987). Principles of field spectroscopy. *International Journal of Remote Sensing* **8**, 1807-1827.

Miralles, D. J., and Slafer, G. A. (1995). Yield, biomass and yield components in dwarf, semi-dwarf and tall isogenic lines of spring wheat under recommended and late sowing dates. *Plant Breeding* **114**, 392-396.

Monteith, J. L. (1965). Light distribution and photosynthesis in field crops. *Annals of Botany* **29**, 17-37.

Monteith, J. L. (1993). The exchange of water and carbon by crops in a mediterranean climate. *Irrigation Science* **14**, 85-91.

Moreau, L., Monod, H., Charcosset, A., and Gallais, A. (1999). Marker-assisted selection with spatial analysis of unreplicated field trials. *Theoretical and Applied Genetics* **98**, 234-242.

Mossedaq, F., and Smith, D. H. (1994). Timing nitrogen application to enhance spring wheat yields in a Mediterranean climate. *Agronomy Journal* **86**, 221-226.

Moussavi-nik, M. (1997). Seed quality and crop establishment in wheat. PhD, University of Adelaide, Adelaide.

Moussavi-nik, M., Hollamby, G. J., Pearson, J. N., and Rengel, Z. (1996). Effects of seed size and embryo size on early growth of wheat. *In* "Eighth Assembly of the Wheat Breeding Society of Australia" (R. A. Richards, C. W. Wrigley, H. M. Rawson, G. J. Rebetzke, J. L. Davidson and R. I. S. Brettle, eds.), pp. 123-126. The Wheat Breeding Society of Australia, Canberra, ACT.

Moussavi-nik, M., Pearson, J. N., Hollamby, G. J., and Graham, R. D. (1998). Dynamics of nutrient remobilization during germination and early seedling development in wheat. *Journal of Plant Nutrition* **21**, 421-434.

Moussavi-nik, M., Rengel, Z., Pearson, J. N., and Hollamby, G. (1997). Dynamics of nutrient remobilisation from seed of wheat genotypes during imbibition, germination and early seedling growth. *Plant & Soil* **197**, 271-280.

Murray, G. M., and Kuiper, J. (1988). Emergence of wheat may be reduced by seed weather damage and azole fungicides and is related to coleoptile length. *Australian Journal of Experimental Research* **28**, 253-261.

Nageswara Rao, R. C., Williams, J. H., Rao, V. M., and Wadia, K. D. R. (1992). A hand-held red-infrared radiometer for measuring radiation interception by crop canopies. *Field Crops Research* **29**, 353-360.

Nelson, J. C. (1997). QGENE: software for marker-based genomic analysis and breeding. *Molecular Breeding* **3**, 229-235.

Nerson, H. (1980). Effects of population density and number of ears on wheat yield and its components. *Field Crops Research* **3**, 225-234.

Odiemah, M., and Atta, M. (1985). The quality of winter wheat seed harvested at different times after sowing. *Cereal Research Communications* **13**, 379-385.

Palta, J. A., and Fillery, I. R. (1993a). Nitrogen accumulation and remobilisation in wheat of N-15-urea applied to a duplex soil at seeding. *Australian Journal of Experimental Agriculture* **33**, 233-238.

Palta, J. A., and Fillery, I. R. P. (1993b). Postanthesis remobilisation and losses of nitrogen in wheat in relation to applied nitrogen. *Plant & Soil* **156**, 179-181.

Palta, J. A., and Fillery, I. R. P. (1995a). N application enhances remobilization and reduces losses of pre-anthesis N in wheat grown on a duplex soil. *Australian Journal of Agricultural Research* **46**, 519-531.

Palta, J. A., and Fillery, I. R. P. (1995b). N application increases pre-anthesis contribution of dry matter to grain yield in wheat grown on a duplex soil. *Australian Journal of Agricultural Research* **46**, 507-518.

Palta, J. A., Kobata, T., Turner, N. C., and Fillery, I. R. (1994). Remobilization of carbon and nitrogen in wheat as influenced by postanthesis water deficits. *Crop Science* **34**, 118-124.

Passioura, J. B. (1977). Grain yield, harvest index, and water use of wheat. *Journal of the Australian Institute of Agricultural Science*, 117-120.

Passioura, J. B., Condon, A. C., and Richards, R. A. (1993). Water deficits, the development of leaf area and crop productivity. *In* "Water Deficits - Plant Responses from Cell to Community" (J. A. C. Smith and H. Griffiths, eds.), pp. 253-264. Bios Scientific Publishers, Oxford, UK.

Paterson, A. H., Tanksley, S. D., and Sorrells, M. E. (1991). DNA markers in plant improvement. *Advances in Agronomy* **64**, 39-90.

Pearson, R. L., Miller, L. D., and Tucker, C. J. (1976). Hand-held spectral radiometer to estimate gramineous biomass. *Applied Optics* **15**, 416-418.

Penuelas, J., Isla, R., Filella, I., and Araus, J. L. (1997). Visible and near-infrared reflectance assessment of salinity effects on barley. *Crop Science* **37**, 198-202.

Perry, D. A. (1980). Seed vigour and seedling establishment. *In* "Advances in Research and Technology of Seeds" (J. R. Thompson, ed.), pp. 25-40. Centre for Agricultural Publishing and Documentation, New York.

Perry, M., and Hillman, B. (1991). "The wheat book. A technical manual for wheat producers," Department of Agriculture, Western Australia, Perth, WA.

Perry, M. W. (1987). Water use efficiency of non-irrigated field crops. *In* "Fourth Australian Agronomy Conference" (T. G. Reeves, ed.), pp. 83-99. Australian Society of Agronomy, La Trobe University, Melbourne.

Perry, M. W., Anderson, W. K., and Delane, R. (1989). Early sowing: One key to improved yields of cereal crops. *Western Australian Journal of Agriculture* **30**, 26-29.

Perry, M. W., and D'Antouno, M. F. (1989). Yield improvement and associated characteristics of some Australian spring wheat cultivars introduced between 1860 and 1982. *Australian Journal of Agricultural Research* **40**, 457-472.

Peterson, C. M., Klepper, B., and Rickman, R. W. (1982). Tiller development at the coleoptilar node in winter wheat. *Agronomy Journal* **74**, 781-784.

Peterson, C. M., Klepper, B., and Rickman, R. W. (1989). Seed reserves and seedling development in winter wheat. *Agronomy Journal* **81**, 245-251.

Pheloung, P. C., and Siddique, K. H. M. (1991). Contribution of stem dry matter to grain yield in wheat cultivars. *Australian Journal of Plant Physiology* **18**, 53-64.

Pinter, P. J., Jr. (1986). Effect of dew on canopy reflectance and temperature. *Remote Sensing of Environment* **19**, 187-205.

Power, J. F., and Alessi, J. (1978). Tiller development and yield of standard and semidwarf spring wheat varieties as affected by nitrogen fertilizer. *Journal of Agricultural Science, UK* **90**, 97-108.

Powles, S. B., Preston, C., Bryan, I. B., and Jutsum, A. R. (1997). Herbicide resistance: Impact and management. *Advances in Agronomy* **58**, 57-93.

Puckridge, D. W., and Donald, C. M. (1967). Competition among wheat plants sown at a wide range of densities. *Australian Journal of Agricultural Research* **18**, 193-211.

Radford, B. J., Wilson, B. J., Cartledge, O., and Watkins, F. B. (1980). Effect of wheat seeding rate on wild oat competition. *Australian Journal of Experimental Agriculture and Animal Husbandry* **20**, 77-81.

Rasyad, A., Sanford, D. v., TeKrony, D. M., and Van-Stanford, D. A. (1990). Changes in seed viability and vigour during wheat seed maturation. *Seed Science and Technology* **18**, 259-267.

Rawson, H. M. (1971). Tillering patterns in wheat with special reference to the shoot at the coleoptile node. *Australian Journal of Biological Science* **24**, 829-841.

Rawson, H. M. (1991). Rapid leaf growth in wheat and its links with flowering. *Australian Journal of Plant Physiology* **18**, 109-119.

Rawson, H. M., Gardner, P. A., and Long, M. J. (1987). Sources of variation in specific leaf area in wheat grown at high temperature. *Australian Journal of Plant Physiology* **14**, 287-298.

Rawson, H. M., and Ruwali, K. N. (1972). Ear branching as a means of increasing grain uniformity in wheat. *Australian Journal of Agricultural Research* **23**, 551-559.

Rebetzke, G. J., and Richards, R. A. (1996). Improving the establishment and early vigour of wheat. *In* "Proceedings of the 8th Australian Agronomy Conference" (M. Asghar, ed.), pp. 466-469. The Australian Society of Agronomy, Toowoomba, Queensland.

Rebetzke, G. J., and Richards, R. A. (1999). Genetic improvement of early vigour in wheat. *Australian Journal of Agricultural Research* **50**, 291-301.

Rebetzke, G. J., Richards, R. A., and Fischer, V. M. (1996). Selection for increased early vigour of Australian wheats. *In* "Eighth Assembly of the Wheat Breeding Society of Australia" (R. A. Richards, C. W. Wrigley, H. M. Rawson, G. J. Rebetzke, J. L. Davidson and R. I. S. Brettle, eds.), pp. 160-162. The Australian Society of Wheat Breeding, Canberra, ACT.

Reeves, T. G., and Brooke, H. D. (1977). The effect of genotype and phenotype on the competition between wheat and annual ryegrass (*Lolium rigidum* Gaud.). *In* "Sixth Conference of the Asian-Pacific Weed Science Society", Vol. 1, pp. 167-172, Jakarta, Indonesia.

Reeves, T. G., Nietschke, B. S., Hollamby, G. J., and Powles, S. B. (1993). Integrated weed management - The role of competitive cultivars. *In* "Seventh Australian Agronomy Conference" (G. K. McDonald and W. D. Bellotti, eds.), pp. 352. Australian Society of Agronomy, Adelaide, South Australia.

Regan, K. L., Siddique, K. H. M., Tennant, D., and Abrecht, D. G. (1993). Early maturity improves grain yield and water use efficiency of wheat in low rainfall regions of Western Australia. *In* "Seventh Australian Agronomy Conference" (G. K. McDonald and W. D. Bellotti, eds.), pp. 286-289. Australian Society of Agronomy, Adelaide, South Australia.

Regan, K. L., Siddique, K. H. M., Tennant, D., and Abrecht, D. G. (1997). Grain yield and water use efficiency of early maturing wheat in low rainfall Mediterranean environments. *Australian Journal of Agricultural Research* **48**, 595-603.

Regan, K. L., Siddique, K. H. M., Turner, N. C., and Whan, B. R. (1992). Potential for increasing early vigour and total biomass in spring wheat. II. Characteristics associated with early vigour. *Australian Journal of Agricultural Research* **43**, 541-553.

Rengel, Z., and Graham, R. D. (1995). Importance of seed Zn content for wheat growth on Zn-deficient soil .1. Vegetative growth. *Plant & Soil* **173**, 259-266.

Richards, M. C., and Whytock, G. P. (1993). Varietal competitiveness with weeds. *Aspects of Applied Biology* **34**, 345-354.

Richards, R. A. (1983). Manipulation of leaf area and its effect on grain yield in droughted wheat. *Australian Journal of Agricultural Research* **34**, 23-31.

Richards, R. A. (1987). Physiology and the breeding of winter-grown cereals for dry areas. *In* "Drought Tolerance in Winter Cereals" (J. P. Srivastava, E. Porceddu, E. Acevedo and S. Varma, eds.), pp. 133-49. John Wiley & Sons Ltd, Chichester, U.K.

Richards, R. A. (1988a). Possible early generation selection criteria for yield of rainfed wheat in southern Australia. *In* "Ninth Australian Plant Breeding Conference" (K. S. McWhirter, R. W. Downes and B. J. Read, eds.), pp. 305-306, Sydney, NSW.

Richards, R. A. (1988b). A tiller inhibitor gene in wheat and its effect on plant growth. *Australian Journal of Agricultural Research* **39**, 749-757.

Richards, R. A. (1991). Crop improvement for temperate Australia: Future opportunities. *Field Crops Research* **26**, 141-169.

Richards, R. A. (1992a). The effect of dwarfing genes in spring wheat in dry environments. I. Agronomic characteristics. *Australian Journal of Agricultural Research* **43**, 517-527.

Richards, R. A. (1992b). The effect of dwarfing genes in spring wheat in dry environments. II. Growth, water use and water-use efficiency. *Australian Journal of Agricultural Research* **43**, 529-539.

Richards, R. A. (1996). Defining selection criteria to improve yield under drought. *Plant Growth Regulation* **20**, 157-166.

Richards, R. A., and Condon, A. C. (1994). New 'yield genes' for wheat. *In* "Seventh Australian Wheat Breeding Assembly" (J. Paull, I. S. Dundas, K. J. Shepherd and G. J. Hollamby, eds.), pp. 159-163. Wheat Breeding Society of Australia, Adelaide, South Australia.

Richards, R. A., Lopez Castaneda, C., Gomez Macpherson, H., and Condon, A. G. (1993). Improving the efficiency of water use by plant breeding and molecular biology. *Irrigation Science* **14**, 93-104.

Richards, R. A., Rebetzke, G. J., Condon, A. G., and Mickelson, B. J. (1996). Targeting traits to increase the yield of wheat. *In* "Eighth Assembly, Wheat Breeding Society of Australia" (R. A. Richards, C. W. Wrigley, H. M. Rawson, G. J. Rebetzke, J. L. Davidson and R. I. S. Brettle, eds.), pp. 54-56. Wheat Breeding Society of Australia, Canberra, ACT.

Richards, R. A., Rebetzke, G. J., van Herwaarden, A. F., Duggan, B. L., and Condon, A. G. (1997). Improving yields in rainfed environments through physiological plant breeding. *Annals of Arid Zone* **36**, 255-266.

Richards, R. A., and Townley-Smith, T. F. (1987). Variation in leaf area development and its effect on water use, yield and harvest index of droughted wheat. *Australian Journal of Agricultural Research* **38**, 983-992.

Ries, S. K., Ayers, G., Wert, V., and Everson, E. H. (1976). Variation in protein, size and seedling vigor with position of seed in heads of winter wheat cultivars. *Canadian Journal of Plant Science* **56**, 823-837.

Ries, S. K., and Everson, E. H. (1973). Protein content and seed size relationships with seedling vigor of wheat cultivars. *Agronomy Journal* **65**, 884-886.

Riley, M. M., Adcock, K. G., and Bolland, M. D. A. (1993). A small increase in the concentration of phosphorus in the sown seed increased the early growth of wheat. *Journal of Plant Nutrition* **16**, 851-864.

Ritchie, J. T. (1972). Model for predicting evaporation from a row crop with incomplete cover. *Water Resources Research* **8**, 1204-13.

Sadras, V. O., and Connor, D. J. (1991). Physiological basis of the response of harvest index to the fraction of water transpired after anthesis: a simple model to estimate harvest index for determinate species. *Field Crops Research* **26**, 227-239.

Salopelto, J., and Peltonen, J. (1995). Impact of seed vigour on the grain yield of spring wheat under short and northern growing season. *Acta Agriculturae Scandinavica Section B-Soil & Plant Science* **45**, 57-62.

Sedgley, R. H., and Seaton, K. A. (1987). Ideotypes for the central wheatbelt of W.A. Part 2- Wheat. *In* "Fourth Australian Agronomy Conference" (T. G. Reeves, ed.), pp. 337. Australian Society of Agronomy, Parkville, Vic., La Trobe University.

Setter, T., and Belford, R. (1990). Waterlogging: how it reduces plant growth and how plants can overcome its effects. *Western Australian Journal of Agriculture* **31**, 51-55.

Shackley, B. J., and Anderson, W. K. (1995). Responses of wheat cultivars to time of sowing in the southern wheatbelt of Western Australia. *Australian Journal of Experimental Agriculture* **35**, 579-587.

Sharma, R. C. (1995). Tiller mortality and its relationship to grain yield in spring wheat. *Field Crops Research* **41**, 55-60.

Shepherd, K. D., Cooper, P. J. M., Allan, A. Y., Drennan, D. S. H., and Keatinge, J. D. H. (1987). Growth, water use and yield of barley in Mediterranean-type environments. *Journal of Agricultural Science, Cambridge* **108**, 365-378.

Siddique, K. H. M., Belford, R. K., Perry, M. W., and Tennant, D. (1989a). Growth, development and light interception of old and modern wheat cultivars in a Mediterranean-type environment. *Australian Journal of Agricultural Research* **40**, 473-487.

Siddique, K. H. M., Belford, R. K., and Tennant, D. (1990a). Root : shoot ratios of old and modern, tall and semi-dwarf wheats in a Mediterranean environment. *Plant and Soil* **121**, 89-98.

Siddique, K. H. M., Kirby, E. J. M., and Perry, M. W. (1989b). Ear : stem ratio in old and modern wheat varieties; relationship with improvement in number of grains per ear and yield. *Field Crops Research* **21**, 59-78.

Siddique, K. H. M., and Sedgley, R. H. (1987). Canopy development modifies the water economy of chickpea (*Cicer arietinum L.*) in south Western Australia. *Australian Journal of Agricultural Research* **37**, 599-610.

Siddique, K. H. M., Tennant, D., Perry, M. W., and Belford, R. K. (1990b). Water use and water use efficiency of old and modern wheat cultivars in a Mediterranean-type environment. *Australian Journal of Agricultural Research* **41**, 431-447.

Sinclair, T. R., Tanner, C. B., and Bennett, J. M. (1984). Water-use efficiency in crop production. *BioScience* **34**, 36-40.

Skinner, R. H., and Nelson, C. J. (1994). Role of leaf appearance rate and the coleoptile tiller in regulating tiller production. *Crop Science* **34**, 71-75.

Slafer, G. A., and Kernich, G. C. (1996). Have changes in yield (1900-1992) been accompanied by a decreased yield stability in Australian cereal production. *Australian Journal of Agricultural Research* **47**, 323-334.

Slafer, G. A., and Rawson, H. M. (1997). Phyllochron in wheat as affected by photoperiod under two temperature regimes. *Australian Journal of Plant Physiology* **24**, 151-158.

Slafer, G. A., Satorre, E. H., and Andrade, F. H. (1994). Increases in grain yield in bread wheat from breeding and associated physiological changes. *In* "Genetic improvement of field crops" (G. A. Slafer, ed.), pp. 1-68. Marcel Dekker, New York.

Smith, R. C. G., Hick, P. T., Gilmour, R., Regan, K. L., Elliot, G. A., Portman, P., and Turner, N. C. (1992). Use of field spectroscopy to rank cereal plots according to biomass. *In* "6th Australasian Remote Sensing Conference", pp. 3-90 - 3-98, Wellington, New Zealand.

Smith, R. C. G., Wallace, J. F., Hick, P. T., Gilmour, R. F., Belford, R. K., Portmann, P. A., Regan, K. L., and Turner, N. C. (1993). Potential of using field spectroscopy during early growth for ranking biomass in cereal breeding trials. *Australian Journal of Agricultural Research* **44**, 1713-1730.

Snape, J. W. (1989). Doubled haploid breeding: Theoretical basis and practical applications. *In* "Review of advances in plant biotechnology 1985-88. Second international symposium on genetic manipulation in crops." (A. Mujeeb Kazi and L. A. Sitch, eds.), pp. 19-30. CIMMYT, Mexico, DF.

Snape, J. W. (1996). The contribution of new biotechnologies to wheat breeding. *In* "Increasing yield potential in wheat: Breaking the barriers . Proceedings of a workshop held in Obregón, Sonora, Mexico" (M. P. Reynolds, S. Rajaram and A. McNab, eds.), pp. 167-181. CIMMYT, Mexico.

Snape, J. W. (1998). Golden calves or white elephants - biotechnologies for wheat improvement. *Euphytica* **100**, 207-217.

Snape, J. W., Quarrie, S. A., Laurie, D. A., Borner, A., and Worland, A. J. (1996). Comparative mapping and its use for the genetic analysis of agronomic characters in wheat. *Euphytica* **89**, 27-31.

Soetono, and Donald, C. M. (1980). Emergence, growth and dominance in drilled and square-planted barley crops. *Australian Journal of Agricultural Research* **31**, 455-470.

Standard, S. A., Perret, D., and Bray, C. M. (1983). Nucleotide levels and loss of vigour and viability in germinating wheat embryos. *Journal of Experimental Botany* **34**, 1047-1054.

Stapper, M., and Harris, H. C. (1989). Assessing the productivity of wheat genotypes in a Mediterranean climate, using a crop-simulation model. *Field Crops Research* **20**, 129-152.

Steven, M. D., Biscoe, P. V., Jaggard, K. W., and Paruntu, J. (1986). Foliage cover and radiation interception. *Field Crops Research* **13**, 75-87.

Stone, P. J., Savin, R., Wardlaw, I. F., and Nicolas, M. E. (1995). The influence of recovery temperature on the effects of a brief heat shock on wheat. I. Grain growth. *Australian Journal of Plant Physiology* **22**, 945-954.

Tashiro, T., and Wardlaw, I. F. (1990). The effect of high temperature at different stages of ripening on grain set, grain weight and grain dimensions in the semi-dwarf wheat 'Banks' *Annals of Botany* **65**, 51-61.

Taylor, G., Allison, M., and Coleman, L., eds. (1991). "Winter cereal management guide,". South Australian Department of Agriculture, Adelaide, South Australia.

TeKrony, D. M., and Egli, D. E. (1991). Relationship of seed vigour to crop yield: A review. *Crop Science* **31**, 816-822.

Tennant, D., Scholz, G., Dixon, J., and Purdie, B. (1992). Physical and chemical characteristics of duplex soils and their distribution in the south-west of Western Australia. *Australian Journal of Experimental Agriculture* **32**, 827-843.

Thorne, G. N., Pearman, I., Day, W., and Todd, A. D. (1988). Estimation of radiation interception by winter wheat from measurements of leaf area. *Journal of Agricultural Science, Cambridge* **110**, 101-108.

Thorne, G. N., Thomas, S. M., and Pearman, I. (1979). Effects of nitrogen nutrition on physiological factors that control the yield of carbohydrate in the grain. *In* "Crop physiology and cereal breeding. Proceedings of a Eucarpia workshop" (J. H. J. Spiertz and T. Kramer, eds.), pp. 90-95. Centre for Agricultural Publishing and Documentation, Wageningen, the Netherlands.

Tompkins, D. K., Fowler, D. B., and Wright, A. T. (1991). Water use by no-till winter wheat influence of seed rate and row spacing. *Agronomy Journal* **83**, 766-769.

Tucker, C. J. (1979). Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment* **8**, 127-150.

Tucker, C. J., Holben, B. N., Elgin, J. H., Jnr, and McMurtrey, J. E. (1981). Remote sensing of total dry-matter accumulation in winter wheat. *Remote Sensing of Environment* **11**, 171-189.

Turner, N. C., and Nicolas, M. E. (1987). Drought resistance of wheat for light-textured soils in a Mediterranean climate. *In* "Drought tolerance in winter cereals" (J. P. Srivastava, E. Porceddu, E. Acevedo and S. Varma, eds.), pp. 203-215. John Wiley and Sons Ltd., Chichester; UK.

Turner, N. C., Nicolas, M. E., Hubick, K. T., and Farquhar, G. D. (1989). Evaluation of traits for the improvement of water use efficiency and harvest index. *In* "Drought resistance in cereals" (F. W. G. Baker, ed.), pp. 177-189. CAB International, Wallingford; UK.

Turner, N. C., Prasertsak, P., and Setter, T. L. (1994). Plant spacing, density, and yield of wheat subjected to postanthesis water deficits. *Crop Science* **34**, 741-748.

Turner, N. C., Tennant, D., Hamblin, A. P., Henson, I. E., Jensen, C. R., and Perry, M. W. (1987). Influence of nitrogen on the yield, water use and water deficits of wheat grown in a Mediterranean climate. *In* "4th Australian Agronomy Conference", pp. 254. Australian Society of Agronomy, Parkville, Vic.

van den Boogaard, R., Alewijnse, D., Veneklaas, E. J., and Lambers, H. (1997). Growth and water-use efficiency of 10 *Triticum aestivum* cultivars at different water availability in relation to allocation of biomass. *Plant, Cell and Environment* **20**, 200-210.

van den Boogaard, R., Veneklaas, E. J., and Lambers, H. (1996a). The association of biomass allocation with growth and water use efficiency of two *Triticum aestivum* cultivars. *Australian Journal of Plant Physiology* **23**, 751-761.

van den Boogaard, R., Veneklaas, E. J., Peacock, J. M., and Lambers, H. (1996b). Yield and water use of wheat (*Triticum aestivum*) in a Mediterranean environment: cultivar differences and sowing density effects. *Plant and Soil* **181**, 251-262.

van Herwaarden, A. F. (1996). Haying-off in wheat: enduring myth or current problem? *In* "Eighth Australian Agronomy Conference" (M. Asghar, ed.), pp. 566-569. The Australian Society of Agronomy, Toowoomba, Queensland.

van Herwaarden, A. F., Farquhar, G. D., Angus, J. F., and Richards, R. A. (1996). Physiological responses of six spring wheat varieties to nitrogen fertilizer. *In* "Eighth Australian Agronomy Conference" (M. Asghar, ed.), pp. 570-573. The Australian Society of Agronomy, Toowoomba, Queensland.

Van Oosterom, E. J., and Acevedo, E. (1992). Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. I. Morphological traits. *Euphytica* **62**, 1-14.

Venn, N. R., Turner, N. C., and Fillery, I. R. P. (1987). Influence of post seeding application of nitrogen on grain yield and water stress of wheat in a Mediterranean climate. *In* "4th Australian Agronomy Conference", pp. 255. Australian Society of Agronomy, Parkville, Vic.

Voltas, J., Romagosa, I., and Araus, J. L. (1997). Grain size and nitrogen accumulation in sink-reduced barley under Mediterranean conditions. *Field Crops Research* **52**, 117-126.

Wardlaw, I. F. (1967). The effect of water stress on translocation in relation to photosynthesis and growth. 1. Effect during grain development in wheat. *Australian Journal of Biological Science* **20**, 25-39.

Webber, G. D., Cocks, P. S., and Jefferies, B. C. (1976). "Farming systems in South Australia," Department of Agriculture and Fisheries, Adelaide, Australia.

Wellington, P. S. (1966). Germination and seedling emergence. *In* "The growth of cereals and grasses" (F. L. Milthorpe and J. D. Ivins, eds.), pp. 3-19. Butterworths, London.

Whan, B. R. (1976a). The association between coleoptile length and culm length in semidwarf and standard wheats. *Journal of the Australian Institute of Agricultural Science* **42**, 194-196.

Whan, B. R. (1976b). The emergence of semi-dwarf and standard wheats, and its association with coleoptile length. *Australian Journal of Experimental Agriculture* **16**, 411-416.

Whan, B. R., Carlton, G. P., and Anderson, W. K. (1991). Potential for increasing early vigour and total biomass in spring wheat. I. Identification of genetic improvements. *Australian Journal of Agricultural Research* **42**, 347-361.

Whan, B. R., Carlton, G. P., Siddique, K. H. M., Regan, K. L., Turner, N. C., and Anderson, W. K. (1993). Integration of breeding and physiology: Lessons from a water-limited environment. *In* "International crop science I. International Crop Science Congress Ames" (D. R. Buxton, R. Shibles, R. A. Forsberg, B. L. Blad, K. H. Asay, G. M. Paulsen and R. F. Wilson, eds.), pp. 607-614. Crop Science Society of America, Madison, WI; USA.

Whan, B. R., Delane, R., and Gilmour, R. (1988). The potential of reduced tillering wheats in dry environments. *In* "Seventh International Wheat Genetics Symposium" (T. E. Miller and R. M. D. Koebner, eds.), pp. 907-911. Institute of Plant Science Research; Cambridge; UK, Cambridge, UK.

Wicks, G. A., Ramsel, R. E., Nordquist, P. T., Schmidt, J. W., and Challaiah (1986). Impact of wheat cultivars on establishment and suppression of summer annual weeds. *Agronomy Journal* **78**, 59-62.

Young, I. M., Montagu, K., Conroy, J., and Bengough, A. G. (1997). Mechanical impedance of root growth directly reduces leaf elongation rates of cereals. *New Phytologist* **135**, 613-619.

Yunusa, I. A. M., Belford, R. K., Tennant, D., and Sedgley, R. H. (1993a). Row spacing fails to modify soil evaporation and grain yield in spring wheat in a dry Mediterranean environment. *Australian Journal of Agricultural Research* **44**, 661-676.

Yunusa, I. A. M., Sedgley, R. H., Belford, R. K., and Tennant, D. (1993b). Dynamics of water use in a dry mediterranean environment. I. Soil evaporation little affected by presence of plant canopy. *Agricultural Water Management* **24**, 205-224.

Yunusa, I. A. M., Sedgley, R. H., and Siddique, K. M. H. (1994). Influence of mulching on the pattern of growth and water use by spring wheat and moisture storage on a fine textured soil. *Plant & Soil* **160**, 119-130.

Yunusa, I. A. M., Siddique, K. H. M., Belford, R. K., and Karimi, M. M. (1993c). Effect of canopy structure on efficiency of radiation interception and use in spring wheat cultivars during the pre-anthesis period in a mediterranean-type environment. *Field Crops Research* **35**, 113-122.

Zadoks, J. C., Chang, T. T., and Konzak, C. F. (1974). A decimal code for the growth stages in cereals. *Weed Research* **14**, 415-421.

Zaicou, C. M., and Gill, G. S. (1992). Effect of crop seeding rates and chemical control of brome grass on crop yield and brome grass seed output. *In* "Proceedings of the 1st International Weed Control Congress", Vol. 2, pp. 589-591. Weed Science Society of Victoria; Melbourne; Australia.

APPENDICES

Appendix A : Potting mixes

University of California mix

400 litre of coarse washed sand (Golden Grove) is sterilised at 100°C for 30 minutes in a sterilising mixer. One bale of Euroturf® peatmoss (300 litres) is added and mixed for 10 seconds. The temperature of the combined sand / peatmoss drops to about 80°C.

After about 10 minutes more cooling, the following fertilisers are added and mixed with the sand / peat mix for 20 seconds. The short mixing times are to ensure that sufficient air porosity remains in the finished soil. The UC mix should have a pH ~ 6.8.

Fertilisers:	Calcium hydroxide	700 g
	Calcium carbonate	480 g
	Nitrophoska (15-4-12)	600 g

Lucern / Medic mix without perlite

350 litres of white sand (Golden Grove coarse, white, concrete) was mixed with 350 litres of grey sand (Mt Compass) for 5 minutes. After this, 480 g of Ag Lime and 600 g of Nitrophoska were added and the soil was further mixed for about 15 seconds. The mix is then spread evenly in a sterilising bin and holes are punched in the mix using the "medic mix hole puncher" with the holes covering the entire mix as evenly as possible. The mix is pasturised at 80°C for 30 minutes. The final mix shouls have a pH ~ 6.5.

Appendix B : Fertilisers

Nitrophoska Analysis

N	Total nitrogen	15%
	5% NH_4 ammonia form	
	4% NO_3 nitrate form	
	1% NH_2 amide form	
	5% IBDU	
P	Total phosphorous	3.90%
	3.9% citrate soluble, of which	
	1.2% water soluble	
K	Potassium sulphate	12.4%
Mg	Magnesium carbonate	1.25%
Ca	Dicalcium phosphate	3.40%
S	Sulphates	5.30%
Fe	Iron oxide	0.30%
Cu	Copper oxides	0.0002%
Zn	Zinc oxide	0.0070%
B	Calcium borate	0.0100%
Mo	Molybdenum oxide	0.0003%

Aquasol™ soluble fertiliser

20 g of Aquasol™ soluble fertiliser (Hortico Aust Pty, Ltd) was dissolved in 10 litres of water and applied evenly where required.

N	Total nitrogen	23%
	1.8% as mono-amonium phosphate	
	2.6% as potassium nitrate	
	18.6% as urea	
P	Total Phosphorus	4.0%
	4.0% as mono-ammonium phosphate	
K	Total potassium	18.0%
	7.8% as potassium nitrate	
	10.2% as potassium chloride	
Zn	Zinc sulphate	0.05%
Cu	Copper sulphate	0.06%
Mo	Sodium molybdate	0.0013%
Mn	Sulphate	0.15%
Fe	Sodium ferric EDTA	0.06%
B	Sodium borate	0.011%

Appendix C : Light interception and yield ranking

Table C.1 Light interception and yield ranking for raw and TwoD adjusted data from Chapter 6, Experiment 1.

Cross No.	Pedigree	Density	Anth.	Raw Data		TwoD Adjusted	
		m^{-2}	DAS	LI %	Yield g/m²	LI %	Yield g/m²
CO4153-401	AUS22600;GK-SAGVAN;/SCHOMBURGK	161	116	119	56	51	285
CO4153-402	AUS22600;GK-SAGVAN;/SCHOMBURGK	156	112	199	130	95	334
CO4155-401	TAU628//7/5AROONA;AG3/AROONA	167	112	147	158	19	216
CO4156-401	TAU641//7/5AROONA;AG3/AROONA	172	114	224	223	280	114
CO4156-402	TAU641//7/5AROONA;AG3/AROONA	222	132	93	1	319	214
CO4156-403	TAU641//7/5AROONA;AG3/AROONA	178	116	150	236	316	230
CO4160-401	7/5AROONA;AG3/AROONA;/;CO3040;OXLEY//ZENATI	167	118	253	237	195	27
CO4160-402	7/5AROONA;AG3/AROONA;/;CO3040;OXLEY//ZENATI	183	122	85	102	168	125
CO4160-403	7/5AROONA;AG3/AROONA;/;CO3040;OXLEY//ZENATI	178	115	86	136	285	138
CO4160-404	7/5AROONA;AG3/AROONA;/;CO3040;OXLEY//ZENATI	178	117	123	115	243	151
CO4167-401	CO1650-201;MKR211-7/RAC177/FLD'OR//RAC177+SR2;/;F84.4697;(KT	189	115	174	83	340	338
CO4167-402	CO1650-201;MKR211-7/RAC177/FLD'OR//RAC177+SR2;/;F84.4697;(KT	178	114	261	229	89	296
CO4189-401	RAC606;7141HR;9E/3WT111/3WT211/7;/;CO2720-401;VS/3*177//BYO/	183	115	241	183	108	53
CO4189-402	RAC606;7141HR;9E/3WT111/3WT211/7;/;CO2720-401;VS/3*177//BYO/	200	118	101	179	149	13
CO4191-401	RAC595;CO2084-203;RAC311H/3/75IRN217;/;CO2477-445;VS/3*177	228	115	342	11	186	140
CO4191-402	RAC595;CO2084-203;RAC311H/3/75IRN217;/;CO2477-445;VS/3*177	183	124	124	40	141	271
CO4191-403	RAC595;CO2084-203;RAC311H/3/75IRN217;/;CO2477-445;VS/3*177	200	114	311	174	112	88
CO4191-404	RAC595;CO2084-203;RAC311H/3/75IRN217;/;CO2477-445;VS/3*177	172	122	140	42	56	277
CO4195-401	MACHETE/;3005;CO2532;VS/3*177/4*SPR	167	116	181	163	132	112
CO4195-402	MACHETE/;3005;CO2532;VS/3*177/4*SPR	156	125	76	131	287	347
CO4196-401	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	139	124	197	152	192	50
CO4196-402	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	222	114	22	22	230	33
CO4196-403	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	211	124	244	23	12	3
CO4196-404	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	178	116	52	67	260	302
CO4196-405	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	233	132	216	231	292	233
CO4196-406	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	183	114	297	209	91	273
CO4196-407	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	306	125	263	251	245	152
CO4196-408	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	167	133	219	103	207	95
CO4196-409	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	150	111	335	93	113	123
CO4196-410	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	139	122	98	263	81	276
CO4196-411	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	194	116	315	281	226	188
CO4196-412	RAC520-4;MDN/4*RAC177;/;CO2477-536;VS/3*177	139	113	281	187	4	179
CO4197-401	CRANBROOK/;CO2477-536;VS/3*177	200	117	100	9	100	242
CO4197-402	CRANBROOK/;CO2477-536;VS/3*177	217	116	167	210	77	18
CO4197-403	CRANBROOK/;CO2477-536;VS/3*177	172	114	201	125	27	195
CO4197-404	CRANBROOK/;CO2477-536;VS/3*177	178	116	10	16	263	200
CO4197-405	CRANBROOK/;CO2477-536;VS/3*177	167	114	81	29	88	304
CO4197-406	CRANBROOK/;CO2477-536;VS/3*177	217	119	178	248	170	77
CO4197-407	CRANBROOK/;CO2477-536;VS/3*177	189	113	151	33	21	137
CO4199-401	13THIBSWN518/;CO2532-406;VS/3*177//SPR	156	116	183	198	313	42
CO4201-401	C3/3WI111/3WT211/7//;CO2477-536;VS/3*177	167	117	324	224	36	250
CO4201-402	C3/3WI111/3WT211/7//;CO2477-536;VS/3*177	200	113	344	324	31	109
CO4201-403	C3/3WI111/3WT211/7//;CO2477-536;VS/3*177	144	121	106	339	134	24
CO4201-404	C3/3WI111/3WT211/7//;CO2477-536;VS/3*177	261	123	34	14	30	37
CO4201-405	C3/3WI111/3WT211/7//;CO2477-536;VS/3*177	144	110	221	227	176	172
CO4201-406	C3/3WI111/3WT211/7//;CO2477-536;VS/3*177	217	116	229	272	193	183

Cross No.	Pedigree	Density	Anth.	Raw Data		TwoD Adjusted	
				LI	Yield	LI	Yield
		m^{-2}	DAS	%	g/m^2	%	g/m^2
CO4201-407	C3/3WI111/3WT211/7//;CO2477-536;VS/3*177	189	111	284	283	119	66
CO4201-408	C3/3WI111/3WT211/7//;CO2477-536;VS/3*177	206	115	343	301	9	89
CO4201-409	C3/3WI111/3WT211/7//;CO2477-536;VS/3*177	250	122	230	215	308	204
CO4201-410	C3/3WI111/3WT211/7//;CO2477-536;VS/3*177	178	112	339	328	69	22
CO4202-401	RAC571;14IBSWN189;/;CO2477-437;VS/3*177	200	121	300	177	187	325
CO4202-402	RAC571;14IBSWN189;/;CO2477-437;VS/3*177	89	116	225	336	198	311
CO4202-403	RAC571;14IBSWN189;/;CO2477-437;VS/3*177	261	117	191	193	303	289
CO4202-404	RAC571;14IBSWN189;/;CO2477-437;VS/3*177	167	122	304	299	7	29
CO4203-401	CO1218-219;76ECN-43/COOK;/;RAC608;VS/3*177//SPR	150	121	347	292	328	69
CO4203-402	CO1218-219;76ECN-43/COOK;/;RAC608;VS/3*177//SPR	233	112	232	348	104	345
CO4204-401	CO1284-209;75IRN-193/RAC88;/;CO2477-437;VS/3*177	200	116	250	305	216	175
CO4204-402	CO1284-209;75IRN-193/RAC88;/;CO2477-437;VS/3*177	156	123	338	25	275	57
CO4204-403	CO1284-209;75IRN-193/RAC88;/;CO2477-437;VS/3*177	200	116	207	241	90	20
CO4204-404	CO1284-209;75IRN-193/RAC88;/;CO2477-437;VS/3*177	178	116	70	49	271	94
CO4204-405	CO1284-209;75IRN-193/RAC88;/;CO2477-437;VS/3*177	206	116	157	76	76	9
CO4204-406	CO1284-209;75IRN-193/RAC88;/;CO2477-437;VS/3*177	206	115	293	280	190	107
CO4204-407	CO1284-209;75IRN-193/RAC88;/;CO2477-437;VS/3*177	150	112	249	325	153	133
CO4204-408	CO1284-209;75IRN-193/RAC88;/;CO2477-437;VS/3*177	222	116	307	274	276	105
CO4204-409	CO1284-209;75IRN-193/RAC88;/;CO2477-437;VS/3*177	161	114	333	82	320	113
CO4205-401	CO1452-208;MED17/MOROCCO//RAC117/RAC177;/;CO2477-405;VS/3*17	256	118	17	247	338	346
CO4205-402	CO1452-208;MED17/MOROCCO//RAC117/RAC177;/;CO2477-405;VS/3*17	244	114	184	317	223	102
CO4206-401	CO1489-203;TAN71/WARIQUAM//9THIBSWN-87;/;CO2477-445;VS/3*177	194	116	41	124	273	148
CO4206-402	CO1489-203;TAN71/WARIQUAM//9THIBSWN-87;/;CO2477-445;VS/3*177	122	106	337	219	347	199
CO4206-403	CO1489-203;TAN71/WARIQUAM//9THIBSWN-87;/;CO2477-445;VS/3*177	167	113	187	173	130	298
CO4206-404	CO1489-203;TAN71/WARIQUAM//9THIBSWN-87;/;CO2477-445;VS/3*177	228	114	332	329	298	220
CO4206-405	CO1489-203;TAN71/WARIQUAM//9THIBSWN-87;/;CO2477-445;VS/3*177	172	118	15	110	92	104
CO4206-406	CO1489-203;TAN71/WARIQUAM//9THIBSWN-87;/;CO2477-445;VS/3*177	222	115	289	111	267	269
CO4206-407	CO1489-203;TAN71/WARIQUAM//9THIBSWN-87;/;CO2477-445;VS/3*177	128	120	146	27	339	156
CO4206-408	CO1489-203;TAN71/WARIQUAM//9THIBSWN-87;/;CO2477-445;VS/3*177	261	115	62	2	148	84
CO4206-409	CO1489-203;TAN71/WARIQUAM//9THIBSWN-87;/;CO2477-445;VS/3*177	217	119	235	120	124	281
CO4207-401	;CO1763-206/;CO2470-401	183	120	53	218	106	236
CO4207-402	;CO1763-206/;CO2470-401	167	118	336	289	318	268
CO4209-401	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	211	118	14	51	188	173
CO4209-402	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	322	117	190	333	237	87
CO4209-403	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	183	111	135	170	183	316
CO4209-404	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	178	116	321	291	311	110
CO4209-405	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	156	121	61	52	283	165
CO4209-406	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	233	114	246	262	294	300
CO4209-407	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	211	116	212	334	221	184
CO4209-408	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	194	112	287	286	327	254
CO4209-409	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	172	118	202	176	324	283
CO4209-410	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	194	116	320	212	314	261
CO4209-411	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	161	114	206	164	257	228
CO4209-412	CO1650-201MKR211-7/3/177/FLO'OR//177;/;CO2477-536;VS/3*177	172	131	309	204	224	154
CO4210-401	5920-TX78;MADDEN/RAC177;/;30475;Sr21/3*CDO//4*416	156	115	45	3	238	189
CO4210-402	5920-TX78;MADDEN/RAC177;/;30475;Sr21/3*CDO//4*416	178	120	58	206	228	131
CO4210-403	5920-TX78;MADDEN/RAC177;/;30475;Sr21/3*CDO//4*416	278	114	252	153	118	124
CO4212-401	RAC416-1;CONDOR/PETITROJO;/;F84.3532;KT/242//KT/242	222	116	328	19	122	90
CO4212-402	RAC416-1;CONDOR/PETITROJO;/;F84.3532;KT/242//KT/242	133	113	223	268	129	160
CO4212-403	RAC416-1;CONDOR/PETITROJO;/;F84.3532;KT/242//KT/242	189	116	161	30	78	209
CO4212-404	RAC416-1;CONDOR/PETITROJO;/;F84.3532;KT/242//KT/242	117	110	305	169	211	16
CO4212-405	RAC416-1;CONDOR/PETITROJO;/;F84.3532;KT/242//KT/242	178	118	192	182	290	337
CO4212-406	RAC416-1;CONDOR/PETITROJO;/;F84.3532;KT/242//KT/242	189	125	334	320	251	76
CO4212-407	RAC416-1;CONDOR/PETITROJO;/;F84.3532;KT/242//KT/242	172	118	272	343	120	115

Cross No.	Pedigree	Density	Anth.	Raw Data		TwoD Adjusted	
				LI	Yield	LI	Yield
		m^{-2}	DAS	%	g/m^2	%	g/m^2
CO4213-401	CO1213-205;76ECN-36/70ECN-44DRP(---;/;30475;Sr21/3*CDO//4*41	161	113	217	213	348	136
CO4214-401	RAC569/;CO2420-407;VS/3*177	144	112	18	34	166	79
CO4214-402	RAC569/;CO2420-407;VS/3*177	244	114	215	319	61	217
CO4216-401	9IBSWN322;WeXCNO;NO66;/;82.170;9e+Tt1/2LNC//4*416	156	116	194	275	305	328
CO4220-401	EMU'S'/ROMANY;CO858;/;CO2522-438;VS/3*177	183	115	182	90	75	201
CO4220-402	EMU'S'/ROMANY;CO858;/;CO2522-438;VS/3*177	183	115	83	245	246	190
CO4220-403	EMU'S'/ROMANY;CO858;/;CO2522-438;VS/3*177	150	117	3	37	86	263
CO4220-404	EMU'S'/ROMANY;CO858;/;CO2522-438;VS/3*177	183	118	32	96	146	301
CO4220-405	EMU'S'/ROMANY;CO858;/;CO2522-438;VS/3*177	167	115	87	167	231	308
CO4220-406	EMU'S'/ROMANY;CO858;/;CO2522-438;VS/3*177	156	111	312	311	315	251
CO4220-407	EMU'S'/ROMANY;CO858;/;CO2522-438;VS/3*177	194	116	12	135	137	180
CO4220-408	EMU'S'/ROMANY;CO858;/;CO2522-438;VS/3*177	211	116	9	154	15	305
CO4225-401	CO3040;OXLEY//ZENATI;/;VERAN/3*RAC177;CO2477-14//GABO	211	115	30	161	93	234
CO4226-401	;CO3040/4/RAC430-6/RVN//9IBWSN180/3/CO2767/Sr26/6*177-6010S	183	116	5	332	343	75
CO4240-401	;CO4093/;CO4056	117	116	103	240	18	44
CO4240-402	;CO4093/;CO4056	178	114	180	137	10	319
CO4240-403	;CO4093/;CO4056	183	115	2	55	310	249
CO4240-404	;CO4093/;CO4056	133	128	317	340	165	252
CO4254-401	RAC549/RAC569	206	113	7	7	317	12
CO4255-401	MACHETE/RAC569	156	119	238	235	206	262
CO4257-401	RAC520/RAC569	178	120	82	129	256	240
CO4257-402	RAC520/RAC569	167	113	114	80	172	147
CO4257-403	RAC520/RAC569	167	113	239	108	6	245
CO4258-401	RAC177/RAC569	250	114	51	155	264	260
CO4259-401	HAHN'S'2/PRL'S'//;CO2498-406;RAC416/Sr21/3*CDO	128	118	171	99	151	314
CO4262-401	AROONA/RAC569	178	112	291	284	291	288
CO4263-401	BANKS/RAC569	194	118	175	128	220	185
CO4265-401	HAHN'S'2/PRL'S'//RAC495	206	121	57	107	277	58
CO4265-402	HAHN'S'2/PRL'S'//RAC495	194	111	254	323	265	221
CO4265-403	HAHN'S'2/PRL'S'//RAC495	144	125	313	200	299	121
CO4265-404	HAHN'S'2/PRL'S'//RAC495	156	124	268	253	278	145
CO4265-405	HAHN'S'2/PRL'S'//RAC495	217	118	170	221	272	210
CO4265-406	HAHN'S'2/PRL'S'//RAC495	194	113	227	228	184	31
CO4265-407	HAHN'S'2/PRL'S'//RAC495	183	114	195	39	248	70
CO4265-408	HAHN'S'2/PRL'S'//RAC495	183	118	271	294	201	130
CO4265-409	HAHN'S'2/PRL'S'//RAC495	150	133	240	196	45	186
CO4265-410	HAHN'S'2/PRL'S'//RAC495	172	121	38	100	218	25
CO4266-401	BWA/RAC569	117	114	28	10	194	218
CO4266-402	BWA/RAC569	211	115	113	132	84	266
CO4266-405	BWA/RAC569	172	115	237	146	279	63
CO4266-406	BWA/RAC569	200	125	303	139	159	129
CO4267-401	CDO/RAC569	189	119	164	211	219	335
CO4268-401	COOK/RAC569	300	117	196	61	121	324
CO4268-402	COOK/RAC569	139	115	275	243	177	159
CO4273-401	MDN/RAC569	194	116	198	64	179	119
CO4273-402	MDN/RAC569	161	112	188	109	156	348
CO4275-401	MWA/RAC569	72	120	49	70	293	36
CO4275-402	MWA/RAC569	156	112	330	261	37	177
CO4275-403	MWA/RAC569	156	112	120	273	123	81
CO4275-404	MWA/RAC569	133	106	134	13	164	118
CO4277-401	TAKARI/RAC569	156	116	185	57	14	167
CO4277-402	TAKARI/RAC569	194	114	160	58	208	291
CO4277-403	TAKARI/RAC569	172	112	156	222	225	287
CO4277-404	TAKARI/RAC569	161	117	11	265	175	329

Cross No.	Pedigree	Density	Anth.	Raw Data		TwoD Adjusted	
		m^{-2}	DAS	LI %	Yield g/m²	LI %	Yield g/m²
CO4278-401	WGL/RAC569	156	114	129	316	20	258
CO4278-402	WGL/RAC569	217	114	269	307	72	144
CO4279-401	RAC575/RAC569	194	117	208	191	185	299
CO4279-402	RAC575/RAC569	178	114	159	32	158	286
CO4279-403	RAC575/RAC569	178	105	145	43	73	47
CO4279-404	RAC575/RAC569	189	121	39	114	309	80
CO4279-405	RAC575/RAC569	178	116	25	85	43	116
CO4281-401	CDO/COOK	139	119	121	277	306	74
CO4281-402	CDO/COOK	206	113	35	121	136	310
CO4281-404	CDO/COOK	194	116	152	171	269	244
CO4281-405	CDO/COOK	178	114	242	306	203	315
CO4281-406	CDO/COOK	128	114	91	44	163	168
CO4281-407	CDO/COOK	150	119	37	151	55	49
CO4281-408	CDO/COOK	194	121	97	150	171	212
CO4281-409	CDO/COOK	106	120	285	257	266	99
CO4281-410	CDO/COOK	122	115	149	342	39	150
CO4282-401	RAC417-2/RAC560	150	116	346	250	233	280
CO4282-402	RAC417-2/RAC560	167	122	251	48	8	237
CO4288-401	KITE/ISR493	194	134	203	53	191	192
CO4288-402	KITE/ISR493	122	119	290	194	332	241
CO4288-403	KITE/ISR493	239	105	112	65	125	232
CO4288-404	KITE/ISR493	161	112	138	73	162	181
CO4289-401	MACHETE/ISR493	189	111	210	84	25	127
CO4289-402	MACHETE/ISR493	206	114	8	141	79	32
CO4291-401	WARIGAL/ISR493	100	115	255	166	102	182
CO4291-402	WARIGAL/ISR493	228	116	200	246	334	51
CO4300-401	RAC628//VERANOPOLIS/3*RAC177	167	115	65	17	116	279
CO4300-403	RAC628//VERANOPOLIS/3*RAC177	161	115	46	119	114	132
CO4300-404	RAC628//VERANOPOLIS/3*RAC177	111	118	96	208	87	239
CO4300-405	RAC628//VERANOPOLIS/3*RAC177	144	111	163	199	209	207
CO4300-406	RAC628//VERANOPOLIS/3*RAC177	244	123	24	26	65	174
CO4300-407	RAC628//VERANOPOLIS/3*RAC177	189	113	102	60	152	54
CO4302-401	RAC632/4/CO1650-204;MKR211-7/3/FLD'OR//RAC177;	194	118	326	338	321	142
CO4302-402	RAC632/4/CO1650-204;MKR211-7/3/FLD'OR//RAC177;	217	114	117	15	296	229
CO4302-403	RAC632/4/CO1650-204;MKR211-7/3/FLD'OR//RAC177;	189	117	245	312	240	320
CO4302-404	RAC632/4/CO1650-204;MKR211-7/3/FLD'OR//RAC177;	139	116	292	226	97	264
CO4303-401	RAC633/CO1070;TZPP/ECN76-023;	144	114	90	68	131	265
CO4311-401	5920-TX78;MADDEN/RAC177;/CO1452-208;MED17/MOROCCO//RAC117/RA	128	131	295	188	35	312
CO4313-401	RAC416-1/CDO	144	120	13	59	182	333
CO4314-401	RAC417-5/RAC549	178	120	298	293	337	231
CO4314-402	RAC417-5/RAC549	144	120	169	8	34	323
CO4315-401	CO1213-205;76ECN36/70ECN44;DRP(...);;/RAC549	156	123	110	97	96	163
CO4323-401	7923;3AG14/5CDO;82ECN-175;//;RAVEN/(LNC/ISR493//RAC177SR26);	267	123	218	287	42	106
CO4323-402	7923;3AG14/5CDO;82ECN-175;//;RAVEN/(LNC/ISR493//RAC177SR26);	83	120	276	347	282	336
CO4323-403	7923;3AG14/5CDO;82ECN-175;//;RAVEN/(LNC/ISR493//RAC177SR26);	172	123	141	50	325	193
CO4327-401	KAYTIL/SCHOMBURGK	89	120	322	181	117	307
CO4330-401	AUS17886;AIFENO#3;/;RAVEN/(LNC/ISR493//RAC177+SR26);CO1657-4	239	116	99	168	54	86
CO4330-402	AUS17886;AIFENO#3;/;RAVEN/(LNC/ISR493//RAC177+SR26);CO1657-4	200	117	89	117	83	274
CO4337-401	F84.6296;AUS77GG'S';/;F84.4667;AUS21544	222	121	214	282	38	60
CO4337-402	F84.6296;AUS77GG'S';/;F84.4667;AUS21544	200	126	270	279	63	272
CO4337-403	F84.6296;AUS77GG'S';/;F84.4667;AUS21544	200	111	143	165	58	38
CO4338-401	SUN88E;86DPN073;/;CO1452-208;MED17/MOROCCO//RAC117/RAC177	194	119	95	77	259	330
CO4338-402	SUN88E;86DPN073;/;CO1452-208;MED17/MOROCCO//RAC117/RAC177	128	114	118	271	329	327
CO4338-403	SUN88E;86DPN073;/;CO1452-208;MED17/MOROCCO//RAC117/RAC177	139	118	36	91	202	331

Cross No.	Pedigree	Density	Anth.	Raw Data		TwoD Adjusted	
				LI	Yield	LI	Yield
		m^{-2}	DAS	%	g/m²	%	g/m²
CO4338-404	SUN88E;86DPN073;/;CO1452-208;MED17/MOROCCO//RAC117/RAC177	167	114	319	260	161	275
CO4338-405	SUN88E;86DPN073;/;CO1452-208;MED17/MOROCCO//RAC117/RAC177	156	120	209	232	52	82
CO4338-406	SUN88E;86DPN073;/;CO1452-208;MED17/MOROCCO//RAC117/RAC177	139	112	92	47	70	169
CO4338-407	SUN88E;86DPN073;/;CO1452-208;MED17/MOROCCO//RAC117/RAC177	122	119	296	309	139	292
CO4338-408	SUN88E;86DPN073;/;CO1452-208;MED17/MOROCCO//RAC117/RAC177	183	119	50	5	150	253
CO4341-401	RAC583/RAC580	106	131	233	89	71	34
CO4344-401	CO1288-403;75IRN560/76ECN022;/RAC569	217	114	318	298	94	149
CO4344-402	CO1288-403;75IRN560/76ECN022;/RAC569	256	119	177	138	33	139
CO4344-403	CO1288-403;75IRN560/76ECN022;/RAC569	206	114	266	264	46	98
CO4346-401	CO1871-402;PELA506/MDN//(WW15/M1238-2/K);/HARTOG	139	116	236	266	64	278
CO4346-402	CO1871-402;PELA506/MDN//(WW15/M1238-2/K);/HARTOG	111	122	72	326	197	187
CO4346-403	CO1871-402;PELA506/MDN//(WW15/M1238-2/K);/HARTOG	144	119	137	252	49	157
CO4351-401	21-49*85/RAC594	183	122	47	31	142	171
CO4352-401	131R;3AG14/4*CDO//LNC/3/6*RAC177;/;CO1452-208;MED17/MCO//RAC	194	117	74	207	80	256
CO4352-402	131R;3AG14/4*CDO//LNC/3/6*RAC177;/;CO1452-208;MED17/MCO//RAC	183	121	158	172	167	158
CO4360-401	TIMMO/3/MAYA74/GUTHA//RAC430-9/4/SCHOMBURGK	200	118	288	255	234	255
CO4360-402	TIMMO/3/MAYA74/GUTHA//RAC430-9/4/SCHOMBURGK	200	117	193	258	189	178
CO4360-403	TIMMO/3/MAYA74/GUTHA//RAC430-9/4/SCHOMBURGK	172	116	234	314	212	223
CO4362-401	TIMMO/WARIGAL//SCHOMBURGK	133	114	211	202	205	128
CO4364-401	4-11;79INT1037;/;CHINA-2;AUS110;//SR26/6*177/3/ZENB/RAC117/4	139	115	260	341	199	306
CO4364-402	4-11;79INT1037;/;CHINA-2;AUS110;//SR26/6*177/3/ZENB/RAC117/4	150	114	258	175	217	14
CO4364-403	4-11;79INT1037;/;CHINA-2;AUS110;//SR26/6*177/3/ZENB/RAC117/4	150	121	148	162	173	344
CO4372-401	RAC416-1/CDO	244	118	265	327	312	282
CO4372-402	RAC416-1/CDO	128	117	75	185	32	92
CO4372-403	RAC416-1/CDO	200	114	172	249	2	1
CO4372-404	RAC416-1/CDO	228	115	279	322	236	161
CO4372-405	RAC416-1/CDO	144	116	294	337	344	248
CO4372-406	RAC416-1/CDO	111	116	88	74	342	62
CO4372-407	RAC416-1/CDO	183	116	222	122	249	122
CO4372-408	RAC416-1/CDO	206	120	173	148	330	72
CO4372-409	RAC416-1/CDO	139	114	144	78	157	120
CO4372-410	RAC416-1/CDO	144	114	257	156	341	246
CO4372-411	RAC416-1/CDO	89	111	154	178	169	166
CO4372-412	RAC416-1/CDO	194	114	77	197	11	78
CO4372-413	RAC416-1/CDO	139	115	153	35	302	162
CO4372-414	RAC416-1/CDO	94	116	179	104	322	267
CO4372-415	RAC416-1/CDO	206	120	56	234	213	143
CO4372-416	RAC416-1/CDO	144	121	247	106	127	71
CO4372-417	RAC416-1/CDO	161	118	133	143	323	97
CO4372-418	RAC416-1/CDO	156	121	23	94	82	61
CO4372-419	RAC416-1/CDO	117	121	273	346	336	52
CO4372-420	RAC416-1/CDO	122	114	256	216	286	225
CO4372-421	RAC416-1/CDO	139	120	341	288	295	67
CO4372-422	RAC416-1/CDO	117	120	213	186	111	43
CO4372-423	RAC416-1/CDO	139	120	228	75	300	108
CO4372-424	RAC416-1/CDO	150	119	286	239	16	40
CO4372-425	RAC416-1/CDO	122	114	111	95	181	73
CO4372-426	RAC416-1/CDO	167	120	264	81	284	342
CO4372-427	RAC416-1/CDO	128	120	33	256	200	83
CO4372-428	RAC416-1/CDO	150	115	127	105	66	238
CO4372-429	RAC416-1/CDO	139	121	186	267	47	303
CO4372-430	RAC416-1/CDO	156	115	20	195	67	196
CO4372-431	RAC416-1/CDO	233	115	107	144	62	11
CO4372-432	RAC416-1/CDO	206	119	78	12	48	176

Cross No.	Pedigree	Density	Anth.	Raw Data		TwoD Adjusted	
				LI	Yield	LI	Yield
		m^{-2}	DAS	%	g/m^2	%	g/m^2
CO4372-433	RAC416-1/CDO	206	114	205	6	346	322
CO4372-434	RAC416-1/CDO	228	116	329	201	301	332
CO4372-435	RAC416-1/CDO	189	105	139	134	262	155
CO4372-436	RAC416-1/CDO	117	114	1	140	147	134
CO4372-437	RAC416-1/CDO	161	115	278	46	288	39
CO4372-438	RAC416-1/CDO	250	117	126	304	180	8
CO4372-439	RAC416-1/CDO	222	116	64	66	274	211
CO4372-440	RAC416-1/CDO	144	115	316	331	222	219
CO4372-441	RAC416-1/CDO	111	116	54	101	98	215
CO4372-442	RAC416-1/CDO	222	116	162	87	68	100
CO4372-443	RAC416-1/CDO	133	114	44	88	214	235
CO4372-444	RAC416-1/CDO	172	123	26	149	155	224
CO4372-445	RAC416-1/CDO	183	118	306	21	345	341
CO4372-446	RAC416-1/CDO	172	125	165	112	232	55
CO4372-447	RAC416-1/CDO	117	115	79	69	178	170
CO4382-401	RAC592/3/CO1982-405;((WExCNO-NO66/ZBZ)JAR'S')//RAC98/ARGIX	100	114	226	225	57	28
CO4382-402	RAC592/3/CO1982-405;((WExCNO-NO66/ZBZ)JAR'S')//RAC98/ARGIX	122	115	66	86	5	21
CO4382-403	RAC592/3/CO1982-405;((WExCNO-NO66/ZBZ)JAR'S')//RAC98/ARGIX	94	118	125	133	28	64
CO4382-404	RAC592/3/CO1982-405;((WExCNO-NO66/ZBZ)JAR'S')//RAC98/ARGIX	100	120	69	71	174	111
CO4382-405	RAC592/3/CO1982-405;((WExCNO-NO66/ZBZ)JAR'S')//RAC98/ARGIX	150	115	48	203	101	91
CO4382-406	RAC592/3/CO1982-405;((WExCNO-NO66/ZBZ)JAR'S')//RAC98/ARGIX	183	115	274	344	13	6
CO4382-407	RAC592/3/CO1982-405;((WExCNO-NO66/ZBZ)JAR'S')//RAC98/ARGIX	144	118	128	147	24	35
CO4389-401	RAC655/29361;Sr21/4*LNC//4*BYO;	128	116	142	28	133	339
CO4389-402	RAC655/29361;Sr21/4*LNC//4*BYO;	133	122	243	318	85	318
CO4389-403	RAC655/29361;Sr21/4*LNC//4*BYO;	183	131	168	290	210	17
CO4389-404	RAC655/29361;Sr21/4*LNC//4*BYO;	206	115	60	20	110	30
CO4389-405	RAC655/29361;Sr21/4*LNC//4*BYO;	189	121	68	285	289	48
CO4389-406	RAC655/29361;Sr21/4*LNC//4*BYO;	167	120	314	315	103	146
CO4389-407	RAC655/29361;Sr21/4*LNC//4*BYO;	133	113	262	345	261	321
CO4389-408	RAC655/29361;Sr21/4*LNC//4*BYO;	139	114	189	189	29	15
CO4389-409	RAC655/29361;Sr21/4*LNC//4*BYO;	161	115	283	321	235	153
CO4389-410	RAC655/29361;Sr21/4*LNC//4*BYO;	122	120	310	254	244	164
CO4389-411	RAC655/29361;Sr21/4*LNC//4*BYO;	250	120	299	192	247	45
CO4389-412	RAC655/29361;Sr21/4*LNC//4*BYO;	167	117	31	54	268	194
CO4389-413	RAC655/29361;Sr21/4*LNC//4*BYO;	144	118	280	302	270	226
CO4389-414	RAC655/29361;Sr21/4*LNC//4*BYO;	139	114	16	36	204	5
CO4389-415	RAC655/29361;Sr21/4*LNC//4*BYO;	117	113	4	4	227	243
CO4389-416	RAC655/29361;Sr21/4*LNC//4*BYO;	156	115	115	242	255	46
CO4389-417	RAC655/29361;Sr21/4*LNC//4*BYO;	100	114	132	98	229	65
CO4389-418	RAC655/29361;Sr21/4*LNC//4*BYO;	128	121	267	276	115	56
CO4389-419	RAC655/29361;Sr21/4*LNC//4*BYO;	156	119	59	220	196	26
CO4389-420	RAC655/29361;Sr21/4*LNC//4*BYO;	211	122	231	259	242	247
CO4389-421	RAC655/29361;Sr21/4*LNC//4*BYO;	167	120	116	217	105	19
CO4389-422	RAC655/29361;Sr21/4*LNC//4*BYO;	133	120	176	300	144	23
CO4389-423	RAC655/29361;Sr21/4*LNC//4*BYO;	100	122	21	38	281	96
CO4389-424	RAC655/29361;Sr21/4*LNC//4*BYO;	106	115	42	41	326	191
CO4389-425	RAC655/29361;Sr21/4*LNC//4*BYO;	111	120	84	205	26	7
CO4389-426	RAC655/29361;Sr21/4*LNC//4*BYO;	144	133	327	297	297	101
CO4389-427	RAC655/29361;Sr21/4*LNC//4*BYO;	67	120	340	313	128	203
CO4389-428	RAC655/29361;Sr21/4*LNC//4*BYO;	117	116	105	295	40	295
CO4389-429	RAC655/29361;Sr21/4*LNC//4*BYO;	106	115	308	159	53	227
CO4389-430	RAC655/29361;Sr21/4*LNC//4*BYO;	133	115	204	303	239	126
CO4389-431	RAC655/29361;Sr21/4*LNC//4*BYO;	117	114	27	24	143	68
CO4389-432	RAC655/29361;Sr21/4*LNC//4*BYO;	83	116	67	233	145	2

Cross No.	Pedigree	Density	Anth.	Raw Data		TwoD Adjusted	
				LI	Yield	LI	Yield
		m^{-2}	DAS	%	g/m²	%	g/m²
CO4403-402	BLADE/4ATSN044	139	114	301	214	258	259
CO4403-403	BLADE/4ATSN044	122	118	108	72	331	309
CO4404-401	ROSELLA/CO2952-6	117	123	55	308	3	343
CO4404-402	ROSELLA/CO2952-6	217	119	302	230	107	202
CO4407-401	MEC3/CO2477-451	200	111	325	63	250	206
CO4408-401	MEC3/KITE	183	109	73	296	307	317
CO4408-402	MEC3/KITE	111	110	155	62	335	135
CO4410-401	RAC639/19IBWSN077	150	117	109	145	241	208
CO4410-402	RAC639/19IBWSN077	222	114	6	18	59	326
CO4410-403	RAC639/19IBWSN077	206	119	94	238	50	222
CO4410-404	RAC639/19IBWSN077	167	119	136	310	23	293
CO4410-405	RAC639/19IBWSN077	178	111	259	45	304	205
CO4410-406	RAC639/19IBWSN077	139	121	323	330	253	197
CO4410-407	RAC639/19IBWSN077	139	115	43	269	126	117
CO4410-408	RAC639/19IBWSN077	128	110	348	157	160	59
CO4410-409	RAC639/19IBWSN077	272	114	122	160	60	141
CO4410-410	RAC639/19IBWSN077	183	114	277	270	74	270
CO4410-411	RAC639/19IBWSN077	111	116	63	118	138	297
CO4410-412	RAC639/19IBWSN077	150	115	71	79	1	340
CO4410-413	RAC639/19IBWSN077	189	115	345	244	41	213
CO4410-414	RAC639/19IBWSN077	122	118	282	335	22	10
CO4410-415	RAC639/19IBWSN077	150	118	29	116	154	313
CO4410-416	RAC639/19IBWSN077	89	117	131	184	109	290
CO4410-417	RAC639/19IBWSN077	200	119	248	278	333	284
CO4410-418	RAC639/19IBWSN077	144	131	166	127	44	257
CO4410-419	RAC639/19IBWSN077	122	115	19	142	215	294
CO4410-420	RAC639/19IBWSN077	144	118	40	113	140	198
CO4410-421	RAC639/19IBWSN077	106	118	331	180	17	93
CO4418-401	CIII/4*RAC41656862//C3/4*RAC416:DT56874	228	115	104	190	254	85
CO4418-402	CIII/4*RAC41656862//C3/4*RAC416:DT56874	161	117	80	126	99	103
CO4418-404	CIII/4*RAC41656862//C3/4*RAC416:DT56874	144	119	220	123	135	4
CO4418-405	CIII/4*RAC41656862//C3/4*RAC416:DT56874	139	120	130	92	252	41