



Australian
National
University

Stabilising the flowering time of wheat in response to autumn rainfall decline in southern Australia

A thesis submitted for the degree of

Doctor of Philosophy

of

The Australian National University

by

Bonnie Maree Flohr

March 2018

© Copyright by Bonnie Maree Flohr 2018

All Rights Reserved

Statement of authorship

All work presented in this thesis is my own, unless otherwise stated. Cooperative work and specific contributions by others are referred to at the beginning of each chapter and in the acknowledgements. The material presented in this thesis does not contain work used for the award of any other degree or diploma.



Bonnie Maree Flohr

Acknowledgements

The research presented in this thesis is funded by the Grains Research and Development Corporation (GRDC) through the Grains Research Scholarship (GRS10934) and the Early Sowing Project (CSP00178), and The Australian National University (ANU). Thank you for providing me with the opportunity to undertake this study. I am also thankful to The Commonwealth Scientific and Industrial Research Organisation (CSIRO) for hosting me, and providing an insightful experience, which has greatly assisted to increase my networks in the industry.

I would like to acknowledge the following for providing material and technical assistance for data used in this thesis; BCG and Yield Prophet[®] for access to sowing time data, AGT for providing pre-release seed of Longsword, Living Farm and WANTFA for hosting and management of the Cunderdin field site, Leigh Davis of SARDI for management of the Minnipa field site, Kelly Angel of BCG for management of the Berriwillock site and Ben Trevaskis for access to near-isogenic lines. I thank Farmlink staff for accommodating the Temora research experiments in 2015 and 2016, and for being as helpful as possible.

From the Crop Adaptation building I am extremely grateful to the hard working research team; Tony Swan, Brad Rheinheimer, Laura Goward and Mel Bullock. Not only did they provide excellent technical assistance and advice, but also laughs and interesting conversation which made many laborious days of field work more enjoyable. I would also like to acknowledge assistance provided by Alec Zwart (experimental design and statistical analysis) and Julianne Lilley (APSIM assistance). I also thank all other associates in the building who have shown interest in my studies, given encouragement, and assisted along the way, particularly Tony Fischer for commenting on draft chapters.

I thank my sisters Jo, Lou and Gabi and their little people for providing me with lighter moments. I especially thank Lou for reading, listening and being interested in my research during the writing up period. I also thank my friends for providing distractions, particularly Jack Koci for his phone calls to debrief each of our latest PhD related drama. I thank Barb Pocock for her encouragement and reviewing some sections.

I am grateful to my three supervisors, Dr. James Hunt, Dr. John Kirkegaard and Professor John Evans for their approachability throughout the PhD.

James, I cannot express enough my sincere gratitude for the continuous patience, encouragement and guidance of my Ph.D study. Thank you for working side-by-side with me in the field and introducing me to the world of research agronomy. It has been a privilege, and I could not have asked for a better advisor and mentor. John K, thank you for sharing your vast knowledge and advice throughout the process, and in general being a wonderful research role model. John E, thank you for the constructive comments and discussions, and for guiding me through the university system.

I am grateful to my parents, Janet and Gary Flohr, who have supported me in every aspect in life up to this point. I am especially grateful for your hard work and sacrifice to give my sisters and I an education, and a childhood in the Mallee where I learnt to appreciate the agricultural industry. I am grateful to Dad for the many crop inspections, for taking me with him to industry events since I was a teenager, and instilling the work ethic and resilience that prepared me to complete this thesis.

I reserve my greatest heartfelt thanks for Paul, who has been patient with me during the tougher moments, helped me with processing samples on weekends and public holidays, and provided a general calm influence which I really appreciated during these times. Undoubtedly your unwavering support and reassurances helped me to the finish line.

Abstract

Wheat (*Triticum aestivum*) production is important to global food security and the livelihoods of those who cultivate it. Increases in water-limited potential yield (PY_w) and farm yield (FY) are necessary to keep pace with global demand, and in order for Australian growers to remain competitive in a changing climate and with declining terms of trade. In drought prone environments such as south-eastern Australia, alignment of the key developmental stage of flowering to the period that is optimal for the local climate is a critical determinant of yield. The optimal flowering period (OFP) begins when the risk of frost decreases, and ends to avoid increasing temperature, heat and water stress during grain fill. Flowering time is a function of the interaction between the speed of plant development (genetic, G), establishment date (management, M) and prevailing seasonal conditions (environment, E). Autumn rainfall decline, extreme spring weather and increasing farm size challenge traditional G x M combinations which are currently used to achieve the OFP in south-eastern Australia i.e. predominately fast developing spring wheats sown in late-April to early May.

The objective of this study was to identify novel G x M combinations that stabilise flowering and maximise yield under changing rainfall patterns and recent changes to farming systems. This study used crop simulation and conducted field experiments in Temora, New South Wales (NSW); Berriwillock, Victoria; Minnipa, South Australia and Cunderdin, Western Australia. Firstly, OFPs were quantified in south-eastern Australia, the area most affected by autumn rainfall decline to align novel G x M strategies accordingly. Simulation demonstrated that the predicted timing and duration of OFPs varied with site and season. The relative importance of seasonal water supply and demand and extremes of temperature in defining the window also varied.

To identify the physiological changes associated with breeding, the PY_w and other parameters were quantified and compared at common sowing or flowering dates with a historic set of NSW cultivars released between 1901 and 2014. Genetic improvement through this period, increased grain yield at a rate of $26 \text{ kg ha}^{-1} \text{ pa}^{-1}$ regardless of sowing or flowering dates. The slow development and stable flowering observed in historic cultivars and superior partitioning to grain of modern cultivars were independent, and could potentially be combined in new cultivars to achieve future yield gains. Yield results for a novel fast-winter genotype (FW, with photoperiod insensitivity

and requiring vernalisation) grown in a diverse set of environments, supported this hypothesis. The FW development pattern extended sowing windows while achieving 10-20% higher yields than current spring cultivars. The flowering stability index (1 minus the ratio of range in thermal time for flowering for each cultivar, to the range in thermal time of sowing dates) of the FW genotype was improved for the sowing dates currently used by farmers.

Finally, novel agronomic packages to capture the higher yield potential of FW cultivars was investigated using simulation. Reliance on irregular rainfall to establish FW wheat could be reduced, and early establishment opportunities increased by sowing genotypes with long coleoptiles into stored sub-soil moisture accumulated during fallow.

Combining the G x M flowering date stabilising factors; winter wheat, long coleoptile, early sowing and fallow reduced the reliance on autumn rainfall for timely crop establishment to provide a further buffer against seasonal climate variability.

Consequently, simulated whole farm yield was increased as a greater area of wheat flowered during the optimal period.

To achieve the productivity increases demonstrated here requires continued collaboration between agronomists and breeders. This includes the development of winter wheat cultivars with long coleoptiles that are adapted to different growing season lengths and OFPs, such that crops can be established earlier and emerge from a greater depth than current cultivars.

‘No race can prosper ‘till it learns
that there is as much dignity in
tilling a field as in writing a
poem’

- *Booker T. Washington*

‘Life is a grindstone, it either
grinds you down or polishes you
up, depending on what you are
made of’

- *A favorite quote of my
Grandmother’s, Marie Pocock*

Table of contents

Statement of authorship	I
Acknowledgements.....	III
Abstract.....	VII
Table of contents	XI
List of abbreviations	XVII
List of tables and figures	XIX
Chapter 1	29
General introduction.....	29
1.1 The significance of flowering date stability in the Australian wheat belt	31
1.2 Options to stabilise flowering time and increase PYw and FY of wheat	37
1.2.1 Vernalisation sensitivity.....	37
1.2.2 Fallow.....	41
1.2.3 Long coleoptile.....	42
1.3 Formulation of research questions.....	42
Chapter 2	49
Water and temperature stress define the optimal flowering period for wheat in south-eastern Australia	49
Abstract.....	51
1. Introduction.....	52
2. Materials and Methods	54
2.1 Site selection and crop simulation approach.....	54
2.2 Crop management set up.....	57
3. Results.....	60
3.1 Defining optimal flowering periods	60
3.2 Relative importance of temperature extremes (frost and heat) and water stress in determining OFP	66

3.3 Implications for sowing time and genotype	68
3.4 Evidence of climate change	69
4. Discussion.....	72
4.1 Variation in optimal flowering periods	72
4.2 Relative importance of temperature extremes (frost and heat) and water stress in determining OFP	74
4.3 Implications for sowing time and genotype.....	74
4.4 Climate change impacts on flowering and sowing dates	76
5. Conclusion	77
6. Supplementary material	78
Chapter 3	85
Genetic yield gain in southern New South Wales wheat cultivars released between 1901-2014 as revealed from synchronous flowering during the optimum period	85
Abstract.....	87
1. Introduction.....	88
2. Materials and methods.....	90
2.1 Site, treatments and agronomy.....	90
2.2 Flowering date- and sowing date-balanced data sets	91
2.3 Measurements and calculations	92
2.4 Data analysis	94
3. Results	95
3.1 Growing conditions and flowering dates	95
3.2 Yield and flowering date stability	98
3.3 Chronological changes in yield physiology.....	99
3.4 Chronological changes in DM and partitioning.....	101
3.5 Chronological changes in development	105
4. Discussion.....	107
4.1 Rate of yield gain	107

4.2 Foundations of yield gain.....	108
4.3 Change in phenology.....	110
4.4 Future yield gain	112
5. Conclusion	114
6. Supplementary material	115
Chapter 4	127
Fast winter wheat phenology can stabilise flowering date and maximise grain yield in semi-arid Mediterranean and temperate environments	127
Abstract.....	129
1. Introduction.....	130
2. Materials and methods	133
2.1 Analysis of wheat sowing time using the Yield Prophet® database	133
2.2 Field experiments	133
2.3 Cultivar selection	138
2.4 Statistical analyses	139
3. Results.....	140
3.1 Analysis of sowing time data from Yield Prophet® database	140
3.2 Seasonal conditions.....	142
3.3 Field experiments comparing cultivar response (excluding NILs) to time of sowing	144
3.3 Effect of sowing date in near isogenic lines.....	149
3.4 Development	151
4. Discussion.....	155
4.1 Sowing date analysis	155
4.2 FW genotype vs. commonly grown genotypes	155
4.3 Suitability of FW genotypes to Mediterranean environments	158
4.4 Suitability of FW genotypes to temperate environments.....	159
4.5 Implications for agronomy and genotype by management interactions	160

5. Conclusion	161
Chapter 5	163
Genotype x management strategies to stabilise the flowering time of wheat in the south-eastern Australian wheat belt	163
Abstract.....	165
1. Introduction.....	166
2. Method.....	169
2.1 General simulation setup.....	169
2.2 Soil water	171
2.3 Genotypes.....	171
2.4 Strategy details.....	172
2.5 Analysis.....	175
3. Results	176
3.1 Productivity increases from G x M strategies	176
3.2 Yield variability	179
3.3 Flowering date.....	181
4. Discussion.....	184
4.1 WW-LC for flowering date stability.....	184
4.2 Optimal phenology and rotation in the LRZ.....	186
4.3 Optimal phenology and rotation in the M and HRZ	189
5. Conclusions	190
6. Supplementary material.....	191
Chapter 6	195
Overview of the thesis.....	195
Contribution of the thesis.....	197
6.1 Water and temperature stress define optimal flowering periods.....	198
6.2.1 Development duration and partitioning are de-coupled.....	199

6.2.2	PYw gain of NSW cultivars released between 1901 and 2014 is 26 kg/ha p.a. (or 0.4% p.a.).....	201
6.3	Early sowing combined with fast-winter genotype stabilises flowering time and yield in diverse environments.....	203
6.4	Long coleoptile winter wheat and fallow rotation reduces reliability on autumn rainfall	205
6.5	Recommendations	206
6.6	Concluding remarks	207
	References	213
	Appendix	225
1.	Experiment layout	225
2.	Dissemination of thesis results to the industry.....	227

List of abbreviations

APSIM	Agricultural Production Simulator
DM	Dry matter
DR	Double ridge
EY	Economic yield
FD	Flowering date
FS	Fast-spring
FSLC	Fast-spring long coleoptile
FW	Fast-winter
FY	Farm yield
G x M	Genotype x management
HI	Harvest index
HRZ	High rainfall zone
LRZ	Low rainfall zone
MRZ	Medium rainfall zone
MS	Mid-spring
MW	Mid-winter
NIL	Near Isogenic Lines
NSW	New South Wales
OFP	Optimal flowering period
PAR	Photosynthetically active radiation
PAWC	Plant available water content
PNW	Pacific North West
PY	Potential yield
PY _w	Water-limited potential yield
RUE	Radiation use efficiency
SA	South Australia
SD	Sowing date
SEA	South eastern Australia
TOS	Time of sowing
TS	Terminal spikelet
TT	Thermal time
VD	Vernal days

Vic	Victoria
VSS	Very slow spring
WA	Western Australia
WUE	Water use efficiency
WW	Winter wheat
WWLC	Winter wheat long coleoptile

List of tables and figures

Chapter 1

Figure 1: National wheat statistics for south-eastern Australia (southern NSW, Vic, SA) (ABARES 2017). Solid line is value for each year, dotted line is 10 year rolling mean.

..... 33

Table 1: extracted from Hunt (2017), showing the five major development genes of wheat, and alleles carried by different cultivars as per Eagles *et al.* (2010); Cane *et al.* (2013); Harris *et al.* (2017b) and their resultant development speed (slow, mid and fast) and pattern (winter, spring). Different vernalisation alleles are denoted by letters where *w*=highly vernalisation sensitive, *v*=vernalisation sensitive, *b*= vernalisation insensitivity, *a* =vernalisation insensitive. Different photoperiod alleles are *a*=insensitive, *b*, *c* and *d*=sensitive, with level of sensitivity depending on which genome they are on and which other *Ppd* and *Vrn* alleles are present..... 39

Table 2: Research questions pursued in the thesis, the status of publication and contribution statements for each chapter..... 43

Chapter 2

Figure 1: Dry-land cereal-cropping areas in Australia (shaded) and the locations used for this study..... 55

Table 1: The 28 locations, where (a) and (b) refer to different soil types at the same location used in the study, and corresponding long-term mean annual rainfall, patch point dataset (PPD) station number, APSoil file number used in the simulation study.. 56

Table 2: Temperature criteria for frost and heat stress during sensitive Zadoks growth stages and corresponding estimated yield reduction, from Bell *et al.* (2015). Yield reduction was calculated for each day and multiplied, so that increasing numbers of stress events results in cumulative reduction in yield. 59

Table 3: Optimal flowering periods (OFPs), peak mean of frost and heat limited yield (kg ha^{-1}) and corresponding flowering date and sowing date range for a mid-fast cultivar over 51-years (1963-2013), for the 28 locations where (a) and (b) refer to different soil types at the same location, ranked in alphabetical order..... 61

Figure 2: The relationship between optimal flowering period (shaded grey) of a mid-fast cultivar of wheat (Table 3), and mean annual rainfall (mm) (line) (Table 2) for 28 locations, where (a) and (b) refer to different soil types at the same location. 62

Figure 3: The relationship between frost and heat limited (FHL) yield (kg ha^{-1}) and flowering date for a mid-fast cultivar of wheat at A) Lameroo, SA and B) Temora, NSW split into percentiles. Lines represent the simulated 10th, 20th, 30th, 40th, 50th, 60th, 70th, 80th and 90th percentiles of yield and corresponding flowering date values generated from 16 sowing dates over 51-years (1963-2013). Darkened line is the optimum flowering period for the 10th and 90th percentiles defined by $\geq 95\%$ of the maximum mean yield. 63

Figure 4: The optimal flowering period (OFP) for a mid-fast cultivar of wheat determined by APSIM simulation for A) Waikerie, SA B) Minnipa, SA C) Yarrawonga, VIC D) Inverleigh, VIC E) Urana, NSW F) Dubbo, NSW. Black lines represent the frost and heat limited (FHL) 15-day running mean yield (kg ha^{-1}). Grey lines represent the standard deviation of the FHL mean yield (kg ha^{-1}). Grey columns are the estimated OFP defined as $\geq 95\%$ of the maximum mean yield from 51 seasons (1963-2013). All locations shown as in Figure 4 are located in Supplementary Figure 1..... 65

Figure 5: Potential yield (kg ha^{-1}) (— — broken grey line), frost and heat limited yield (kg ha^{-1}) (solid grey line) and the mean heat (●●● dotted black line), frost (solid black line) and mean water stress from floral initiation to maturity (●●● dotted grey line) indices (0 to 1) applied to yield plotted against flowering date for a mid-fast cultivar of wheat. A) Waikerie, SA B) Temora, NSW C) Longerenong, Vic. Grey columns are the estimated optimal flowering period defined as $\geq 95\%$ of the maximum mean yield in 51 seasons (1963-2013). 67

Figure 6: The 15-day running mean yield (kg ha^{-1}) and flowering date of different wheat development types at A) Temora, NSW and B) Lameroo, SA over a 51-year simulation (1963-2013). Mean yields are for a mid-fast developing spring wheat (solid line), a very slow developing spring wheat (dotted line), and winter wheat (broken line). Grey columns are the estimated optimal flowering period defined as $\geq 95\%$ of the maximum mean yield of a mid-fast cultivar. 68

Table 4: Simulated flowering date corresponding to peak mean frost and heat limited yield (kg ha^{-1}) and sowing date for cultivars of different development type at Temora, NSW and Lameroo, SA. 69

Figure 7: Estimated optimal flowering period (OFP) for mid-fast cultivar of wheat at A) Lameroo, SA and B) Longerenong, Vic C) Charlton, Vic for 35 years (1963-1997) (light grey column) and 16 years (dark grey column) (1998-2013). Mean frost and heat limited yield (kg ha^{-1}) for 1963-1997 (broken line) and for 1998-2013 (solid line). Estimated OFP is defined by $\geq 95\%$ of the maximum mean yield. 70

Figure 8: Growing season rainfall (columns) and average minimum and maximum temperature for September (solid lines) at Lameroo, SA. Broken lines are 10-year rolling means for rainfall and for minimum and maximum temperatures. 71

Figure S1: Optimal flowering period of wheat for 22 locations simulated and not displayed in Figure 4. The optimal flowering period for a mid-fast cultivar of wheat determined by APSIM simulation for 1) Lock, SA 2) Cleve, SA 3) Cummins, SA 4) Hart, SA 5) Maitland, SA 6) Saddleworth, SA 7) Bordertown, SA 8) Lameroo, SA 9) Walpeup Vic 10) Hopetoun a, Vic 11) Hopetoun b, Vic 12) Swan Hill a, Vic 13) Swan Hill b, Vic 14) Charlton, Vic 15) Longernong, Vic 16) Kerang, Vic 17) Mathoura, NSW 18) Temora, NSW 19) Cootamundra, NSW 20) Bogan Gate a, NSW 21) Bogan Gate b, NSW 22) Merriwagga, NSW 23) Condobolin, NSW 24) Trangie, NSW 25) Nyngan, NSW. Black lines represent the frost and heat limited (FHL) 15-day running mean yield (kg ha⁻¹). Grey lines represent the standard deviation of the FHL mean yield (kg ha⁻¹). Grey columns are the estimated OFP defined as $\geq 95\%$ of the maximum mean yield from 51 seasons (1963-2013). 51

Chapter 3

Table 1: Sowing dates of the field experiments at Temora in 2015 and 2016. 91

Table 2: The time of sowing that generated near-simultaneous flowering dates (flowering date-balanced data) within the optimal flowering window for cultivars grown in 2015 and 2016. Grey shading indicates that cultivar was not grown in 2016. 92

Figure 1: Cumulative thermal time (°C days) for Temora, NSW. Black line 2016, broken black line 2015, grey line average of years 2005-2016. 96

Table 3. Flowering dates (Z65) of flowering date (FD)- and sowing date (SD)-balanced data sets in 2015 and 2016 growing seasons in Temora, NSW. Grey shading indicates that cultivar was not grown in 2016. FD balanced data correspond to the sowing date from Table 2, while SD balanced data correspond to time of sowing 3. 96

Figure 2: Mean grain yield plotted against flowering date for a historic set of wheat cultivars sown at four time of sowing in Temora, NSW in 2015 (■) and 2016 (●). Sowing date details are shown in Table 1. Each marker represents a different time of sowing and sowing date moves later from left to right. Cultivars are presented in order of release. Grey columns are the optimal flowering period as per Flohr *et al.* (2017b). The 5% LSD value is 0.7 t/ha and the P-Value of year x TOS x cultivar interaction is <0.001. 98

Figure 3: Chronological deviation changes in yield and yield components in 2015 (■, □) and 2016 (●, ○) in New South Wales wheat cultivars released between 1901 and 2014. Solid symbols (●, ■) are for cultivars that flower simultaneously, and hollow symbols (○, □) for cultivars sown on the same date. Deviation is the difference between the trait value for a given cultivar and the mean of each season for that trait. Bold text corresponds to flowering date balanced data, and un-bold text corresponds to sowing date balanced data. P-values and R² are related to the regression fitted to data. Symbols (■, ●) are cultivar Longsword, which has not been included in the regressions or means shown. 100

Figure 4: Chronological deviation changes in DM production and radiation interception in 2015 (■, □) and 2016 (●, ○) in New South Wales wheat cultivars released between 1901 and 2014. Solid symbols (●, ■) are for cultivars that flower simultaneously, and hollow symbols (○, □) for cultivars sown on the same date. Deviation is the difference between the trait value for a given cultivar and the mean of each season for that trait. Bold text corresponds to flowering date balanced data, and un-bold text corresponds to sowing date balanced data. P-values and R² are related to the regression fitted to data. Symbols (■, ●) are cultivar Longsword, which has not been included in the regressions or means shown..... 103

Figure 5: Chronological deviation changes in harvest index, plant height and stem weight at Z70 in 2015 (■, □) and 2016 (●, ○) in New South Wales wheat cultivars released between 1901 and 2014. Solid symbols (●, ■) are for cultivars that flower simultaneously, and hollow symbols (○, □) for cultivars sown on the same date. Deviation is the difference between the trait value for a given cultivar and the mean of each season for that trait. Bold text corresponds to flowering date balanced data, and un-bold text corresponds to sowing date balanced data. P-values and R² are related to the regression fitted to data. Symbols (■, ●) are Longsword, which has not been included in the regressions or means shown..... 104

Figure 6: Chronological deviation changes in development for cultivars used in the experiment in 2015 (■, □) and 2016 (●, ○) in New South Wales wheat cultivars released between 1901 and 2014. Solid symbols (●, ■) are for cultivars that flower simultaneously, and hollow symbols (○, □) for cultivars sown on the same date. Deviation is the difference between the trait value for a given cultivar and the mean of each season for that trait. Bold text and broken line correspond to flowering date (FD)-balanced regression, and un-bold text corresponds to sowing date (SD)-balanced regression. If the analysis did not find the FD- and SD- balanced regressions

significantly different, a common solid line was fitted to both sets of data. P-values and R^2 are related to the regression fitted to SD- or FD-balanced data, whereas 2015 and 2016 numbers are the mean value for each experimental season. Symbols (■, ●) are Longsword, which has not been included in the regressions or means shown. 106

Table S1. Comparison of functions (linear vs. logistic) fitted to variable vs. year of release plots in Figures 3-6, and plots of locally weighted linear regressions (LOESS). Akaike Information Criterion (AIC) and Schwarz Bayes Information Criterion (BIC) describe the goodness of fit of a function corrected for the number of parameters each function contains, where lower values suggest a better fit..... 115

Figure S1. Chronological deviation changes in dry matter production between sowing and maturity (Z89) in 2015 (■, □) and 2016 (●, ○) in New South Wales wheat cultivars released between 1901 and 2014. Solid symbols (●, ■) are for cultivars that flower simultaneously, and hollow symbols (○, □) for cultivars sown on the same date. Deviation is the difference between the trait value for a given cultivar and the mean of each season for that trait. Bold text corresponds to flowering date balanced data, and unbold text corresponds to sowing date balanced data. P-values and R^2 are related to the regression fitted to data. Symbols (■, ●) are cultivar Longsword, which has not been included in the regressions or means shown. 124

Chapter 4

Figure 1: Duration and timing of the different development phases of winter wheat, fast and slow developing spring wheat in relation to the months of the year, typical optimal sowing windows and flowering period for southern Australia (Flohr *et al.* 2017b) and the autumn period during which rainfall has recently declined in southern Australia (Cai *et al.* 2012). 132

Table 1: Location, plot size, target plant density, mean and year of experiment growing season rainfall (April to October), time of sowing (TOS), cultivars grown and cultivar development type of either fast-spring (FS), mid-spring (MS), very-slow spring (VSS), fast-winter (FW) or mid-winter (MW)..... 135

Table 2. The five major development genes of wheat, and alleles carried by commercial cultivars and near-isogenic lines which govern response to vernalisation (Vrn; v=sensitive, a, b, e=insensitive) and photoperiod (Ppd; b, c=sensitive, a=insensitive). 139

Figure 2: Mean sowing date for different regions from 2008-2015 from the Yield Prophet® data base, and P-value, R^2 and the slope of the linear function fitted to the

data. The number next to marker is the number of fields included in the mean sowing date for each year. Error bars are the standard deviation around the mean for each year.

..... 141

Figure 3: Number of fields sown at weekly time intervals for wheat growing regions in Western Australia (total fields 600, median sowing date 15 May), South Australia (total fields 359, median sowing date 10 May), Victoria (total fields 358, median sowing date 9 May), southern New South Wales where (total fields 228, median sowing date 8 May) for combined seasons 2013, 2014 and 2015 from the Yield Prophet® database. 141

Figure 4: Cumulative thermal time (°C d) for A) Temora, NSW black line 2016, broken black line 2015, grey line average of years 2005-2016, and adjusted vernal days (●●●● 2015 and ●●●● 2016) B) Berriwillock in 2015 vs. mean 1997-2016 C) Minnipa in 2015 vs mean 1998-2016 and D) Cunderdin in 2015 vs mean 1990-2016. Accumulated degree days in the year of the experiment (black line) and long term mean for each site (grey line). 143

Table 3: Flowering date stability (higher number indicates a cultivar is more stable), mean yield and mean standard deviation of yield for cultivars. Figures are averaged across all times of sowing for two seasons at Temora, NSW in 2015 and 2016. 145

Table 4. The effect of sowing date on mean spikelet sterility (%) for cultivars at maturity. Time of sowing (TOS) ranged from mid-April to mid- May at Temora, NSW in 2015 and 2016. 146

Figure 5: Mean grain yield (t/ha) of commercial cultivars, a fast developing spring wheat (○), mid-fast developing spring wheat (Δ), very-slow spring wheat (□), fast developing winter wheat (Longsword, ●), and mid-winter wheat (▲) plotted against flowering date and minimum (°C, dark grey shading) and maximum temperatures (°C, light grey shading) at A) Temora, 2015 B) Temora, 2016 C) Berriwillock, 2015 and D) Minnipa, 2015 E) Cunderdin, 2015 shown as grain yield vs. time of sowing vs. temperature (flowering dates not recorded). Cultivar and sowing date details for each site are shown in Table 1. Each marker represents a different time of sowing and sowing date moves later from left to right. Broken lines are the optimal flowering period (OFP) as per Flohr *et al.* (2017). The vertical line is 5% LSD, P-Value of TOS x cultivar interaction at Temora, Minnipa and Cunderdin is <0.001, and at Berriwillock <0.005.

..... 148

Figure 6: Mean grain yield (t/ha) of near-isogenic lines with development patterns representing a fast developing winter wheat (●), fast developing spring wheat (○), very-slow spring wheat (□) and mid-winter wheat (▲) plotted against flowering date and

minimum (°C, dark grey shading) and maximum temperatures (°C, light grey shading) at A) Temora, 2015 B) Temora, 2016 C) Minnipa, 2015. D) Cunderdin, 2015 shown as grain yield vs. time of sowing. Cultivar and sowing date details for each site are shown in Table 1. Each marker represents a different time of sowing and sowing date moves later from left to right. Broken lines are the optimal flowering period (OFP) as defined by Flohr *et al.* (2017). The vertical line is 5% LSD, P-Value of TOS x cultivar interaction is <0.001..... 150

Figure 7: Developmental patterns of mid-winter (MW), fast-winter (FW, Longsword), very-slow spring (VSS), mid-spring (MS) and fast-spring (FS) cultivars sown in Temora, NSW in 2015 and 2016. In 2015 time of sowing (TOS) were 17 April, 27 April, 7 May and 15 May and in 2016 TOS were 17 April, 27 April, 6 May and 15 May. White area is calendar days from sowing to double ridge (DR), light area grey is calendar days from DR to terminal spikelet (TS) and dark grey area is calendar days from TS to flowering (An). Number written without brackets is cumulative degree day and number within brackets is vernal days to reach DR. Vertical box is the optimal flowering period for Temora as per Flohr *et al.* (2017). 153

Figure 8: Developmental patterns of Sunstate-MW, Sunstate-FW, Sunstate-VSS and Sunstate-FS near isogenic lines sown in Temora, NSW in 2015 and 2016. In 2015 time of sowing (TOS) were 17 April, 27 April, 7 May and 15 May and in 2016 TOS were 17 April, 27 April, 6 May and 15 May, and. White area is calendar days from sowing to double ridge (DR), light area grey is calendar days to reach terminal spikelet (TS) and dark grey area is calendar days to reach flowering (An). Number written without brackets is cumulative degree day °C and number within brackets is vernal days to reach DR. Vertical box is the optimal flowering period for Temora as per Flohr *et al.* (2017). 154

Chapter 5

Table 1: The 9 locations and corresponding long-term mean annual rainfall, patch point data set (PPD) station number, APSoil file number, plant available water content (PAWC), depth and depth of top layer used in the simulation study..... 170

Figure 1: Dry-land cereal cropping in south-eastern Australia (shaded), rainfall isohyets and the locations used for this study. 170

Figure 2. Summary of continuous cropping, forage legume and long fallow strategies relative to months of the year in south-eastern Australia..... 172

Table 2: A summary of the genetic x management strategies simulated for the low, medium and high rainfall zones in SA, Vic and NSW using APSIM 7.8, where short coleoptile length is 50 mm and long coleoptile length is 110 mm. 173

Table 3: Sowing windows for fast-winter (FW), slow-winter (SW), mid-winter (MW) and fast-spring (FS) genotypes and optimal flowering periods (OFP) as per Flohr et al. (2017b) used in the simulation study. 173

Figure 3. The distribution of simulated grain yield for the total 20 day sowing program from 1990-2016 for the 12 genotype (winter vs. spring wheats and long vs. short coleoptile) x management (sowing date, fallow length and sowing depth) strategies. The box and whisker plot shows the minimum, 25th percentile, median, 75th percentile and maximum grain yield for each strategy over the time period. On the left hand side CW, FL and LF signify rotation of either continuous wheat, forage legume or long fallow respectively, WW and FS signify winter wheat or fast spring wheat genotype and LC signifies a long coleoptile genotype. Numbers on the right hand side are the average yield (kg/ha) over the total period and sowing program. Grey shaded box and whisker plots indicate strategies that sow winter wheat with a long coleoptile ge 179

Figure 4. Simulated yield and annual rainfall for years 1997-2016 for strategies baseline, 3, 6 and 11 at a) Cootamundra, and b) Walpeup. Rotation is either continuous wheat (CW), forage legume (FL) or long fallow (LF), and genotype is winter wheat with a long coleoptile (WW-LC). 180

Figure 5. The distribution of simulated flowering dates for the total 20 day sowing program from 1990-2016 for the 12 genotype (winter vs. spring wheats and long vs. short coleoptile) x management (sowing date, fallow length and sowing depth) strategies. On the left hand side CW, FL and LF signify rotation of either continuous wheat, forage legume or long fallow, respectively, WW and FS signify winter wheat or spring wheat genotype and LC signifies a long coleoptile genotype. A higher stability index indicates a strategy that promotes greater flowering date stability over the whole farm and seasons, and bold text highlights the most stable strategy. Grey shaded box and whisker plots indicate strategies that sow a long coleoptile winter wheat genotype. Yellow shaded column represents the optimal flowering period for each site defined by Flohr *et al.* (2017b). Details of each strategy (baseline - 11) are in Table 3. 183

Table 4: The mean initial plant available water (mm) at sowing (15 March) at each location in which a winter wheat genotype is established under different rotations. ... 183

Figure S1. Validation of flowering time for APSIM cultivar V4-P1 used in simulations at locations Saddleworth, Lameroo, Waikerie, Walpeup and Condobolin. Observed

flowering dates were recorded in Temora, New South Wales in 2015 and 2016 and Minnipa, South Australia in 2015. Flowering dates were simulated using the same sowing dates and under the same seasonal conditions as field experiments from Flohr *et al.* (2017c). 191

Table S1. P-values of two-tailed t-test between yield of the baseline strategy vs. yield of strategies 1 to 11, and slope of the linear function for deviation of yield from the environmental mean and the environmental mean (mean of all strategies at a particular location). Bold text highlights significant differences, a slope closer to zero suggest the strategy is equally stable as the environmental mean, a positive slope indicates that the strategy is more stable than the environmental mean, and a negative slope indicates the strategy is less stable as per Eberhart and Russell (1966)...... 192

Chapter 6

Table 1: A map of research questions pursued in the thesis, and the main outcomes. .209

Chapter 1

General introduction



Image 1. Field experiment in Temora, NSW in September 2016

1.1 The significance of flowering date stability in the Australian wheat belt

Wheat is cultivated on more than 200 million hectares per year, supplying 21% of food worldwide (Ortiz *et al.* 2008). Wheat is a staple food in more than 40 countries, and is successfully grown in a wide range of environments including South America, Australia, North America, Europe and Asia (Bushuk 1998). In the past 50 years, cereal production has doubled as a consequence of the ‘Green Revolution’, achieved through the introduction of dwarfing and disease resistance genes, greater inputs of fertiliser, pesticides, and improved agricultural systems (Tilman *et al.* 2002). To meet the projected demand driven by population growth, income per capita and demand for biofuel, yield needs to increase by another 38% between 2005 and 2050 (Fischer *et al.* 2014).

Three key terms are used when discussing yield gain and global food security; farm yield (FY), potential yield (PY) and water-limited potential yield (PY_w). FY is determined from field, farm, district, regional or national averages, whereas PY is defined as the measured yield of the best cultivar, grown with optimal agronomy and without manageable biotic and abiotic stresses (Fischer 2015). PY_w is the same as PY except yield is limited by the amount of seasonal available water (van Ittersum *et al.* 2013). PY_w is the most sensible term to use when discussing PY in water-limited environments such as Australia. Recently estimated FY across countries ranges from 1.8 to 8.6 t/ha, but PY is significantly higher ranging from 2.6 to 10.8 t/ha (Fischer *et al.* 2014). Yield gap is defined as the difference between PY and FY (van Ittersum *et al.* 2013), and can be expressed as a percentage of FY (Fischer 2015). The average global wheat yield gap is 48% (Fischer *et al.* 2014).

Researchers, agronomists, breeders and farmers involved in crop production aim to increase FY by closing the yield gap, or increasing PY. Increases in FY have been associated with PY increases (Fischer 2015). Increases in PY in wheat are associated with cultivar improvement, such as increased grain number, harvest index, increased grain weight and total dry matter, increased radiation use efficiency, photosynthesis and stem-stored carbohydrate at flowering (van Ittersum *et al.* 2013; Fischer *et al.* 2014). The genetic component of PY_w is quantified by growing a number of historic and modern cultivars side by side under typical rain fed conditions, with otherwise optimal agronomy and no pests or diseases (Fischer 2009). Experiments like these are not only important for quantification of breeding success, but also for identification of

physiological traits for future cultivar improvement (Sadras and Lawson 2011).

Increases in FY occur through adoption of agronomy, and involve incremental changes in multiple technologies (Fischer *et al.* 2014; Hochman *et al.* 2017). Yield gain in both PY_w and FY are important for global food security.

Grain cropping in Australia is dominated by wheat production which was valued at \$34 billion in 2016/17 season (ABARES 2017). Around 12.4 million hectares are planted annually to wheat, of which a majority is rain fed and exported to over 50 countries (Anderson *et al.* 2016; AEGIC 2017). Australia only produces 3% of the world's wheat (~25 million t/yr) but accounts for a much larger portion (10-15%) of the world's 100 million tonne annual global wheat trade (AEGIC 2017). A survey of Australian farms undertaken in 2012 found that cereal crops provide 60-90% of farm income, with pulses, oilseeds, sheep or cattle providing the remaining income (Edwards *et al.* 2012). Of the farm area cropped per farm, an average of 58% is sown to wheat (Edwards *et al.* 2012) signalling the importance of the wheat industry not only to global food security and the nation's economy, but to the profitability and longevity of Australian farmers. As competitors in the global wheat trade (e.g. Russia and the Ukraine) continue to increase exports at a lower cost of production in comparison to Australia, Australian producers need to increase FY without increasing production costs in order to remain competitive (AEGIC 2016b; Anderson *et al.* 2016).

The semi-arid wheat belt of southern Australia has a predominately Mediterranean climate, with a cool wet season during which rain-fed wheat and other grain crops are grown, and a hot, dry season where land is left fallow. In this region annual rainfall ranges from 300 to 700 mm (Kirkegaard *et al.* 2014). There are pockets in the wheat belt where the climate is more temperate, and rainfall is higher and more reliable. In both temperate and Mediterranean environments the amount and variation of rainfall drives relatively low and highly variable yield from season to season (Fig. 1), compared to countries such as China, the UK and USA (Hochman *et al.* 2017). Frost, heat and drought are the main environmental yield-limiting constraints (Richards 1991). Frost costs the Australian grains industry ~\$700 million every year (An-Vo *et al.* 2018), and between 1964 and 2007, drought and extreme heat are estimated to have reduced crop national yields by ~ 20% in Australia (Lesk *et al.* 2016).

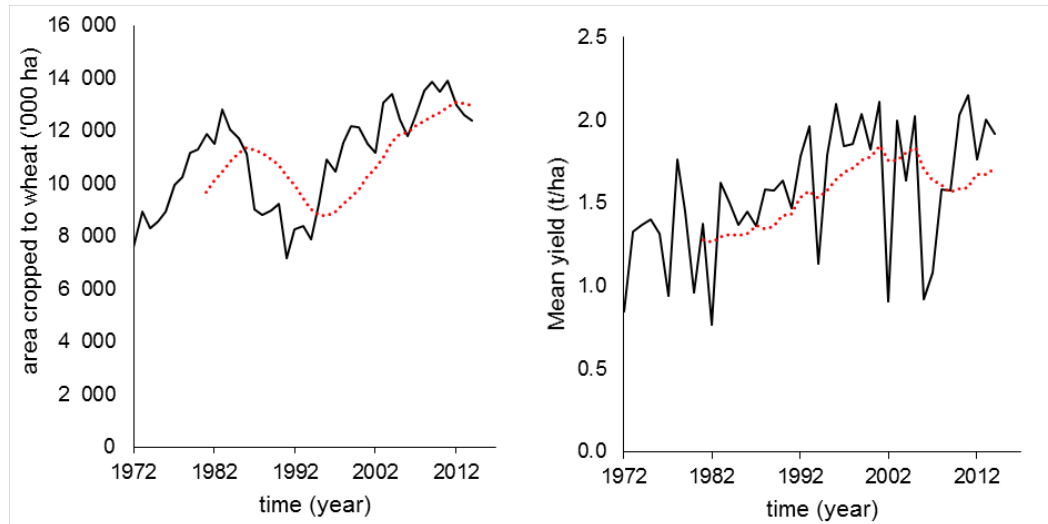


Figure 1: National wheat statistics for south-eastern Australia (southern NSW, Vic, SA) (ABARES 2017). Solid line is value for each year, dotted line is 10 year rolling mean.

Reduced sheep numbers, access to nitrogen fertiliser and a greater herbicide selection has supported continuous wheat cropping sequences in recent decades (Kirkegaard *et al.* 2011). For dry land wheat production in southern Australia, establishment of wheat is generally reliant on autumn rainfall to provide seed-bed moisture for germination. Since the start of the 20th century, the Australian wheat industry has been based on fast-developing spring cultivars established following rainfall in autumn (April-May), and growth during winter to mature at the end of spring to minimise exposure to drought and heat stress. Planting a farm can take 2-4 weeks, depending on equipment and land area to be covered. Crops are harvested in early summer, and between harvest and planting of the subsequent crop there is a 4-6 month period, known as the summer fallow (Hunt and Kirkegaard 2011). During the summer fallow, best practice is to control weeds using herbicides to conserve rain that falls during summer for use by the subsequent crop (Hunt *et al.* 2013). Accumulation of rainfall for the subsequent crop can be increased by extending the fallow period through crop rotation e.g. cereal hay crop cut at flowering conserves more soil water than a crop harvested at maturity (Kirkegaard and Hunt 2010; Kirkegaard *et al.* 2014). The fallow can be extended further by foregoing a whole season of crop production, referred to as long fallow (Ridge 1986; Fischer and Armstrong 1990). Long fallow reliably increases wheat yields, having the greatest benefit in low yielding environments (Angus *et al.* 2015) and on heavy soil types (Ridge 1986). Due to increasing land pressures, the area of long fallow has

decreased in southern Australia (Oliver *et al.* 2010), and higher value rotational break-crops that maintain some of the benefits of long fallows e.g. forage legumes (Bodner *et al.* 2015) have proved more popular.

In Australia, historic cultivar experiments have documented chronological changes and yield gain of local cultivars in Western Australia (WA) (Perry and D'Antuono 1989; Siddique *et al.* 1989a; Siddique *et al.* 1989b) and South Australia (SA) (Sadras and Lawson 2011). However, no published studies have considered cultivars adapted to the important grain producing region in the southern half of New South Wales (NSW). Studies from WA and SA demonstrated that Australian breeders have increased PY_w at a similar rate as the international figure of $\sim 0.5\%$ p.a. (Fischer 2009). Even though genetic increases in PY_w have increased at a comparable rate as those overseas, Hochman *et al.* (2017) observed a stall in PY_w in Australia between 1990 and 2015. The authors concluded that the 27% decline in PY_w can be attributed to reduced rainfall (28% reduction over 26 year period) and rising daily maximum temperatures (1.05°C increase over the 26 year period, Hochman *et al.* 2017). Whilst PY_w has decreased during this period, FY has been stable because Australian wheat farmers have closed the yield gap (Hochman *et al.* 2017). Leading farmers are achieving $\sim 80\%$ of PY_w using available advanced technologies in agronomic management and improved cultivars (van Rees *et al.* 2014). For those growers to increase FY, an increase in PY_w is necessary. However the average yield gap in Australia is much larger at $\sim 50\%$ (Hochman *et al.* 2017). To overcome this yield gap, underperforming growers need to adopt technologies and practices that overcome their current constraints to yield.

The rainfall decline noted by Hochman *et al.* (2017) has largely been from autumn, particularly in April–May (Murphy and Timbal 2008; Pook *et al.* 2009; Cai *et al.* 2012; Verdon-Kidd *et al.* 2014). See Figure 2 of Cai *et al.* (2012) for autumn rainfall trends since 1951 in SEA. The rainfall decline is associated with movement in the position and expansion of the sub-tropical dry zone (Cai *et al.* 2012; Cai and Cowan 2013), which has resulted in a decline in the synoptic systems (cut-off lows) that historically deliver autumn rainfall to SEA (Pook *et al.* 2009). This was particularly severe during the Millennium Drought experienced in Australia 1996-2009 (Verdon-Kidd *et al.* 2014) where hot, dry springs were also experienced more consistently, and during which time national yields decreased. Rainfall decline, and climate variability has been attributed to anthropogenic climate change (Cai and Cowan 2013), and is likely to persist. Autumn

rainfall decline, and the further shifts projected (CSIRO and Bureau of Meteorology 2015; Watson *et al.* 2017), make wheat production in Australia difficult in an already highly variable climate. Autumn rainfall decline has been most severe in the south-eastern Australian (SEA) wheat belt (Cai *et al.* 2012). The SEA wheat belt stretches from central New South Wales (south of Dubbo) through to Victoria, and South Australia, and in this area ~7 million hectares are sown to wheat annually (ABARES 2017). This region is therefore chosen as the focus of this study (Fig. 2).

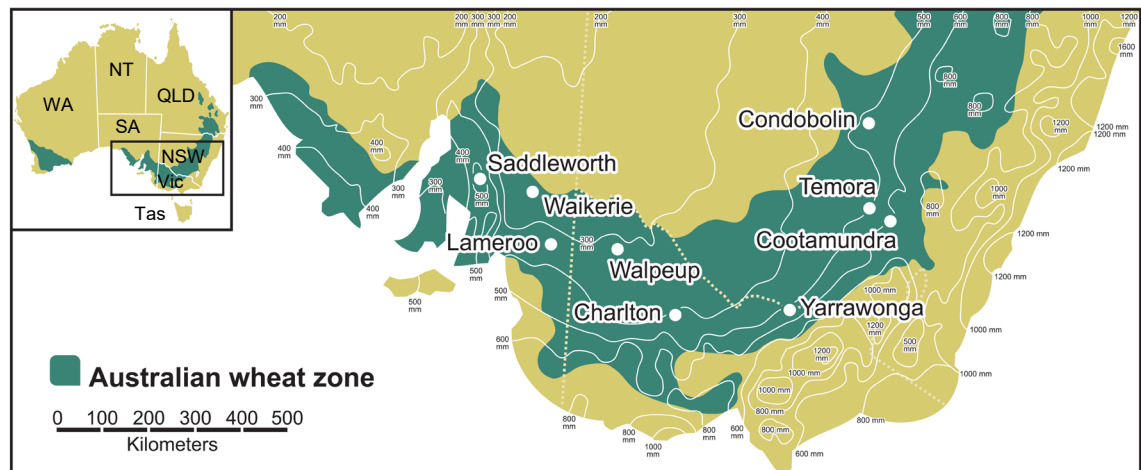


Figure 2. Dry-land cereal cropping in south-eastern Australia (enlarged) and rainfall isohyets (Australian Government 2017). Australian states, Western Australia (WA), Northern Territory (NT), South Australia (SA), Queensland (QLD), New South Wales (NSW), Victoria (Vic) and Tasmania (Tas). Map data: Google Earth (<http://earth.google.com>).

In SEA wheat genotypes with a spring development pattern have predominantly been grown since the end of the 19th century, when William Farrer identified that cultivars from the northern hemisphere which required vernalisation and longer days to flower, were not suited to the southern Australian growing season (Pugsley 1983). Since the release of the cultivar Federation by Farrer in 1901, Australian wheat breeders have continued to follow Farrer's lead and significant PY_w progress has been made by breeders selecting cultivars that develop from autumn establishment to flower during the optimal period (Richards *et al.* 2014). The Millennium Drought (Verdon-Kidd *et al.* 2014) provided an additional impetus to breed fast-developing wheats that could be sown after adequate autumn rainfall and mature quickly before the onset of terminal

drought. Today the most widely grown genotypes continue to be those with little photoperiod or vernalisation sensitivity, with fast-spring (FS) and mid-spring (MS) types dominating grain deliveries in the 2015/16 growing season (GrainCorp 2016).

The phenological progression of fast spring cultivars that are currently favoured, is largely driven by temperature accumulation alone (Eagles *et al.* 2009). Although faster and earlier development is advantageous for escaping drought, the consequence of having reduced sensitivity to vernalisation and photoperiod is that seasonal temperature variation can alter crop development rates such that flowering does not reliably occur within the optimal flowering period (Loss and Siddique 1994). Therefore, the greatest implication of autumn rainfall decline is that if rains do not fall during the optimal establishment time for fast developing cultivars (late April/ early May), crops flower too late and yield is reduced by drought and heat. If crops are established too early they suffer yield reductions caused by frost damage and/or insufficient biomass accumulation.

Flowering during the environment's optimal period is critical to grain yield as grain number is determined just prior to and at flowering (Fischer 1985) and grain yield is most sensitive to stresses during this period, including drought (Giunta *et al.* 1993; del Moral *et al.* 2003) and extreme high (Shpiler and Blum 1990; Tashiro and Wardlaw 1990; Ferris *et al.* 1998) and low temperatures (Boer *et al.* 1993; Fuller *et al.* 2007). The optimum temperature to facilitate pollination and fertilisation is in the range 18-24°C, with a minimum of 9°C and maximum of 31°C (Porter and Gawith 1999). In temperate climates such as northern Europe, flowering date has a broad optimum. However, in environments with a distinct dry season, flowering outside narrow optimal flowering periods can result in drastic yield reductions (Bodner *et al.* 2015). The wheat belt of SEA is one such environment. In these environments flowering date stability is closely associated with high and stable yields, so stabilising flowering is one pathway to increased FY.

In the last 20 years the average farm size has doubled in most cropping zones of Australia (Anderson *et al.* 2016). The mechanisation of agriculture, the availability of no-till farming equipment, reduced livestock numbers and a wide selection of herbicides have supported a shift towards greater farm size to achieve economies of scale and counter declining terms of trade (Fletcher *et al.* 2016). A larger cropped area per farmer has naturally driven progressively earlier sowing (Fletcher *et al.* 2016). Farmers are

typically sowing crops in late April and early May (Anderson *et al.* 2016; Fletcher *et al.* 2016), a sowing window that is suitable to the development of existing fast-spring wheat cultivars, but coincides with recent autumn rainfall decline. Furthermore, existing cultivars are not suited to the wider sowing window necessary to get the larger cropped area planted and still flower during the local optimal period. The combination of autumn rainfall decline and increasing farm size has further exacerbated the need to stabilise flowering in SEA. To achieve flowering time stability, novel genotype and management synergies need to be identified and implemented.

1.2 Options to stabilise flowering time and increase PY_w and FY of wheat

1.2.1 Vernalisation sensitivity

Wheat breeders select cultivars with developmental patterns that are adapted to target environments with the aim to achieve stable yields i.e. reduce the risk of crop failure from season to season (Cockram *et al.* 2007; Kamran *et al.* 2014). From germination to harvest, the cereal plant develops through an orderly series of development phases (Slafer and Rawson 1994). The timing and coordination of these stages depends on the genotype (G), environment (E), and establishment date or management (M) (Fischer 2009). For the last century, crop physiologists and agronomists have studied the effect of temperature and photoperiod on plant development to ensure critical development stages occur at the optimal period (Fischer, 2011). An understanding of crop development can assist in decision making at the grower level (e.g. nitrogen and pesticide application) and help explain changes in yield in response to stress at the plant physiological level (Kirby and Appleyard 1981). Many key measurements relevant to yield physiology are made at flowering, as flowering signifies the stage of development where resources to reach PY_w have largely been accumulated (Slafer *et al.* 2015b).

Globally, wheat breeders have selected two major types of development patterns: winter and spring types, which differ in their responses to vernalising temperatures (Pugsley 1983). Three main gene systems control development in wheat, vernalisation (response to low temperatures, Trevaskis 2010), photoperiod (response to day length, Slafer and Rawson 1995a) and earliness per se (temperature accumulation, Sukumaran *et al.* 2016). The vernalisation gene system accounts for ~70-75%, the photoperiod gene system for ~20-25%, and earliness per se for ~5% of the variability in the heading time of bread wheat (Stelmakh 1998; Kamran *et al.* 2014).

In the absence of any conflicting literature, it is assumed that all wheat genotypes are sensitive to temperature for development (earliness per se). True winter wheats must have vernalisation sensitive alleles at the three major vernalisation (*Vrn*) loci, whereas vernalisation is not a requirement for spring wheats (Table 1). Both spring and winter cultivars also carry sensitive or insensitive photoperiod (*Ppd*) alleles. Photoperiod plays a greater role in spring wheats, as winter wheat are only responsive to photoperiod after the vernalisation requirement is satisfied (Davidson *et al.* 1985). There is genetic variation in each, which determine differences in time to flowering among genotypes (Table 1, Cockram *et al.* 2007). A description of each of the genetic controls of flowering are shown below, and Table 1 shows the resultant development speed of *Vrn* and *Ppd* allele combinations. It should be noted that the five major genes (Table 1) do not account for all of the variation in speed of development i.e. the same haplotype can result in a different development speed due to differences in other major genes (Hunt 2017).

Vernalisation (cold) sensitivity: Cultivars with vernalisation sensitivity require exposure to temperatures in the range of -2°C to 15°C, with an optimum of 5°C before switching from vegetative growth to reproductive growth (Porter and Gawith 1999; Trevaskis 2010). Recently winter alleles (*v*) at the VRN1 loci have been linked to deeper root growth, likely associated with a longer vegetative phase (Voss-Fels *et al.* 2018). The greatest advantage of vernalisation sensitivity over photoperiod sensitivity is greater flowering time stability from broad sowing dates (Penrose and Martin 1997). Because vernalisation sensitive cultivars must experience a winter before they will flower, winter cultivars have a broader flexibility in time of establishment whilst maintaining high yield, and are therefore better suited to earlier establishment (Richards 1991; Penrose 1993, Penrose and Martin 1997).

Photoperiod (daylength) sensitivity: The duration of day light that wheat plants are exposed to can alter the speed at which they develop. Wheat is a 'long day' plant and in photoperiod-sensitive genotypes flowering is accelerated under long days, and slowed under short days (Slafer and Rawson 1995b). The *b* allele on Ppd-B1 has been associated with increased time from sowing to heading (Cane *et al.* 2013).

Earliness per se (temperature accumulation): Wheat rate of development is temperature dependent and is optimal at 20-25 °C and ceases at ~0°C and 37°C (Porter and Gawith 1999). Accumulation of temperature is measured in thermal time, and is

calculated as the sum of daily average temperature (minus base temperature) over a given period (Slafer and Rawson 1995b). The calculation of thermal time allows growth stages to be expressed independently of variable daily temperature influxes, and is referred to later in this thesis.

Table 1: extracted from Hunt (2017), showing the five major development genes of wheat, and alleles carried by different cultivars as per Eagles *et al.* (2010); Cane *et al.* (2013); Harris *et al.* (2017b) and their resultant development speed (slow, mid and fast) and pattern (winter, spring). Different vernalisation alleles are denoted by letters where *w*=highly vernalisation sensitive, *v*=vernalisation sensitive, *b*= vernalisation insensitivity, *a* =vernalisation insensitive. Different photoperiod alleles are *a*=insensitive, *b*, *c* and *d* =sensitive, with level of sensitivity depending on which genome they are on and which other *Ppd* and *Vrn* alleles are present.

Development speed and pattern	Example cultivar	<i>Ppd-B1</i>	<i>Ppd-D1</i>	<i>Vrn-A1</i>	<i>Vrn-B1</i>	<i>Vrn-D1</i>
Very slow winter	Hereward	<i>b</i>	<i>c</i>	<i>w</i>	<i>v</i>	<i>v</i>
Slow winter	Marombi	<i>a</i>	<i>b</i>	<i>w</i>	<i>v</i>	<i>v</i>
Slow winter	Revenue	<i>a</i>	<i>a</i>	<i>v</i>	<i>v</i>	<i>v</i>
Mid-winter	Wedgetail	<i>b</i>	<i>a</i>	<i>v</i>	<i>v</i>	<i>v</i>
Fast winter	Osprey	<i>a</i>	<i>a</i>	<i>v</i>	<i>v</i>	<i>v</i>
Very slow spring	Eaglehawk	<i>b</i>	<i>b</i>	<i>b</i>	<i>v</i>	<i>a</i>
Slow spring	Bolac	<i>b</i>	<i>a</i>	<i>a</i>	<i>v</i>	<i>v</i>
Mid-spring	Yipti	<i>b</i>	<i>d</i>	<i>a</i>	<i>a</i>	<i>v</i>
Fast spring	Mace	<i>a</i>	<i>a</i>	<i>v</i>	<i>a</i>	<i>v</i>
Very fast spring	Axe	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>v</i>

Yield gain of Australian wheat cultivars has been associated with increasingly faster development achieved through low levels of sensitivity to photoperiod and vernalisation (Perry and D'Antuono 1989; Siddique *et al.* 1989a; Siddique *et al.* 1989b; Richards 1991). Studies have hypothesized that breeding for earlier flowering has resulted in chronological decrease in duration of pre-flowering growth through a shorter vegetative phase and improved partitioning of resources to the spike to increase grain/m² (Kirby *et al.* 1989; Siddique *et al.* 1989b; Siddique *et al.* 1990b). Future PY_w gain through plant breeding is likely to be achieved through further increases in partitioning of assimilates to the growing spike that lead to increased grain/m² (Slafer *et al.* 2015a). One way to increase yield is through increased light interception and pre-flowering dry matter production (Reynolds *et al.* 2012). In Australian cultivars, pre-flowering dry matter can

be increased by introducing sensitivity to vernalisation and early sowing. The benefits would be twofold: increased dry matter production through extended development phases, and the removal of risk of fast development in warm winters (Anderson and Smith 1990; Penrose and Martin 1997). In practice, vernalisation sensitive (i.e. winter genotypes) cultivars with greater dry matter production can only increase partitioning of assimilates to the developing grain and lift PY_w , if pre-flowering development duration and superior partitioning are not irreversibly linked to faster development.

Penrose (1993) and Coventry *et al.* (1993) demonstrated that winter genotypes sown early could yield at least as well if not better than spring genotypes sown later. Even though winter cultivars have shown potential for SEA, Australian wheat breeding programs have released few winter cultivars (Hunt 2017). The trend in Australia to breed faster, less stable genotypes has potentially removed G x M advantages associated with a longer yield formation phase delivered by early sowing and slow development. Given recent autumn rainfall decline and increasing farm size, an opportunity exists to use summer and early autumn rainfall in place of autumn breaking rain to establish novel genotypes of slow development (Fig. 3, Kirkegaard and Hunt 2010; Hunt and Kirkegaard 2011). A greater range of cultivars that cover a broader range of sowing dates yet flower at the optimum time would also enhance management options available to growers (Mac-Indoe 1937; Martin 1981; Fischer 2011). Given the large spatial variability in length of the growing season and annual rainfall in the SEA wheat belt, a single genotype for the whole wheat belt is not appropriate, and G x M synergies need to be region specific.

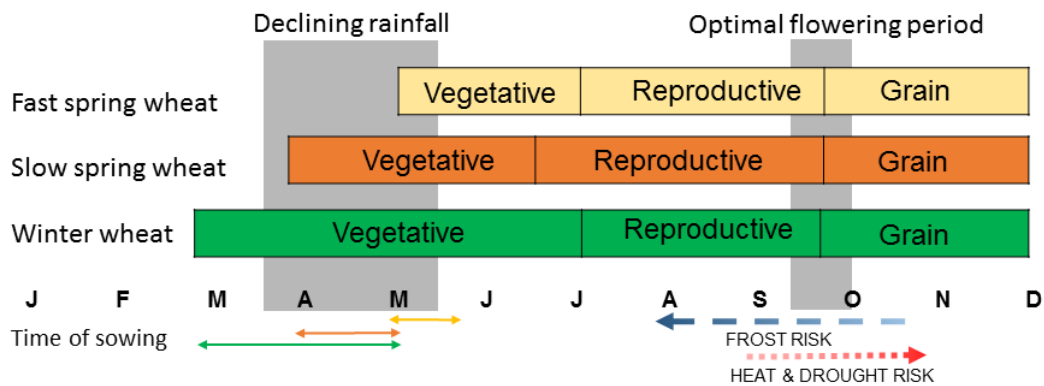


Figure 3: Duration and timing of the different development phases of winter wheat and fast and slow developing spring wheats in relation to the months of the year. Typical optimal sowing windows are represented by arrows colour coded to the wheat type the risks of frost and heat/drought are indicated by broken arrows and colour gradients. Grey bands represent the autumn period during which rainfall has recently declined in south-eastern Australia (Cai *et al.* 2012) and the optimal flowering period which minimises the risks from both frost and heat/drought.

1.2.2 Fallow

While the available time period over which to establish winter wheat is greater than fast-spring cultivars, the early establishment of winter wheat is still reliant on irregular rainfall events in late summer/ early autumn, and opportunities to plant do not always occur (Penrose 1993). As with fast-spring crops, late established winter wheat crops risk flowering outside the optimal period and suffering from drought and heat stress. The practice of long fallow i.e. leaving a field out of crop production for an entire season, has been used to conserve soil moisture for subsequent crops and manage production risk associated with southern Australia's variable climate (Schultz 1971; Ridge 1986; Oliver *et al.* 2010). Rotation with legume pastures contributed to significant increases in national wheat yield from the middle of the 20th century (Kirkegaard and Hunt 2010). Since the end of the 20th century, the area of long fallow declined with the availability of adapted and profitable break-crops, such as canola and grain legumes (Sadras and Roget 2004). With greater availability of crop options, the summer fallow (typically November –April) can be extended (October-April) through crop rotation, increasing stored soil water without foregoing a season of income. International studies have

shown that reliance on irregular autumn rainfall can be reduced, and early establishment opportunities increased, by growing winter wheat cultivars that have the ability to be sown and emerge from a greater depth (i.e. 10-15 cm), on stored soil moisture accumulated during fallow periods (Schillinger and Young, 2014; Schillinger, 2016). Such practices would be novel to Australia, and require evaluation in the modern farming context.

1.2.3 Long coleoptile

In order to facilitate establishment on stored soil water, wheat cultivars with long coleoptiles that can be safely sown at a greater depth are required (Rebetzke *et al.* 2007a). Modern Australian cultivars have short coleoptiles and struggle to emerge if sown at depths exceeding 50 mm (Reithmuller 1990). Short coleoptiles are a consequence of the introduction of dwarfing (*Rht*) genes which reduced plant height and improved harvest index in modern cultivars (Richards 1992b). However it is feasible to breed short stature, high harvest index cultivars with long coleoptiles using alternative dwarfing genes (Rebetzke *et al.* 1999; Rebetzke *et al.* 2007b). The early establishment of long coleoptile winter wheat cultivars would offer a novel avenue to increase PY_w and FY. If successful, long coleoptile winter wheat cultivars may break the historic trend of breeding fast-developing spring wheats, whilst lifting FY by stabilising the flowering time of wheat to the optimal period. The feasibility of this concept requires further investigation in environments experiencing rainfall decline and a change in sowing time.

1.3 Formulation of research questions

The overarching objective of this thesis was to identify novel genetic (G) x management (M) strategies to stabilise flowering time and lift FY and PY_w in the increasingly variable climate of the SEA wheat belt. The thesis addressed this overarching question by means of four distinct but related research activities, answering relevant sub-questions, set out in the four following chapters. The structure of this analysis and the questions addressed are summarised in Table 2.

Table 2: Research questions pursued in the thesis, the status of publication and contribution statements for each chapter.

Overarching objective: Identify novel G x M to achieve flowering date stability	
Chapter, topic and journal	Research question addressed
<p>Chapter 1</p> <p><u>Topic:</u> General introduction</p>	<p>Background information and framing of research questions</p>
<p>Chapter 2</p> <p><u>Topic:</u> Optimal flowering periods</p> <p><u>Journal:</u> <i>Published, Field Crops Research</i>, 209, 108-119</p> <p><u>Contribution statement:</u> BF wrote the manuscript. BF carried out the simulation experiments with support of JH. All authors discussed the results and contributed to the final manuscript.</p>	<ol style="list-style-type: none"> 1. What are the optimal flowering periods in the SEA cropping zone as defined by temperature and water supply and demand? 2. What sowing dates are required for widely grown mid-fast developing cultivars to flower during the optimal period?
<p>Chapter 3</p> <p><u>Topic:</u> Change in yield potential & growth and development traits of popular wheat cultivars released in southern New South Wales between 1901-2014</p> <p><u>Journal:</u> <i>Published, European Journal of Agronomy</i>, 98, 1-13</p> <p><u>Contribution statement:</u> BF and JH conceived, designed and analysed the experiments and interpreted the results. BF wrote the manuscript and designed and prepared figures and tables. BF managed the collection of data from field experiments under the supervision of JH, and with assistance from TS and BR. JK and JE contributed valuable comment to the final manuscript.</p>	<ol style="list-style-type: none"> 1. How much observed yield gain is associated with: (i) earlier flowering, (ii) reduced duration to flowering, (iii) inherently better partitioning to grain? 2. What is the genetic yield gain of New South Wales wheat cultivars released between 1901 and 2014?
<p>Chapter 4</p>	<ol style="list-style-type: none"> 1. What sowing dates are farmers currently practicing?

<p><u>Topic:</u> Novel fast-winter genotype</p> <p><u>Journal:</u> <i>Published, Field Crops Research</i>, 223, 12-25</p> <p><u>Contribution statement:</u> BF and JH conceived, designed and analysed the experiments. BF wrote the manuscript, designed and prepared figures and tables. BF managed the collection of data from Temora field experiments under the supervision of JH, and with assistance from TS and BR. BT created and provided NILs that were grown in the experiment. AZ helped design the Temora experiment and analyse results, AF managed WA experiment. BF, JH, JK, JE provided critical feedback and helped shape the final manuscript. Raw data from WA, SA, and Victoria was not collected by BF, but collected as part of the greater GRDC project</p>	<p>2. Can a fast-winter genotype stabilise flowering across the early sowing dates being practiced by farmers in southern Australia?</p>
<p>Chapter 5</p> <p><u>Topic:</u> Novel G x M strategies</p> <p><u>Journal:</u> <i>Published, Crop and Pasture Science</i>, 69, 547-560</p> <p><u>Contribution statement:</u> BF and JH conceived and designed the simulation experiments. BF conducted the simulations with assistance from JL. BF analysed results, wrote the manuscript, designed and prepared figures. JH, JK and JE provided critical feedback and helped shape the final manuscript.</p>	<p>1. Can novel genotype x management strategies reduce reliance on autumn rainfall for establishment and increase FY by allowing a greater portion of wheat to flower during the optimal period?</p>
<p>Chapter 6</p> <p><u>Topic:</u> Overview of the thesis</p>	<p>Summary of key findings and implications for farm practice and future research</p>

Bonnie Flohr (BF) James Hunt (JH) John Kirkegaard (JK) John Evans (JE) Tony Swan (TS)
Brad Rheinheimer (BR) Ben Trevaskis (BT) Alec Zwart (AZ) Julianne Lilley (JL) Andrew
Fletcher (AF)

Given the diversity of climates in the SEA wheat zone, it was first necessary to discover the OFP at multiple locations using an established crop growth model APSIM and half a century of weather records. APSIM is a cropping systems simulation model developed in Australia (Keating *et al.* 2003; Holzworth *et al.* 2014). APSIM enables the study of interactions between plant, soil, climate and management on grain yield. The study deployed APSIM in Chapter 2 and Chapter 5 (Version 7.6 and 7.8 respectively) because it is well validated for wheat (Hochman *et al.* 2007; Lilley and Kirkegaard 2007; Brown *et al.* 2014) and fallow periods (Hunt and Kirkegaard 2011; Zeleke and Nendel 2016). The first research question addressed in the thesis was: *what are the optimal flowering periods in the SEA cropping zone as defined by temperature and water supply and demand? Second, what sowing dates are required for widely grown mid-fast developing cultivars to flower during the optimal period?*

Experiments with historic wheat genotypes are important to quantify breeding success and for identifying the physiology needed for future cultivar improvement. A comprehensive field experiment at Temora (southern NSW) over two years was conducted with 12 genotypes released in NSW between 1901 and 2014 with 4 sowing times and multiple harvests. This experiment also addresses the knowledge gap around the genetic gain in yield of southern NSW cultivars. In previous historic wheat studies, only a single sowing date has been used (e.g. Siddique *et al.* 1989a; Sadras and Lawson 2011). An important and novel aspect of the work presented here was the use of multiple sowing dates. Multiple sowing dates enable comparison between genotypes that are flowering concurrently within the defined optimal flowering period, thereby controlling for the large genetic differences in duration of life cycle that is common across such sets. Using this method it is possible to separate out the effect of speed of development from flowering time on observed yield gain in southern NSW. These field experiments address the following questions: *what is the genetic gain in yield of wheat cultivars released in New South Wales between 1901 and 2014? How much observed yield gain is associated with earlier flowering? How much yield gain is associated with reduced duration to flowering? How much yield gain is associated with inherently better partitioning to grain?*

Given the minor role that slow developing cultivars have played in the Australian farming system thus far, Chapter 4 focussed on comparing the flowering behaviour of a novel winter genotype to elite modern spring genotypes. The chapter firstly quantified the sowing dates used by farmers that are sowing wheat, and then assesses the suitability and associated optimal sowing dates of the novel genotype with field experiments in different environments in southern Australia. The key research question addressed was; *can a fast-winter genotype stabilise flowering across the early sowing dates being practiced by farmers in southern Australia?*

Existing literature suggests that a key limitation to the breeding and adoption of winter wheats in many environments of SEA is a lack of establishment opportunities. Chapter 5 investigated this limitation using simulation modelling (APSIM) to investigate the effect of manipulating genotype (winter vs. spring wheats and long vs. short coleoptile) and management (sowing date, sowing depth and fallow length) on flowering date and PY_w in low, medium and high rainfall zones of SEA. The central question of Chapter 5 was: *can novel genotype x management strategies reduce reliance on autumn rainfall for establishment and increase PY_w by allowing a greater portion of wheat to flower during the optimal period?*

The final chapter (Chapter 6) provides a summary of the key findings from this research, their implications for practical action along with suggestions for further research. Extension of the findings from this research has commenced with the farming community, which is summarised in Appendix 1.

Chapter 2

*Water and temperature stress define the optimal
flowering period for wheat in south-eastern
Australia*

STATUS: Published in April 2017

Flohr BM, Hunt JR, Kirkegaard JA, Evans JR, 2017, Water and temperature stress define the optimal flowering period for wheat in south-eastern Australia. *Field Crops Research* **209**, 108-119



Image 2: Flowering wheat plot at Temora, NSW on 8 October 2015

Abstract

Across the Australian wheat belt, the time at which wheat flowers is a critical determinant of yield. In all environments an optimal flowering period (OFP) exists which is defined by decreasing frost risk, and increasing water and heat stress. Despite their critical importance, OFPs have not been comprehensively defined across south eastern Australia's (SEA) cropping zone using yield estimates incorporating temperature, radiation and water-stress. In this study, the widely validated cropping systems model APSIM was used to simulate wheat yield and flowering date, with reductions in yield applied for frost and heat damage based on air temperatures during sensitive periods. Simulated crops were sown at weekly intervals from April 1 to July 15 of each year. The relationship between flowering date and grain yield was established for 28 locations using 51-years (1963-2013) of climate records. We defined OFPs as the flowering period which was associated with a mean yield of $\geq 95\%$ of maximum yield from the combination of 51 seasons and 16 sowing dates. OFPs for wheat in SEA varied with site and season and the relative importance of seasonal water supply and demand and extremes of temperature in defining the window also varied. Quantifying OFPs will be a vital first step to identify suitable genotype x sowing date combinations to maximise yield in different locations given recent and predicted regional climate shifts including the decline in autumn rainfall.

1. Introduction

In all environments there exists a period during which wheat (*Triticum aestivum* L.) must flower in order for grain yield to be maximised, herein referred to as the optimal flowering period (OFP). Flowering during the optimal period is critical to grain yield as grain number is determined just prior to and at flowering (Fischer 1985) and grain yield is most sensitive to stresses during this period, including drought (Giunta *et al.* 1993; del Moral *et al.* 2003) and extreme high (Shpiler and Blum 1990; Tashiro and Wardlaw 1990; Ferris *et al.* 1998) and low temperatures (Boer *et al.* 1993; Fuller *et al.* 2007). In temperate climates such as northern Europe, flowering date has a broad optimum. However, in environments with a distinct dry season, flowering outside narrow OFPs can result in drastic yield reductions (Bodner *et al.* 2015). The wheat belt of south eastern Australia (SEA) is one such environment, which has a predominantly Mediterranean climate with a cool wet season during which rain-fed wheat and other grain crops are grown, and a hot, dry season where land is left fallow. Whilst rainfall in the north-east of the region is equi-seasonal in distribution, cropping is still confined to the cool season by high summer temperatures and insufficient precipitation to sustain summer crops (Potgieter *et al.* 2002; Chenu *et al.* 2013). In the 2012/ 2013 season the south eastern states of Australia (New South Wales, Victoria and South Australia) produced over 14 Mt of wheat, 63% of Australia's total wheat production (Commonwealth of Australia 2013). The majority of annual production is exported, making the region important for global food security.

In SEA, spring wheat cultivars are established following rainfall in April-May (austral autumn) and grow during winter to mature at the end of spring. Significant yield progress has been made by breeders selecting cultivars with development patterns such that once established in autumn they will flower during the optimal period (Richards 1991; Richards *et al.* 2014). However, since 1996, rains that could once be relied upon by farmers to establish crops in April-May have declined significantly (Pook *et al.* 2009; Cai *et al.* 2012). This decline was particularly severe during the millennium drought (Verdon-Kidd *et al.* 2014) at which time wheat crops established and flowered too late and yield was reduced by terminal drought and heat (Commonwealth of Australia 2013). Reduced autumn rainfall has been attributed to anthropogenic climate change (Murphy and Timbal 2008; Cai *et al.* 2012) and is likely to persist. New combinations of management and genetics will be required to stabilise flowering date in

order to overcome the observed yield decline (Kirkegaard and Hunt 2010), and maintain the viability of SEA wheat farms and their contribution to global food security. A clear first step in this process is to identify the current OFP for environments in the SEA wheat belt.

A combination of environmental factors (precipitation, soil type, temperature) influence the opening, closing and duration of the OFP. Previous authors have stated that OFPs in SEA occur after the last spring frost and before the onset of heat and water stress (Anderson and Smith 1990; Richards 1991; Zheng *et al.* 2012). Untimely spring frosts (September to October) are common in the Australian wheat belt (Boer *et al.* 1993; Fuller *et al.* 2007; Zheng *et al.* 2012; Zheng *et al.* 2015). A yield penalty of 10 % as a direct result of frost is common (Fuller *et al.* 2007), and more catastrophic events are frequent (Crimp *et al.* 2015). Zheng *et al.* (2015) analysed the frost and heat patterns of the Australian wheat belt, and found that the only regions that could be classified as almost “frost free” were some areas of the coastline in South Australia and north-east of central Queensland, while frosts occurred in other regions in 80% of years. Wheat is most sensitive to frost during reproductive growth stages. When wheat ears are exposed to freezing temperature after heading, frost damage will reduce the number of grain and sometimes cause death of entire ears (Fuller *et al.* 2007).

High temperatures during sensitive reproductive growth stages can also result in a yield penalty (Ferris *et al.* 1998). Gomez-Macpherson and Richards (1995) found that grain yield declined by 1.3% per day that sowing was delayed after late-May due to high temperatures around the time of anthesis and grain-fill. High temperature events (>35°C) during the period between head emergence to 10 days after anthesis can significantly reduce grain number and quality (Tashiro and Wardlaw, 1990). Similarly, heat shock during the grain filling period can also cause grain abortion and degrade grain quality (Randall and Moss 1990; Stone and Nicolas 1995).

Perhaps the most important determinant of the OFP is the pattern of water supply and demand experienced in a given environment (Bodner *et al.* 2015). Whilst drought patterns in SEA are well described (Chenu *et al.* 2013), the effect of seasonal water supply and demand in determining OFPs has been overlooked in previous analyses of OFPs e.g. Zheng *et al.* (2012), Zheng *et al.* (2013), Bell *et al.* (2015). In all of these studies OFPs were defined only by temperature extremes, which ignores the critical role that water supply and demand plays in defining OFPs in SEA.

To obtain an accurate definition of the OFP for a specific environment, Anderson and Smith (1990) suggest that time of sowing experiments should be conducted over a range of seasons. Anderson *et al.* (1996) defined the optimal flowering period from field experiments by "...using the mean flowering dates ...of the sites and the optimum flowering period was taken to be 10 days either side of the mean optimum date [for grain yield]". Experiments like these are expensive, and the recommendations to farmers are specific to the experimental conditions (e.g. temperature, rainfall and soil water holding capacity) during the period of the experiments, and may not reflect long-term climatic patterns (Asseng *et al.* 2001). More recently, Zheng (2012) analysed heat and frost patterns of the wheat belt to calculate flowering windows based on occurrence of last frost days and first heat days.

Alternatively, an analysis of historic climate records using a crop simulator such as APSIM (Keating *et al.* 2003; Holzworth *et al.* 2014) allows one to identify management strategies to achieve optimum sowing date and flowering period (Asseng *et al.* 2001; Zheng *et al.* 2012) and can account for both temperature and water stress simultaneously. This is especially useful in the seasonally variable production environments of SEA (Asseng *et al.* 2001; Turner 2004; Asseng and Pannell 2013).

This study sought to define OFPs in SEA to assess management (sowing date) and genetic (genotype) interventions to overcome yield reductions due to the decline in autumn rainfall. It uses APSIM to incorporate the seasonal effects of water supply and demand, radiation and temperature on grain yield. By using the potential yield predictions to integrate the effects of temperature and radiation as well as water supply and demand, it extends the work of Zheng *et al.* (2012) who used only air temperature records alone (i.e. frost, heat) to define OFPs for the entire Australian wheat belt.

2. Materials and Methods

2.1 Site selection and crop simulation approach

Locations were selected to represent environments where wheat is grown in the cropping belt of SEA (Fig. 1, Table 1), and based on the availability of accurate soil characterization from the APSoil database (Dalglish *et al.* 2009) and patched-point meteorological weather stations from the SILO database (Jeffrey *et al.* 2001). At some sites (Hopetoun, Swan Hill and Bogan Gate), two different soil files were selected to compare the effect of soil type on the OFP. The cropping systems model Agricultural

Production Systems SIMulator (APSIM), version 7.6 (Keating *et al.* 2003; Holzworth *et al.* 2014) was used to simulate wheat flowering date and yield using 51 years (1963-2013) of climate data. Simulation of wheat growth, development and yield in APSIM has been extensively validated in numerous studies across southern Australia (Asseng *et al.* 2001; Lilley *et al.* 2003; Lilley and Kirkegaard 2007; Carberry *et al.* 2009; Hochman *et al.* 2009a), and no further validation was undertaken here. The key APSIM modules used in the analysis were Wheat (wheat crop growth and development) and Manager (specifying sowing rules).



Figure 1: Dry-land cereal-cropping areas in Australia (shaded) and the locations used for this study.

Table 1: The 28 locations, where (a) and (b) refer to different soil types at the same location used in the study, and corresponding long-term mean annual rainfall, patch point dataset (PPD) station number, APSoil file number used in the simulation study.

State		Location	Latitude, Longitude	Mean annual rainfall	PPD station No.	APSoil File no.
SA	1	Maitland	-34.3745, 137.6733	502	22008	261
	2	Hart	-33.7322, 138.4922	458	21000	286
	3	Cleve	-33.7011, 136.4937	400	18014	316
	4	Cummins	-34.2644, 135.7266	428	18023	37
	5	Lock	-33.5676, 135.7561	390	18046	318
	6	Minnipa	-32.8542, 135.1542	343	18053	352
	7	Saddleworth	-34.0844, 138.7815	493	23315	104
	8	Lameroo	-35.3288, 140.5175	385	25509	253
	9	Waikerie	-34.1778, 139.9806	258	24018	104
	10	Bordertown	-36.3125, 140.7718	479	25501	344
Vic	11	Walpeup	-35.1201, 142.0041	331	76064	726
	12	Hopetoun(a)	-35.7344, 142.3703	342	77018	716
	12	Hopetoun(b)	-35.7344, 142.3703	342	77018	714
	13	Kerang	-35.8674, 143.8007	356	80024	733
	14	Swan Hill(a)	-35.3406, 143.5533	344	77042	718
	14	Swan Hill(b)	-35.3406, 143.5533	344	77042	719
	15	Charlton	-36.2715, 143.345	403	80067	736
	16	Longerenong	-36.6722, 142.2991	413	79028	746
NSW	17	Yarrawonga	-36.0281, 146.0044	509	81057	208
	18	Inverleigh	-38.243, 143.9887	553	90167	737
	19	Mathoura	-35.7228, 144.7865	360	74129	203
	20	Nyngan	-31.5495, 147.1961	441	51039	246

21	Urana	-35.3305, 146.2652	441	74110	212
22	Temora	-34.4061, 147.5248	510	73038	179
23	Cootamundra	-34.6299, 148.0364	618	73142	180
24	Dubbo	-32.2385, 148.6089	591	65012	197
25	Bogan Gate(a)	-33.1074, 147.8008	495	50004	188
25	Bogan Gate(b)	-33.1074, 147.8008	495	50004	189
26	Merriwagga	-33.9247, 145.5205	356	75142	697
27	Condobolin	-33.0664, 147.2283	437	50052	688
28	Trangie	-31.9861, 147.9489	492	51049	683

APSIM calculates flowering date i.e. anthesis (and other crop stages) by accumulation of thermal time. The APSIM Wheat model calculates thermal time based on mean daily temperature $((T_{max} + T_{min})/2)$ using crown temperature. Crown temperature is derived from air temperature using original routines in CERES-Wheat (Zheng *et al.* 2014). The length of each crop stage between emergence and floral initiation is determined by the accumulation of thermal time, and cultivar-specific factors accounting for vernalisation and photoperiod responses (Ritchie 1991). The length of each crop stage from floral initiation to maturity is determined only by accumulation of thermal time. The root-mean-square error (RMSE) in the ability for APSIM-Wheat to predict flowering time is 6.2 days (Zheng *et al.* 2013).

2.2 Crop management set up

All simulated crops were sown at 150 plants/m², at a depth of 30 mm with a row spacing of 300 mm. In APSIM cultivars are allocated a vernalisation and photoperiod “factor” which represent sensitivity to vernalising temperatures and day length where high values are more sensitive. The model then uses these factors to calculate cultivar specific developmental rates. The cultivar parameters selected here represent a spring wheat of mid to fast phenological development, typical of varieties grown in SEA (e.g. Scout, Spitfire, Mace etc.). This was based on the APSIM base cultivar with vernalisation sensitivity of 1.5 and photoperiod sensitivity of 3.0. For comparison, a winter wheat (e.g. Wedgetail) with vernalisation sensitivity of 4, photoperiod sensitivity

of 0, and an intermediate facultative wheat (e.g. Eaglehawk) with a vernalisation sensitivity of 2.5 and photoperiod sensitivity of 4 were also simulated at selected sites (Temora, NSW and Lameroo, S.A) under the same management parameters to observe any change in yield and OFP.

APSIM-Manager was used to sow a crop on a fixed date at weekly intervals from 1 April to 15 July of each year. Nitrogen was applied as NO_3 with a fertilizer rule, which was maintained above 100 kg/ha in the top three layers of the soil throughout the season such that nitrogen supply did not limit yield. In the simulation, the initial plant available water was set to 0 mm and not reset in subsequent seasons, and the crop received 15 mm of irrigation at sowing to ensure that it would emerge shortly after it was sown. APSIM assumes crops are grown free of weeds and disease. As highlighted in the recent review by Barlow *et al.* (2015), APSIM does not currently account for frost and heat events in its yield predictions. Therefore, a reduction for frost and heat damage based on air temperature obtained from patched point meteorological weather stations was applied as per Bell *et al.* (2015). To estimate the effect of heat or frost stress events on grain yield during sensitive growth stages, temperature ranges were categorized into mild, medium and severe stress with a corresponding impact on yield during different growth stages, these estimations are based on the literature and expert opinion (Bell *et al.* 2015) (Table 2). Yield reductions were cumulative for multiple events that occurred during the sensitive stages of plant growth (Table 2). The combination of management rules and frost and heat rules ensure that the OFP was defined for each environment by the combination the drought pattern, temperature and radiation. Outputs from the simulation were annual potential grain yield and annual grain yield modified for frost and heat damage, referred to as the frost and heat limited (FHL) yield hereafter, at different sowing dates and corresponding flowering dates. To quantify the effect of stress on the OFP, the mean stress index of frost and heat, and the mean water stress between floral initiation and maturity applied to the crop was plotted for selected sites, with 0 indicating zero effect on grain yield, and 1 having the greatest effect on grain yield.

Table 2: Temperature criteria for frost and heat stress during sensitive Zadoks growth stages and corresponding estimated yield reduction, from Bell *et al.* (2015). Yield reduction was calculated for each day and multiplied, so that increasing numbers of stress events results in cumulative reduction in yield.

Temperature	Stress level	Zadoks sensitive stage	Yield reduction per day
0 to 2 ⁰ C	Mild	60-69	10%
-2 to 0 ⁰ C	Moderate	60-75	20%
< -2 ⁰ C	Severe	60-79	90%
32 to 34 ⁰ C	Mild	60-79	10%
34 to 36 ⁰ C	Moderate	60-79	20%
>36 ⁰ C	Severe	60-79	30%

For each location, over the 51 years x 16 sowing dates of simulation, the FHL yield was attributed to the predicted flowering date in each simulation. OFPs were defined by calculating a 15-day running mean of FHL yield over the 51 years of simulation. In order to avoid periods with small sample sizes at the early extremes of flowering time affecting the mean, only 15 day periods with at least 15 data points were used.

Flowering dates corresponding to $\geq 95\%$ of the peak mean FHL yield defined the dates of the OFP for each location. A criterion of 95% assumes that growers seek to maximise yield and that 5% is an acceptable level of yield loss that growers would be willing to bear for a management action (sowing time x cultivar selection) that costs very little to achieve. Three lines were plotted, the 15-day running mean, the positive standard deviation, and the negative standard deviation associated with the running mean. To demonstrate how the OFP changes from season to season, the 15-day running mean of yield was split into 10, 20, 30, 40, 50, 60, 70, 80 and 90th percentiles for selected locations.

The APSIM simulation was also used to estimate the optimal sowing date range for each location to achieve the OFPs. To define the sowing range, the sowing dates that corresponded to the flowering dates that achieved the highest 15-day running mean yield were split into earliest sowing date, 25th percentile, median, 75th percentile and latest sowing dates.

To observe effects of recent rainfall decline and increasing temperatures within the 51-year simulation, APSIM output for yield and flowering date was analysed for two time periods 1963-1997 and 1998-2013. The 15-year time period (1998-2013) includes the period of April-May rainfall decline experienced at many of the sites in the south-eastern wheat belt described by Cai *et al.* (2012).

3. Results

3.1 Defining optimal flowering periods

Yield and OFP varied across 28 locations according to the temperature, radiation and rainfall patterns and soil type of each environment (Table 3). The highest peak mean FHL yield was in Maitland (4910 kg ha⁻¹), followed by Inverleigh (4841 kg ha⁻¹). The lowest yielding location was Waikerie (1819 kg ha⁻¹). The open and close dates and duration varied significantly across the wheat belt. The earliest OFP open date was at Minnipa (22 August), while the latest was at Inverleigh (12 October). The longest and shortest durations of the OFP were Inverleigh (26 days) and Nyngan (4 days), and the latest and earliest close dates were Inverleigh (6 November) and Nyngan and Waikerie (29 August). Timing of the OFP was related to mean annual rainfall (Fig. 2) and consequently yield, although high annual rainfall often coincided with a cooler growing season in SEA (data not shown) e.g. Inverleigh, so effects of temperature and water availability are confounded. The duration of the OFP is affected by the criteria used to define OFP (95% of maximum yield), as it biases toward defining shorter windows in low yielding environments (5% equates to a lower absolute yield value), which alerts growers to the critical importance of managing flowering time carefully in those environments to maximise yield. However, there was no clear relationship between rainfall amount (and thus yield) and duration of the OFP (Fig. 2).

Table 3: Optimal flowering periods (OFPs), peak mean of frost and heat limited yield (kg ha^{-1}) and corresponding flowering date and sowing date range for a mid-fast cultivar over 51-years (1963-2013), for the 28 locations where (a) and (b) refer to different soil types at the same location, ranked in alphabetical order.

Location	Optimal flowering period		Peak mean yield (kg ha^{-1}) and corresponding flowering date		Sowing date range for corresponding peak mean yield				
	Open	Close	yield	flowering date	Earliest	25 th percentile	Median	75 th percentile	Latest
Bogan Gate (a)	19-Sep	3-Oct	4283	27-Sep	12-May	16-May	21-May	27-May	1-Jun
Bogan Gate (b)	18-Sep	1-Oct	3650	21-Sep	6-May	8-May	13-May	17-May	21-May
Bordertown	26-Sep	15-Oct	3577	7-Oct	16-May	23-May	29-May	3-Jun	9-Jun
Charlton	21-Sep	30-Sep	2920	23-Sep	29-Apr	6-May	7-May	10-May	14-May
Cleve	7-Sep	18-Sep	3402	13-Sep	13-May	15-May	20-May	24-May	30-May
Condobolin	11-Sep	19-Sep	2435	15-Sep	29-Apr	2-May	7-May	10-May	15-May
Cootamundra	6-Oct	20-Oct	4338	12-Oct	6-May	13-May	20-May	24-May	31-May
Cummins	8-Sep	28-Sep	3843	18-Sep	15-May	19-May	24-May	27-May	1-Jun
Dubbo	13-Sep	26-Sep	3881	18-Sep	6-May	7-May	11-May	15-May	18-May
Hart	21-Sep	2-Oct	4242	24-Sep	6-May	8-May	13-May	18-May	22-May
Hopetoun (a)	7-Sep	11-Sep	2900	8-Sep	1-May	5-May	10-May	14-May	19-May
Hopetoun (b)	4-Sep	9-Sep	1903	5-Sep	20-Apr	22-Apr	25-Apr	29-Apr	30-Apr
Inverleigh	12-Oct	6-Nov	4841	22-Oct	2-Jun	11-Jun	15-Jun	24-Jun	1-Jul
Kerang	12-Sep	18-Sep	3131	15-Sep	25-Apr	29-Apr	3-May	5-May	9-May
Lameroo	28-Aug	20-Sep	3154	7-Sep	26-Apr	29-Apr	2-May	6-May	11-May
Lock	4-Sep	14-Sep	3049	9-Sep	6-May	7-May	13-May	15-May	20-May
Longerenong	6-Oct	10-Oct	2749	7-Oct	9-May	12-May	16-May	25-May	27-May
Maitland	16-Sep	9-Oct	4910	1-Oct	27-May	29-May	5-Jun	10-Jun	14-Jun
Mathoura	15-Sep	22-Sep	2268	18-Sep	26-Apr	30-Apr	3-May	6-May	9-May
Merriwagga	27-Aug	10-Sep	2619	31-Aug	22-Apr	25-Apr	27-Apr	29-Apr	6-May
Minnipa	22-Aug	8-Sep	3514	25-Aug	29-Apr	30-Apr	6-May	6-May	8-May
Nyngan	26-Aug	29-Aug	2234	27-Aug	27-Apr	30-Apr	2-May	7-May	9-May
Saddleworth	9-Sep	24-Sep	3857	17-Sep	6-May	10-May	15-May	17-May	23-May
Swan Hill (a)	1-Sep	20-Sep	3673	15-Sep	26-Apr	2-May	6-May	9-May	12-May
Swan Hill (b)	1-Sep	10-Sep	2805	5-Sep	19-Apr	24-Apr	27-Apr	30-Apr	3-May
Temora	25-Sep	10-Oct	3038	3-Oct	4-May	6-May	13-May	18-May	22-May
Trangie	12-Sep	30-Sep	4746	22-Sep	13-May	14-May	21-May	25-May	30-May
Urana	18-Sep	29-Sep	3282	23-Sep	30-Apr	4-May	8-May	12-May	16-May
Waikerie	23-Aug	29-Aug	1819	25-Aug	22-Apr	23-Apr	27-Apr	29-Apr	3-May
Walpeup	8-Sep	17-Sep	3318	11-Sep	29-Apr	1-May	4-May	10-May	13-May
Yarrawonga	25-Sep	2-Oct	3594	28-Sep	30-Apr	2-May	8-May	13-May	17-May

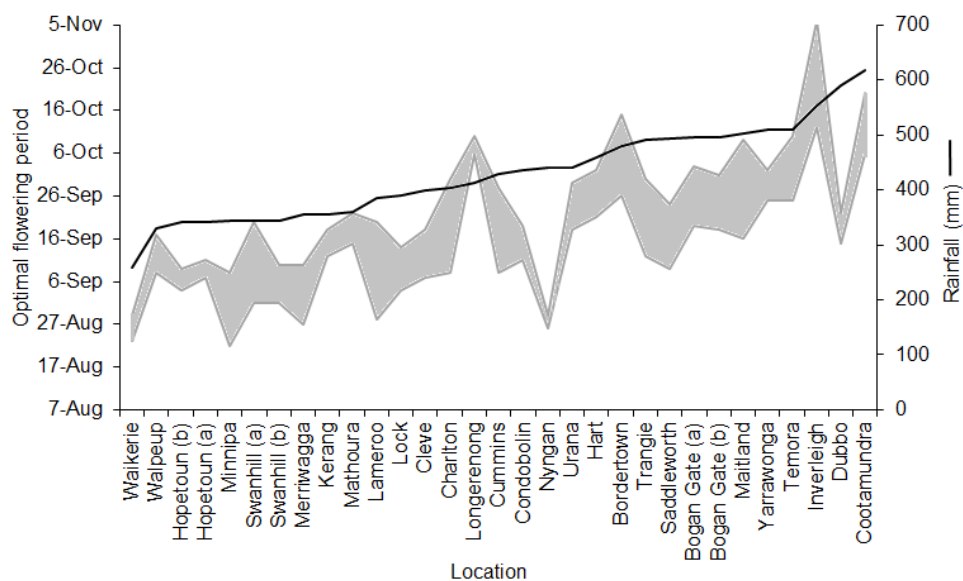


Figure 2: The relationship between optimal flowering period (shaded grey) of a mid-fast cultivar of wheat (Table 3), and mean annual rainfall (mm) (line) (Table 2) for 28 locations, where (a) and (b) refer to different soil types at the same location.

The 10th-90th percentiles of FHL yield simulated at each flowering date (Fig. 3) reveal the seasonal variability in the OFP. Depending on which environment factor had the greatest effect on yield at each location i.e. frost, radiation, heat or drought, the OFP shifted accordingly. At some locations, e.g. Lameroo (Fig. 3A), in low yielding seasons the OFP was earlier than in more favourable seasons, as early flowering allowed crops to escape spring drought. At other locations with high incidence of frost, e.g. Temora (Fig. 3B), the OFP was later in less favourable seasons, as later flowering allowed crops to escape frost. Higher yielding seasons also had a broader optimal period, and in the cases above largely overlapped with the optima in lower yielding seasons. In a practical sense, given seasonal conditions are unknown at sowing, wheat producers should aim to have crops flowering in the period bounded by 95% of the mean maximum yield achieved (Table 3).

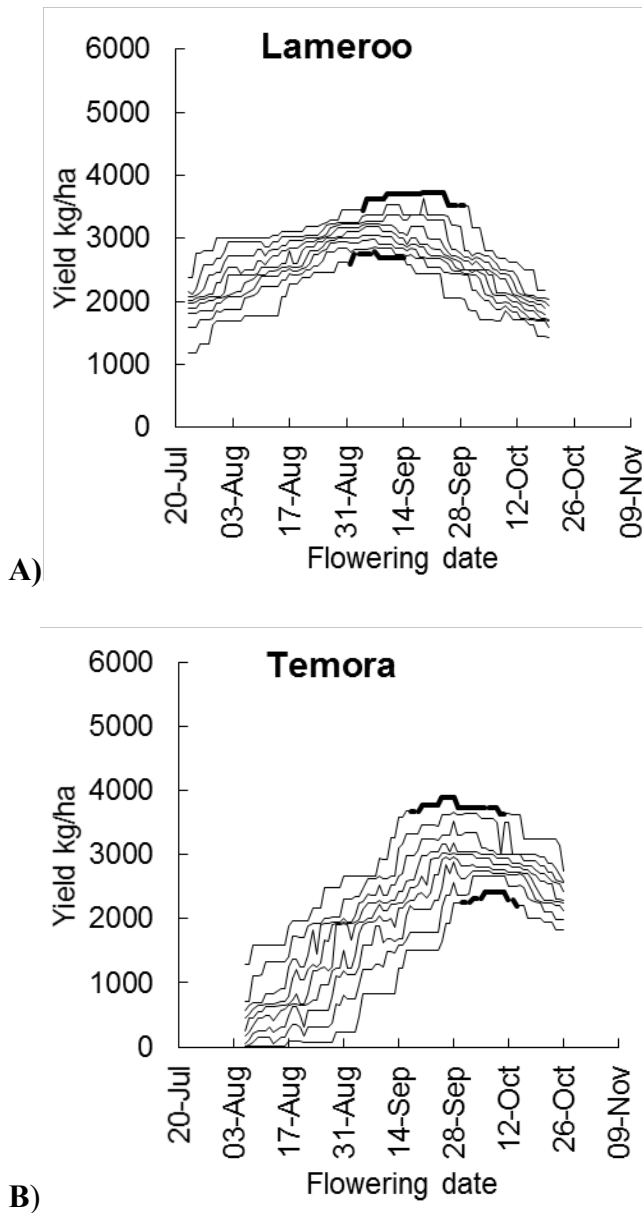


Figure 3: The relationship between frost and heat limited (FHL) yield (kg ha^{-1}) and flowering date for a mid-fast cultivar of wheat at A) Lameroo, SA and B) Temora, NSW split into percentiles. Lines represent the simulated 10th, 20th, 30th, 40th, 50th, 60th, 70th, 80th and 90th percentiles of yield and corresponding flowering date values generated from 16 sowing dates over 51-years (1963-2013). Darkened line is the optimum flowering period for the 10th and 90th percentiles defined by $\geq 95\%$ of the maximum mean yield.

Figure 4 shows how OFP have been defined using FHL yield. Figure 4 shows just 6 diverse locations, the same figures for all 28 locations can be found in Supplementary Figure 1. The degree of the incline or decline of the curves before or after the optimum for a location illustrates the influence of sub-optimal radiation and/or frost (before optimum), or accelerated development and/or drought and/or heat on grain yield (after optimum). For example, Minnipa (Fig. 4B) curves have a gentle incline showing that radiation and frost are less of a determinant on OFP, but the sharper decline after the optima shows heat and water stress play a larger role after peak yield is reached. In comparison, in locations such as Inverleigh and Dubbo (Fig. 4D and 4F), frost or sub-optimal radiation are greater determinants of the OFP, as seen by the sharp incline of the curves. The positive and negative standard deviation lines in Figure 4 show the variation around the mean, and reflect seasonal variability and the stability of a location's environment.

In this analysis we compared two different soils at three locations; Swan Hill, Hopetoun and Bogan Gate (Table 1). In each instance, there was a heavier textured soil with higher plant available water capacity (PAWC), and a soil with a lower PAWC. At Swan Hill the OFP for the lighter soil (APSoil file 719) was 10 days shorter than for the heavier soil (APSoil file 718) (Table 3). In Hopetoun, the flowering period for the lighter soil began 3 days later but was of similar duration as that of the heavier soil (5 and 6 days respectively) (Table 3). The flowering period for the two soils at Bogan Gate were very similar (Table 3). There was some indication that OFP on low PAWC soils were earlier than for higher PAWC soils, presumably because higher PAWC soils were more able to buffer against terminal drought.

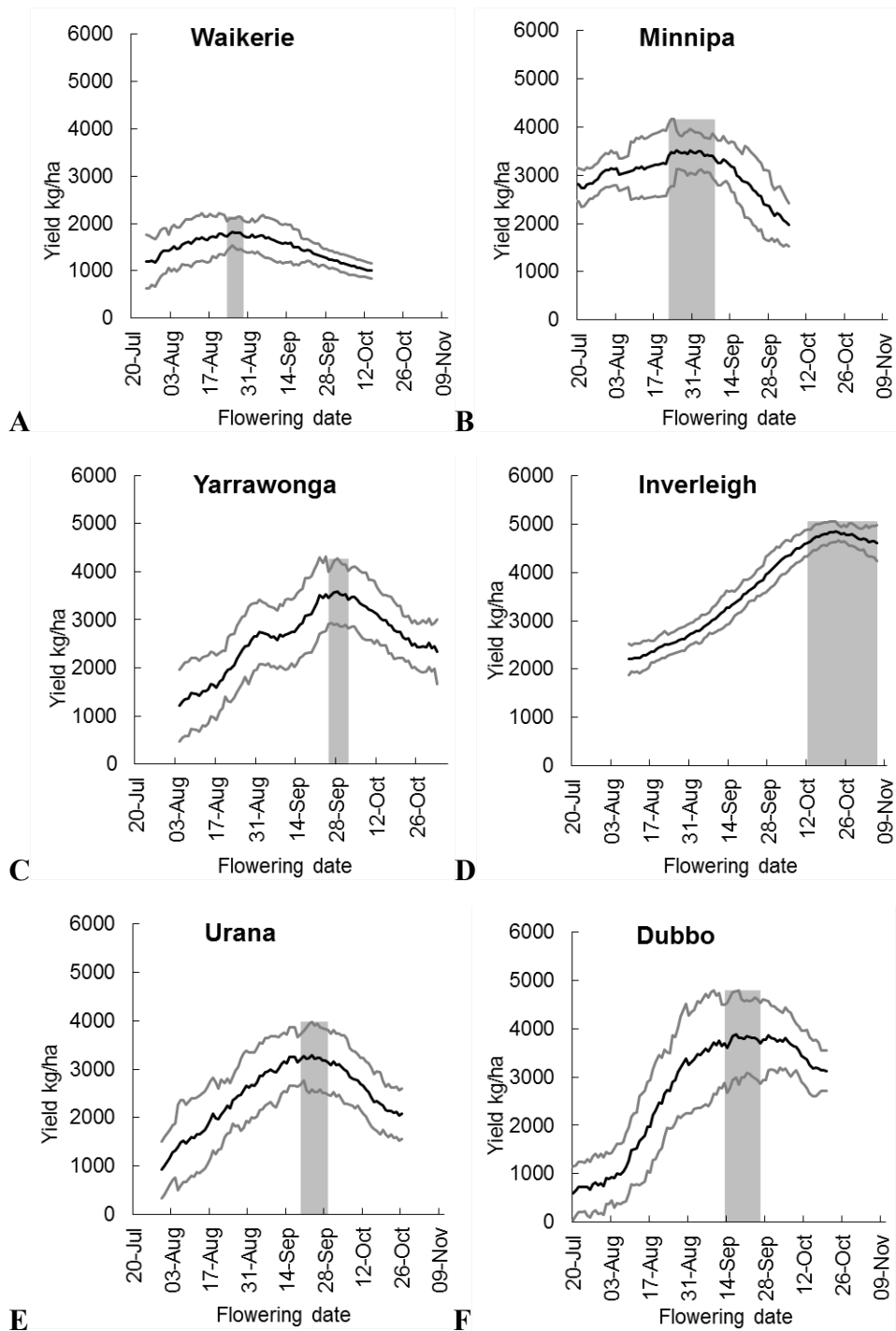


Figure 4: The optimal flowering period (OFP) for a mid-fast cultivar of wheat determined by APSIM simulation for A) Waikerie, SA B) Minnipa, SA C) Yarrawonga, VIC D) Inverleigh, VIC E) Urana, NSW F) Dubbo, NSW. Black lines represent the frost and heat limited (FHL) 15-day running mean yield (kg ha^{-1}). Grey lines represent the standard deviation of the FHL mean yield (kg ha^{-1}). Grey columns are the estimated OFP defined as $\geq 95\%$ of the maximum mean yield from 51 seasons (1963-2013). All locations shown as in Figure 4 are located in Supplementary Figure 1.

3.2 Relative importance of temperature extremes (frost and heat) and water stress in determining OFP

The OFP which has been defined for wheat in Figure 4 represents the combined effect of frost, heat and water stress and radiation on wheat physiological processes and yield. Figure 5 shows three of these sites again, but provides greater detail on how the OFP moves in response to these stresses, and how by using APSIM yield in addition to heat and frost rules gives a more accurate definition of the OFP, compared to using temperature extremes alone.

Figure 5A for Waikerie demonstrates how using extreme temperatures alone to calculate OFP can result in severe overestimates in the timing of its occurrence. The point at which heat and frost damage lines intersect (where combined damage is lowest), is 8 September, however the flowering date for peak FHL yield is 25 August, 14 days earlier. The peak potential yield (APSIM without frost and heat damage) is earlier again, at 9 August. At Temora and Longerenong there is a similar pattern, although the shifts were less extreme (Fig. 5B, 5C). At Temora the intercept of the frost and heat indices is the 9 October, but the peak FHL yield is achieved from a flowering date on 28 September. Without applying the heat and frost indices, the peak potential yield was achieved by flowering on the 5 September. At Longerenong, the intercept of the frost and heat index is 15 October, but the peak FHL yield and peak potential yield is achieved from a flowering date on 7 October. In all of these figures the combined effect of water stress, frost and heat during the reproductive phase in defining OFP is clear. Although only three examples are shown, similar patterns are observed at other sites included in this study. These examples clearly demonstrate that integration of both extreme temperatures and radiation, as well as water supply and demand as per our method are essential for accurate definition of OFPs.

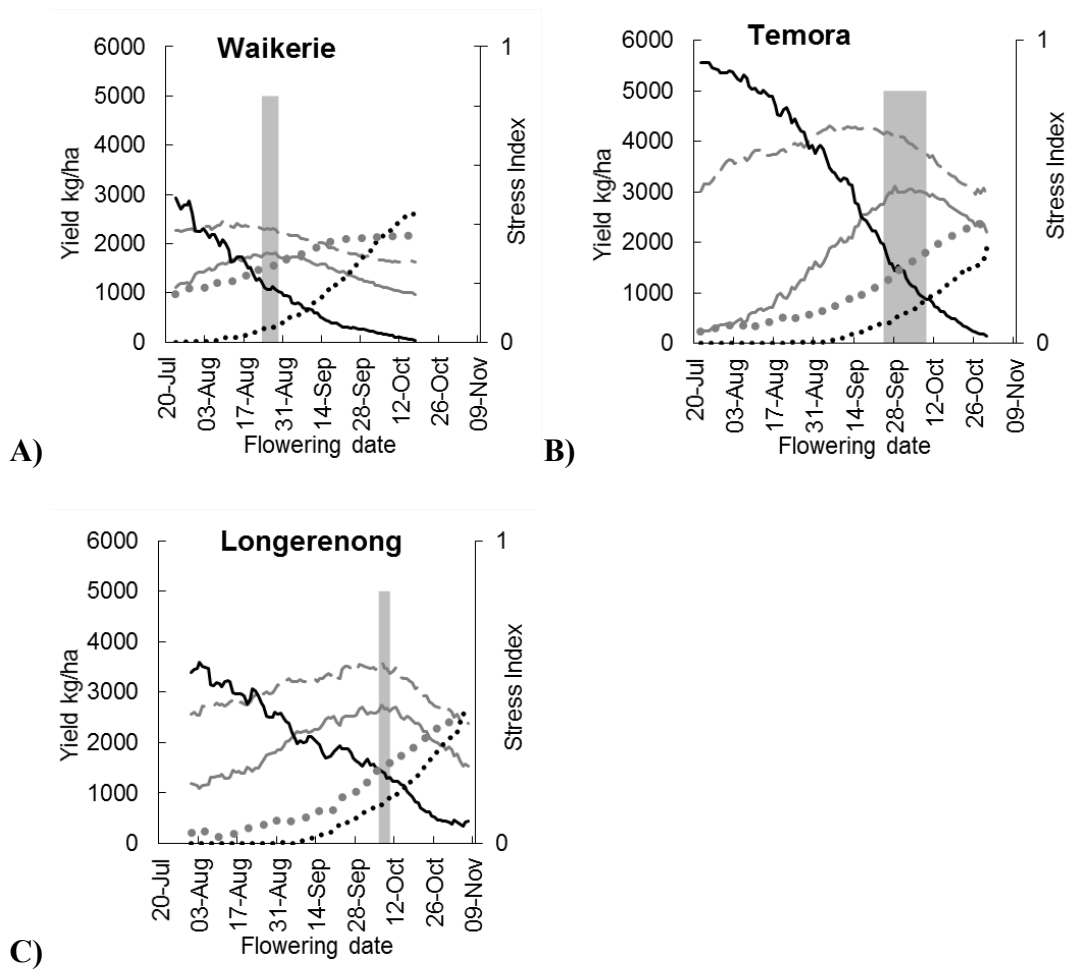


Figure 5: Potential yield (kg ha^{-1}) (— — broken grey line), frost and heat limited yield (kg ha^{-1}) (— solid grey line) and the mean heat (●●● dotted black line), frost (— solid black line) and mean water stress from floral initiation to maturity (●●● dotted grey line) indices (0 to 1) applied to yield plotted against flowering date for a mid-fast cultivar of wheat. A) Waikerie, SA B) Temora, NSW C) Longerenong, Vic. Grey columns are the estimated optimal flowering period defined as $\geq 95\%$ of the maximum mean yield in 51 seasons (1963-2013).

3.3 Implications for sowing time and genotype

Figure 6 and Table 4 illustrate that OFP for mid-fast, very-slow spring and winter cultivars are very similar in the environments where this comparison was made, but that the slower developing cultivars sown early have similar or higher yield potential.

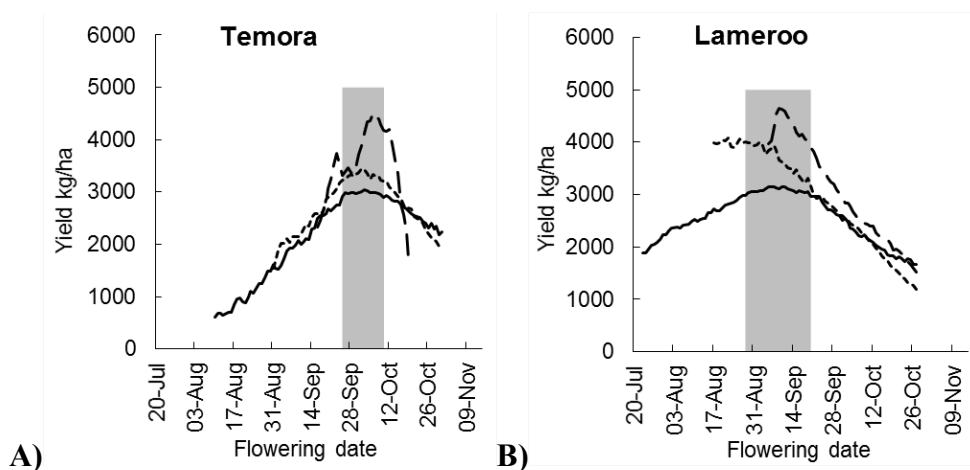


Figure 6: The 15-day running mean yield (kg ha^{-1}) and flowering date of different wheat development types at A) Temora, NSW and B) Lameroo, SA over a 51-year simulation (1963-2013). Mean yields are for a mid-fast developing spring wheat (solid line), a very slow developing spring wheat (dotted line), and winter wheat (broken line). Grey columns are the estimated optimal flowering period defined as $\geq 95\%$ of the maximum mean yield of a mid-fast cultivar.

Table 4: Simulated flowering date corresponding to peak mean frost and heat limited yield (kg ha⁻¹) and sowing date for cultivars of different development type at Temora, NSW and Lameroo, SA.

Maturity type	Temora			Lameroo		
	Peak mean yield (kg/ha)	Flowering date peak mean	Sowing date corresponding to peak yield	Peak mean yield (kg/ha)	Flowering date peak mean	Sowing date corresponding to peak yield
Winter	4514	9-Oct	12-Apr	4653	9-Sep	2-Apr
Very slow spring	3444	2-Oct	19-Apr	4086	22-Aug	22-Mar
Mid fast spring	3038	3-Oct	14-May	3154	7-Sep	6-May

3.4 Evidence of climate change

There is evidence that OFPs have shifted over the 51-year period considered in this study. At Lameroo the OFP for the years 1963-1997 was 4 to 19 September, Longerenong was 27 September to 2 October, and Charlton was 22 to 30 September. For the years 1998-2013 the OFP in Lameroo was 25 August to 8 September (Fig. 7A), Longerenong 8 to 11 September (Fig. 7B), and in Charlton 1-4 September (Fig. 7C). This can be attributed to lower than average rainfall and higher than average temperatures at flowering. Figure 8 illustrates climate change in Lameroo with a summary of September temperatures and growing season rainfall during the 51-year simulated time period.

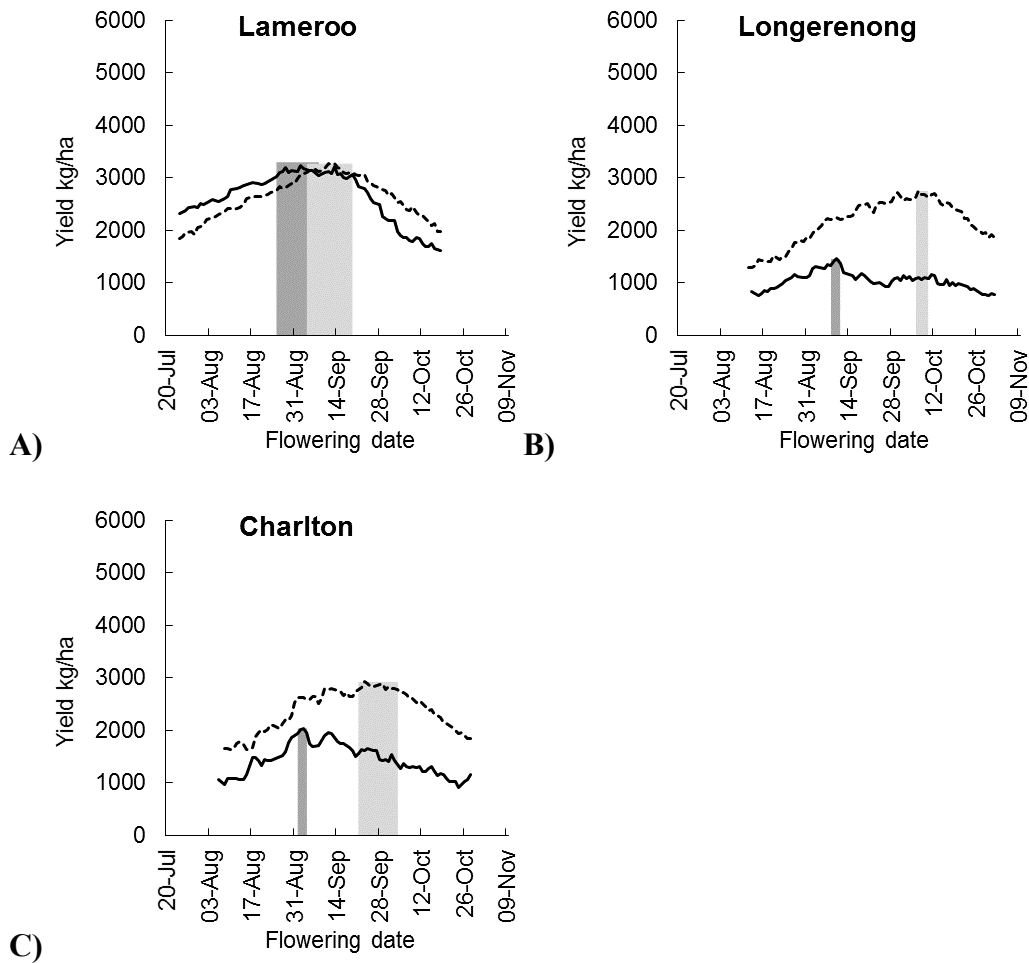


Figure 7: Estimated optimal flowering period (OFP) for mid-fast cultivar of wheat at A) Lameroo, SA and B) Longerenong, Vic C) Charlton, Vic for 35 years (1963-1997) (light grey column) and 16 years (dark grey column) (1998-2013). Mean frost and heat limited yield (kg ha^{-1}) for 1963-1997 (broken line) and for 1998-2013 (solid line). Estimated OFP is defined by $\geq 95\%$ of the maximum mean yield.

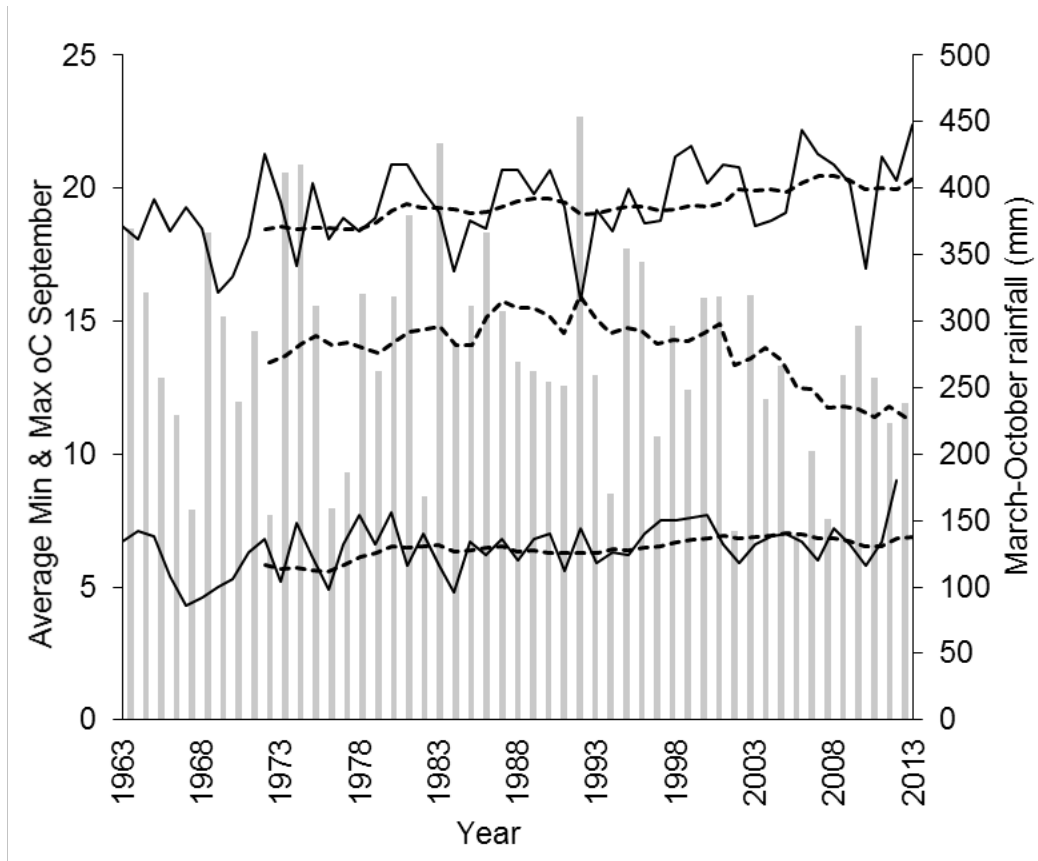


Figure 8: Growing season rainfall (columns) and average minimum and maximum temperature for September (solid lines) at Lameroo, SA. Broken lines are 10-year rolling means for rainfall and for minimum and maximum temperatures.

4. Discussion

4.1 Variation in optimal flowering periods

Variation in OFP duration indicated that defining OFP as 10 days either side of the optimum as proposed by Anderson *et al.* (1996) was not appropriate in all environments. We have used $\geq 95\%$ of maximum yield to define the OFP, and differences in the duration of OFPs were an indication of seasonal variability in a given environment, and the possible reasons causing the variability could be numerous. Wide OFPs may suggest that rainfall, frost and heat were more variable, as highest yields were achieved across a broader range of flowering dates e.g. Lameroo. Conversely wide OFP can also suggest a benign environment, resulting in a wide and stable environment for flowering e.g. Inverleigh. A narrower OFP suggests that an environment was less variable because optimal conditions for flowering occurred at approximately the same date in each season. Alternatively, a narrow period may indicate that the environment restricts the OFP due to overlap between the period of declining frost risk and the period of increasing drought and heat risk e.g. Hopetoun. Regardless of the reasons behind the duration of the OFP, a narrow OFP indicates an environment in which growers must be timely with sowing and cultivar selection in order to maximise yields.

Defining the OFP as $\geq 95\%$ of maximum yield as we have done here does have its limitations. Firstly, in low yielding environments the difference in absolute yields of crops that flower inside the OFP and those that flower outside will be very small e.g. at Waikerie where maximum mean yield was 1819 kg/ha and the OFP will be deemed to have ended when yields fall below 1728 kg/ha which is a small difference in absolute terms. An alternative approach would be to nominate an absolute yield value as the threshold e.g. 0.3 t/ha, however in a low yielding environment 0.3 t/ha represents a large portion of production. Our criteria has also defined very narrow OFPs in some environments (e.g. Longerenong 6-10 October) and it may be more appropriate to use a less stringent criterion e.g. $\geq 90\%$ of maximum yield which at Longerenong would expand the OFP to 23 September to 15 October. However, any criteria used to define OFP will ultimately be arbitrary and useful mainly for comparing environments rather than informing management. Supplementary Figure 1 can be used to visually estimate how the OFP might change using different criteria. From a management perspective, growers in all environments will be best to target the flowering date that corresponds to

the maximum mean yield defined in Table 3, and know that moving away from this date is likely to reduce yield.

Zheng *et al.* (2012) also identified the OFP for two of the sites simulated here, Waikerie and Dubbo. At both sites the OFP in the Zheng *et al.* (2012) study were of a longer duration and later in the season than estimated here. While exact dates were not given in Zheng *et al.* (2012), for Waikerie the approximate OFP was the first week of September to mid- October, whereas by including water stress as a factor we found it to be much earlier and shorter from 23 August to 29 August. For Dubbo, Zheng *et al.* (2012) calculated the OFP from the last week of September to mid- November, while here it was 13 to 26 September. These differences in OFP reflect the methods used to calculate the OFP. Zheng *et al.* (2012) considered only the risk of heat and frost periods (i.e. temperature extremes) to define OFP, while here we also accounted for water stress and radiation effects on yield. This indicates that estimates of OFP defined only by extremes of temperature tend to be later in the season than when effects of drought are included.

The OFPs identified by our simulation method are well validated by recent field studies conducted in close proximity to the study locations. Field experiments likewise integrate effects of drought, frost and heat on grain yield. In a time of sowing by cultivar experiment at a field site 16 km south of Saddleworth, Hunt *et al.* (2014) found that highest yields were achieved by treatments that flowered on 21 September, which falls within the OFP defined here of 12 to 23 September. Flohr *et al.* (2017a) report two years of field data from Temora in which highest yields were achieved by cultivars that flowered on 29 September in the relatively hot and dry year of 2015, and 10 October in the very favourable year of 2016. Hunt *et al.* (2014) found that in 2013 highest yields were achieved by treatments that flowered between 24 September and 1 October. Harris *et al.* (2017a, 2016) conducted experiments at a site 80 km south of Temora, and found that highest yields were achieved by treatments that flowered around 3 October in 2015 and 7 October in 2016. All but one of these dates fall within the OFP defined in this paper of 25 September to 10 October, and are in close agreement with the optimal heading date of 1 October stated in Penrose (1997) via personal communication from R. Martin. In the hotter, drier environment of Condobolin, Harris *et al.* (2017a) reported that highest yields came from treatments that flowered around 7 September, which is slightly earlier than the window of 11 to 19 September defined here. Fettell *et al.* (2011) describes the Condobolin environment "...frost frequently drops substantially between

September 14 and 24, but average maximum temperature and evaporative demand increase rapidly from September 19 to 30” and found that highest yields came from treatments that flowered between 18 and 23 September in 2006, around 24 and 31 August in 2009 and between 27 September and 7 October in 2010, flowering sometimes earlier and sometimes later than our defined OFP. Gomez-Macpherson and Richards (1995) found that highest yields at Condobolin were achieved later than this (30 September to 10 October), however their experiments were conducted in 1989 and 1990 prior to the recent warming and drying of the Australian climate that has likely shifted OFP (Figure 7). As stated previously, the strength of our approach over field experiments is a large reduction in cost and the ability to define OFPs for many more sites and seasons.

4.2 Relative importance of temperature extremes (frost and heat) and water stress in determining OFP

Previous authors have defined OFPs by the occurrence of the last frost event and first heat event (Zheng *et al.* 2012). We have shown that OFPs are actually defined by a trade-off between drought, radiation, frost and heat, rather than extremes of temperature alone (Fig. 5). Any crop flowering on the optimal date for yield in a given combination of site and season may experience all three abiotic stresses to varying degrees during their critical period. The OFP we have presented represents the period that minimises the combined yield reduction from all three stresses. To our knowledge, this is the first comprehensive study to identify OFP for wheat across south-eastern Australia that captures the impact of these stresses across a wide range of climate and soil-type variation. The approach would be applicable to other crops (e.g. barley, canola, grain legumes) where yield is also dependant on flowering in an optimal period.

4.3 Implications for sowing time and genotype

Defining OFP is useful because it allows identification of appropriate sowing date x genotype combinations to optimise yield for a specific environment (Anderson *et al.* 1996). Timing of flowering in a given environment is a function of sowing date, genotype (cultivar) and prevailing seasonal temperatures. Sowing date and cultivar selection are two major management decisions made by wheat producers at the start of the growing season, the objective being to select combinations that lead to crops flowering during the OFP. Throughout the history of wheat cultivation, farmers and wheat breeders have selected developmental patterns which best match the conditions

under which they are grown (Cockram *et al.* 2007; Kamran *et al.* 2014). Since the introduction of photoperiod insensitive semi-dwarf wheat cultivars during the 1970s, breeding programs in SEA have focussed overwhelmingly on spring wheats of mid- to fast-maturity (Davidson *et al.* 1985; Eagles *et al.* 2009). The development pattern of these cultivars matched the timing of once reliable autumn planting rains in April-May with OFPs in spring. However, optimal sowing times for mid-fast cultivars (predominantly April-May, Table 3) which allow them to flower in the OFPs unfortunately coincides with the most severe period of recent rainfall decline identified by Cai *et al.* (2012) and Pook *et al.* (2009). New combinations of genotype x management will be required to ensure crops continue flowering in the OFPs. Strategies could include using stored soil water from either summer rainfall (Hunt and Kirkegaard 2011; Verburg *et al.* 2012; Hunt *et al.* 2013), or long fallow (Oliver *et al.* 2010) to establish crops. This practice has been shown to be successful in low rainfall locations in the Pacific Northwest of the USA (Schillinger and Young 2014) and has previously been proposed for SEA by Kirkegaard and Hunt (2010). This practice would be facilitated by using genotypes with long coleoptiles which would allow them to emerge on stored soil water from greater soil depths (Rebetzke *et al.* 2007a). Another option would be to use winter wheat genotypes which can be established much earlier than spring genotypes when soil water is available, but still flower during the OFP as demonstrated by Penrose and Martin (1997). Establishment would then occur prior to the traditional sowing window, as late summer and early autumn rainfall has been more reliable in recent decades (Hunt and Kirkegaard 2011). Previous simulation and field experiments have demonstrated that winter genotypes sown early yield as well as (Gomez-Macpherson and Richards 1995; Kirkegaard *et al.* 2014; Frischke *et al.* 2015) or better (Coventry *et al.* 1993; Moore 2009; Bell *et al.* 2015) than spring genotypes sown later. Figure 6 and Table 4 support these findings. Now that OFP have been accurately defined, breeders and agronomist can use our definitions to target OFP in any given season, and depending how the season breaks, provide growers with new genotype (development type, long coleoptile) x sowing (early autumn sowing, deeper sowing) strategies, such as listed above, for specific environments to maximise yield in a variable climate.

The sowing date ranges targeting OFP estimated in this study (Table 3) are consistently of shorter duration than those currently recommended by state departments of

agriculture. For example, the recommended sowing date of mid-fast spring maturity types sown in the Victorian Mallee is between the last week of April, and the second week of June (Department of Economic Development Jobs Transport and Resources and GRDC 2015). According to our simulations, Kerang, situated at the south eastern corner of the Victorian Mallee has an optimal sowing date range of 25 April to 9 May, with a median sowing date of May 3. Similar conclusions can be reached at other sites in this analysis such as Longerenong in the Wimmera region of Victoria, Charlton in North Central Victoria and Yarrowonga in North Eastern Victoria, and also some sites in NSW (Matthews *et al.* 2015). Whilst state recommendations appear to correctly estimate the start of the sowing period, they greatly overestimate the end of the optimal period. Currently no “sowing date guide” exists for South Australian farmers, but we believe trends to be similar there.

4.4 Climate change impacts on flowering and sowing dates

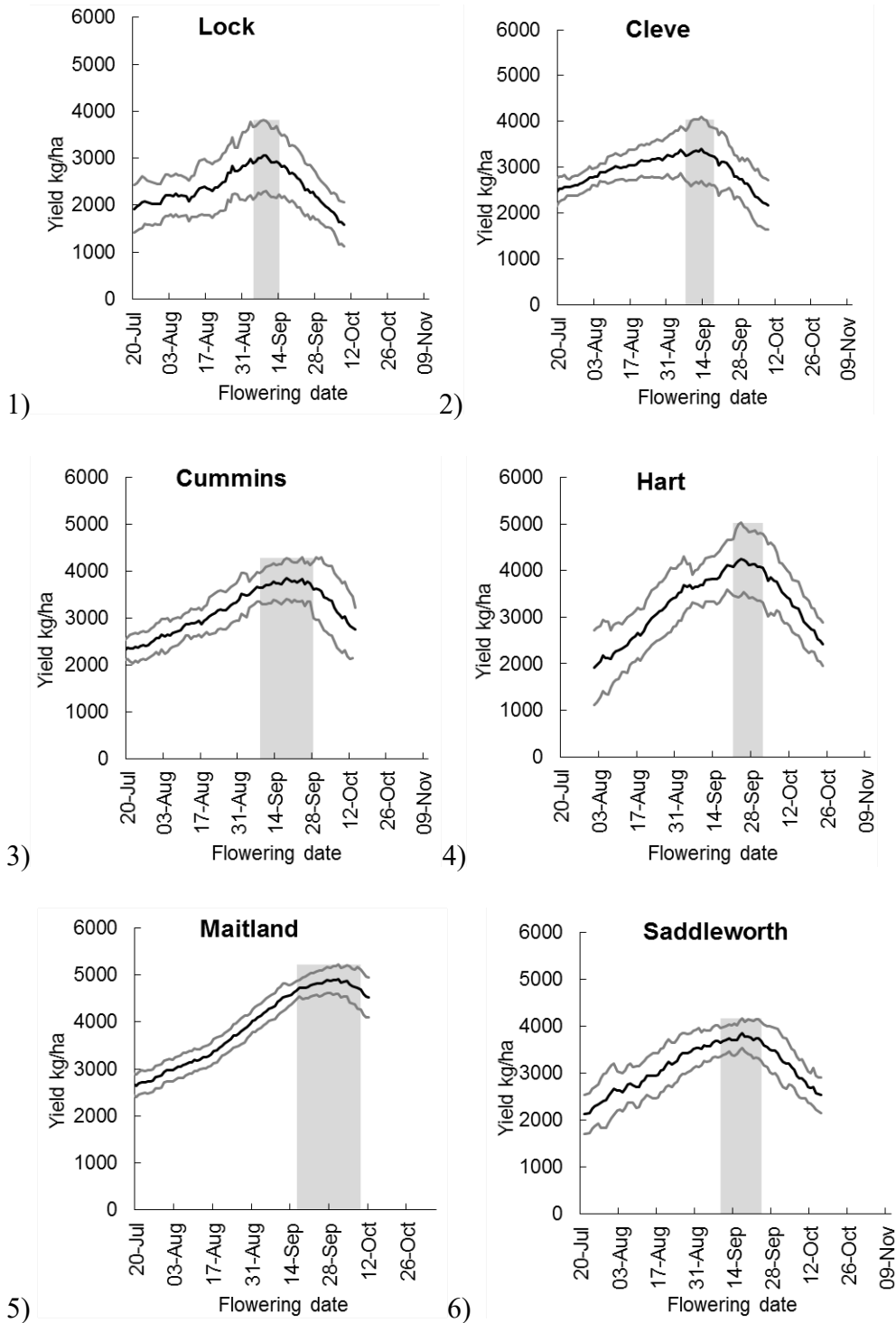
Global minimum and maximum temperatures are increasing (IPCC 2013). By 2030, Australian temperatures are predicted to rise between 1.9°C and 5°C (CSIRO and Bureau of Meteorology 2015). Figure 7 shows that OFPs have shifted at three sites, Lameroo, Longerenong and Charlton over the 51-year period considered in this study. A shift to an earlier OFP can be expected in other areas of the SEA wheat-belt where autumn rainfall decline and increased spring drought has been experienced in the period 1998-2013, particularly prevalent during millennium drought. APSIM has been used to analyse crop development under future climates in numerous studies. Zheng *et al.* (2012) studied wheat development under future climate scenarios, and estimated that both sowing and flowering dates would occur earlier. Yang *et al.* (2014) also predicted through simulation that flowering will be 11 days earlier on average in the Australian wheat belt. This was explained by earlier last frost days and earlier first heat events in future climates. However, predictions of increased minimum temperatures and decline in frost incidence for SEA incorporated in the studies of Zheng *et al.* (2012) and Yang *et al.* (2014) are at odds with observed increases in the occurrence and severity of late-season frosts across the region (Crimp *et al.* 2015). The Millennium drought (1996-2009) occurred within the 1998-2013 simulated time period, and was characterised by lower than average rainfall and higher temperatures (Fig. 8). Our study has demonstrated that in low rainfall sites and seasons, highest yields were achieved when the wheat crops flowered earlier, escaping spring drought (Fig. 2, 3, 5 and 7). This

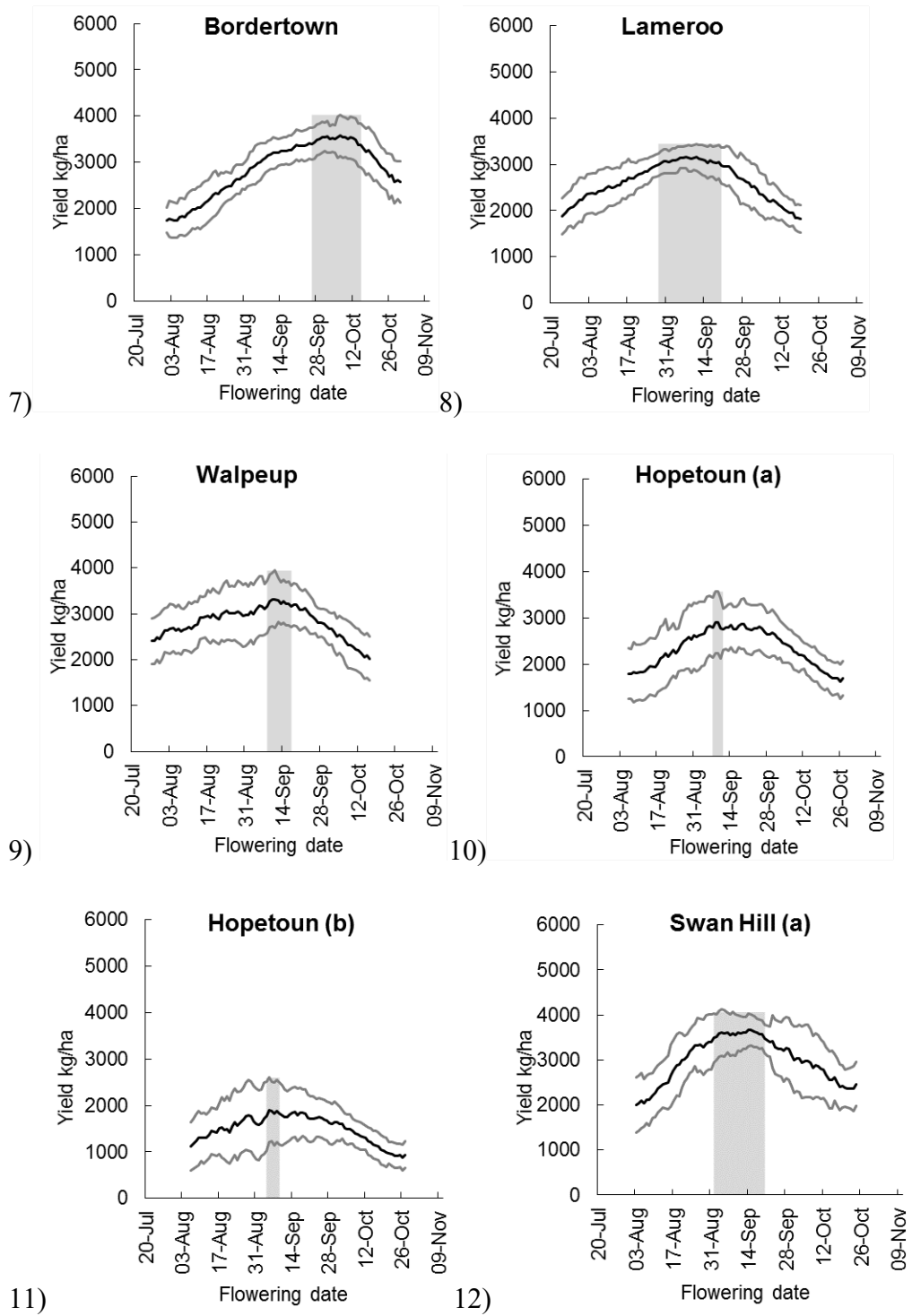
emphasizes the importance of considering patterns of water supply and demand when defining flowering periods rather than temperature extremes alone.

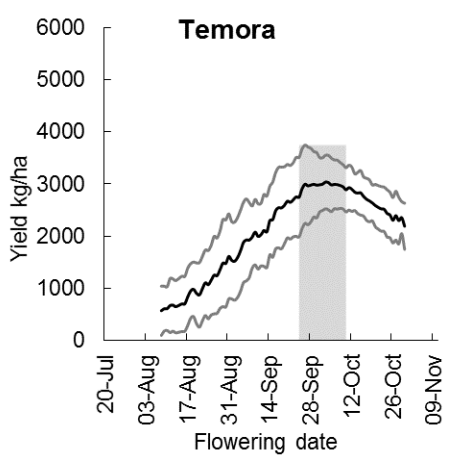
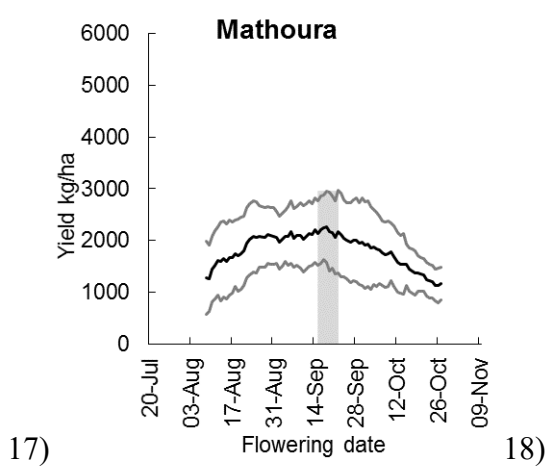
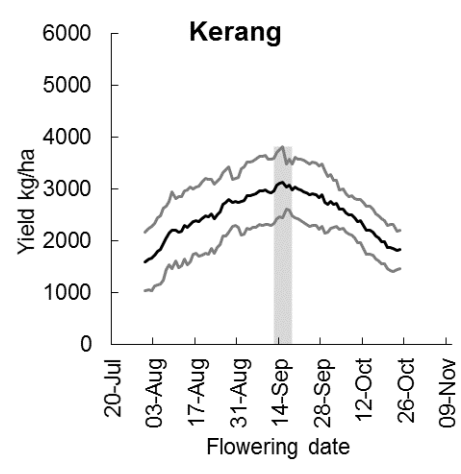
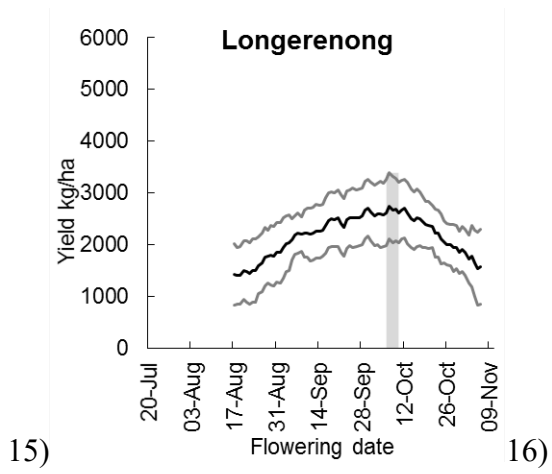
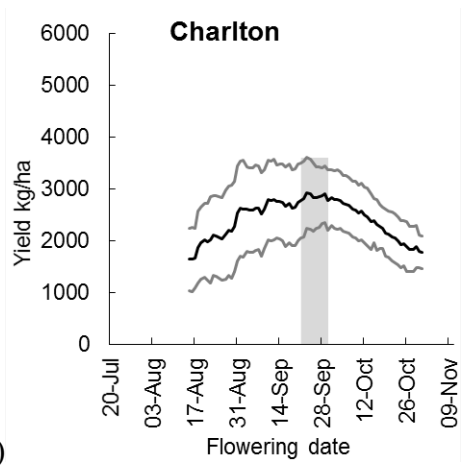
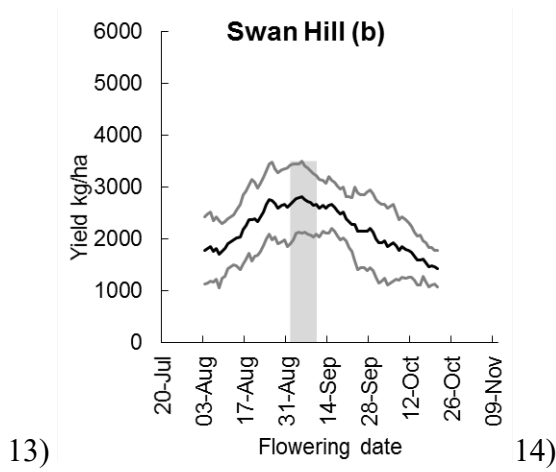
5. Conclusion

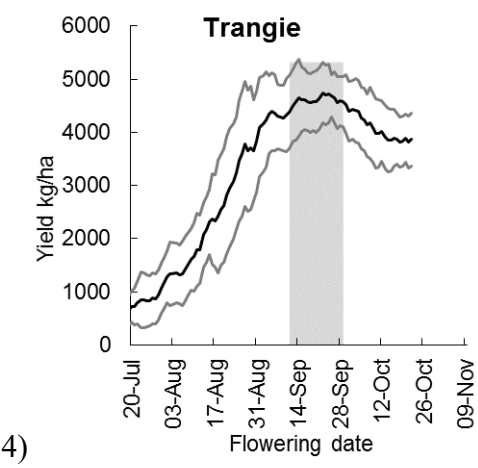
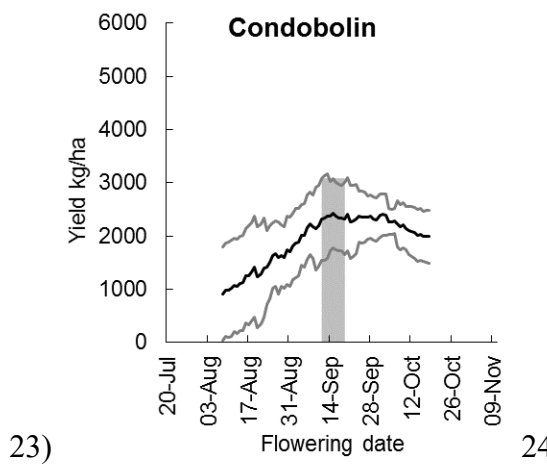
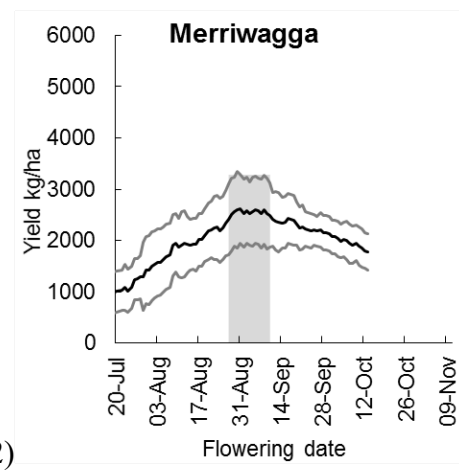
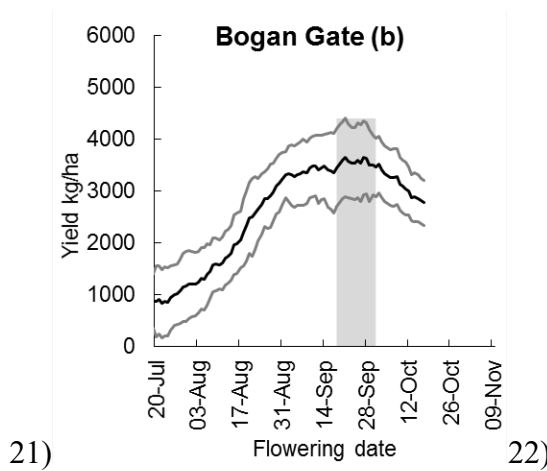
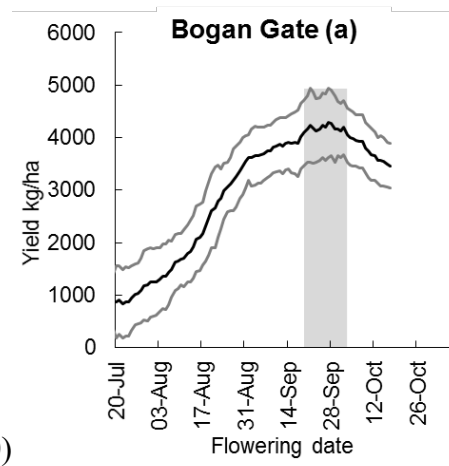
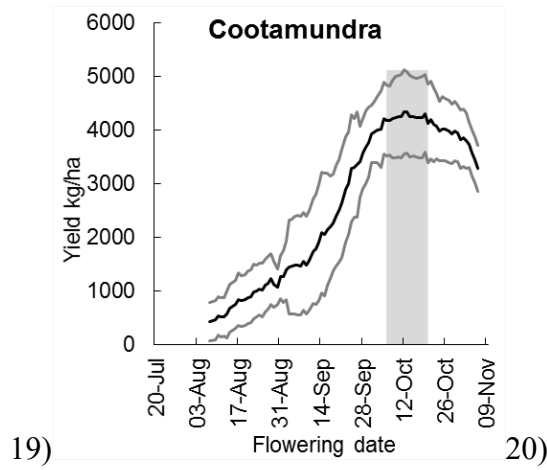
OFPs for wheat in SEA vary with site and season and are driven by the combined effects of seasonal water supply and demand, and extremes of temperature during critical periods of development. Sowing dates required for current cultivars to achieve OFPs coincide with a period of marked autumn rainfall decline which has reduced grain yields across the SEA region. Further work to identify new G x M strategies that target OFPs which account for water and temperature stress is required, to avoid current and future yield losses associated with autumn rainfall decline.

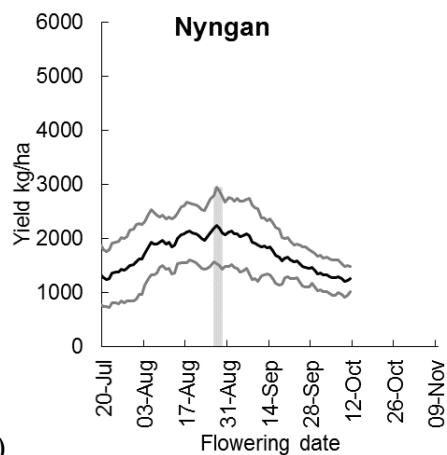
6. Supplementary material











25)

Figure S1: Optimal flowering period of wheat for 22 locations simulated and not displayed in Figure 4. The optimal flowering period for a mid-fast cultivar of wheat determined by APSIM simulation for 1) Lock, SA 2) Cleve, SA 3) Cummins, SA 4) Hart, SA 5) Maitland, SA 6) Saddleworth, SA 7) Bordertown, SA 8) Lameroo, SA 9) Walpeup Vic 10) Hopetoun a, Vic 11) Hopetoun b, Vic 12) Swan Hill a, Vic 13) Swan Hill b, Vic 14) Charlton, Vic 15) Longernong, Vic 16) Kerang, Vic 17) Mathoura, NSW 18) Temora, NSW 19) Cootamundra, NSW 20) Bogan Gate a, NSW 21) Bogan Gate b, NSW 22) Merriwagga, NSW 23) Condobolin, NSW 24) Trangie, NSW 25) Nyngan, NSW. Black lines represent the frost and heat limited (FHL) 15-day running mean yield (kg ha^{-1}). Grey lines represent the standard deviation of the FHL mean yield (kg ha^{-1}). Grey columns are the estimated OFP defined as $\geq 95\%$ of the maximum mean yield from 51 seasons (1963-2013).

Chapter 3

Genetic yield gain in southern New South Wales wheat cultivars released between 1901-2014 as revealed from synchronous flowering during the optimum period

STATUS: Published May 2018

Flohr BM, Hunt JR, Kirkegaard JA, Evans JR, Swan A, Rheinheimer B, 2017, Genetic yield gain in southern New South Wales wheat cultivars released between 1901-2014 revealed from synchronous flowering during the optimum period, *European Journal of Agronomy* **98**, 1-13



Image 3. Plots ready for harvest in Temora, NSW on November 2016

Abstract

Quantifying historic increases in water-limited potential yield (PY_w) achieved through breeding provides insight into associated changes in physiology and can assist with future cultivar improvement. We compared PY_w of bread wheat cultivars popular in southern New South Wales, Australia released between 1901 and 2014. In both 2015 and 2016, cultivars were sown at multiple sowing dates to allow comparisons to be made at a consistent optimal flowering date (early October), and thus control for the large differences in life cycle duration. Seasonal conditions were close to average in 2015 and extremely favorable in 2016. In both, grain yield increased across the historic period studied at 26 kg/ha per annum, regardless of whether a common sowing date or flowering date was used. Yield gain was not linear, and there was a period of rapid yield increase during the middle of the 20th century, that culminated with the release of semi-dwarf cultivars. Yield gain was relatively slower from the 1980s until the present day, possibly due to selection for grain quality traits (grain size and protein) at the expense of grain number. Historic yield increases were not associated with an earlier flowering date, but with an interplay between greater grain number/m² and greater grain weight which was the result of increased partitioning of assimilates to spikes, and greater number of grains per unit spike weight (fruiting efficiency). Greater partitioning to the spike in modern cultivars was associated with reduced dry matter (DM) production prior to flowering. Modern cultivars have a less stable flowering time across sowing dates, and shorter life cycle, but improved partitioning in modern cultivars appeared decoupled from shorter developmental phases prior to flowering. The performance of the novel vernalisation sensitive cultivar Longsword showed that future yield gain may be achieved through the combination of early sowing and slow development, increased DM production and superior partitioning to grain.

1. Introduction

Despite regular drought and generally low yields in comparison to countries such as China, the UK and USA, Australian average farm yield (FY) for wheat has increased on average from 0.5 t/ha to 2 t/ha over the 20th century (Hochman *et al.* 2017). FY is determined through field, farm, district, regional or national averages, whereas potential yield (PY) is defined as the measured yield of the best cultivar, grown with optimal agronomy and without manageable biotic and abiotic stresses (Fischer 2015). Water-limited potential yield (PY_w) is the same as PY, but yield is limited by the amount of seasonal available water (Fischer 2015). Increases in PY_w, achieved through wheat breeding are an important component of the production increases observed in Australia and around the world that have enabled wheat production to keep pace with global demand (Fischer *et al.* 2014). Today, further increases in wheat yield are necessary in order for Australian growers to cover increasing costs of production and remain competitive in a global market. Hochman *et al.* (2017) demonstrated that whilst national PY_w (as estimated by simulation) has decreased since 1990 due to declining rainfall and increasing temperatures, FY has been stable due to Australian wheat farmers closing the yield gap (where yield gap = PY-FY as per Fischer 2015). This reduction in yield gap is likely due to adoption of advanced technologies both in agronomic management such as those described by Kirkegaard *et al.* (2014), and genetic yield improvements made by breeding.

One method to accurately estimate the genetic component of increases in PY_w and FY is to grow a number of historic and modern cultivars side by side under typical rain fed conditions, with otherwise optimal agronomy and no pests or diseases (Fischer 2009). This method allows quantification of yield improvement under current agronomy and climate, insight into associated changes in physiology and can assist with future improvement (Sadras and Lawson 2011). Such studies have documented chronological changes in local cultivars in Western Australia (WA) (Perry and D'Antuono 1989; Siddique *et al.* 1989a; Siddique *et al.* 1989b) and South Australia (SA) (Black *et al.* 2008; Saunders 2008; Sadras and Lawson 2011; Kitonyo *et al.* 2017). However, no published studies have considered cultivars adapted to the important grain producing region in the southern half of New South Wales (NSW). The studies from WA and SA demonstrated that Australian breeders have increased PY_w by breeding cultivars which flower earlier, have reduced plant height, increased harvest index (HI) and grain number

per m² (grain/m²) (Fischer *et al.* 2014). Fischer *et al.* (2014) predicted similar findings in other parts of eastern Australia, though publications are scarce.

Compared to the west of the country, high rainfall regions of south-eastern Australia experience cooler winters, relatively mild springs and typically have an optimal flowering period for wheat from late September to mid-October (Flohr *et al.* 2017b). Significant yield progress has been made by breeders selecting cultivars that develop from autumn establishment to flower during the optimal flowering period (Richards *et al.* 2014). Cultivar rate of reproductive development is dependent on sensitivity to temperature (earliness *per se*), vernalisation (response to cold) and photoperiod (response to daylength) (Slafer *et al.* 2015b). Since the release of the cultivar Federation (1901), cultivars have varied in sensitivity to vernalisation and photoperiod, but generally sensitivity to both has decreased with time (Pugsley 1983; Davidson *et al.* 1985; Richards 1991; Eagles *et al.* 2009). Although faster development is advantageous in drought the consequence of reduced sensitivity to vernalisation and photoperiod, is that seasonal temperature variation can alter crop development rates such that flowering does not reliably occur within the optimal flowering period (Loss and Siddique 1994). Vernalisation sensitivity has been linked to greater flowering date stability and extended sowing date opportunities (Penrose and Martin 1997; Flohr *et al.* 2017c). Depending on development rate (fast, mid, slow etc.), different sowing dates are required for crops to flower within the optimal flowering period to maximize yield (Kerr *et al.* 1992; Flohr *et al.* 2017b). Therefore flowering date is a function of cultivar rate of development and time of sowing (TOS), in which sowing time can be controlled (to a degree) by breeders, agronomists and farmers.

Bodner *et al.* (2015) and Flohr *et al.* (2017b) have stressed the importance of time of flowering on grain yield in drought prone environments. Thus it is logical that previous historic wheat experiments, which have generally been sown later than is optimal for all cultivars, have associated some of the yield increase observed to faster development and earlier flowering dates (Perry and D'Antuono 1989; Siddique *et al.* 1989a; Siddique *et al.* 1989b; Richards 1991). Studies have also hypothesized that breeding for earlier flowering has resulted in chronological decrease in duration of pre-flowering growth, through a shorter vegetative phase and improved partitioning of resources to the spike to increase grain/m² (Kirby *et al.* 1989; Siddique *et al.* 1989b; Siddique *et al.* 1990b). Most of these experiments have been planted on a single date, erring on the late side of the

optimal sowing date, and consequently not all cultivars flowered within the optimal flowering period. Thus genetic yield gain observed from these studies may be confounded by the effects of sowing date, which although historically dependent on timing of opening rains, can now usually be manipulated by growers through management such that it can be optimal for cultivars with different development speeds (Anderson *et al.* 1996). Therefore the questions still remain; how much observed yield gain is due to earlier flowering, how much yield gain is due to reduced duration to flowering, and how much yield gain is due to inherently better partitioning of assimilates to grain?

To answer these questions we measured yield gain and associated change in the phenology and physiology of an historic cultivar set sown with multiple sowing dates, such that flowering of at least some sowings occurred concurrently and within the defined optimal flowering period, thereby controlling for the large genetic differences in duration of life cycle that is common across such sets. A secondary aim was to fill the gap in relation to quantifying the genetic yield gain and change in physiology of popular southern NSW bread wheat cultivars. Thirdly, to compare the growth and development patterns of a novel wheat ideotype (fast-winter) that may interact with management (earlier sowing) to offer significant future increases in PY_w .

2. Materials and methods

2.1 Site, treatments and agronomy

A field experiment using an historic set of milling quality spring wheat cultivars was conducted at the Temora Agriculture Innovation Centre (-34.4064°S, 147.5259°E), NSW in 2015 and 2016. Cultivars were selected based on historic popularity (Fitzsimmons 1991; Brennan and Bialowas 2001; GrainCorp 2014) among growers in southern NSW since 1900. The last cultivar in the series (Condo) was chosen on the basis of high yield in national variety evaluation trials (ACAS 2007), being the highest yielding and highest quality cultivar in southern NSW at the time of its release in 2014. Seed of historic lines was obtained from the Australian Winter Cereals Collection, and grown in rows at Black Mountain, Australian Capital Territory in 2013 to confirm type, purity and to bulk seed for field experiments. The fast-winter cultivar Longsword (Flohr *et al.* 2017c; Hunt 2017), recently released (2017) by Australian Grains Technology (AGT) was also included in the series to compare against modern and historic spring

cultivars, but was not included in chronological regressions or means shown in the results.

All cultivars were sown at four TOS (Table 1) between mid-April to mid-May and had four replicates. Twelve wheat cultivars were grown in 2015 and ten in 2016 (Table 2). TOS is defined as the calendar date at which seeds become imbibed and begin the process of germination. For instance, this could be the date on which they are planted into a moist seed bed, or the date on which they received rainfall/irrigation after being sown into a dry seed bed. In 2016 the first two TOS were irrigated with 15 mm of water which was applied to all plots of that TOS using pressure compensating drip irrigation. This irrigation is assumed not to have contributed to crop transpiration and yield, as 2016 experienced an extremely wet winter and spring during which the soil profile filled below rooting depth. In 2015 the target plant density was 120 plants/m², and plots were 12 m x 1.8 m with 305 mm row spacing. In 2016 the target plant density was 140 plants/m², and plots were 10 m x 1.8 m with 305 mm row spacing. In all experiments, chemical fertilisers and pesticides were applied such that nutrients, weeds, pests or diseases did not limit yield.

Table 1: Sowing dates of the field experiments at Temora in 2015 and 2016

Time of sowing	2015	2016
1	17 April	15 April
2	27 April	27 April
3	7 May	6 May
4	15 May	15 May

2.2 Flowering date- and sowing date-balanced data sets

The results section of this paper compares two sets of data, flowering date (FD)-balanced data and sowing date (SD)-balanced data. FD-balanced data only uses data collected from cultivar*sowing date combinations that generated near-simultaneous flowering dates during the optimal flowering period of 25 September to 10 October in Temora (as per Flohr *et al.* 2017b). Table 2 shows the sowing date which resulted in simultaneous flowering for each cultivar in each season. The SD-balanced data set uses cultivar*sowing date treatments that were sown on the same sowing date. The sowing date used for this data set in both seasons was TOS 3. TOS 3 represents a common sowing date to the area where the research experiment was conducted. In 2015 this was 7 May, and in 2016 6 May. Only a single TOS in each year (7 May in 2015 and 6 May

in 2016) is shown for cultivar Longsword. In both years, flowering of Longsword occurred within the optimal flowering period, and represented both FD- and SD-balanced data for this cultivar (Table 2), and suitable for comparison to historic and modern cultivars.

Table 2: The time of sowing that generated near-simultaneous flowering dates (flowering date-balanced data) within the optimal flowering window for cultivars grown in 2015 and 2016. Grey shading indicates that cultivar was not grown in 2016.

Cultivars	Year of release	2015 sowing date with simultaneous flowering	2016 sowing date with simultaneous flowering
Federation	1901	1	1
Ford	1916	2	
Ranee	1924	2	2
Bencubbin	1929	2	
Gabo	1945	4	4
Olympic	1956	1	1
Heron	1959	2	2
Condor	1973	2	3
Banks	1979	2	3
Janz	1989	2	3
Gregory	2004	2	3
Condo	2014	4	4
Longsword	2017	3	3

2.3 Measurements and calculations

To compare the two experimental seasons to the long term average at Temora (station number 073151, 6 km from the site), degree days i.e. $TT = \sum ((T_{\min} + T_{\max})/2) - T_{\text{base}}$ accumulated using 0°C as the base temperature and starting from the first sowing date were calculated for each season, using data available from the Commonwealth Bureau of Meteorology (BoM) website (Australian Government 2017). Half-hourly air temperatures at the experimental site were also recorded using iButton integrated data loggers (Maxim Integrated, San Jose CA, USA) housed in a radiation screen at 1.5 m height. From the regular iButton recordings, cardinal air temperature and adjusted degree days were calculated for each TOS, where $T_{\text{base}} = 0^{\circ}\text{C}$, $T_{\text{optimal}} = 23^{\circ}\text{C}$ and $T_{\text{max}} =$

37°C as per Porter and Gawith (1999). Adjusted calculations of thermal time (TT) were used to estimate TT between critical development stages of treatments.

Flowering date (Z65, Zadoks *et al.* 1974) was recorded as the calendar date when 50% of the spikes in each plot had visible anthers. The calendar date at which double ridge (DR, growth stage 2.5 as per Waddington *et al.* 1982) and terminal spikelet (TS, growth stage 4 as per Waddington *et al.* 1982) occurred was recorded using the methods described by Kirby and Appleyard (1981). A mean flowering date stability index was calculated as 1 minus the ratio of range in thermal time for flowering across sowings for each cultivar to the range in thermal time in sowing dates for each year. A higher stability index indicates less change in flowering date for a large range in sowing date.

Dry-matter (DM) was measured at Z39 (flag leaf emerged on the main stem), Z70 (end of flowering) and Z89 (maturity) by cutting all above ground plant parts in a quadrant 0.5 m width x 1.2 m (four inside rows) per replicate. Gregory was used as the indicator cultivar to take Z39 cuts i.e. when Gregory reached Z39 a cut for all cultivars was made for that TOS. Cultivars were sampled individually at Z70, and cuts were taken 7 days after reaching Z65 (50% flowering). At Z39 and Z70, total wet weight was recorded, samples were subsampled (a random number of stems at Z39, and 20 stems at Z70) and a wet weight of the sub-sample was recorded, and dried at 70°C for at least 48 hours to record a dry weight so that DM in g/m² could be calculated. At Z70, 20 stems were partitioned into stem, green leaf, dead leaf, and head and dried at 70°C for at least 48 hours to record a dry weight. At Z89 20 stems were partitioned into stem, leaf, grain and chaff and dried at 70°C for at least 48 hours to record a dry weight, and an additional 5 spikes were collected to count spikelets and calculate an average spikelet per spike. Individual grain weight was measured by weighing 200 grains dried at 70°C for at least 48 hours. Harvest index was calculated as the ratio of the grain to the total DM of the sample taken at maturity. At maturity plant height was recorded with a ruler, excluding awns. In 2015 grain yields were measured by machine harvest of the inside four rows of six row plots and are reported at 12% moisture, in 2016 yield was measured by hand-harvesting and threshing 2.0 m² (two 0.83 x 1.2 m quadrants taken from the inside four rows of six row plots) and are also reported at 12% moisture. Harvest grain moisture was determined via Near Infrared (NIR) technology, and grain yield was corrected to 0% moisture and divided by grain weight (also 0% moisture) to calculate grain/m². Growth rates (g/°C day) between Z39 and Z70 was calculated as DM divided by

accumulated thermal time for each cultivar. Fruiting efficiency (grains/g spike) was calculated by dividing grain/m² by spike g/m² at Z70 (Slafer *et al.* 2015a).

In both seasons shortwave radiation was recorded every 10 minutes using a pyranometer (Apogee Instruments, USA) situated at the experimental site and at 1.5 m height. Regular pyranometer recordings were summed to calculate a daily incoming shortwave radiation in MJ/day. Canopy light interception of photosynthetically active radiation (PAR) was recorded around solar noon using a ceptometer (AccuPAR LP-80; Pullman, WA, USA) at 4 positions per plot at the time of Z39 and Z70 DM sampling. Values of daily fractional PAR interception were obtained by interpolation between reading dates of interception; and these were multiplied by the daily solar radiation recorded from the pyranometer to calculate daily radiation interception (MJ/m²/day), assuming PAR was equal to 0.5 shortwave radiation (Monteith 1972). Radiation use efficiency (RUE, g/MJ) was calculated as the ratio of crop growth to cumulative intercepted PAR from Z39 to Z70.

2.4 Data analysis

The experiment was a split-plot design with sowing time as the main plot and cultivar as the sub-plot with four replicates and spatial optimisation, designed with DiGger software (Coombes 2002). All measurements were analysed using linear mixed models (REML) accessed via the GenStat 18 user interface (VSN International 2013) with year, sowing date and cultivar as fixed effects and whole plot and block as random effects.

To account for seasonal differences, trait deviation was calculated as the difference between the trait value for a given cultivar and the mean of each season for that trait. Chronological trends of the mean deviation of traits vs. year of release were analysed using simple linear and non-linear regression via the GenStat 18 user interface to obtain a P-value, R² value, Akaike information criterion (AIC) and Schwarz Bayes information criterion (BIC). Initially, linear regressions were fitted separately to FD- and SD-balanced data sets. Using simple linear regression with grouping applied (data grouped as FD-balanced and SD-balanced) it was then tested if FD and SD regressions were significantly different. If the analysis did not find the regressions were significantly different, a common line was fitted to both sets of data. Some traits exhibited a non-linear relationship with year of release, and in these instances a locally weighted linear regression (LOESS) with 2 degrees of freedom were fitted to help guide appropriate

selection of function type. Logistic (s-shaped) or split-line regressions were then fitted where appropriate. The AIC and BIC values from these regression were compared to the values from the linear regression to ensure that they provided a better fit (lower AIC and BIC) than the simple linear function, and only used for analysis if these criteria were satisfied (Archontoulis and Miguez 2015). In the case of split-line regressions, the analysis output supplied an x-axis value where the data “broke”, and separate linear functions were then fitted to the data split at this value. AIC, BIC and R² values for all functions fitted are supplied in Supplementary Table 1.

3. Results

3.1 Growing conditions and flowering dates

The monthly TT accumulation (°C) from the two seasons is summarised in Figure 1. In 2015, Temora had a cooler than average growing season and growing season (April-October) rainfall of 276 mm (long-term average 262 mm). Temora experienced several frost events just prior to the optimal flowering period (between the 23rd and 26th of September) where minimum temperatures ranged from -0.5 to -2.2 °C. During the optimal flowering period in 2015, Temora also experienced 3 days where maximum temperatures were over 30⁰C, when many treatments were flowering (Table 3). Yield and trait data used to analyse chronological trends in FD-balanced data were only from treatments that flowered at a similar date during the optimal period, therefore the impact of frost and heat events was minimised. In SD-balanced data, yield and trait data was affected depending on the development stage of the treatment at the time of the frost and heat events, and favoured cultivars with development suited to early-May sowing (TOS 3).

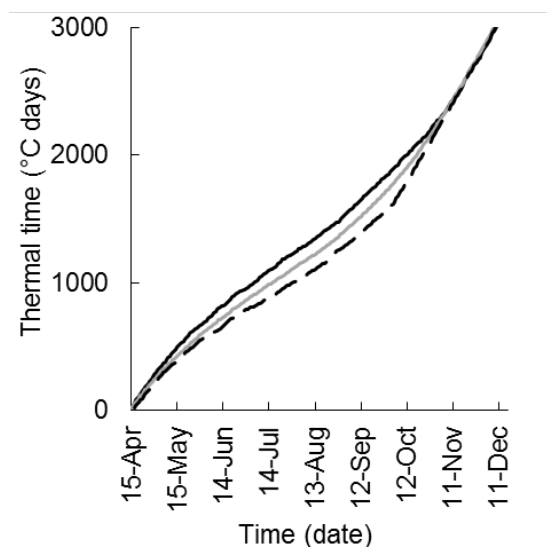


Figure 1: Cumulative thermal time (°C days) for Temora, NSW. Black line 2016, broken black line 2015, grey line average of years 2005-2016.

Table 3. Flowering dates (Z65) of flowering date (FD)- and sowing date (SD)-balanced data sets in 2015 and 2016 growing seasons in Temora, NSW. Grey shading indicates that cultivar was not grown in 2016. FD balanced data correspond to the sowing date from Table 2, while SD balanced data correspond to time of sowing 3.

Cultivar	2015		2016	
	FD	SD	FD	SD
Federation	6-Oct	12-Oct	5-Oct	16-Oct
Ford	8-Oct	13-Oct		
Ranee	6-Oct	9-Oct	5-Oct	9-Oct
Bencubbin	7-Oct	11-Oct		
Gabo	7-Oct	5-Oct	1-Oct	24-Sep
Olympic	6-Oct	12-Oct	1-Oct	12-Oct
Heron	5-Oct	8-Oct	3-Oct	6-Oct
Condor	6-Oct	9-Oct	1-Oct	1-Oct
Banks	5-Oct	8-Oct	28-Sep	28-Sep
Janz	7-Oct	11-Oct	28-Sep	28-Sep
Gregory	6-Oct	11-Oct	2-Oct	2-Oct
Condo	7-Oct	3-Oct	2-Oct	20-Sep
Longsword	10-Oct	10-Oct	9-Oct	9-Oct

The 2016 growing season in Temora had an above average temperature and rainfall (590 mm in April-October). The season of 2016 was so favourable (no water stress, sufficient nitrogen and zero frost or heat events at or surrounding the optimal flowering

time) that record yields (up to 8 t/ha) were achieved in modern cultivars, and yields shown actually represent PY not PY_w . As a result of above average rainfall and high nitrogen application there was lodging of the tall cultivars at early time of sowings. While care was taken to hand-harvest these plots to reduce grain loss, lodging occurred during grain fill and yield was likely reduced in these plots. Table 3 shows that flowering occurred near concurrently in FD-balanced data, and that flowering dates of some SD-balanced treatments flowered outside of the optimal flowering period.

3.2 Yield and flowering date stability

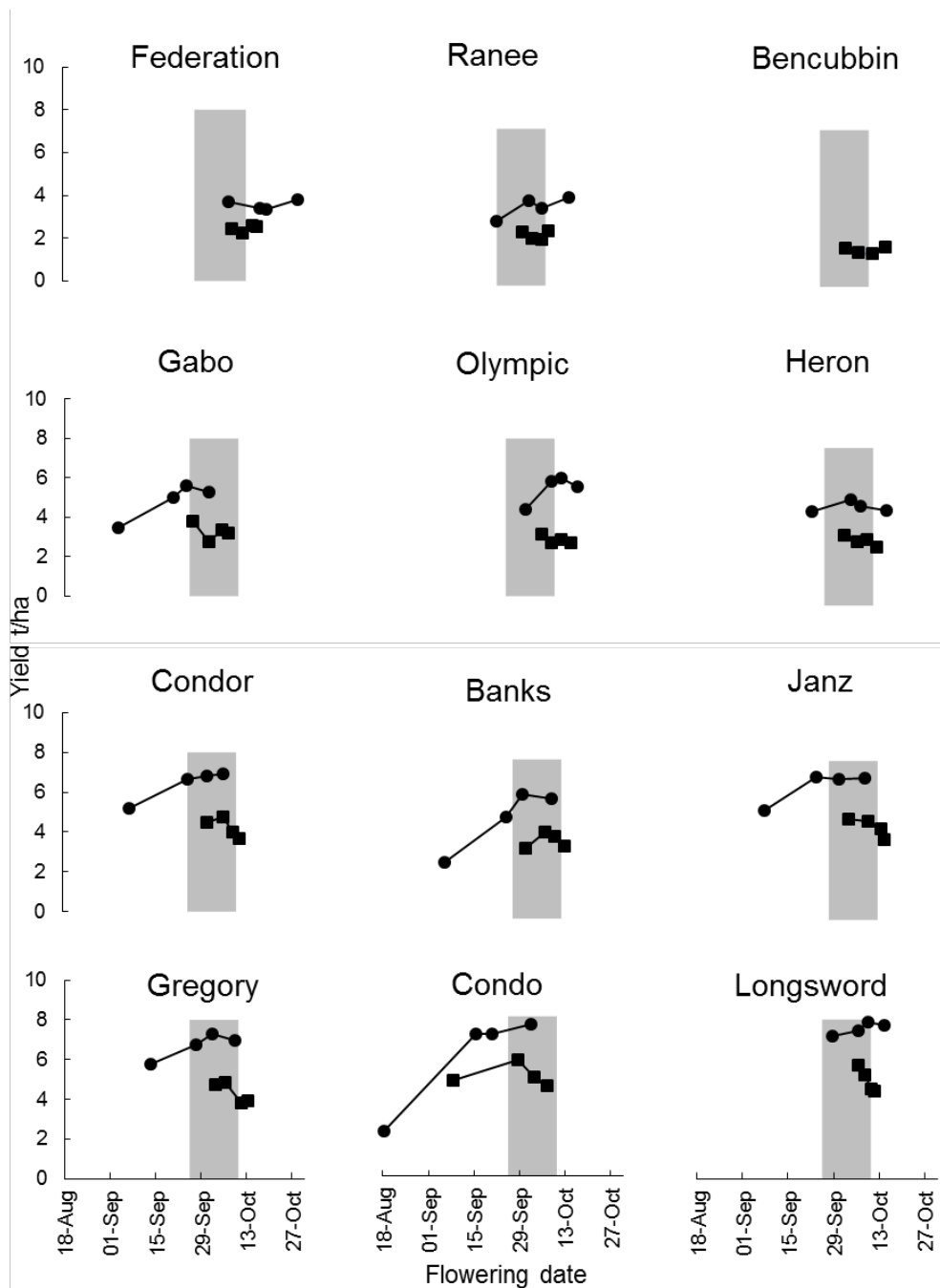


Figure 2: Mean grain yield plotted against flowering date for a historic set of wheat cultivars sown at four time of sowing in Temora, NSW in 2015 (■) and 2016 (●). Sowing date details are shown in Table 1. Each marker represents a different time of sowing and sowing date moves later from left to right. Cultivars are presented in order of release. Grey columns are the optimal flowering period as per Flohr *et al.* (2017b). The 5% LSD value is 0.7 t/ha and the P-Value of year x TOS x cultivar interaction is <0.001.

All cultivars yielded higher in the more favourable season of 2016 (Fig. 2). Modern cultivars flowered within the optimal flowering period more consistently from later sowing dates, and older cultivars from earlier sowing dates. Longsword flowered within the optimal flowering period from multiple TOS, and achieved yields similar or higher than modern cultivars. A majority of the highest yielding treatments (TOS) for each cultivar flowered during the optimal flowering period defined by Flohr *et al.* (2017b).

3.3 Chronological changes in yield physiology

Grain yield was affected by year ($P < 0.001$), cultivar ($P < 0.001$) and TOS ($P < 0.001$), and all interactions were significant ($P < 0.001$). The two seasons were contrasting, and data are presented as per Sadras and Lawson (2011) as deviation from the seasonal mean. A logistic function fitted to the relationship between yield and year of release showed a superior fit in comparison to a linear function ($R^2 = 0.83$ vs 0.79 , AIC = 116 vs 121, BIC = 123 vs 125). There were no significant differences between curves fitted to different years, or FD or SD balanced data and a common curve was used (Fig. 3A). It showed that yield gain has progressed in three phases, with rapid gains made during the middle of the century culminating in the release of semi-dwarf cultivars, and less rapid gains made in the first half of the 20th century, and over the last 30 years. A LOESS with 2 degrees of freedom was also fitted to the data ($R^2 = 0.83$, AIC = 115, BIC = 121) and confirmed the differential rates of yield gain over the years of release studied, with inflections during the 1940s and 1980s (Table S1). Averaged over the entire period studied (1901-2014), grain yield has increased at a rate of ~26 kg/ha per year (Fig. 3A).

Increase in grain yield has been driven by an associated increase in grain/m² (Fig. 3B), grain/spike (Fig. 3C), grain/spikelet (Fig. 3D), spike g/m² (Fig. 3E), fruiting efficiency (Fig. 3F) and grain weight (Fig. 3G) with year of release. A logistic function fitted to the relationship between grain/spike and grain/spikelet and year of release showed superior fit in comparison to a linear function (Table S1). Fig. 3C and 3D show that grain/spike and spikelet increased rapidly with the release of the first semi-dwarfs in the 1970s.

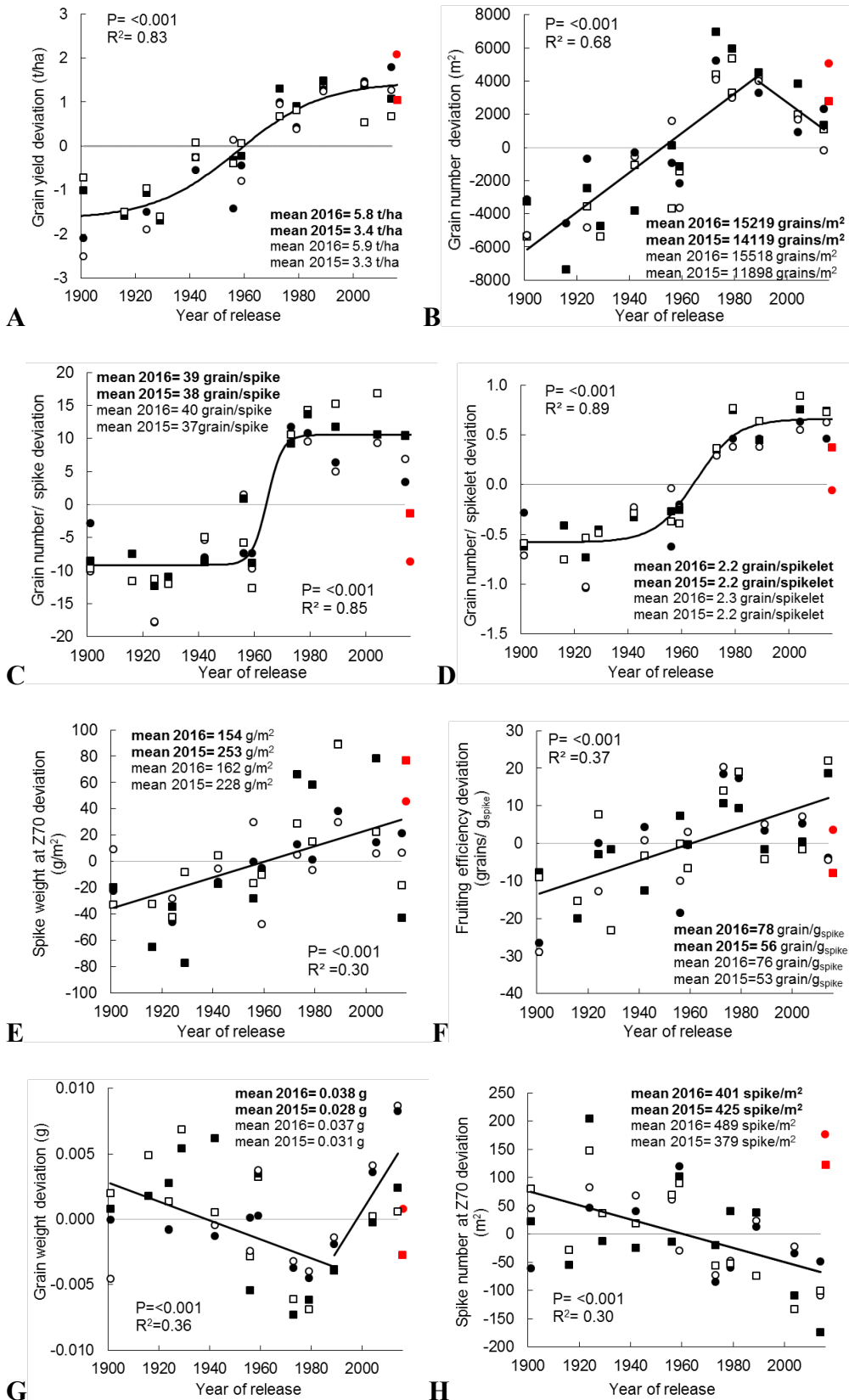


Figure 3: Chronological deviation changes in yield and yield components in 2015 (■, □) and 2016 (●, ○) in New South Wales wheat cultivars released between 1901 and 2014. Solid symbols (●, ■) are for cultivars that flower simultaneously, and hollow symbols

(○, □) for cultivars sown on the same date. Deviation is the difference between the trait value for a given cultivar and the mean of each season for that trait. Bold text corresponds to flowering date balanced data, and un-bold text corresponds to sowing date balanced data. P-values and R^2 are related to the regression fitted to data. Symbols (■, ●) are cultivar Longsword, which has not been included in the regressions or means shown.

When data were analysed using split-line regression, grain/m² and grain weight were found to change differentially over similar periods (Fig. 3B, G). Although break points in the regression were identified in the year 1988 for grain/m², and 1987 for grain weight, the break occurred between the cultivars Janz (1989 release) and Gregory (2004 release). Condo (2014) was consistently the highest yielding cultivar, and while it appears grain/m² and grain/spikelet have been a major contributor to yield increase, in the very favourable season of 2016 Condo also had the highest grain weight of all the treatments (46 mg) (Fig. 3G).

The very favourable season of 2016 increased the fruiting efficiency of cultivars compared to the relatively dry and hot spring experienced in 2015. Also contributing to the greater fruiting efficiency was low spike weight due to low radiation (data not shown) and warm temperatures experienced in the 2016 season (Fig. 1).

The yield of Longsword was competitive with modern spring cultivars in both seasons. Yield of Longsword was associated with greater grain/m² through increased spike weight and spike no./m², but not grain/spikelet or spike as for the modern high yielding spring cultivars (Fig.3)

3.4 Chronological changes in DM and partitioning

Grain/m² and potential grain size are predetermined during the critical growth period between spikelet initiation and Z70 in wheat (Slafer *et al.* 2015b). In our experiments we made physiological measurements (DM, PAR interception) at Z39 and Z70. There was no significant difference among genotypes in growth from sowing to Z39 (Fig. 4A). Data show that DM produced between sowing and Z70 and between Z39 and Z70, PAR interception at Z39 and Z70 and total MJ/m² intercepted during this period have decreased over time (Fig. 4B, C, D, E, F), but growth rates per °Cd have remained constant over the same period (Fig. 4G). RUE showed a near-significant increase (Fig.

4H, $P=0.09$). Longsword had higher DM production between sowing and Z70 and during the critical growth period, but other traits (PAR interception, growth rates and RUE) have generally followed modern cultivars.

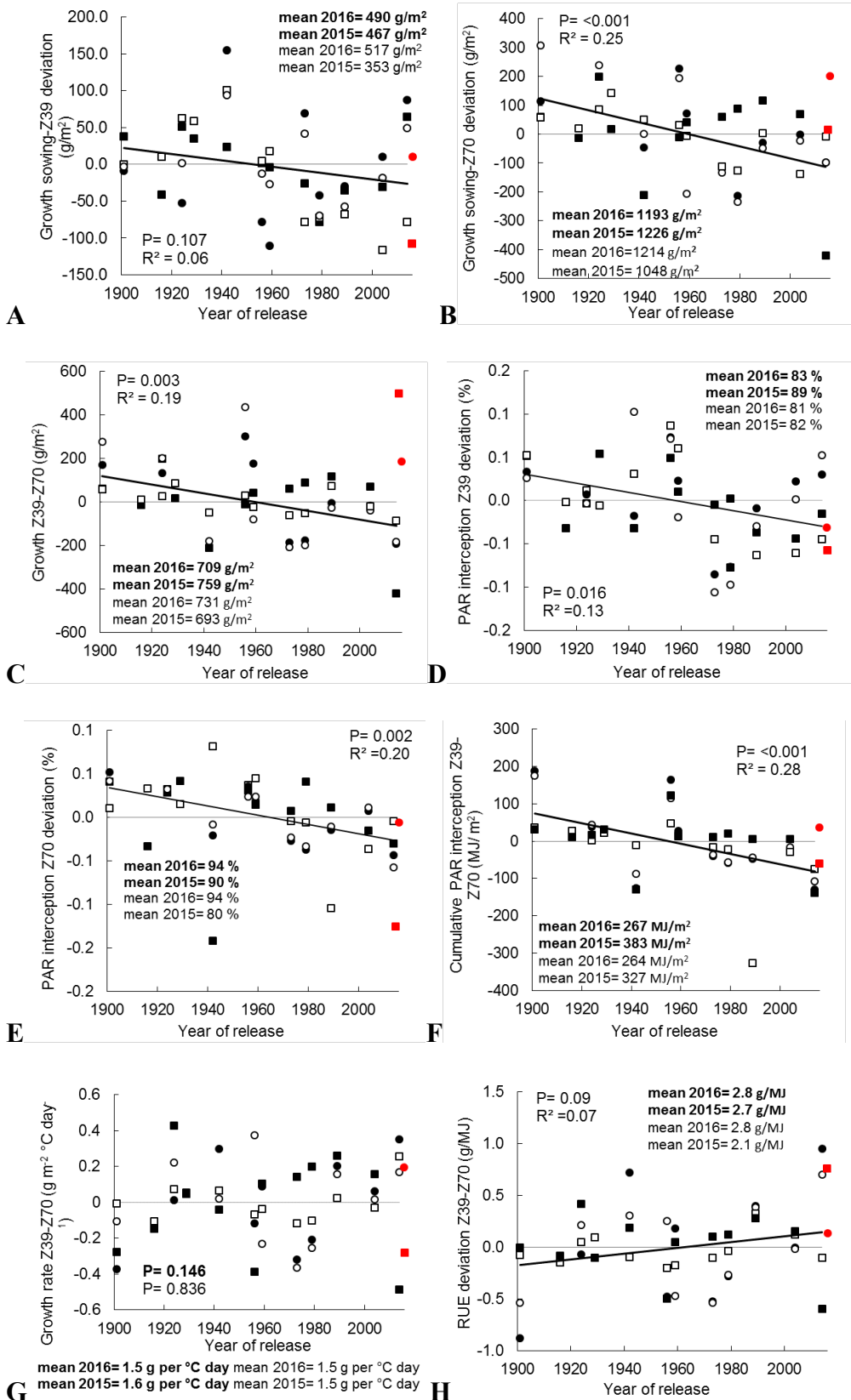


Figure 4: Chronological deviation changes in DM production and radiation interception in 2015 (■, □) and 2016 (●, ○) in New South Wales wheat cultivars released between 1901 and 2014. Solid symbols (●, ■) are for cultivars that flower simultaneously, and hollow symbols (○, □) for cultivars sown on the same date. Deviation is the difference between the trait value for a given cultivar and the mean of each season for that trait. Bold text corresponds to flowering date balanced data, and un-bold text corresponds to sowing date balanced data. P-values and R^2 are related to the regression fitted to data. Symbols (■, ●) are cultivar Longsword, which has not been included in the regressions or means shown.

HI ranged from 0.21 to 0.39 in 2015 and 0.21 to 0.45 in 2016 (Fig. 5A), with a significant rate of increase of ~ 0.002 per year ($P < 0.001$). Contributing to the improved HI was reduced plant height from ~ 1.4 m to 0.9 m (Fig. 5B) and reduced mean stem g/m^2 from 841 (Federation) to 623 (Condo) g/m^2 (Fig. 5C). A logistic function fitted to plant height (Fig. 5B) implies that plant height was systematically reduced until ~ 1970 's, thereafter plant height has been maintained without further change. HI for Longsword was not as high as Condo (2014), which can be associated with greater spike g/m^2 (Fig. 5H) and stem g/m^2 (Fig. 5C) in Longsword treatments.

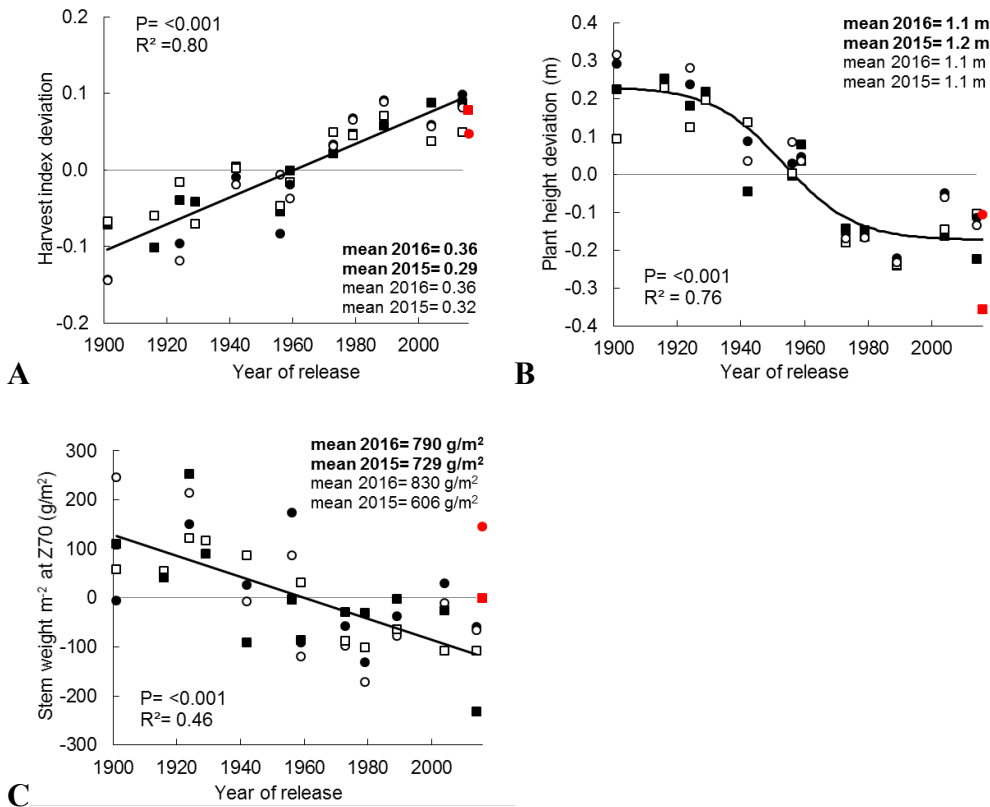


Figure 5: Chronological deviation changes in harvest index, plant height and stem weight at Z70 in 2015 (■, □) and 2016 (●, ○) in New South Wales wheat cultivars released between 1901 and 2014. Solid symbols (●, ■) are for cultivars that flower simultaneously, and hollow symbols (○, □) for cultivars sown on the same date. Deviation is the difference between the trait value for a given cultivar and the mean of each season for that trait. Bold text corresponds to flowering date balanced data, and unbold text corresponds to sowing date balanced data. P-values and R^2 are related to the regression fitted to data. Symbols (■, ●) are Longsword, which has not been included in the regressions or means shown.

3.5 Chronological changes in development

Modern cultivars have become less stable in flowering time (Fig. 6A), require less °C days to double ridge (Fig. 6B), have a shorter duration between double ridge to terminal spikelet (Fig. 6C), double ridge to Z65 (Fig. 6D) and sowing to Z65 (Fig. 6E). A regression for flowering date stability was also fitted excluding Condo (2014 release) as Condo heavily influenced the downward trend (Fig. 6A). With Condo removed, a negative regression persisted $P=0.027$, $R^2=0.20$. The fast winter cultivar Longsword had a very stable flowering time over a wide sowing window in both seasons. When Longsword was sown in the first week of May (TOS 3), the thermal time from double ridge to Z65 was similar to modern spring cultivars as was the thermal time from sowing to Z65 (Fig. 6D, E). However thermal time from sowing to double ridge of Longsword was longer than many cultivars released in the last 30 years (Fig. 6B).

In all development figures, mean thermal time (°C days) was greater when data was FD-balanced. Negative regressions for °C days between double ridge to terminal spikelet and double ridge to Z65 (Fig. 6C and D) were only significant when data was FD-balanced.

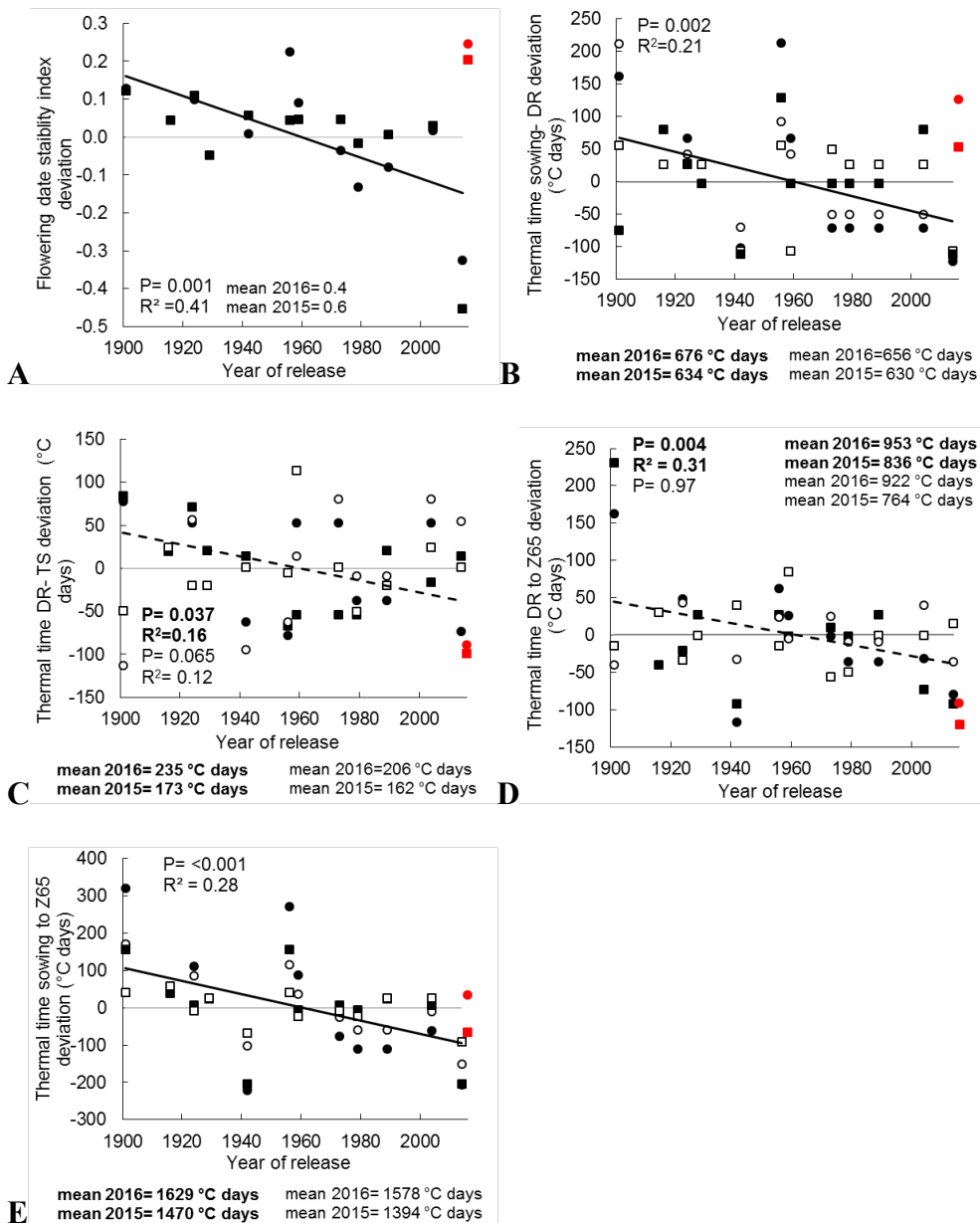


Figure 6: Chronological deviation changes in development for cultivars used in the experiment in 2015 (■, □) and 2016 (●, ○) in New South Wales wheat cultivars released between 1901 and 2014. Solid symbols (●, ■) are for cultivars that flower simultaneously, and hollow symbols (○, □) for cultivars sown on the same date. Deviation is the difference between the trait value for a given cultivar and the mean of each season for that trait. Bold text and broken line correspond to flowering date (FD)-balanced regression, and un-bold text corresponds to sowing date (SD)-balanced regression. If the analysis did not find the FD- and SD- balanced regressions significantly different, a common solid line was fitted to both sets of data. P-values and R^2 are related to the regression fitted to SD- or FD-balanced data, whereas 2015 and

2016 numbers are the mean value for each experimental season. Symbols (■, ●) are Longsword, which has not been included in the regressions or means shown.

4. Discussion

4.1 Rate of yield gain

We have found an increase in grain yield in southern NSW cultivars released between 1901 and 2014 (Fig. 3A). The annual rate of yield progress in our collection of historic wheats was 26 kg/ha per annum (p.a.), or when presented as relative to the mean yield of the most recently released cultivar (6 t/ha), progress is ~ 0.4% p.a. of Condo (2014 release). The positive increase was not linear; yield gain was slow for the first three decades, followed by a greater rate of genetic gain during the middle of the century (approximately 1940s to 1980s), with slower improvements thereafter. The shape of the trend in yield improvement found in this study diverges from the linear trend found in other Australian studies (Sadras and Lawson 2011). However similar trends can be found in data presented from other countries and in Australia e.g. Austin *et al.* (1980) in the UK, Cox *et al.* (1988) in the US, Slafer and Andrade (1989) in Argentina and Perry and D'Antuono (1989) in WA, with the greatest period of yield gain associated with the introduction of semi-dwarf cultivars. A plateau in genetic PY in recent decades has been observed in experiments from Mediterranean Spain (Acreche *et al.* 2008; Sanchez-Garcia *et al.* 2013) and the Yaqui Valley, Mexico (Fischer and Edmeades 2010). Acreche *et al.* (2008) discussed that yield stall observed in Spanish cultivars was a result of modern cultivars not being bred in Mediterranean target environments, but introduced from sub-tropical or temperate environments of Mexico or France. This could also be true for the cultivars used in our study. During the periods of rapid yield gains, favoured cultivars were derived from breeding programs located in southern NSW itself (Condor, Heron) or nearby Victoria (Ranee, Olympic). From the 1980s onward, cultivars from sub-tropical Queensland (Banks, Janz, Gregory) dominated, and were in part favoured due to their superior grain quality and thus higher market value. We hypothesise that lack of yield gain in recent decades is associated with either dominance of cultivars bred in environments substantially different to that of southern NSW, or the breeding programs involved placing greater emphasis on quality and foliar disease resistance at the expense of yield, as discussed by Hunt *et al.* (2017).

The observed yield progress across the period studied (26 kg/ha or 0.4% p.a.) is in close agreement to the yield gain reported in cultivars released between 1926-1984 by Anthony and Brennan (1987) of 0.6% p.a., and similar to that found by Sadras and Lawson (2011) for SA cultivars of 25 kg/ha p.a. (~0.4% p.a.), the 0.5% p.a. estimated by Fischer (2009) and to those in international studies (Fischer *et al.* 2014). There was no difference in yield gain when comparing FD- vs. SD-balanced data in our two-year field experiment. Therefore, change in flowering date has not contributed to yield gain for southern NSW cultivars, in agreement with the study by Sadras and Lawson (2011) for SA cultivars. However, in less favourable seasons, one would expect the earliness observed in modern cultivars critical to the escape of spring drought and associated higher yields. Multiple sowing dates revealed that cultivars with fast development yielded more when sown later, and cultivars with slower development yielded more when sown early (Fig. 2 and 6E). A chronological trend towards faster duration of developmental phases prior to flowering was observed (Fig. 6). This may have contributed to yield gain and will be discussed in section 4.3.

4.2 Foundations of yield gain

It is widely documented that increases in PY_w seen around the world are largely associated with increased partitioning of assimilates to the growing spike prior to flowering through reduced plant height which improved HI (Fischer 1984; Perry and D'Antuono 1989; Siddique *et al.* 1989a; Siddique *et al.* 1989b; Slafer and Andrade 1993; Sadras and Lawson 2011). Likewise, in popular NSW cultivars, yield gain can also be attributed to improved partitioning, particularly for reproductive structures (spike g/m^2 , grain/spike and per spikelet, Fig. 3) and high HI (Fig. 5A). Shorter stems accounted for a lower fraction of total DM and resulted in greater partitioning to the developing spike and therefore spike g/m^2 at Z70 (Fig. 3E, 5C). These findings agree with Perry and D'Antuono (1989); Siddique *et al.* (1989a); Siddique *et al.* (1989b), who showed reduced stem g/m^2 reduces competition for assimilates resulting in more florets and greater survival of florets. Plant height has plateaued since ~1970s (Figure 5B), suggesting either that optimum height has been reached, or since the introduction of semi-dwarf cultivars, breeders have not attempted to further reduce plant height. Acreche *et al.* (2008) also found a similar trend in Spanish cultivars released between 1940 and 1998. Grain/spike and spikelet (Fig. 3C, D) also supported the rapid yield gain following the introduction of semi-dwarf cultivars, but further increase in both has

slowed since. When discussing spike g/m^2 it is important to note that historic cultivars up until the release of Condor (1973) (Federation, Bencubbin, Ford, Rancee, Gabo, Olympic and Heron) were awnless. After Condor, all cultivars released had awns and the weight of awns would contribute to our calculations of spike g/m^2 .

Sadras and Lawson (2011) found that before 1982, grain/ m^2 increased and grain weight decreased; subsequently grain/ m^2 stabilised and grain weight increased. Likewise, Calderini *et al.* (1995) found grain weight decreased between 1900 and 1980 and then increased in a set of Argentinean wheat cultivars. Our study also found reversals in the chronological trends in grain weight and grain/ m^2 (Fig. 3B, G). Condo's (2014 release) grain yield was associated with increased grain weight but grain/ m^2 was similar to that of cultivars released around the 1960s. In FD- and SD-balanced data, grain weight decreased until 1987, but then increased. In FD- and SD-balanced data, grain/ m^2 increased until 1988 and then decreased, probably indicating a shift in breeding objectives towards physical grain quality in recent decades.

SA cultivars released after the early 1980s accumulated more DM (Sadras and Lawson 2011). Other key studies show that breeding has increased HI with little effect on total DM production (Perry and D'Antuono 1989; Siddique *et al.* 1989b; Slafer and Andrade 1991; Calderini and Slafer 1999). In contrast, we found a chronological decrease in DM accumulated between sowing and Z70 (Fig. 4B) and between Z39-Z70 (Fig. 4C). Decrease in growth is likely to be contributing to high HI. Loss and Siddique (1994) discuss that once the minimum structures (stem, leaves, tillers) have been produced, it is more efficient for the plant to partition growth directly into the spike than to produce additional vegetative growth for later translocation during grain development, saving metabolic energy (Fondy and Geiger 1980) and increasing WUE (Siddique *et al.* 1990a).

Our data show that modern cultivars intercepted less radiation at noon (Fig. 4 D, E, F) at two critical growth stages. Despite lower radiation interception, modern cultivars have maintained the same growth rates as historic cultivars (Fig. 4G). Sadras and Lawson (2011) and Yunusa *et al.* (1993) found that RUE has improved in modern SA and WA cultivars, but we did not observe a significant increase in RUE in our data (Fig. 4H). While historic cultivars intercept more PAR at noon, modern cultivars use radiation more efficiently (Siddique *et al.* 1989a). In the field, modern cultivars were visibly a darker green colour, consistent with a trend for greater chlorophyll content per unit leaf

area (Watanabe *et al.* 1994). Modern wheat cultivars also had more erect canopies compared to the historic wheats, which were observed to have relatively pale and long, floppy leaves in the field. Erect leaf display is associated with a smaller light extinction coefficient (also observed by Yunusa *et al.* 1993) and allows sunlight to penetrate more deeply into the canopy, spreading absorption across a greater leaf area. The combination of changes result in equivalent growth rates. These data could be looked at as per Sadras *et al.* (2012) and Sadras and Lawson (2013).

Slafer *et al.* (2015a) propose future yield gains will be achieved through improved fruiting efficiency. There are only a handful of studies that have observed chronological changes in fruiting efficiency, and no clear trend has been shown. Here, in both FD- and SD-balanced data, there was an increase in fruiting efficiency ($P < 0.001$). Our results are in agreement with studies from Spain, the UK and Argentina (Abbate *et al.* 1998; Shearman *et al.* 2005; Acreche *et al.* 2008) but at odds with other studies from Argentina which showed neither a positive or negative chronological trend (Slafer and Andrade 1993). This suggests Australian breeders have increased not only spike g/m^2 at Z70, but also increased the efficiency converting spike dry weight into greater grain/ m^2 . When comparing an early-sown, slow-developing cultivar to a later-sown, faster-developing cultivar under irrigation, Fischer (2016) found that there was no difference in grain/ m^2 , but the slower developing cultivar had poorer fruiting efficiency. Our data also showed that the slower developing cultivar Longsword, had lower fruiting efficiency than the fast developing Condo (Fig. 3F). Should fruiting efficiency be a useful selection trait in the future, a greater understanding of the effect of environment (and hence genetic x environment interactions) will be necessary, given that fruiting efficiency was variable between the two contrasting seasons shown here.

4.3 Change in phenology

Genetic yield gain has been associated with shorter time from sowing to flowering in Mediterranean environments (Kirby *et al.* 1989; Siddique *et al.* 1989a; Giunta *et al.* 2007). In an average and above average season, we observed that yield gain was not associated with changes in flowering date, in agreement with the study by Sadras and Lawson (2011). However, we found chronological differences in phenology leading up to flowering (Fig. 6) while Sadras and Lawson (2011) did not when observing a different set of cultivars. Modern cultivars required less thermal time to reach Z65, e.g. on average Federation required 328 °C days, or 22 days more than Condo to reach Z65.

The trend to breed increasingly faster development in Australian cultivars can be observed in Figure 2. Figure 2 shows that older cultivars achieved highest yields when planted early, as this resulted in flowering during the optimal period. For modern cultivars, highest yields were achieved when planted later when treatments also flowered during the optimal period. This field experimental evidence confirms the modelling that suggested grain yield is maximised when crops flower during the optimal period in drought prone environments (Flohr *et al.* 2017b). The shift to fast development has been thought to contribute to drought avoidance and better alignment of development to autumn rainfall and the optimal flowering period. However our data supports the associations made by various studies that faster development has resulted in less time for vegetative growth, reduced excessive tillers (Kirby *et al.* 1989; Siddique *et al.* 1989a; Fischer 2016) and reduced nodal root development (Siddique *et al.* 1990a) which has increased partitioning of assimilates to spike growth and increased grain/m² and HI (Richards 1991). This also supports Passioura (1977) who found that HI was a function of pre- and post-flowering evapotranspiration. Therefore, if pre-flowering duration and growth are reduced, this should reduce pre-flowering evapotranspiration and lead to an increase in HI.

Our data indicate that yield gain is associated with reduced duration of vegetative growth brought about by faster development (Fig. 6). This may not be causal and may have occurred through selection for both yield and faster development. Data collected on Longsword provides some clarity on the two possible hypotheses. Longsword had a similar pre-flowering growth duration (Fig 6B, E) and DM production (Fig 4B, C) to older cultivars. However, Longsword had improved HI (~0.4, Fig. 5A) and equivalent yields to the most modern cultivars. The fact that superior partitioning has occurred in cultivars with both slow (e.g. Longsword) and fast (e.g. Condo) development indicates that improved partitioning is not always linked to shorter duration of pre-flowering growth. Longer growth duration during the critical growth period (DR to TS) can potentially be used as a means to increase DM partitioning to the developing spike and thereby increase yield. Further research to separate these two possibilities would be beneficial, and could be confirmed independent of “genetic noise” by comparing the growth and development characteristics of near-isogenic lines, which differ only in flowering time (*Vrn* and *Ppd* genes) but are otherwise genetically similar.

Siddique *et al.* (1989a) found historic cultivars had a shorter duration between double ridge and terminal spikelet than modern cultivars. Though not significant ($P=0.065$), a similar trend was found in the SD-balanced data. However we found the reverse in FD-balanced data. In FD-balanced data, modern NSW cultivars had a significantly shorter duration from double ridge to terminal spikelet (Fig. 6C). In the WA experiments of Siddique *et al.* (1989a) and Siddique *et al.* (1989b), a single sowing date of 27 and 28 May was used which favoured fast developing cultivars. The consistent trend we found of greater mean thermal time to reach double ridge, terminal spikelet and Z65 when data was FD-balanced compared to SD-balanced (Fig 6B, C, E) show that the duration of phenology between cultivars has been changed through breeding over the last century. Observing the phase duration of cultivars which flower concurrently reveals differences that are not obvious when comparing cultivars sown on the same date.

4.4 Future yield gain

Future yield gain through plant breeding is likely to be achieved through further increases in partitioning of assimilates to the growing spike that lead to increased grain/m² (Slafer *et al.* 2015a). One consequence would be to further increase HI. A theoretical maximum HI for wheat in the UK is ~0.62 (Austin *et al.* 1980), which suggests Australian wheat breeders may still have opportunity to increase HI i.e. in 2016 Condo achieved 0.45. Richards (1992a) has shown that the optimal height for modern cultivars is 0.7-1 m, suggesting that there may still be a benefit in reducing height in Australian cultivars (Condo average height was 1 m). Alternatively, selecting for taller plants can increase biomass, however maintaining high harvest index in such selections would be imperative. Depending on how fast growth proceeds relative to development, to continue the trend of using faster development to increase HI risks insufficient accumulation of assimilates during the growing season which will limit yield potential (Fischer 1979, 2016). Additionally there is greater risk of cultivars flowering too early, resulting in frost induced floret sterility (Flohr *et al.* 2017b). A consequence of breeding high-yielding, fast-developing cultivars has been poorer flowering date stability (Fig. 6A) and thus cultivars are limited to a narrow sowing window (Fig. 2). In the future, cultivars that have a stable flowering time and can reliably maximize yield from a wide sowing window, will offer greater farm system flexibility in an increasingly variable climate (Flohr *et al.* 2017c).

Reynolds *et al.* (2012) suggest that greater partitioning to the developing spike at flowering will be realised through increased photosynthesis and pre-flowering DM production. Barley is an example of a cereal which is able to produce more DM and grain using the same amount of water as wheat (Siddique *et al.* 1989a; Siddique *et al.* 1990b; Richards 1991). To achieve this in wheat, cultivars with growth patterns different to those that are most popular today may be required (Hunt 2017). Anderson and Smith (1990) and Penrose and Martin (1997) have previously suggested incorporating a vernalisation requirement into an existing cultivar to remove the risk of fast development in a warm winter, and increase DM production through longer developmental phases. Wheat breeders in the UK have previously had success with increasing pre-flowering DM to increase yield in winter wheats (Shearman *et al.* 2005). Longsword is a photoperiod insensitive ‘fast’ winter wheat (obligate vernalisation requirement) from a cross between the high-yielding spring cultivar (Mace) and a CIMMYT-derived spring breeding line. Longsword showed some key attributes that separated it from modern NSW cultivars. These were: greater number of spikes per unit area (Fig. 3H), greater spike mass per unit area (Fig. 3E), greater DM production between sowing and Z70 and between Z39 and Z70 (Fig. 4B, C), a stable flowering date (Fig 6A) and a longer sowing to double ridge development phase (Fig. 6B). These attributes support the hypothesis of Penrose and Martin (1997). Our data has shown that historic cultivars have a more stable flowering time, greater thermal time requirement to Z70 and longer phases between double ridge- terminal spikelet and double ridge- Z70 i.e. allowing greater radiation interception and DM accumulation. Therefore, future yield increases could be achieved by combining longer durations with modern cultivar canopy characteristics (erect leaves with high chlorophyll content delivering higher RUE) and superior partitioning (provided development duration and partitioning are decoupled), theoretically resulting in greater partitioning of assimilates to the spike e.g. Longsword. The benefits are likely to be three-fold; greater assimilates captured during the growing season, greater partitioning to the spike and stabilized flowering time to increase sowing opportunities to growers.

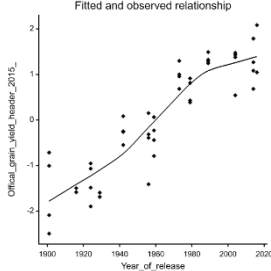
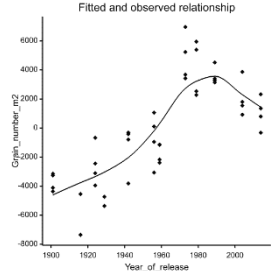
5. Conclusion

Between 1901 and 2014, genetic yield gain of popular southern NSW wheat cultivars showed an s-shaped trend when controlled for either flowering time or sowing date. Analysis showed increases in PY_w have stalled in southern NSW cultivars since the ~1980s. To keep pace with global demand, and ensure southern NSW growers remain competitive, the need to identify avenues to increase PY_w is urgent, especially under an increasingly variable climate. Periods of yield improvement were associated with an interplay between greater grain/m² and increased grain weight, and the result of greater partitioning of assimilates to spikes and higher fruiting efficiency. Modern cultivars have a less stable flowering time across wide sowing windows, and a shorter life cycle. Improved partitioning appeared decoupled from shorter developmental phases prior to flowering. Longer development phases in historic cultivars allowed greater accumulation of DM, which has declined in modern cultivars. We propose that future PY_w gain may be achieved by combining the superior partitioning of modern cultivars with the longer duration of growth, greater DM production and flowering time stability of older cultivars. The performance of a novel vernalisation sensitive cultivar (Longsword) provided evidence to support this hypothesis.

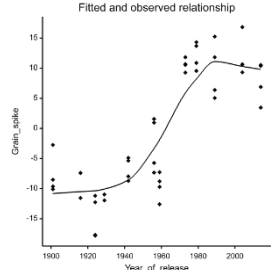
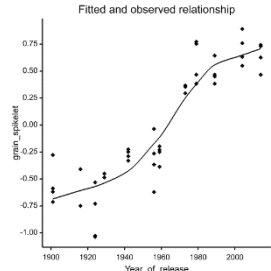
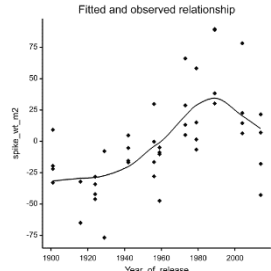
Chapter 3

6. Supplementary material

Table S1. Comparison of functions (linear vs. logistic) fitted to variable vs. year of release plots in Figures 3-6, and plots of locally weighted linear regressions (LOESS). Akaike Information Criterion (AIC) and Schwarz Bayes Information Criterion (BIC) describe the goodness of fit of a function corrected for the number of parameters each function contains, where lower values suggest a better fit.

Variable	Figure	Function fitted	Linear			Split-line R ²	Logistic			LOESS			Fitted LOESS
			AIC	BIC	R ²		AIC	BIC	R ²	AIC	BIC	R ²	
Grain yield (t/ha)	3A	logistic	121	125	0.79		116	123	0.83	115	121	0.83	
Grain number (m ²)	3B	linear split-line	853	856	0.54	0.68	835	843	0.69	825	831	0.76	

Chapter 3

Grain number/ spike	3C	logistic	330	333	0.65	296	304	0.85	304	310	0.81	
Grain number /spikelet	3D	logistic	48	52	0.80	26	33	0.89	30	35	0.87	
Spike weight at Z70 (m ²)	3E	linear	473	477	0.30	470	477	0.41	460	466	0.50	

Chapter 3

Fruiting efficiency (grains/ g _{spike})	3F	linear	373	377	0.37 1	373	380	0.43	366	372	0.49		
Grain weight (g)	3G	linear split-line	-315	-311	0.00	0.36	-317	-310	0.12	-343	-338	0.50	
Spike number at Z70 (m ⁻²)	3H	linear	538	541	0.30	535	542	0.40	532	537	0.42		

Chapter 3

Growth sowing - Z39 (g/m ²)	4A	linear	527	531	0.06	524	531	0.21	520	525	0.24	
Growth sowing-Z70 (g/m ²)	4B	linear	591	595	0.26	595	602	0.26	593	599	0.26	
Growth Z39-Z70 (g/m ²)	4C	linear	607	611	0.19	611	618	0.19	609	615	0.19	

Chapter 3

PAR interception Z39 (%)	4D	linear	-99	-96	0.13	-93	-85	0.07	-114	-109	0.41	
PAR interception Z70 (%)	4E	linear	-121	-117	0.20	-117	-110	0.20	-119	-114	0.21	
Cumulative PAR interception Z39-Z70 (MJ/m ²)	4F	linear	551	555	0.28	555	562	0.28	549	555	0.34	

Chapter 3

Growth rate Z39-70 (gm^2 $^{\circ}\text{C day}^{-1}$)	4G	N/A	34.0	37.6	0.02	36.7	43.9	0.05	30.2	35.5	0.15	
RUE Z39-Z70 (g/MJ)	4H	linear	79.1	82.7	0.07	81.4	88.5	0.10	74.2	79.6	0.20	
Harvest index	5A	linear	-138	-134	0.80	-136	-129	0.81	-144	-139	0.83	

Chapter 3

Plant Height (m)	5B	logistic	-48.2	- 44.7	0.76	- 66.0	- 58.8	0.85	- 74.3	- 69.0	0.87	
Stem weight at Z70 (g/ m ²)	5C	linear	556	559	0.46	554	561	0.52	553	559	0.51	
Flowering date stability index	6A	linear	-24.7	- 22.5	0.41	- 32.3	- 27.9	0.65	- 30.2	- 26.9	0.58	

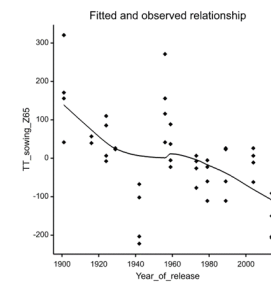
Chapter 3

Thermal time sowing_DR	6B	linear	551	555	0.21	557	564	0.17	551	557	0.25	
Thermal time DR_TS	6C	linear	242	244	0.16	240	245	0.28	237	240	0.35	
Thermal time DR_Z65	6D	linear	255	257	0.31	256	260	0.34	246	249	0.57	

Chapter 3

Thermal time sowing_Z65 6E linear 573 576 0.28

576 584 0.29 569 575 0.36



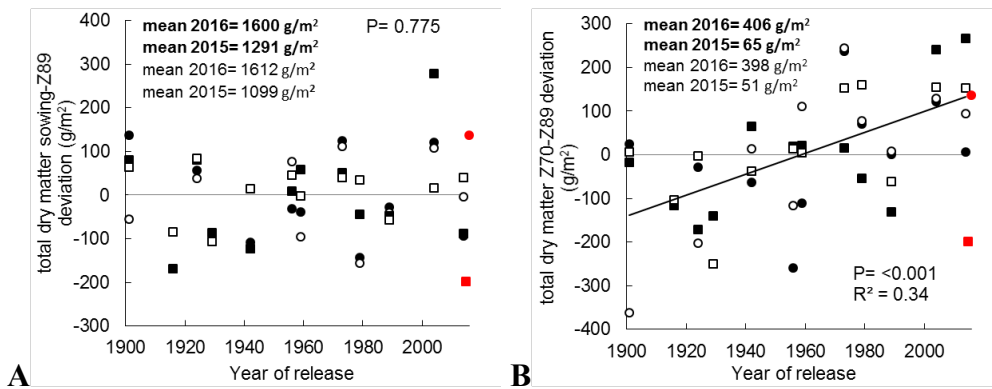


Figure S1. Chronological deviation changes in dry matter production between sowing and maturity (Z89) in 2015 (■, □) and 2016 (●, ○) in New South Wales wheat cultivars released between 1901 and 2014. Solid symbols (●, ■) are for cultivars that flower simultaneously, and hollow symbols (○, □) for cultivars sown on the same date.

Deviation is the difference between the trait value for a given cultivar and the mean of each season for that trait. Bold text corresponds to flowering date balanced data, and unbold text corresponds to sowing date balanced data. P-values and R² are related to the regression fitted to data. Symbols (■, ●) are cultivar Longsword, which has not been included in the regressions or means shown.

Chapter 4

Fast winter wheat phenology can stabilise flowering date and maximise grain yield in semi-arid Mediterranean and temperate environments

STATUS: Published Field Crops Research February 2018

Data use acknowledgement: Raw data presented from WA, SA, and Victoria was not collected by B. Flohr.

Flohr BM, Hunt JR, Kirkegaard JA, Evans JR, Trevaskis B, Zwart A, Swan A, Fletcher AL, Rheinheimer B, 2017, Fast winter wheat phenology can stabilise flowering date and maximise grain yield in semi-arid Mediterranean and temperate environments, Field Crops Research **223**, 12-25



Image 4. Wheat apices of a winter (LHS) and a fast-spring cultivar (RHS) both sown 14 April 2016 in Temora, NSW, photo taken 4 August 2016

Abstract

Australian wheat (*Triticum aestivum*) producers have been sowing crops earlier to adapt to reduced autumn rainfall, extreme spring weather and increasing farm size. Analysis of sowing date records indicate a shift of around 1.5 days/year over a 10 year period. The most suitable development patterns to maintain or increase yield at earlier sowing times have not been identified. Field experiments were conducted over two years at a range of sites and time of sowing (TOS), comparing a novel cultivar with fast-winter (FW) development to current elite spring and winter cultivars, and near-isogenic lines that differed only in major development genes. In cooler environments, the FW exhibited a more stable flowering time across a broader range of TOS compared to spring or slower developing winter cultivars. The optimal sowing window was shorter in warmer environments for the FW. Early-sown FW wheat yielded 8% more than fast-developing spring wheat sown later but flowering concurrently. FW wheat yielded 17% more than the elite mid-winter cultivar, and 18% more than elite slower developing spring cultivars when averaged across all TOS. The FW development pattern has potential to extend sowing periods while achieving 10-20% higher yields and flowering time stability. Wheat cultivars with altered development patterns must be developed to ensure crops flower during optimal periods from earlier sowing times.

1. Introduction

Global wheat yields need to increase by 38% from 2005 to 2050 to meet projected demand (Fischer *et al.* 2014). Australia will make an important contribution to this demand as it is one of the top ten major wheat producing countries and the fourth largest wheat exporter in the world (AEGIC 2016a). In south eastern and south west Australia, the wheat (*Triticum aestivum*) growing season traditionally extends from autumn (April-May) through to late spring. Crops are sown following the onset of autumn rains and lower temperatures, and flower and fill grain before the onset of high temperatures and terminal drought. Frost, heat and drought risk define a distinct optimal flowering period (OFP) for wheat in each region (Flohr *et al.* 2017b). The semi-arid wheat belt of southern Australia has a predominately Mediterranean climate with hot dry summers and cool, wet winters. In this region annual rainfall ranges from 300 to 700 mm (Kirkegaard *et al.* 2014). There are areas in the south-eastern wheat belt where the climate is more temperate, with rainfall more evenly distributed through the year. In both temperate and Mediterranean environments the amount and variation of rainfall drives relatively low and highly variable grain yield from season to season (Hochman *et al.* 2017). In southern Australia, wheat genotypes have predominately been of spring development pattern (weak vernalisation sensitivity) since the end of the 19th century when William Farrer identified that cultivars from the northern hemisphere which required cold (vernalisation) and longer days (photoperiod) to flower were not suited to the southern Australian growing season (Pugsley 1983) when sown on the typical sowing date. Since the release of the cultivar Federation by Farrer in 1901, Australian wheat breeders have continued to follow Farrer's lead and significant yield progress has been made by breeders selecting cultivars that develop from autumn establishment to flower during the optimal period (Richards *et al.* 2014). The Millennium Drought experienced in Australia 1996-2009 (Verdon-Kidd *et al.* 2014), provided an additional impetus to breed fast developing wheats that could be sown after adequate autumn rainfall and mature quickly before the onset of terminal drought. Today, the most widely grown genotypes continue to be those with little photoperiod or vernalisation sensitivity, with fast-spring (FS) and mid-spring (MS) phenology types dominating grain deliveries in the 2015/16 growing season (GrainCorp 2016).

Wheat yield gain in Australian has stalled since 1990, which has been attributed to reduced rainfall and rising temperatures, but balanced by improvements in technology (Hochman *et al.* 2017). Additionally, since the mid 1990's, "breaking" rains that could once be relied upon to establish crops in autumn (April-May) have declined significantly (Pook *et al.* 2009; Cai *et al.* 2012). In response to changing rainfall patterns, extreme spring temperature events, increasing farm size, new technologies and availability of herbicides, Australian wheat producers are sowing progressively earlier (Stephens and Lyons 1998; Anderson *et al.* 2016; Fletcher *et al.* 2016), though the extent of this practice change has not been comprehensively quantified. In drought-prone environments it is critical to optimise sowing such that the crop life-cycle accommodates flowering under optimal conditions to maximise yield (Bodner *et al.* 2015). Commonly grown FS genotypes incur high risk of flowering outside the OFP if sown too early, and suffer yield reductions due to frost damage and/or insufficient biomass accumulation. If sown too late, they risk yield loss through exposure to water and heat stress during the critical period for yield determination (Flohr *et al.* 2017b). Flohr *et al.* (2017b) have proposed that new robust genotype (G) by management (M) strategies need to be developed to stabilise flowering time and yield over wide sowing windows under current and future climates. Growers have already identified that sowing earlier is a beneficial management strategy to increase yield (Fletcher *et al.* 2016), but now require new elite genotypes with life-cycles that align earlier sowing dates with the OFP to maximise yield.

Wheat's wide adaptability and success around the world can largely be attributed to manipulation of flowering time to suit different growing environments. Three main gene systems control flowering in wheat, vernalisation (Trevaskis 2010), photoperiod (Slafer and Rawson 1995a) and earliness *per se* (Sukumaran *et al.* 2016). Vernalisation sensitivity has been noted as a key requirement for cultivars in northern latitudes e.g. cool temperate areas of continental Europe and North America, to ensure sensitive floral organs are not damaged by extreme low temperatures (Kamran *et al.* 2014), though the concept of breeding well-adapted vernalisation sensitive cultivars to environments with distinct OFP such as North Africa and West Asia has been discussed internationally (Fujita *et al.* 1992). Vernalisation sensitivity extends the vegetative phase of the plant, delaying reproductive development until the cold requirement has been saturated by an adequate number of vernal days (Porter and Gawith 1999), and is considered saturated

when the plant apex reaches double ridge (Kirby and Appleyard 1981). Penrose and Martin (1997) showed that obligate vernalisation sensitivity (i.e. winter habit) is more effective at stabilising flowering time from a broad range of sowing dates than photoperiod sensitivity. Penrose (1993) and Coventry *et al.* (1993) also demonstrated that winter genotypes sown early could yield at least as well, if not better than FS genotypes sown later.

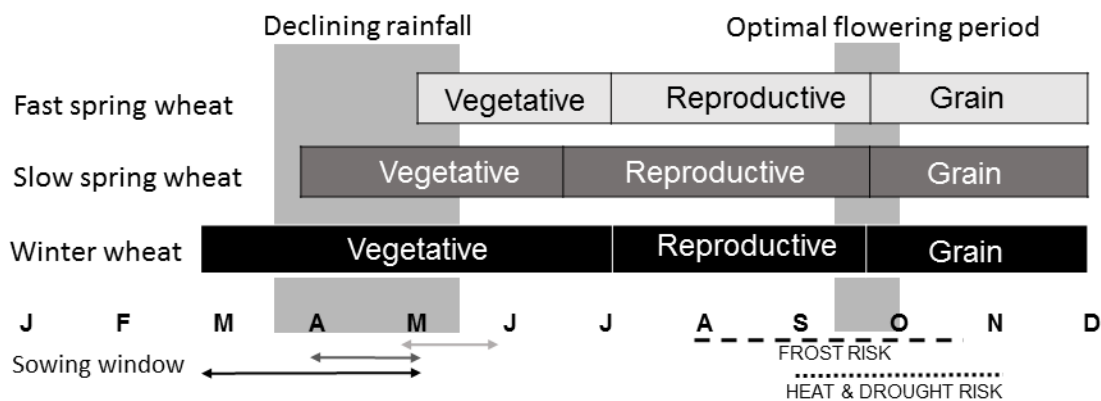


Figure 1: Duration and timing of the different development phases of winter wheat, fast and slow developing spring wheat in relation to the months of the year, typical optimal sowing windows and flowering period for southern Australia (Flohr *et al.* 2017b) and the autumn period during which rainfall has recently declined in southern Australia (Cai *et al.* 2012).

Winter genotypes (obligate vernalisation requirement) do exist in Australian wheat germplasm, but were previously overlooked by growers, agronomists, breeders and researchers due to the late sowing in national variety evaluations which did not express the genotype (G) by management (M) advantages of the longer development phase delivered by early sowing. No milling quality winter wheats have been released during the period 2002-2016 (Hunt 2017). In response to recent research and grower interest in earlier sowing, the wheat breeding company Australian Grains Technology (AGT) have selected Longsword - a photoperiod insensitive 'fast' winter (FW) wheat (obligate vernalisation requirement but short development phase from double ridge to anthesis) from a cross between the high-yielding spring cultivar (Mace) and a CIMMYT-derived spring breeding line. New FW cultivars with better adaptation than those currently available to growers (e.g. Longsword) will further increase benefits to growers, particularly those on mixed farms where dual purpose grazing is possible (Bell *et al.*

2015; Frischke *et al.* 2015). A cultivar with this development pattern has never previously been available to growers in Western Australia (WA), South Australia (SA) or north western Victoria (Hunt 2017).

The aim of this study was to ascertain when growers in southern and western Australia are currently sowing wheat, and to compare the yield and flowering time of Longsword with those of currently grown spring and winter cultivars across a broad range of environments, and at sowing times practiced by growers. In order to isolate the specific impact of crop phenology, the experiment also included related cultivars (near-isogenic lines) that differed in flowering time but were otherwise genetically similar.

2. Materials and methods

2.1 Analysis of wheat sowing time using the Yield Prophet® database

In order to investigate trends in sowing dates for wheat, the sowing date records were obtained from the Yield Prophet® database. Yield Prophet® is an online commercialised version of the crop production model APSIM (Holzworth *et al.* 2014), and is used by farmers to make real-time assessments of crop water and fertiliser requirements and seasonal yield potential. It has been delivered to growers across Australia since 2004 (Hochman *et al.* 2009b). In order to use the service, growers must enter a sowing date for their subscribed fields. Regardless of how many seasons' growers had been subscribed for, sowing dates for all fields sown to wheat and subscribed to the service between 2008 and 2015 (3260 fields) were analysed according to region. Linear functions were fitted to mean sowing dates using least-squares regression in GenStat 18 (VSN International 2013). Sowing dates for fields in regions SA, WA, Vic, and southern New South Wales (NSW) recorded in 2013, 2014 and 2015 were split and summed into weekly intervals.

2.2 Field experiments

Field experiments were conducted at four locations in the southern (Temora, New South Wales; Berriwillock, Victoria; Minnipa, South Australia) and western Australian (Cunderdin) wheat belt (Table 1). Each experiment had 2-4 sowing dates commencing in mid-April and ending in mid-May, and seeds were sown at a depth of 2-4 cm. Details regarding plot size, row spacing, and targeted plant density are shown in Table 1. Time of sowing (TOS) is defined as the calendar date at which seeds become imbibed and begin the process of germination. For instance, this could be the date on which they are

planted into a moist seed bed, or the date on which they received rainfall/irrigation after being sown into a dry seed bed, which is common practice on ~50% of Australian farms (Fletcher *et al.* 2016). Where irrigation has been indicated in Table 1 either 8 (Berriwillock) or 15 mm (Temora) was applied to all plots of that TOS using drip irrigation directly onto the seed row. As this small amount was applied to very dry soil and did not penetrate deeply, it is assumed not to have contributed to crop transpiration and yield. This is certainly the case at Temora in 2016 where an extremely wet winter subsequently filled the soil profile below rooting depth. In all experiments, chemical fertilisers and pesticides were applied such that nutrient limitations, weeds, pests or diseases did not limit yield.

Chapter 4

Table 1: Location, plot size, target plant density, mean and year of experiment growing season rainfall (April to October), time of sowing (TOS), cultivars grown and cultivar development type of either fast-spring (FS), mid-spring (MS), very-slow spring (VSS), fast-winter (FW) or mid-winter (MW).

Site	Year	Soil type	Plot size (m), row spacing (cm)	Targeted plant density (plants /m ²)	Mean growing season rainfall (mm)	Growing season rainfall in year of experiment (mm)	TOS	Cultivars grown	Development type
Temora -34.397, 147.539	2015	Red chromosol	12 x 1.8, 31	120	262	276	17 April	Condo	FS
							27 April	Gregory	MS
							07 May	Longsword	FW
							15 May	Eaglehawk	VSS
								Wedgetail	FW
								Sunstate-FS	FS
								Sunstate-VSS	VSS
	Sunstate- FW	FW							
	Sunstate-MW	MW							
Temora -34.397, 147.539	2016	Red chromosol	10 x 1.8, 31	140	262	591	15 April*	Condo	FS
							27 April*	Gregory	MS
							06 May	Longsword	FW
							15 May	Eaglehawk	VSS
								Wedgetail	FW
								Sunstate-FS	FS
								Sunstate-VSS	VSS

Chapter 4

								Sunstate- FW	FW
								Sunstate-MW	MW
Berriwillock	2015	Vertic calcarosol	12 x 1.8, 30	150	178	139	09 April* 08 May	Scout	FS
-35.640, 142.996								Kiora	MS
								Longsword	FW
								Bolac	VSS
								Wedgetail	MW
Minnipa	2015	Calcarosol	10 x 1.4, 23	120	205	249	13 April 29 April 13 May	Mace	FS
-32.834, 135.151								Cutlass	MS
								Longsword	FW
								Eaglehawk	VSS
								Wedgetail	MW
								Sunstate-FS	FS
								Sunstate-VSS	VSS
								Sunstate- FW	FW
								Sunstate-MW	MW
Cunderdin	2015	Deep sandy duplex	10 x 1.5, 25	150	228	188	14 April 28 April 22 May	Mace	FS
-31.345, 117.144								Magenta	MS
								Longsword	FW
								Eaglehawk	VSS
								Wedgetail	MW
								Sunstate-FS	FS
								Sunstate-VSS	VSS
								Sunstate- FW	FW
								Sunstate-MW	MW

*treatment irrigated a small amount to ensure germination

Flowering date (Zadoks *et al.* 1974) was recorded as the calendar date when 50% of the spikes in each plot had visible anthers. Flowering dates were not recorded at Cunderdin. Grain yield was measured by machine harvest with the exception of Temora in 2016 which was measured by hand-harvesting and threshing 2.0 m² (two 0.83 x 1.2 m quadrats taken from the middle four rows of six row plots). All yields were corrected to 12% moisture content. Additionally in the Temora experiments, the calendar date at which double ridge (Waddington *et al.* 1982) and terminal spikelet (Waddington *et al.* 1982) occurred was recorded using the methods described by Kirby and Appleyard (1981). From the Temora data, a mean flowering date stability index was calculated as 1 minus the ratio of range in thermal time for flowering for each cultivar to the range in thermal time in sowing dates for each year. A higher stability index indicates less change in flowering date for a large range in sowing date. At maturity (Zadoks *et al.* 1974), spikelet number and sterile spikelets in the first floret position were recorded from five heads from each plot in the Temora experiments and an average % of sterile spikelets was determined and assumed to be frost induced sterility as per Reinheimer *et al.* (2004).

Degree day i.e. $TT = \sum ((T_{\min} + T_{\max})/2) - T_{\text{base}}$ accumulation using 0°C as the base temperature and starting from the first sowing date for the season at Temora (station number 073151, 6 km from the site), Minnipa (station number 18195, on site), Cunderdin (station number 19900414, 11 km from the site) and Berriwillock (77094 Swan Hill aerodrome, 70 km from the site) were compared to the average of the number of years of data available from the Commonwealth Bureau of Meteorology (BoM) website for each site. At the Temora site, half-hourly air temperatures were recorded using iButton integrated data loggers (Maxim Integrated, San Jose CA, USA) housed in a radiation screen at 1.5 m height. From the regular recordings, cardinal air temperature and adjusted degree day were calculated for each TOS, where $T_{\text{base}} = 0^{\circ}\text{C}$, $T_{\text{optimal}} = 23^{\circ}\text{C}$ and $T_{\text{max}} = 37^{\circ}\text{C}$ as per Porter and Gawith (1999). Using the same method, vernal days (VD) were calculated using $T_{\text{base}} = -1.3^{\circ}\text{C}$, $T_{\text{optimal}} = 4.9^{\circ}\text{C}$ and $T_{\text{max}} = 15.7^{\circ}\text{C}$ (Porter and Gawith 1999). Adjusted calculations of TT were used to estimate TT between critical development stages of treatments. Using the same method as Flohr *et al.* (2017b) the OFP for Berriwillock (Flohr *et al.* 2017b) was determined and found to be 15-25 September. All other OFP referred to are from Flohr *et al.* (2017b). Where OFP is defined by decreasing frost risk, and

increasing water and heat stress. Flowering as closely as possible to the environmentally determined optima is critical for maximising grain yield.

2.3 *Cultivar selection*

At each site the FW line Longsword was compared to a locally adapted high yielding FS wheat (either Mace, Scout or Condo), a mid-developing spring wheat (MS - either Magenta, Cutlass, Kiora or Gregory), a very-slow developing spring wheat (VSS - EGA Eaglehawk or Bolac) and a mid-developing winter wheat (MW - EGA Wedgetail) (Table 1). Spring cultivars for each site were selected based on their yield performance in National Variety Trials (ACAS 2007). EGA Wedgetail was the last milling quality winter cultivar released in Australia in 2002 and the only milling quality winter cultivar available to growers at the time of the experiments (Hunt 2017).

In four experiments (Temora 2015 & 2016, Minnipa and Cunderdin), Sunstate and three Sunstate background near-isogenic lines (NILs) were also sown in conjunction with the commercial lines (Table 1). The NILs were developed by crossing desired alleles into the recurrent parent Sunstate to backcross five (Steinfort *et al.* 2017). Four NILs that varied in their response to vernalisation and photoperiod were selected for use in the experiments. The alleles of the five major genes governing wheat development present in each of the lines are presented in Table 2. Comparing phenology and yield of NILs has the advantage of removing genetic differences other than phenology that occur when solely comparing yield of commercial cultivars. The development patterns of the NILs corresponded to cultivars with similar development times also grown in the field experiments; Condo/ Mace/ Scout to Sunstate fast-spring (Sunstate-FS), Longsword to Sunstate fast-winter (Sunstate-FW), EGA Eaglehawk/ Bolac to Sunstate very-slow spring (Sunstate-VSS) and EGA Wedgetail to Sunstate mid-winter (Sunstate-MW).

Table 2. The five major development genes of wheat, and alleles carried by commercial cultivars and near-isogenic lines which govern response to vernalisation (Vrn; v=sensitive, a, b, e=insensitive) and photoperiod (Ppd; b, c=sensitive, a=insensitive).

Cultivar	Photoperiod		Vernalisation		
	<i>Ppd-B1</i>	<i>Ppd-D1</i>	<i>Vrn-A1</i>	<i>Vrn-B1</i>	<i>Vrn-D1</i>
Condo	<i>a</i>	<i>a</i>	<i>v</i>	<i>a</i>	<i>a</i>
Mace	<i>a</i>	<i>a</i>	<i>v</i>	<i>a</i>	<i>v</i>
Scout	<i>b</i>	<i>a</i>	<i>v</i>	<i>a</i>	<i>a</i>
Gregory	<i>b</i>	<i>a</i>	<i>v</i>	<i>v</i>	<i>a</i>
Cutlass	<i>b</i>	<i>d</i>	<i>a</i>	<i>a</i>	<i>v</i>
Magenta	<i>b</i>	<i>a</i>	<i>v</i>	<i>a</i>	<i>v</i>
Eaglehawk	<i>b</i>	<i>b</i>	<i>b</i>	<i>v</i>	<i>a</i>
Bolac	<i>b</i>	<i>a</i>	<i>a</i>	<i>v</i>	<i>v</i>
Longsword	<i>a</i>	<i>a</i>	<i>v</i>	<i>v</i>	<i>v</i>
Wedgetail	<i>b</i>	<i>a</i>	<i>v</i>	<i>v</i>	<i>v</i>
Fast-spring (Sunstate-FS)	<i>a</i>	<i>a</i>	<i>v</i>	<i>a</i>	<i>a</i>
Very-slow spring (Sunstate-VSS)	<i>b</i>	<i>b</i>	<i>e</i>	<i>a</i>	<i>a</i>
Fast-winter (Sunstate-FW)	<i>a</i>	<i>a</i>	<i>v</i>	<i>v</i>	<i>v</i>
Mid-winter (Sunstate-MW)	<i>a</i>	<i>b</i>	<i>v</i>	<i>v</i>	<i>v</i>

2.4 Statistical analyses

All experiments were split-plot designs (whole plot = time of sowing, sub-plot = cultivar) with four replicates and spatial optimisation, designed with DiGger software (Coombes 2002). Yields were analysed within sites using linear mixed models (REML) accessed via the GenStat 18 user interface (VSN International 2013) with sowing date and cultivar as fixed effects and site and block structure as random effects. At the Temora site, year was included as a fixed effect factor in the model. Apart from the two year experiment at the Temora site, sites were analysed

separately due to the large interaction between site and treatments. A 5% least significant difference was estimated using twice the Standard Error of the Difference.

3. Results

3.1 Analysis of sowing time data from Yield Prophet® database

All regions showed a trend toward sowing earlier with different rates of change between 2008 and 2015. In WA the rate of change was 1.3 days/year, in SA 1.4 days/year, Victoria 2.0 days/year and southern NSW 1.1 days/year (Fig. 2). During 2013-2015 42% of fields from across all regions were sown prior to 10 May (Fig. 3), a date which approximates optimal time of sowing for current elite fast developing spring cultivars in most environments of Southern Australia (Flohr *et. al.* 2017).

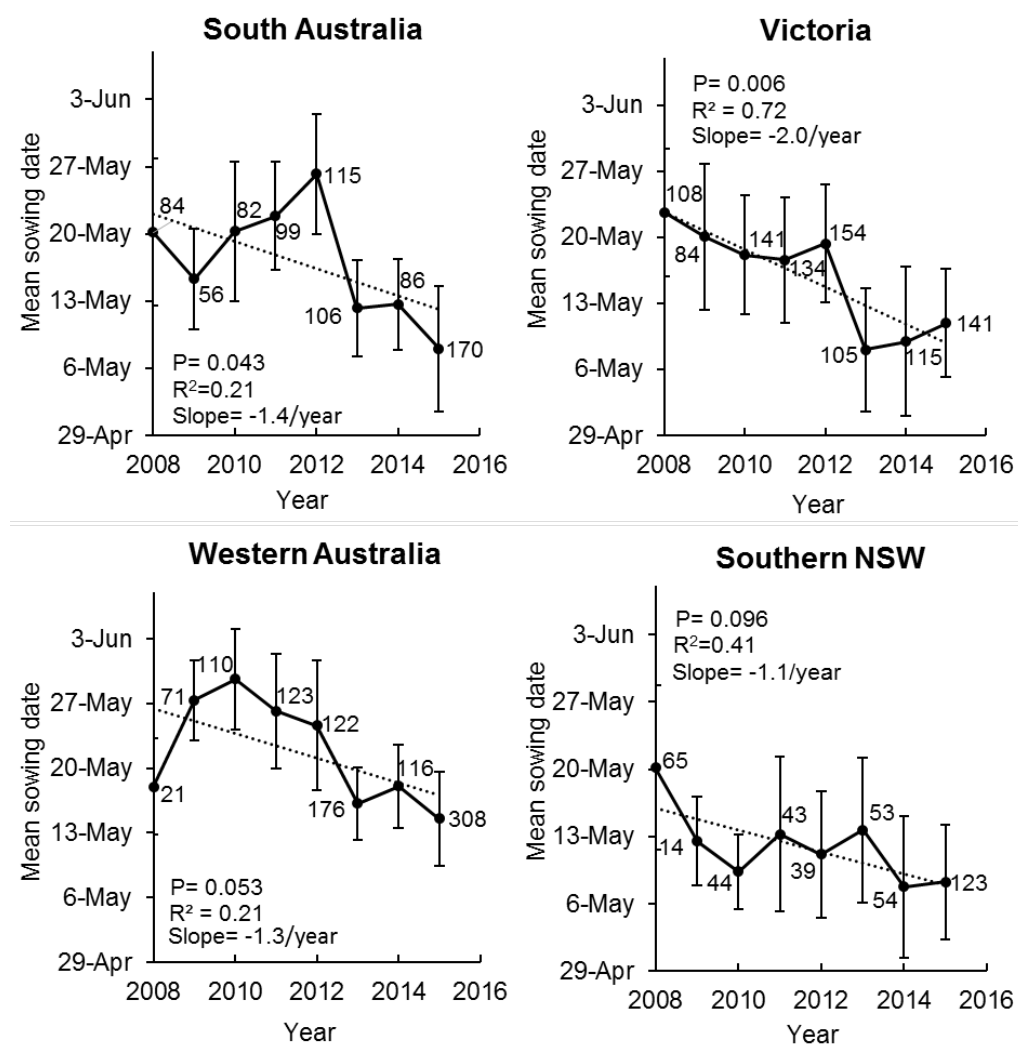


Figure 2: Mean sowing date for different regions from 2008-2015 from the Yield Prophet® data base, and P-value, R2 and the slope of the linear function fitted to the data. The number next to marker is the number of fields included in the mean sowing date for each year. Error bars are the standard deviation around the mean for each year.

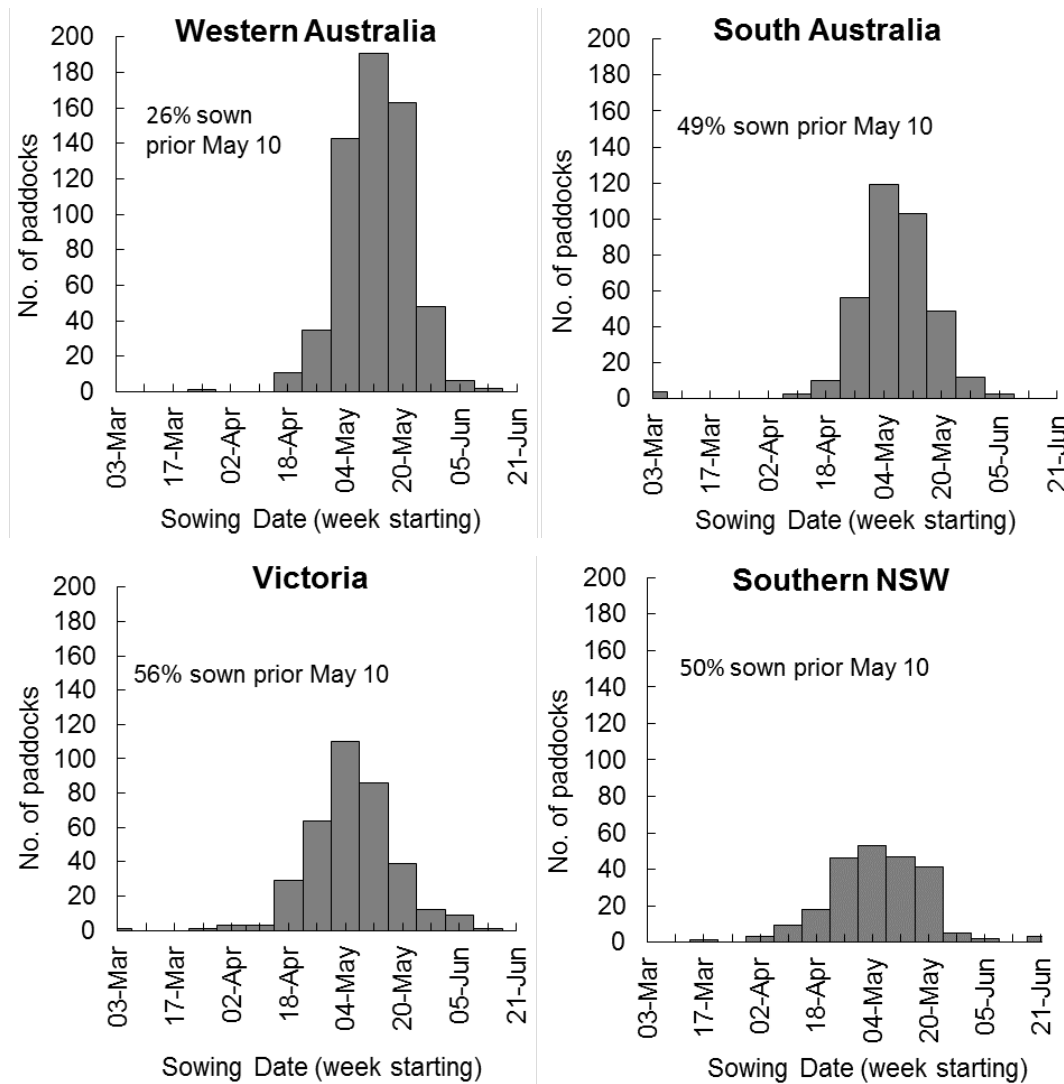


Figure 3: Number of fields sown at weekly time intervals for wheat growing regions in Western Australia (total fields 600, median sowing date 15 May), South Australia (total fields 359, median sowing date 10 May), Victoria (total fields 358, median sowing date 9 May), southern New South Wales where (total fields 228, median sowing date 8 May) for combined seasons 2013, 2014 and 2015 from the Yield Prophet® database.

3.2 Seasonal conditions

The monthly TT accumulation (°C) in the year of experiment for each site is summarised in Figure 4. In 2015, Temora had a cooler than average growing season and growing season (April-October) rainfall of 276 mm (long-term average 262 mm, Table 1). Temora experienced several frost events just prior to the optimal flowering period (between the 23rd and 26th of September) where minimum temperatures ranged from -0.5 to -2.2 °C. During the optimal flowering period in 2015, Temora also experienced 3 days where maximum temperatures were over 30^oC, when many treatments were flowering. The drought stress experienced by the crop in 2015 growing season at Temora can be characterised as stress beginning before flowering and lasted until maturity (ET₃₋₄ as per Chenu *et al.* (2013)). The 2016 growing season in Temora had an above average temperature and rainfall (590 mm in April-October). The season of 2016 was so favourable (no water stress, sufficient nitrogen and zero frost or heat events at or surrounding the optimal flowering time) that yields of up to ~8 t/ha were achieved. Rainfall in Berriwillock in 2015 was well below average, and there were 3 days of extreme heat >35°C during grain fill in early October and drought characterised as severe that lasted until maturity (ET₄ as per Chenu *et al.* (2013)). In Minnipa in 2015, temperature was close to long term average and rainfall was slightly above average and drought characterised as an ET₂ with mild stress post-flowering. In Cunderdin in 2015 there were two frost events, -0.5°C and -0.1°C on October 2 and 4, below average rainfall and characterised as an ET₃₋₄ drought stress.

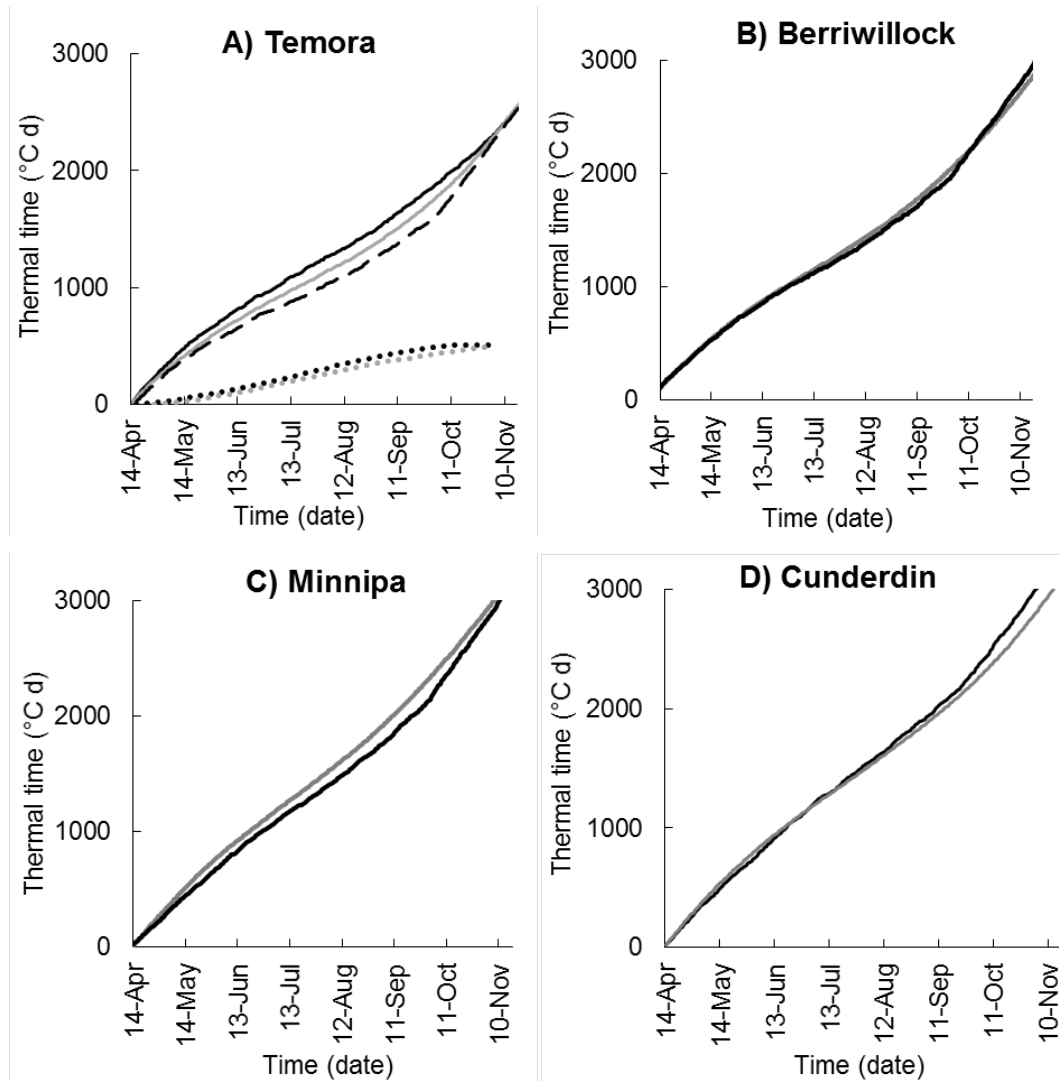


Figure 4: Cumulative thermal time ($^{\circ}\text{C d}$) for A) Temora, NSW black line 2016, broken black line 2015, grey line average of years 2005-2016, and adjusted vernal days (●●●● 2015 and ●●●● 2016) B) Berriwillock in 2015 vs. mean 1997-2016 C) Minnipa in 2015 vs mean 1998-2016 and D) Cunderdin in 2015 vs mean 1990-2016. Accumulated degree days in the year of the experiment (black line) and long term mean for each site (grey line).

3.3 Field experiments comparing cultivar response (excluding NILs) to time of sowing

i. Temperate environment

High rainfall regions of south-eastern Australia such as Temora have equi-seasonal rainfall distribution, experience cooler winters and relatively mild springs and typically have an OFP for wheat from late September to mid-October (Flohr *et al.* 2017b). Grain yields were largely related to the effect of time of sowing on date of flowering (Fig. 5, 6). In both experimental seasons at Temora, there were significant interactions between cultivar and TOS, and the highest yielding genotype x sowing date treatments flowered within the OFP (Fig. 5A, B).

In 2015, treatments that flowered during the OFP were FS sown 27 April to 15 May, FW and MS sown in 17 April to 7 May, and MW and VSS sown 17 April (Fig. 5A). The highest yielding treatments were FS sown 27 April, and FW sown 17 April. Mean yield of commercial cultivars across all TOS were FS>FW>MS>VSS>MW. In 2015 early sown FW yielded 21% more than FS sown later (current practice), or 16% more when both were sown early. In the warmer 2016 growing season, treatments that flowered during the OFP were FS sown in 15 May, the FW and MS cultivars sown 15 April to 6 May, and MW sown in 15 April. Zero treatments of the VSS flowered during the OFP in 2016 (Fig. 5B). In 2016 the highest yielding treatments were FS sown 15 May and FW sown 6 May. In 2016, the favourable spring conditions (high level of plant available water and zero frost or heat events) favoured slow developing cultivars and mean yield across all TOS were FW>MW>MS>VSS>FS. In 2016 FS sown later yielded 6% more than FW sown early, but FW yielded 70% more when both were sown mid-April.

Table 3 summarises the two seasons at Temora, and shows that spring cultivars had a lower stability index (less stable flowering) compared to winter cultivars. The FW line Longsword had the highest mean yield, while FS cultivar i.e. Condo, had greater variability in yield than winter cultivars. Sterile spikelet scoring at Temora showed that FS cultivars had the highest average number of sterile spikelets when sown early (Table 4).

Table 3: Flowering date stability (higher number indicates a cultivar is more stable), mean yield and mean standard deviation of yield for cultivars. Figures are averaged across all times of sowing for two seasons at Temora, NSW in 2015 and 2016.

Cultivar	Flowering date stability index	Mean grain yield (t/ha)	Mean standard deviation of yield (t/ha)
Condo	0.09	5.5	1.3
Gregory	0.50	5.5	0.5
Longsword	0.70	6.3	0.4
Wedgetail	0.73	5.5	0.4
Eaglehawk	0.71	5.3	0.3
Sunstate-FS	0.52	4.6	1.2
Sunstate-VSS	0.72	4.2	0.3
Sunstate-MW	0.53	4.9	0.5
Sunstate-FW	0.70	5.1	0.5
P- Value (cultivar)		<0.001	
LSD		0.2 t/ha	

Table 4. The effect of sowing date on mean spikelet sterility (%) for cultivars at maturity. Time of sowing (TOS) ranged from mid-April to mid- May at Temora, NSW in 2015 and 2016.

Cultivar	Year	Mean spikelet sterility %			
		TOS1	TOS2	TOS3	TOS4
Condo	2015	8	7	7	6
	2016	62	12	5	4
Eaglehawk	2015	4	5	15	7
	2016	4	3	3	2
Gregory	2015	7	8	14	6
	2016	17	11	9	3
Longsword	2015	12	7	8	7
	2016	16	6	8	5
Wedgetail	2015	3	5	8	9
	2016	2	1	2	2
Sunstate-FS	2015	9	5	8	12
	2016	65	12	10	3
Sunstate-VSS	2015	10	14	11	20
	2016	6	3	11	2
Sunstate-FW	2015	12	10	12	12
	2016	32	9	8	5
Sunstate-MW	2015	13	17	17	20
	2016	6	6	8	3
2016 Cultivar. TOS		<0.001			
2015 Cultivar. TOS		0.003			
2016 LSD		10			
2015 LSD		7			

ii. Mediterranean environments

In the medium-low rainfall areas of western and southern Australia which experience cool, wet winters with hot, dry springs (OFP late August- mid September) the FW genotype yielded highest when sown from mid to late April TOS, while yield decreased when sown after these dates (Fig. 5C, D, E). The average yield advantage of FW sown early vs. FS sown late (current practice) in these environments was 7%.

In 2015 the highest yielding treatments at Berriwillock flowered earlier than the defined OFP thus escaping the very hot and dry spring of 2015 (Fig. 5C). The FS cultivar sown early flowered very early (18 August), and was the highest yielding treatment in the experiment. The FW line sown early flowered during the optimal period (15-25 September) for that environment, but achieved a slightly lower yield than the FS (FW 1.6 t/ha vs FS 1.8 t/ha, LSD 0.14 t/ha). In Berriwillock MS, VSS and MW sown 9 April were competitive with the FW and FS treatments. At Minnipa the FS flowered during the OFP when sown from 29 April to 13 May, and the FW only from 13 April sowing (Fig. 5D). The MS cultivar was close to flowering within the OFP from 13-29 April TOS, and zero treatments of the VSS flowered during the optimal period. At Minnipa when both FS and FW were sown early, FW had a 14% yield advantage. While flowering date was not recorded at Cunderdin, FW sown at later TOS yielded less than the spring wheats, indicating it flowered outside the optimal period with later TOS, as occurred at Minnipa (Fig. 5E). At Cunderdin yields were not reported for plots of FS and MS sown 14 April as they ripened early and were damaged by birds, we assume FW sown 14 April was the highest yielding early sown treatment for this site.

The FW sown 14 April at the Cunderdin site showed a disadvantage compared to FS sown later (FW 3.2 t/ha vs FS 3.7 t/ha, LSD 0.4 t/ha). At Minnipa and Cunderdin relatively low yields were observed for VSS and MW regardless of TOS, suggesting that the older, commercially available, slow developing cultivars are not competitive with the elite fast/mid-spring wheats.

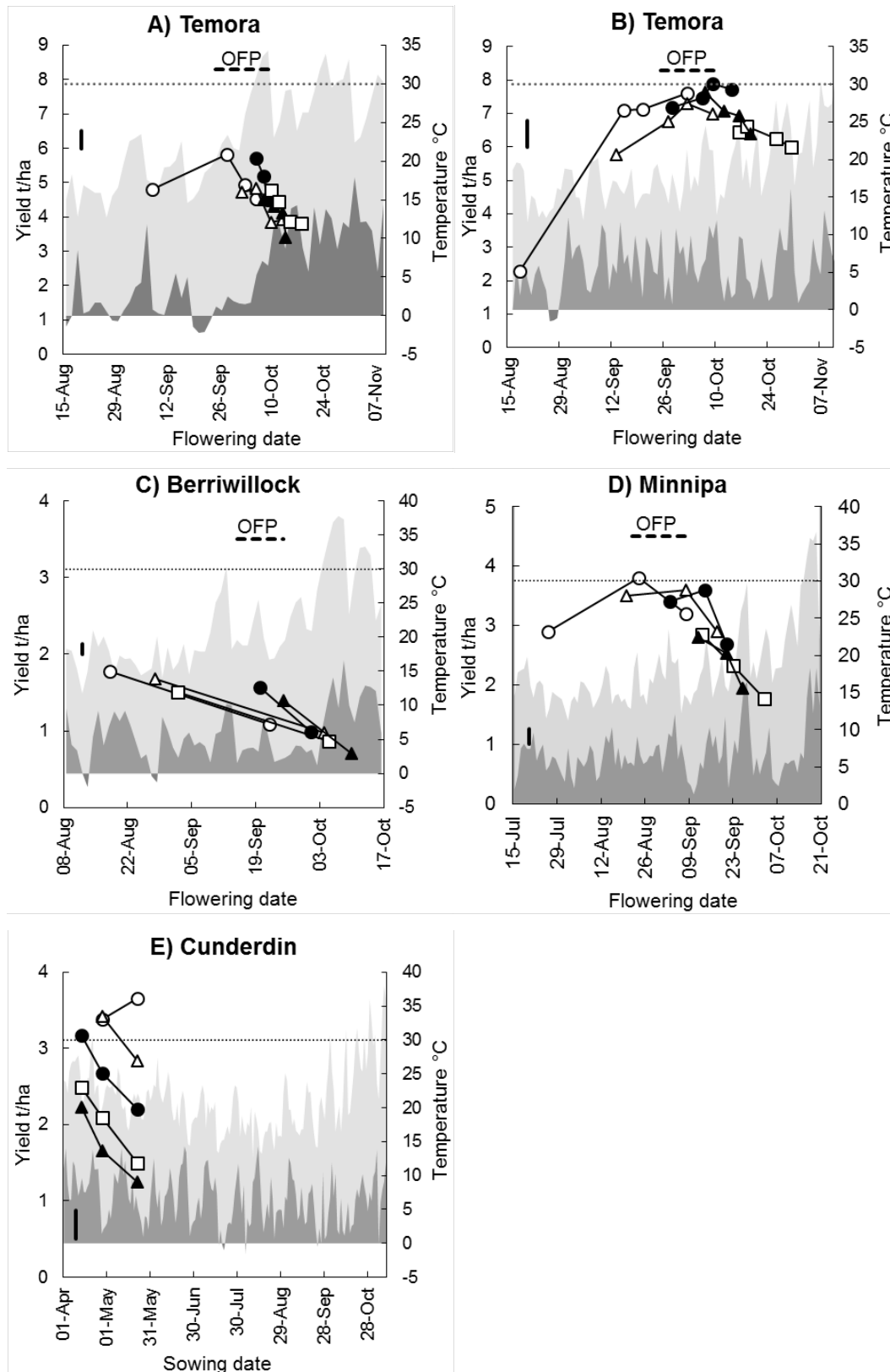


Figure 5: Mean grain yield (t/ha) of commercial cultivars, a fast developing spring wheat (○), mid-fast developing spring wheat (△), very-slow spring wheat (□), fast developing winter wheat (Longsword, ●), and mid-winter wheat (▲) plotted against

flowering date and minimum ($^{\circ}\text{C}$, dark grey shading) and maximum temperatures ($^{\circ}\text{C}$, light grey shading) at A) Temora, 2015 B) Temora, 2016 C) Berriwillock, 2015 and D) Minnipa, 2015 E) Cunderdin, 2015 shown as grain yield vs. time of sowing vs. temperature (flowering dates not recorded). Cultivar and sowing date details for each site are shown in Table 1. Each marker represents a different time of sowing and sowing date moves later from left to right. Broken lines are the optimal flowering period (OFP) as per Flohr *et al.* (2017). The vertical line is 5% LSD, P-Value of TOS x cultivar interaction at Temora, Minnipa and Cunderdin is <0.001 , and at Berriwillock <0.005 .

3.3 Effect of sowing date in near isogenic lines

In the temperate environment, the highest yielding NIL treatments flowered within the OFP (Fig 6A, B). In 2015, the first TOS (17 April) for all cultivars except the Sunstate-VSS flowered within the OFP. The dry and warm conditions during the OFP favoured treatments sown at the first and second TOS for Sunstate-FS, and were the highest yielding treatments. In the contrasting season of 2016, treatments that flowering during the OFP were Sunstate-FS and Sunstate-FW sown 27 April, 6 May and 15 May and Sunstate-MW sown 15 April (Fig. 6B). The highest yielding treatments were Sunstate-FW sown 27 April (7.4 t/ha) and 6 May (7.3 t/ha) and Sunstate-MW sown 15 April (7.4 t/ha). Sunstate-FW sown 15 April was the lowest yielding treatment for this cultivar (5.5 t/ha), all other TOS performed well with yields greater or equal to Sunstate-FS. When sown early in all environments (warm and cool), the Sunstate-VSS line flowered late, outside the OFP, and produced deformed and largely infertile spikes.

This is possibly related to the strong photoperiod sensitivity of this line when it initiates flowering under short days. Across all TOS and both seasons at Temora, FW had 0.8 t/ha yield advantage over Sunstate-FS and similar yields to Sunstate-MW. The Sunstate-VSS line had the most stable flowering date but the lowest mean yield (Table 3).

As with the commercial varieties described in the previous section, in the warmer Mediterranean type environments the slow developing NILs of Sunstate-FW, Sunstate-VSS and Sunstate-MW gave the highest yield at early times of sowing, with yield decreasing with later TOS (Fig. 6C, D). At Minnipa the mean yield

advantage of Sunstate-FW sown 30 days earlier than Sunstate-FS sown at its optimal time (current practice) was 0.2 t/ha. The mean yield advantage of Sunstate-FW over Sunstate-FS when both were sown 30 days earlier than current practice was 0.7 t/ha in Minnipa. The Sunstate-MW line was too slow to flower at Minnipa and yields were reduced relative to Sunstate-FW by terminal drought and heat stress in all but the earliest times of sowing. Similar to the commercial varieties in Cunderdin, Sunstate-FS yielded 0.3 t/ha higher than Sunstate-FW.

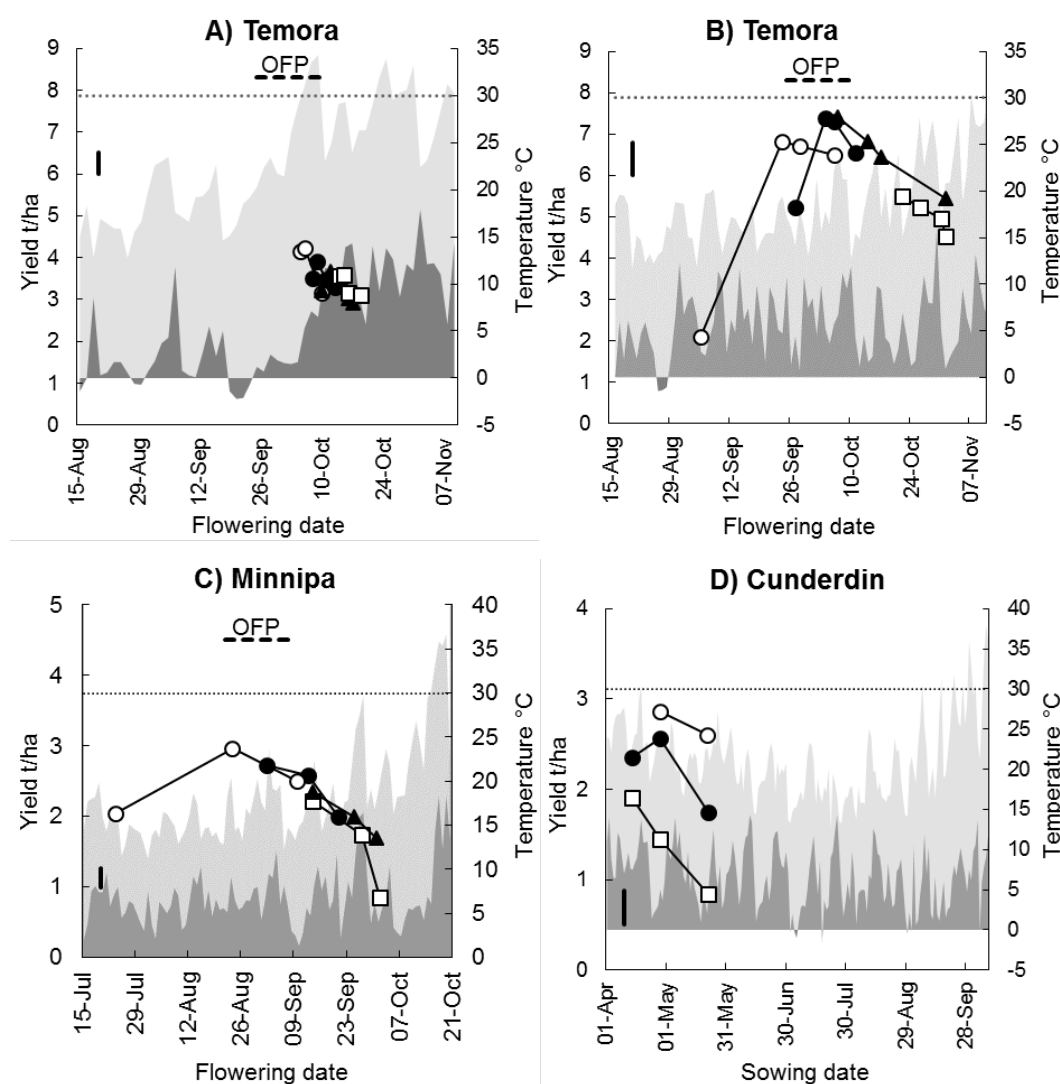


Figure 6: Mean grain yield (t/ha) of near-isogenic lines with development patterns representing a fast developing winter wheat (●), fast developing spring wheat (○), very-slow spring wheat (□) and mid-winter wheat (▲) plotted against flowering date and minimum (°C, dark grey shading) and maximum temperatures (°C, light grey shading) at A) Temora, 2015 B) Temora, 2016 C) Minnipa, 2015. D) Cunderdin, 2015 shown as grain yield vs. time of sowing. Cultivar and sowing date details for

each site are shown in Table 1. Each marker represents a different time of sowing and sowing date moves later from left to right. Broken lines are the optimal flowering period (OFP) as defined by Flohr *et al.* (2017). The vertical line is 5% LSD, P-Value of TOS x cultivar interaction is <0.001.

3.4 Development

Environmental influences on key developmental stages affected cultivars grown in Temora. Figure 7 and 8 show more thermal time was required to reach key development phases (DR, TS, Z65) in 2016 than in 2015, but less VD were required to reach DR in 2016 than 2015. The development of consecutive sowings of each of the five cultivars and four NILs was found to converge. For example cultivar Longsword with four dates between 17 April and 15 May reached flowering within a period of 5 days. This convergence has been summarised for the cultivars shown in Figure 7 and 8 by calculating a flowering date stability index (Table 3). The winter cultivars remained vegetative (up to DR) from early sowings longer than spring cultivars (Fig. 7, 8), demonstrating the mediation role played by vernalisation. In both contrasting seasons, winter cultivars (Longsword and EGA Wedgetail) required more VD than spring cultivars (Condo and Gregory) to reach double ridge and flowered within the OFP from early TOS (Fig. 7). Winter cultivars EGA Wedgetail and Longsword also tended to have a longer DR-TS phase at earlier TOS compared to later TOS. Across both seasons and all time of sowing, EGA Wedgetail had a mean of 249 VD to reach DR (SD \pm 41 VD), Longsword 229 VD (SD \pm 37 VD), EGA Eaglehawk 226 VD (SD \pm 45 VD), Gregory 182 VD (SD \pm 63 VD), Condo 136 VD (SD \pm 48 VD), Sunstate-MW 249 (SD \pm 42), Sunstate-FW 221 (SD \pm 55), Sunstate-VSS 216 (SD \pm 50) and Sunstate-FS 156 (SD \pm 67).

2015

2016

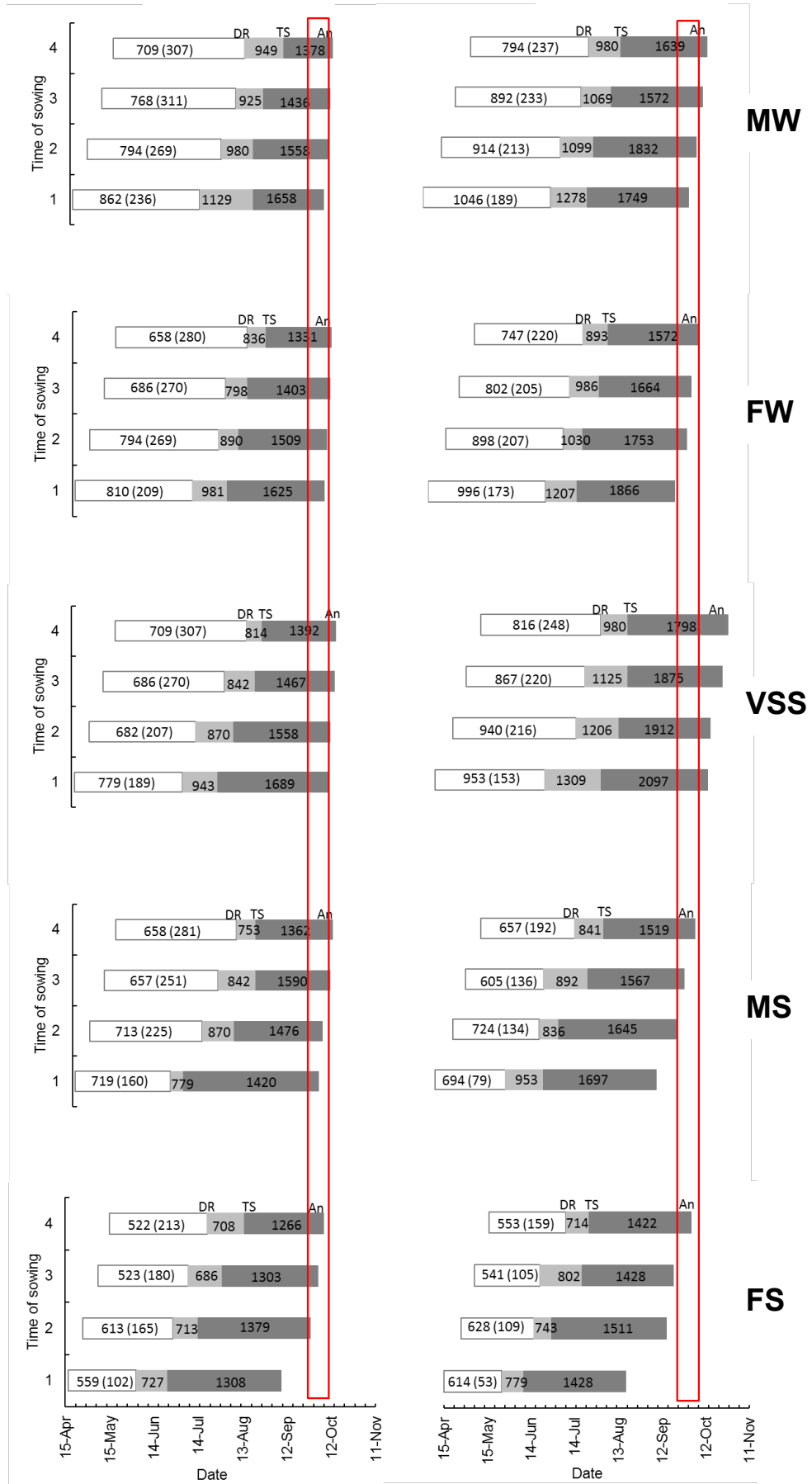


Figure 7: Developmental patterns of mid-winter (MW), fast-winter (FW, Longsword), very-slow spring (VSS), mid-spring (MS) and fast-spring (FS) cultivars sown in Temora, NSW in 2015 and 2016. In 2015 time of sowing (TOS) were 17 April, 27 April, 7 May and 15 May and in 2016 TOS were 17 April, 27 April, 6 May and 15 May. White area is calendar days from sowing to double ridge (DR), light area grey is calendar days from DR to terminal spikelet (TS) and dark grey area is calendar days from TS to flowering (An). Number written without brackets is cumulative degree day and number within brackets is vernal days to reach DR. Vertical box is the optimal flowering period for Temora as per Flohr *et al.* (2017).

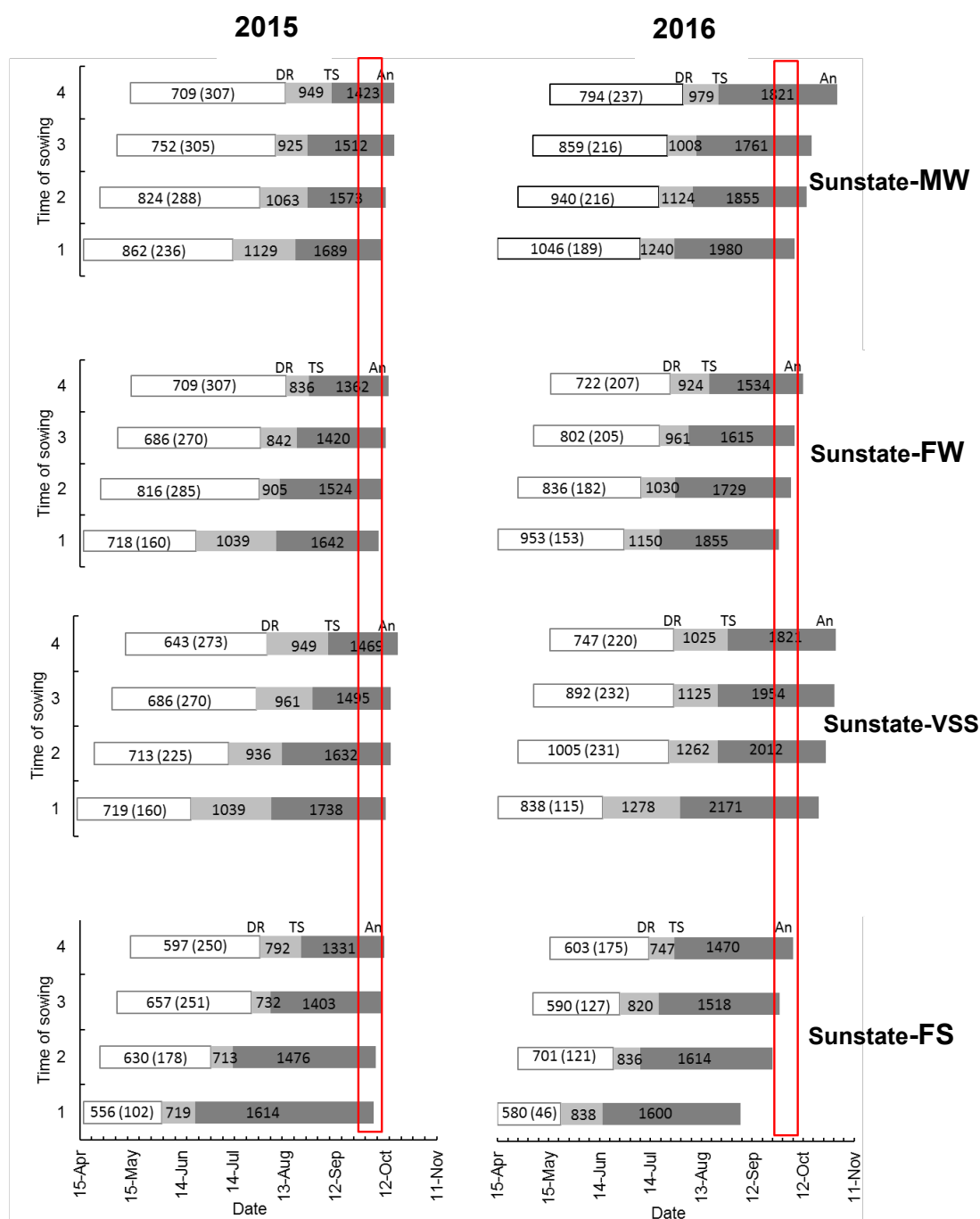


Figure 8: Developmental patterns of Sunstate-MW, Sunstate-FW, Sunstate-VSS and Sunstate-FS near isogenic lines sown in Temora, NSW in 2015 and 2016. In 2015 time of sowing (TOS) were 17 April, 27 April, 7 May and 15 May and in 2016 TOS were 17 April, 27 April, 6 May and 15 May, and. White area is calendar days from sowing to double ridge (DR), light area grey is calendar days to reach terminal spikelet (TS) and dark grey area is calendar days to reach flowering (An). Number written without brackets is cumulative degree day °C and number within brackets is vernal days to reach DR. Vertical box is the optimal flowering period for Temora as per Flohr *et al.* (2017).

4. Discussion

4.1 Sowing date analysis

The move to earlier sowing times revealed in this study is consistent with the shifts reported over a longer period (Anderson *et al.* 2016; Fletcher *et al.* 2016). The mean sowing dates in different regions (SA 10 May, Vic 9 May, sNSW 9 May, WA 16 May) for growers in the Yield Prophet[®] database are now close to those recommended to optimise flowering times for the majority of the existing fast-spring cultivars grown (Flohr *et al.* 2017b). The benefits of early sowing are well documented and include increased frequency of planting opportunities (Hunt *et al.* 2012), increased machinery use efficiency (Fletcher *et al.* 2016), a longer grain yield formation phase (Hunt *et al.* 2012), higher water-use efficiency (Richards 1991; Gomez-Macpherson and Richards 1995; Richards *et al.* 2014), deeper roots for greater water extraction (Incerti and O'Leary 1990; Kirkegaard *et al.* 2014; Kirkegaard *et al.* 2015; Lilley and Kirkegaard 2016), improved early vigour in warm soil temperatures (Penrose 1993) for both greater weed competition (GRDC 2017) and reduced soil evaporation (Batten and Khan 1987; Eastham *et al.* 1999) and increased interception of solar radiation (Stapper and Harris 1989). For growers to fully realise the benefits of early sowing, greater breeding emphasis is needed on cultivars that can achieve the OFP from earlier sowing. Without that, growers will remain at high risk of yield loss to frost, heat and drought in current and future climates (Yang *et al.* 2014; Flohr *et al.* 2017b).

4.2 FW genotype vs. commonly grown genotypes

The novel FW genotype studied here provides greater flexibility in sowing date than FS genotypes to deliver greater yield and flowering time stability, a result consistent with several studies on winter wheat physiology (Mac-Indoe 1937; Batten and Khan 1987; Penrose 1993; Penrose and Martin 1997). The results support the conclusions of recent agronomic studies that well-adapted, slow-developing cultivars are required for early sowing to be viable in current and future climates of Australia (Anderson *et al.* 1996; Kirkegaard and Hunt 2010; Ludwig and Asseng 2010; Bell *et al.* 2015; Fletcher *et al.* 2016; Hunt 2017). In agreement with Fischer and Kohn (1966), grain yield in these trials were largely related to the effect of TOS on flowering date. While FS and MS cultivars such as Mace, Scout and Gregory perform well from sowing dates in early May, spring wheats are less stable in their flowering date when

sown earlier (Fig. 5). Spring wheats have some weak vernalisation sensitivity that speeds development under cold temperatures, but they will flower regardless of cold exposure (Kamran *et al.* 2014). Earlier sown FS cultivars flower too early and yield is reduced by frost (Table 4). FW genotypes can safely extend sowing windows and provide a small yield increase, as demonstrated here by the mean 8% yield advantage of the early-sown FW genotype over the later-sown FS cultivars. This advantage is somewhat less than the 15% reported previously by Penrose (1993), presumably due to the greater diversity of environments in this study. Alternatively, an experiment that was irrigated and in a low frost environment in Mexico, found that there was no difference in yield between a long season wheat sown early and a short season wheat sown later, though the long season wheat cultivar had photoperiod and vernalisation sensitivity and may not be a fair comparison (Fischer 2016). The only yield that could not be attributed to flowering date was Sunstate-FW sown mid-April, which yielded significantly less than Sunstate-FS sown later but flowering concurrently. The commercial FS cultivar (Condo) and equivalent NIL (Sunstate-FS) showed very different mean stability indices (0.09 vs. 0.52). Condo had low stability in both the 2015 and 2016 seasons (0.04 and 0.13 respectively), whereas Sunstate-FS had high stability in 2015 (0.75) and low in 2016 (0.28), suggesting there are background effects not explained by major genes in the NILs. Nonetheless FS genotypes were not stable across wide sowing dates or contrasting seasons. There was an overall yield advantage for the Sunstate-FW of 23% when both were sown in mid-April (current practice), which was very similar to the yield advantage of 22% found between the commercial cultivars both sown early. Sowing earlier with slow developing cultivars offers a novel avenue to increase yield in response to greater farm size and climate variability in southern Australia. The range in latitude of sites used in this study was between 31°S and 36°S (Table 1). Earlier sowing with slower developing cultivars also has the potential to raise yield and maximise resource use in similar regions outside of southern Australia. This could include other wheat production zones in the southern hemisphere affected by autumn rainfall decline described by Cai *et al.* (2012), and wheat producing regions in the northern hemisphere at similar latitudes with Mediterranean and temperate climates such as west Asia and north Africa (Piggin *et al.* 2015).

In environments ending in terminal drought, photoperiod insensitivity has been key to accelerate growth to ensure life cycle is complete before high temperatures (Worland 1996). A large number of Australian cultivars have insensitive alleles to photoperiod (Cane *et al.* 2013) and few VSS genotypes have been released in Australia. Photoperiod sensitivity affects both vegetative and reproductive phases of wheat (Miralles and Richards 2000). In theory, extending the reproductive phase (TS-AN) with photoperiod sensitivity would support increased spike weight and increased number of fertile florets at flowering resulting in higher potential grain yield (Slafer and Rawson 1994, 1996; Whitechurch and Slafer 2002; González *et al.* 2005). Steinfort *et al.* (2017) conclude that the utilisation of sensitivity genes *VRN1* or *Ppd-1* to increase the duration of the reproductive phase is a more complex process than originally proposed. Our results, and those of Penrose and Martin (1997), found photoperiod sensitive wheats such as Eaglehawk, Bolac or the Sunstate-VSS were not competitive with the elite FS/MS cultivars, or wheats with MW or FW genotypes. The flowering date of VSS can be less stable than FW or MW, because the photoperiod requirement can become saturated and trigger early flowering if crops are sown too early (Richards *et al.* 2014). However our results show that the VSS genotype had a high flowering date stability index (~ 0.7), and the lowest standard deviation for grain yield (Table 3). In our experiments, with the exception of Berriwillock, the VSS cultivars and the Sunstate-VSS flowered after the OFP. These findings suggest that the VSS genotype is stable, but is not suited to the environments it was grown in here, and may be better suited to environments with a longer growing season such as more southern latitudes of the wheat belt e.g. southern Victoria. Averaged across all TOS and sites, the FW genotype yielded 18% more than the VSS cultivars EGA Eaglehawk and Bolac. Cane *et al.* (2013) hypothesised several example genotypes that would be suitable for early sowing, some with more emphasis on photoperiod sensitivity, others on vernalisation sensitivity. Our results (Fig. 5, 6, 7, 8, Table 3) demonstrate that cultivars with a greater emphasis on vernalisation sensitivity have higher and more stable yield across a broad range of sowing dates due to more stable and optimum flowering dates in many areas where earlier sowing has increased. Near-isogenic lines for major genes influencing flowering time (Sunstate-FS, Sunstate-VSS, Sunstate-FW,

Sunstate-MW) show that by changing alleles it is possible to improve adaptability and yield of current practice by up to 23% (Fig. 6).

At each site a small number of genotypes were compared, and although comparisons of each maturity type were between the most elite cultivars commercially available, differences observed may be due to differences in yield potential. For example Longsword is a 2017 release, and EGA Wedgetail is a 2002 release, and factors other than phenology may have contributed to higher yield. It should also be noted that comparison between the elite cultivar and equivalent NIL did not always have the same allelic combinations. For example, Sunstate-VSS is *bbeaa* and Eaglehawk is *bbbva*. Therefore while findings are useful for general interpretation, interpretation is limited by confounding comparisons. Even so, data clearly indicated that flowering within the optimum period is critical to achieve higher grain yield in the regions discussed. To confidently provide recommendations to wheat breeders regarding the optimum allelic combinations, and to growers on cultivar x sowing date combinations beyond the environments studied, further research involving a wider range of genotypes across a wider range of latitudes and different seasons would be necessary.

Despite Penrose and Martin (1997) concluding that winter habit should be a major objective for wheat breeding programs in southern NSW, only a few MW varieties have been released in the last 15 years (Hunt 2017). However EGA Wedgetail has remained popular in southern NSW making up 10% of milling quality deliveries to GrainCorp in 2015-2016 (GrainCorp 2016). NSW growers have continued to grow the available winter types for their value as dual purpose crops, where the crop is grazed in the vegetative phase extended with early sowing (Bell *et al.* 2015).

Experiments here did not attempt to defoliate the winter wheats grown, however Figures 7 and 8 show the period where grazing was possible at each TOS (dates prior to double ridge), and the value of grazing has been clearly demonstrated in previous simulation and field experiments (Harrison *et al.* 2011; Harrison *et al.* 2012; Bell *et al.* 2015; Frischke *et al.* 2015).

4.3 Suitability of FW genotypes to Mediterranean environments

Growers in Mediterranean environments (WA, SA and Victoria) currently take a risk in sowing cultivars that are not adapted to early sowing i.e. Scout, Mace. Results

from the Berriwillock site in 2015 provide an example of how sowing FS wheat earlier than recommended has been an effective strategy to increase yields in recent hot, dry seasons (Fig. 5C). It is a strategy that carries high risk of reduced yields in a frosty or higher yielding season, and these experiments show that using slow developing cultivars in early sowing windows is a less risky strategy. A common argument against early sowing and winter wheats is that there is greater competition for assimilates between the growing spike and the elongating stem (Gomez-Macpherson and Richards, 1995) resulting in more stem biomass and less grain, i.e. low harvest index and low water use efficiency. However our results show that even in the dry environments (and in below average seasons, Fig. 4) of Berriwillock and Cunderdin, winter genotypes in modern genetic backgrounds i.e. Longsword, sown early can compete with commonly grown cultivars. Even though early sown winter wheats can have higher evapotranspiration due to an extended vegetative period (Doyle and Fischer 1979), early sown crops have deeper roots to access stored soil water when available (Lilley and Kirkegaard 2016).

Later sowing of FW Longsword resulted in yields declining below those of MS or FS genotypes. This was also true for other slow developing cultivars MW and VSS grown in these environments. This yield response is largely explained by flowering time, as Longsword, Wedgetail and Eaglehawk did not flower during the optimal period from later sowing times (Fig. 5) in warm environments such as Minnipa where vernalisation is slow i.e. a longer length of time is required due to a more mild growing season (Fig. 4D). In these environments, it is likely that FW genotypes will augment current mid and fast developing spring types by further opening the sowing window available to growers, but it is unlikely to replace them as later sown FW will flower outside the OFP. By extending the sowing window, FW cultivars can contribute to timeliness of the sowing program to maximise whole farm yield.

4.4 Suitability of FW genotypes to temperate environments

Southern NSW had the lowest number of fields subscribed to Yield Prophet compared to other regions, and the greatest number of fields were sown in the week starting 9 May. However, our results show that in this environment the potential sowing window for a FW wheat such as Longsword could begin early April and extend into mid-May, where it achieved similar or higher yields to the widely grown MS cultivar Gregory sown at its optimal time.

Penrose (1993) estimated that a sowing opportunity (sowing opportunity defined as >15 mm) for winter wheats in the period between mid-April and early May can be achieved in 75% of years in southern and central NSW. This is similar to Temora, where there was opportunity for early sowing in 70% of years in the last 10 years (2006- 2016) (Australian Government 2017). In the relatively cool environment of Temora, Longsword consistently flowered during the optimal period across a broad range of sowing dates (mid-April to early-May) even in seasons with contrasting temperature extremes (Fig. 4A, B). The mean yield advantage across all seasons and times of sowing at Temora of FW Longsword over FS Condo and MS Gregory was 0.8 t/ha (Table 3). In addition to a higher mean yield, Longsword offered greater yield stability (standard deviation 0.4 t/ha) vs. Condo (standard deviation 1.3 t/ha) or Gregory (standard deviation 0.5 t/ha) associated with greater stability in flowering date (Table 3). Due to the very broad sowing window in this environment, the probability of getting an early establishment opportunity between April and mid-May is higher than getting an establishment opportunity for a mid-fast cultivar i.e. between 4 May and 22 May in Temora (Flohr *et al.* 2017b). This helps resolve the logistical issue of increased farm size described by Fletcher *et al.* (2016) i.e. a larger sowing program that requires more resources for timely establishment and securing a greater area of crop flowering within the OFP to maximise yield. `

4.5 Implications for agronomy and genotype by management interactions

In spite of the potential benefits of sowing winter wheat, a suite of management challenges need to be considered before the full benefits of early sowing with slow developing cultivars can be realised in the environments discussed, including; barley yellow dwarf virus, aphid infestation, take-all and *Septoria tritici* blotch (Penrose 1993; Hunt 2017). Management has been discussed for high rainfall zones of Australia where early sowing has been practiced for a longer period e.g. Penrose (1993); Hunt *et al.* (2015a); Hunt *et al.* (2015b) but in medium and low rainfall areas, research remains site-specific e.g. Hunt *et al.* (2016) and further investigation for optimum management is warranted.

The development patterns and yield advantages shown by the FW genotype addresses the challenge put forward to breeders by Fischer (2011) to "...develop cultivars for which date of anthesis was the same regardless of sowing date". It is likely that the area of wheat sown early will continue to increase as growers seek

improved efficiencies in labour and machinery (Fletcher *et al.* 2016). The FW cultivar Longsword appears to have excellent adaptation to the medium-low and high rainfall environments of southern and western Australia, and was commercially released in late 2017. It will provide further impetus for breeding companies to target FW types with broad adaptation across southern and western Australia and may usher in a new leap in productivity for Australian wheat farmers. There may also be potential for vernalisation to stabilise flowering and yield of other crops such as barley and canola (Kirkegaard *et al.* 2016), and in other Mediterranean and temperate environments which also have distinct OFPs such as North Africa and West Asia, where such genotypes have not yet been utilised (Hoshino and Tahir 1987). Marker-aided selection will aid identification of winter wheats with the desired allele combinations, and is a clear example of how breeders and physiologists can work together to use molecular physiology to achieve breeding objectives.

5. Conclusion

Changing rainfall patterns, extreme spring temperatures and increasing farm size in Australia have driven wheat growers to sow increasingly early, and this demands new G x M strategies to minimise water and temperature stress at flowering and maximise yield. A modern FW genotype (with photoperiod insensitivity and vernalisation sensitivity) can stabilise both flowering time and yield across a broad range of environments using the early establishment dates currently practiced by growers. Given the change in grower sowing times described here, greater breeding effort and national variety trial resources should be applied to winter cultivars with good local adaptation to different agro-ecological environments across the wheat growing areas of southern and western Australia.

Chapter 5

Genotype x management strategies to stabilise the flowering time of wheat in the wheatbelt of south-eastern Australia

STATUS: Published June 2018

Flohr BM, Hunt JR, Kirkegaard JA, Evans JR, Lilley JM, 2017, Genotype x management strategies to stabilise the flowering time of wheat in the south-eastern Australian wheat belt, *Crop & Pasture Science* **69**, 547-560.



Image 5. Sowing the field experiment in Temora, NSW 6 May 2016

Abstract

Growers in the south-eastern Australian wheat belt need increases in water-limited potential yield (PY_w) in order to remain competitive in a changing climate and with declining terms of trade. In drought prone regions, flowering time is a critical determinant of yield for wheat. Flowering time is a function of the interaction between management (M, establishment date), genotype (G, development rate) and prevailing seasonal conditions. Faced with increasing sowing areas and declining autumn rainfall, growers are now sowing current fast-developing spring wheat cultivars too early. To widen the sowing window and ensure optimum flowering dates for maximum yield, new G x M strategies need to be identified and implemented. This study examined the effect of manipulating genotype (winter vs. spring wheats and long vs. short coleoptile) and management (sowing date, fallow length and sowing depth) interventions on yield and flowering date in high, medium and low rainfall zones in south-eastern Australia. Twelve strategies were simulated at 9 sites over the time period 1990-2016. At all sites the highest yielding strategies involved winter wheats with long coleoptiles (WW-LC) established on stored sub-soil moisture from the previous rotation, and achieved a mean yield increase of 1200 kg/ha or 42% compared to the baseline strategy. The results show promise for WW-LC to widen the sowing window, remove the reliance on autumn rainfall for early establishment and thus stabilise flowering and maximise yield. This study predicts that G x M strategies that stabilise flowering have the potential to increase PY_w .

1. Introduction

Increasing climate variability and declining terms of trade are two of the biggest challenges facing the Australian wheat (*Triticum aestivum L.*) industry. Significant decline in autumn (April-May) rainfall since the mid-1990s (Pook *et al.* 2009; Cai *et al.* 2012), with further shifts projected (CSIRO and Bureau of Meteorology 2015) make wheat production in southern Australia difficult in an already highly variable climate. Australian commodities compete on a global market, and overseas competitors such as Russia and the Ukraine continue to increase wheat production at a lower cost per tonne in comparison to Australia (AEGIC 2016b). On average, a large yield gap exists (~50%) for wheat in Australia (Hochman *et al.* 2017). Yield gap is defined as the difference between the water-limited potential yield (PY_w) and on-farm yield (FY) expressed as a percentage of FY. PY_w is defined as the measured or simulated yield of the best cultivar, grown with optimal agronomy and without manageable biotic and abiotic stresses but subject to the environmental constraints of plant available water and temperature (Fischer 2015; Hochman *et al.* 2017). Leading farmers are achieving ~80% of PY_w using available management and cultivars (van Rees *et al.* 2014), which approximates economic yield (EY). In order to stay competitive in a growing global market and under a changing climate, these farmers need an increase in PY_w .

Over the last century or more, Australian wheat breeders have maintained a genetic yield gain of 0.4-0.5% per annum (Siddique *et al.* 1989b; Sadras and Lawson 2011; Flohr *et al.* 2018). Farm-level productivity can be further increased if genetic (G) x management (M) interactions are captured. Historically, yield gain in Australia has been achieved by the interaction between improved cultivars (G) and improved agronomic management practices (M) (Kirkegaard and Hunt 2010; Fischer *et al.* 2014). Flowering time is a function of such G x M interactions i.e. the drivers of flowering are establishment date (M) and cultivar development rate (G). Bodner *et al.* (2015) has stressed the importance of flowering as closely as possible to environmentally determined optima in order to maximize grain yields in drought prone environments. Sowing dates by Australian growers often occur outside the optimal sowing window for the widely grown fast developing spring wheats (typically early to mid-May), and extreme weather during spring has made achieving timely flowering of cereal crops increasingly critical to yield and farm profitability (Fletcher *et al.* 2016). Thus, stabilizing flowering time over a whole wheat farm within the optimal period defined by

Flohr *et al.* (2017b) has the potential to lift PY_w in current and future climates. Given the large spatial variability in growing season length and annual rainfall in the Australian wheat belt, a general management practice for the whole wheat belt is not appropriate, and G x M strategies need to be region-specific.

For dry-land wheat production in southern Australia, establishment of wheat is generally reliant on autumn rainfall to provide seed-bed moisture to germinate seed and allow emergence. Currently favoured fast spring (FS) cultivars have little vernalisation or photoperiod sensitivity, and development is largely driven by temperature accumulation (Eagles *et al.* 2009). If rain does not fall during the optimal establishment time for FS cultivars, crops flower too late and yield is reduced by drought and heat. Having a range of cultivars that cover a broader range of sowing dates, yet flower at the optimum time, would enhance management options (Mac-Indoe 1937; Martin 1981; Fischer 2011). This increases the optimal effective sowing window for wheat, and thereby improves chances of receiving timely establishment rain. Winter wheats (WW, obligate vernalisation requirement), although not traditionally popular in the south-eastern Australian farming system (Hunt 2017), are more stable in their flowering than modern fast developing spring cultivars (Flohr *et al.* 2017c). Penrose (1993) demonstrated that winter genotypes sown early could yield at least as well if not better than FS genotypes sown later. More recently, Flohr *et al.* (2017c) showed in four diverse environments that correctly matching sowing date to cultivar development speed (slow, medium, fast; winter vs. spring habit) can synchronise whole farm flowering, extend the sowing window and increase whole farm yield whilst reducing yield losses due to frost, heat and drought. Unfortunately the early establishment of WW is reliant on irregular rainfall events in late summer/ early autumn, and while the chances to establish WW are greater than FS, planting opportunities do not always exist (Penrose 1993). Rainfall irregularity is further compounded by the autumn rainfall decline detailed by Pook *et al.* (2009) and Cai and Cowan (2013). As with FS, late established WW risk flowering outside the optimal period and suffering from drought and heat. Reliance on irregular rainfall can be reduced, and early establishment opportunities increased by sowing deeper into sub-soil moisture accumulated during fallow periods (Fischer and Armstrong 1990). In south eastern Australia, fallow length can range from 4 to 18 months. The shortest is summer fallow, where weeds are controlled and stubble from the previous crop is retained over the summer period to

conserve summer rainfall (Hunt *et al.* 2013). Fallow length can be extended through crop rotation e.g. a forage legume crop cut prior to grain fill conserves more sub-soil moisture than a crop harvested at maturity (Kirkegaard and Hunt 2010). The fallow can be extended even further by foregoing a whole season of crop production, referred to as long fallow (Ridge 1986).

Long fallow reliably increases wheat yields, having the greatest benefit in low yielding environments (Angus *et al.* 2015) and on heavy soil types (Ridge 1986). Long fallow in rotation with WW is common practice in the semi-arid United States Pacific Northwest (PNW) where annual rainfall is <290 mm, and yield increases of 1.6 t/ha have been observed compared to continuous spring wheat rotations (Schillinger 2016). Similar to south-eastern Australia, the PNW experiences dry autumns, and the long fallow rotation allows early establishment of WW crops on sub-soil moisture stored from the previous season. Due to increasing land pressures, the utilisation of long fallow has decreased in southern Australia (Oliver *et al.* 2010), and higher value rotational break-crops that maintain some of the benefits of long fallows e.g. forage legumes (Bodner *et al.* 2015) have proved more popular. Provided there is good summer fallow weed control, soil water remaining after a break crop can be used by the following crop without losing a season of income (Miller *et al.* 2003; Hunt *et al.* 2013).

In order to allow early establishment from stored soil water alone, seed needs to be sown at a greater depth (~150-180 mm in PNW). Modern Australian cultivars have coleoptiles shortened by dwarfing genes, and struggle to emerge if sown at depths exceeding 50 mm (Reithmuller 1990). In order to allow establishment on stored soil water, cultivars with long coleoptiles that can be safely sown at a greater depth are required (Rebetzke *et al.* 2007a). Kirkegaard and Hunt (2010) demonstrated a ~0.5 t/ha yield increase from a FS cultivar with a long coleoptile at a single site in the Victorian Mallee, but the potential for long coleoptile cereal cultivars to improve yields has not been more widely evaluated across southern Australia.

The benefits of fallows and break-crop rotations are well documented in southern Australia (Kirkegaard *et al.* 2008; Angus *et al.* 2015), as are the opportunities available to exploit sub-soil moisture accumulation (Lilley and Kirkegaard 2007; Hunt and Kirkegaard 2011; Lilley and Kirkegaard 2016). However, there are few studies exploring the advantages or disadvantages of fallow length in combination with different genotypes in high, medium and low rainfall sites in south-eastern Australia.

We propose that combining the G x M flowering date stabilising factors; winter wheat, long coleoptile, early sowing and fallow, will reduce reliance on autumn rainfall for timely crop establishment, provide a buffer against seasonal variability, and lift PY_w by allowing a greater portion of wheat to flower during the optimal period. Here, we evaluate these strategies at a range of locations using the Agricultural Production Systems Simulator (APSIM, Holzworth *et al.* 2014). Given that APSIM assumes crops are grown without weeds, pests or disease and nutrients are non-limiting, simulated yield represents PY_w , and is a useful means to identify where yield gains are possible to guide future experimentation.

2. Method

2.1 General simulation setup

APSIM (version 7.8) was used to simulate 12 genetic (G) x management (M) strategies over a 27 year period (1990-2016). The 1990-2016 time period was chosen because it aligns with recent PY_w decline in Australia (Hochman *et al.* 2017). PY_w decline has been attributed to temperature increases and rainfall decline, particularly during autumn in south-eastern Australia (Pook *et al.* 2009; Cai *et al.* 2012). Therefore simulated PY_w in this time period is most relevant to wheat production today. Simulations were run in high, medium and low rainfall sites in South Australia (SA), Victoria (Vic) and New South Wales (NSW) (Fig. 1, Table 1). Locations were selected to represent environments where wheat is grown in the cropping belt of south-eastern Australia (SEA), where autumn rainfall decline has been prevalent, and based on the availability of accurate soil characterization from the APSoil database (Dalglish *et al.* 2009) and patched-point meteorological weather stations from the SILO database (Jeffrey *et al.* 2001). Simulation of wheat growth, development and yield in APSIM has been extensively validated in numerous studies across southern Australia (Hochman *et al.* 2007; Lilley and Kirkegaard 2007; Brown *et al.* 2014), and is capable of matching observed data to an acceptable level of accuracy. The key APSIM modules used in the analysis were Wheat (wheat crop growth and development), Fieldpea (crop growth and development) and Manager (specifying sowing rules and rotations).

Table 1: The 9 locations and corresponding long-term mean annual rainfall, patch point data set (PPD) station number, APSOIL file number, plant available water content (PAWC), depth and depth of top layer used in the simulation study.

Location	State	Rainfall zone	Mean annual rainfall (mm)	PPD station number	APSOIL file no.	PAWC (mm) to depth (m)	PAWC of top layer (mm)
Saddleworth	SA	High	493	23315	104	121 (1.5)	18
Yarrowonga	VIC	High	509	81057	208	121 (1.8)	10
Cootamundra	NSW	High	618	73142	180	202 (1.8)	17
Lameroo	SA	Medium	385	25509	253	90 (1.5)	6
Charlton	VIC	Medium	403	80067	736	130 (1)	19
Temora	NSW	Medium	510	73038	179	125 (1.2)	22
Waikerie	SA	Low	258	24018	104	67 (1.5)	4
Walpeup	VIC	Low	331	76064	726	179 (1.3)	5
Condobolin	NSW	Low	437	50052	688	233 (1.8)	10

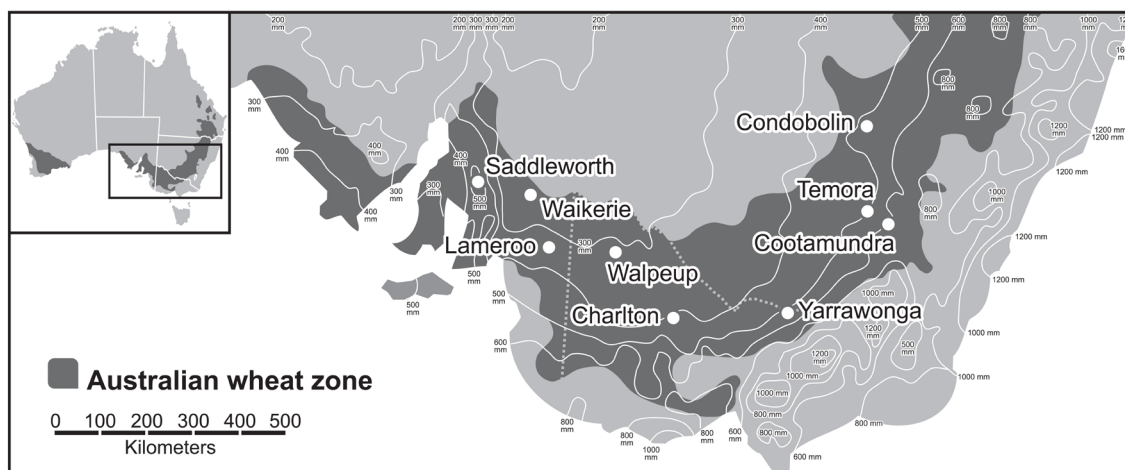


Figure 1: Dry-land cereal cropping in south-eastern Australia (shaded), rainfall isohyets and the locations used for this study.

APSIM assumed crops were grown weed and disease free, but a reduction for frost ($<2^{\circ}\text{C}$) and heat damage ($>32^{\circ}\text{C}$) based on screen temperatures was applied to crop growth as per Bell *et al.* (2015). Yield reductions were cumulative for multiple frost and heat events that occurred during the sensitive stages of plant growth. Nitrogen was applied as NO_3^- with a fertilizer rule, which was maintained above 100 kg/ha in the top three layers of the APSIM soil file throughout the season such that nitrogen supply did

not limit yield. In all strategies wheat was sown and assumed to establish at 150 plants/m² (Anderson and Garlinge 2000; Hunt and Kirkegaard 2011) with a row spacing of 300 mm (Scott *et al.* 2013). Each site was viewed as a hypothetical farm where we assumed that the total area of wheat sown in each season takes 20 days to sow. The simulation was continuous through 1990-2016 such that legacy effects of the different strategies are captured.

2.2 Soil water

In the simulation, the initial plant available water was set to 0 mm and not reset in subsequent seasons; therefore, the effect of initialisation was not accounted for. The depth of the top layer of the soil at each site was 10 cm, and the second layer varied at each site, and ranged between 10 and 30 cm. Soil depth for each location is given in Table 1. In APSIM, seed germinates one day after sowing and when soil water is greater than the crop lower limit (CLL) at whatever depth has been specified in the simulation.

2.3 Genotypes

In APSIM, cultivars are allocated a vernalisation and photoperiod “factor” which represent sensitivity to vernalising temperatures and day length where high values are more sensitive. The model then uses these factors to calculate cultivar-specific developmental rates. The cultivar parameters selected here represent a spring wheat of fast spring (FS) phenological development, typical of cultivars grown in south-eastern Australia (e.g. Scout, Spitfire, Mace etc.). This was based on the APSIM base cultivar with vernalisation sensitivity of 1.5 and photoperiod sensitivity of 3.0, and was used at all sites and strategies where a FS cultivar was sown (Bell *et al.* 2015). At each site FS cultivars were only sown starting at the optimal sowing date for that site as per Flohr *et al.* (2017b) and are shown in Table 3. Winter wheats (WW) were also sown in some strategies, and cultivars of slightly different development speeds were sown according to the length of season in each environment. In environments with a shorter growing season a fast-winter (FW) genotype (e.g. Longsword, Flohr *et al.* 2017c) with a vernalisation sensitivity of 4 and a photoperiod sensitivity of 1 was used. The phenology of the FW genotype was evaluated using data from Flohr *et al.* (2017c) and found to estimate FW phenology to an adequate level, but did show some bias towards earlier flowering ($R^2=0.91$, Fig. S1). In environments with an intermediate growing season a mid-winter (MW) genotype (e.g. Wedgetail) with a vernalisation sensitivity of 3.9 and a photoperiod sensitivity of 3.9 was used, and in environments with a long

growing season a slow-winter genotype (SW) type (e.g. Revenue) with a vernalisation sensitivity of 3.9 and a photoperiod sensitivity of 4.3 was sown. MW and SW parameterisations in APSIM have previously been used and validated (Bell *et al.* 2015).

The impact of a long coleoptile on the cultivars outlined above was investigated. When a cultivar is sown at a depth of 110 mm, APSIM assumes that wheat has a sufficiently long coleoptile to emerge at the specified density from this depth if the soil water is above the CLL. Therefore sowing depth is indicative of coleoptile length (long or short) in APSIM. In this simulation experiment cultivars with short coleoptile were sown at a depth of 30 mm, and cultivars with long coleoptile were sown at a depth of 110 mm (Rebetzke *et al.* 2007a; Kirkegaard and Hunt 2010; Schillinger 2016).

2.4 Strategy details

Table 2 summarises the key differences between the twelve strategies, and Figure 2 summarises the different crop rotations (continuous cropping, forage legume, long fallow). Strategies are additive combinations of genetic (development type, long coleoptile) and management (rotation, fallow length, sowing time, sowing depth) components which aim to maximise yield and maintain a stable flowering date within the optimal flowering period. Optimal sowing dates and optimal flowering period are adapted from Flohr *et al.* (2017b) and were applied to sites as per Table 3.

	Year 1			Year 2					Year 3															
Rotation	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O
Continuous cropping	Summer fallow			Crop					Summer fallow			Crop												
Forage legume	Summer fallow			Forage crop			Summer fallow		Crop															
Long fallow	Long fallow															Crop								

Figure 2. Summary of continuous cropping, forage legume and long fallow strategies relative to months of the year in south-eastern Australia.

Table 2: A summary of the genetic x management strategies simulated for the low, medium and high rainfall zones in SA, Vic and NSW using APSIM 7.8, where short coleoptile length is 50 mm and long coleoptile length is 110 mm.

Strategy number	Strategy acronym	Rotation	Phenology	Sowing date	Coleoptile length
Baseline	Baseline	Continuous wheat	Spring wheat	fixed	short
1	CW-FS-LC	Continuous wheat	Spring wheat	fixed	long
2	FL-FS	Forage legume	Spring wheat	fixed	short
3	FL-FS-LC	Forage legume	Spring wheat	fixed	long
4	LF-FS	Long fallow	Spring wheat	fixed	short
5	LF-FS-LC	Long fallow	Spring wheat	fixed	long
6	CW-Opp-WW	Continuous wheat	Winter wheat	opportunistic	short
7	CW-WW-LC	Continuous wheat	Winter wheat	fixed	long
8	FL-Opp-WW	Forage legume	Winter wheat	opportunistic	short
9	FL-WW-LC	Forage legume	Winter wheat	fixed	long
10	LF-Opp-WW	Long fallow	Winter wheat	opportunistic	short
11	LF-WW-LC	Long fallow	Winter wheat	fixed	long

Table 3: Sowing windows for fast-winter (FW), slow-winter (SW), mid-winter (MW) and fast-spring (FS) genotypes and optimal flowering periods (OFP) as per Flohr et al. (2017b) used in the simulation study.

Locations	Winter cultivar	Sowing window WINTER		Spring cultivar	Open sowing window SPRING	OFP	
		open	close			open	close
Saddleworth	FW	15-Mar	6-May	FS	6-May	9-Sep	24-Sep
Yarrawonga	MW	15-Mar	30-Apr	FS	30-Apr	25-Sep	2-Oct
Cootamundra	SW	15-Mar	6-May	FS	6-May	6-Oct	20-Oct
Lameroo	FW	15-Mar	26-Apr	FS	26-Apr	28-Aug	20-Sep
Charlton	MW	15-Mar	29-Apr	FS	29-Apr	21-Sep	30-Sep
Temora	MW	15-Mar	4-May	FS	4-May	25-Sep	10-Oct
Waikerie	FW	15-Mar	17-Apr	FS	17-Apr	23-Aug	29-Aug
Walpeup	FW	15-Mar	29-Apr	FS	29-Apr	8-Sep	17-Sep
Condobolin	FW	15-Mar	29-Apr	FS	29-Apr	11-Sep	19-Sep

i. Baseline

The baseline strategy represents conventional practice, that is, continuous wheat (Fig. 2) with a FS genotype (Table 2). The wheat crop is sown on a fixed date, and sowing finishes 20 days later regardless of seed bed moisture. This simulates ‘dry sowing’, a common practice by farmers in seasons when there is a late onset of rainfall (Fletcher *et al.* 2016). As specified in section 2.2, seed will germinate when soil water is greater than the CLL. In the results section, yields of the 12 G x M strategies are compared to the yield of this strategy at each site.

ii. Opportunity sowing winter wheat (Opp-WW, strategies 6, 8, 10)

In these strategies two cultivars of differing development are grown, a FS genotype and a WW genotype. Opportunity sowing of a WW only occurs when plant available water in the top two layers of soil exceeds 20 mm after 15 March, so germination begins at sowing. If there is an opportunity to sow a WW, sowing begins, but if the optimal sowing window of the FS cultivar is reached within the 20 day sowing program (Table 4) the cultivar is switched to FS using the same rules as the baseline strategy such that flowering date is synchronised to the optimal flowering period. If no early sowing opportunities arise, a FS genotype is sown at its optimal sowing window on a fixed date regardless of seedbed moisture, and germinates when soil water is greater than the CLL in the first layer. Therefore, in this strategy, the area sown to each genotype changes from year to year based on the timing of rain. Where a fixed sowing date has been indicated for a WW or FS wheat, dates are differential per site and are shown in Table 3.

iii. Forage legume rotation (FL, strategies 2, 3, 8, 9)

In the forage legume rotation, wheat and fieldpea were grown in a 2-year rotation. The pea cultivar Kaspera was sown at 40 plants/m² and terminated at the start of grain fill to simulate hay production and generate a longer fallow period than in strategies with growing continuous grain crops. The field pea crop was sown on 1 June at a depth of 30 mm regardless of seedbed moisture, and germinates when soil water is greater than the CLL in the first layer. Rotations were run in two phases so that a wheat yield was obtained for each season. In reality at the farm scale, this management change would reduce the overall number of wheat crops, and thus total farm wheat production. However, the aim was to quantify the impact that crop sequence can have on subsequent

wheat yield. The disease, weed, and nitrogen benefits of the break crop, although likely, were not simulated, so the sequence impacts relate only to effects on the water balance.

iv. Long fallow (LF, strategies 4, 5, 10, 11)

In long fallow strategies, a wheat crop was sown only every alternate year, with one growing season of fallow. In the year of fallow, weeds were controlled and water was stored for a subsequent wheat crop. This strategy imitates the successful crop sequence reported in dry areas of the Pacific North West of the USA (Schillinger and Young 2014). Rotations were run in two phases so that wheat yield was obtained for each season. As with the forage legume, this management change would reduce the overall number of wheat crops, and thus total farm wheat production. However, the aim was to quantify the impact that this crop sequence could have on subsequent wheat yield.

v. Long coleoptile (LC, strategies 1, 3, 5, 7, 9, 11)

These strategies model the potential impact of a wheat cultivar (both WW and FS genotypes) with a long coleoptile (Rebetzke *et al.* 2007a) that could be sown deeply (110 mm, Kirkegaard and Hunt 2010; Schillinger 2016) into moist soil water remaining e.g. from the previous forage legume or long fallow period. This trait facilitates early sowing on a specific date where stored soil water greater than CLL is too deep for successful germination of current short coleoptile cultivars. This removes reliance on autumn rainfall for timely crop establishment and allows crops to flower during the optimal period.

2.5 Analysis

Box plots were produced for each site and strategy to show the range in flowering date and grain yield generated from the 20 day sowing program over the 27-year time period.

Each boxplot shows a minimum, 25th quartile, median, 75th quartile and maximum value. Mean yield over the 27 years for each strategy and site was also calculated and compared against the mean yield of the baseline strategy. In all strategies, any yield increase from continuous wheat rotations are clear farm productivity increases. In 2-year rotations (forage pea, long fallow) a yield increase of about 100% of the subsequent wheat crop would be needed to maintain whole farm profitability compared to continuous wheat (making allowance for the cost of production of the second wheat crop and the cost of the fallow).

A two-tailed t-test between the yield of the baseline strategy vs. the yield of strategies 1 to 11 was performed to determine if strategies were significantly different. P-values are presented in supplementary Table 1. To determine the yield stability of each strategy, a linear function for the relationship between deviation of yield from the environmental mean and the environmental mean (mean of all strategies at a particular location) was fitted. As per Eberhart and Russell (1966) and Raun *et al.* (1993) the slope from this function reflects stability, where strategies with a slope closer to zero suggest the strategy is equally as stable as the environmental mean over the time period 1990-2016. A positive slope indicates that the strategy is more stable than the environmental mean, and a negative slope indicates the strategy is less stable. The slope for each regression is reported in supplementary Table 1.

A mean flowering date stability index was calculated for each strategy and site as the ratio of range in sowing date (20 days) to range in flowering dates, and is presented on the flowering date box plot.

3. Results

3.1 Productivity increases from *G x M* strategies

Figure 3 summarises the range in grain yield for the 12 strategies at the 9 environments over the 1990-2016 time period. The aim of the *G x M* strategies was to stabilise flowering time to the optimal period at each site, and increase average yield compared to the baseline strategy of the hypothetical farm. All strategies that included WW had significantly greater yields than the baseline strategy (Fig. 3, Table S1). Yield of strategies with FS-LC were often not significantly different from the baseline strategy (Table S1).

Grain yields generally increased with annual rainfall (Table 1, Fig. 4). Average farm yield ranged from 1573 kg/ha in the baseline strategy in Waikerie, to 6451 kg/ha in LF-WW-LC in Saddleworth. The highest yield long-term gain was from LF-WW-LC which yielded an additional 3000 kg/ha (88%) at Saddleworth, and 1700 kg/ha (74%) at Condobolin compared to the baseline yield. CW-FS-LC reduced yield by 200 kg/ha (8%) in Walpeup, with similar negative results in Lameroo, Temora and Saddleworth.

The highest yielding strategies in all rainfall zones all featured WW genotypes, predominately strategies FL-WW-LC, LF-Opp-WW and LF-WW-LC. Although often only a small yield increase relative to the baseline scenario e.g. 189 kg/ha Waikerie, the

CW-Opp-WW strategy increased farm productivity at all sites except Walpeup (-69 kg/ha), and the increase was not significant at Yarrawonga (Table S1). At other sites e.g. Saddleworth, Cootamundra, the yield increase from continuous WW was much higher (1473 kg/ha, 1423 kg/ha respectively).

With the exception of the Cootamundra, Temora, and Yarrawonga sites, LF-WW-LC offered the greatest mean yield advantage ranging from 700 kg/ha (45%) at Waikerie to 3000 kg/ha (88%) at Saddleworth. At Cootamundra, Temora, and Yarrawonga FL-WW-LC offered the greatest mean yield advantage. Across all HRZ sites, CW-WW-LC, FL-WW-LC and LF-WW-LC averaged similar productivity increases of 1500 kg/ha (44%), 1600 kg/ha (47%) and 1700 kg/ha (51%) respectively. CW-WW-LC offers the greatest whole-farm productivity in the HRZ, and legume rotation offers similar productivity increases as long fallow.

Averaged across all MRZ sites, productivity increases were similar for LF-Opp-WW (1100 kg/ha or 39%), FL-WW-LC (1100 kg/ha or 39%) and CW-WW-LC (1000 kg/ha or 36%). Forage legume rotations and long fallow both offer similar productivity increases at MRZ sites.

Averaged across all LRZ sites, the yield advantage of 1300 kg/ha (58%) from LF-WW-LC was greater than that for LF-Opp-WW, 1200 kg/ha (49%). There was a mean 700 kg/ha (33%) mean yield increase from FL-WW-LC and a 600 kg/ha (27%) mean yield increase from LF-FS-LC. Yield increase from CW-WW-LC ranged from 300 to 700 kg/ha (10-30%), where yield increases were mostly achieved in above average rainfall seasons (Fig. 4).

Chapter 5

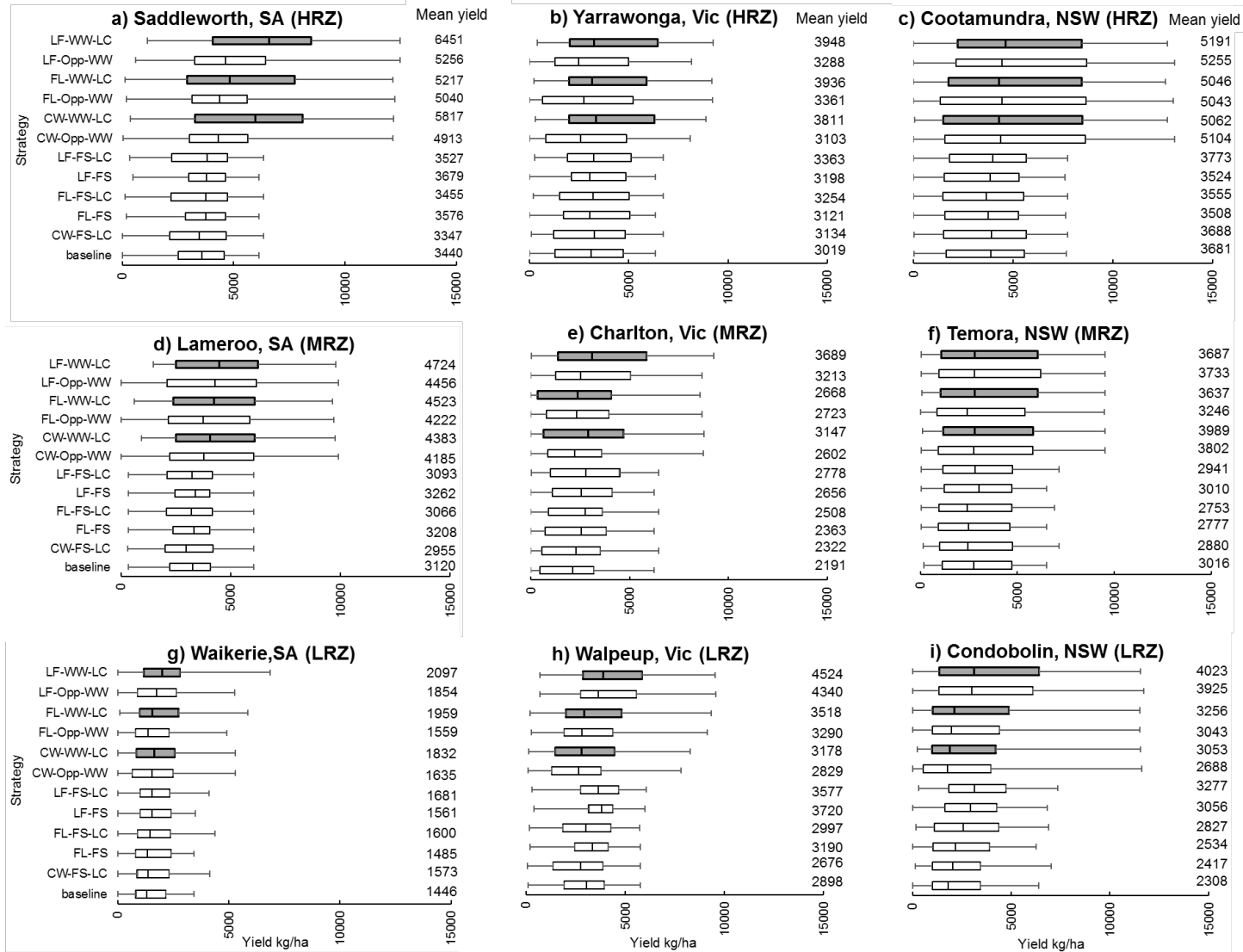


Figure 3. The distribution of simulated grain yield for the total 20 day sowing program from 1990-2016 for the 12 genotype (winter vs. spring wheats and long vs. short coleoptile) x management (sowing date, fallow length and sowing depth) strategies. The box and whisker plot shows the minimum, 25th percentile, median, 75th percentile and maximum grain yield for each strategy over the time period. On the left hand side CW, FL and LF signify rotation of either continuous wheat, forage legume or long fallow respectively, WW and FS signify winter wheat or fast spring wheat genotype and LC signifies a long coleoptile genotype. Numbers on the right hand side are the average yield (kg/ha) over the total period and sowing program. Grey shaded box and whisker plots indicate strategies that sow winter wheat with a long coleoptile ge

3.2 Yield variability

The range in yield achieved from the various strategies provides some idea of the risk and variability of the strategies (Fig. 3). Narrower boxes reflect greater yield stability. Further indication of stability is provided in Table S1. The strategies with the highest slope were LF-WW-LC, FL-WW-LC and CW-WW-LC, and were therefore the most stable compared to the environmental mean. Often the strategies with the broadest range in yield had greater median and mean yields e.g. strategies CW-WW-LC, FL-WW-LC, LF-WW-LC in Saddleworth and Cootamundra. Most of the variation in yield can be explained by seasonal rainfall variation (Fig. 4). A higher mean yield with higher variability is tolerable provided the frequency of lower yields does not increase (i.e. minimum values in Fig. 3). If yield is too low in a sequence of seasons, cash flow may limit farm viability.

Figure 4 shows that continuous wheat and forage legume rotations with WW-LC can achieve similar yields to long fallow in the HRZ (Fig. 4a). However in the LRZ, LF-WW-LC increased yields more than continuous wheat or forage legume rotations, which is particularly evident in below average seasons e.g. 2002, 2004 (Fig. 4b).

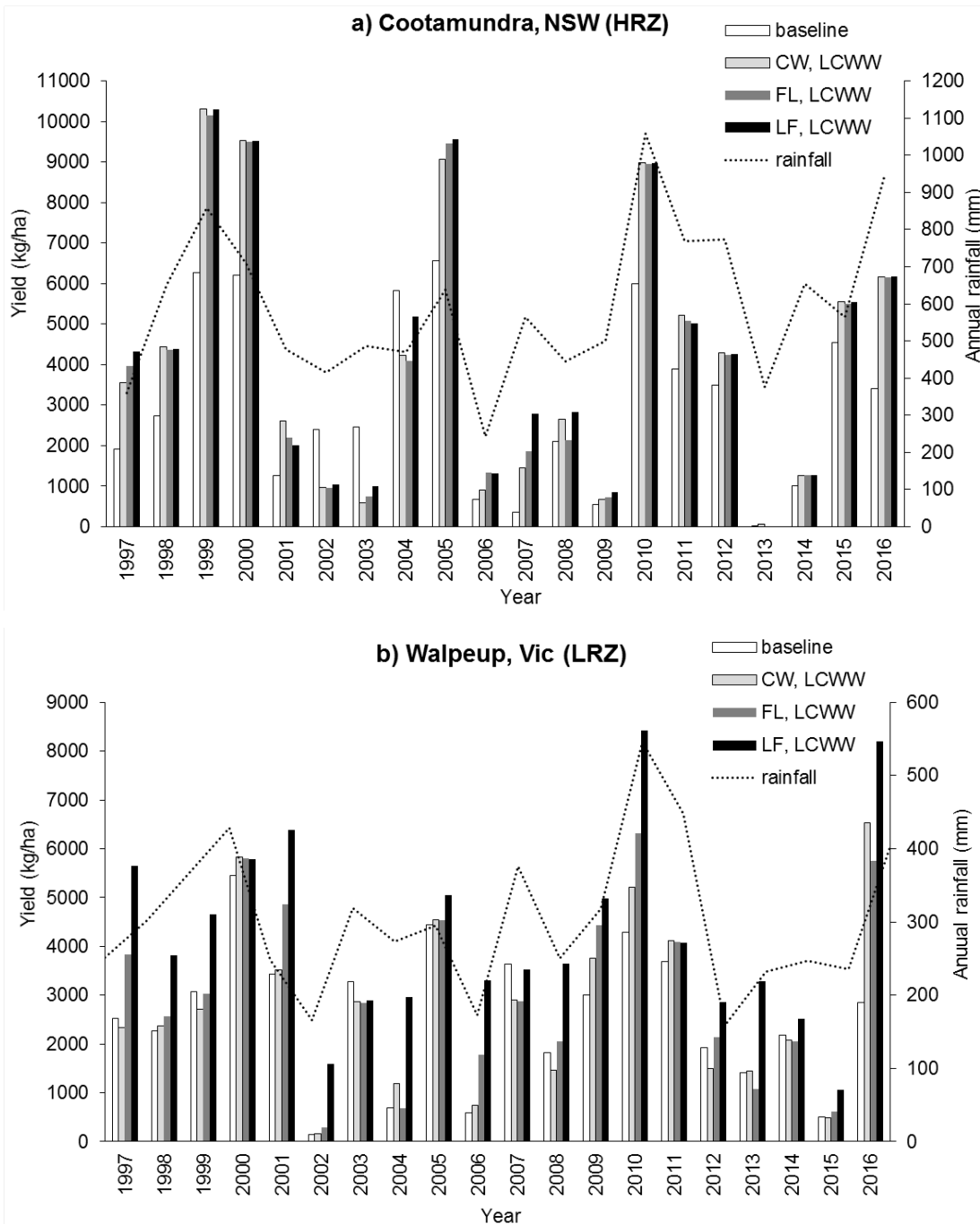


Figure 4. Simulated yield and annual rainfall for years 1997-2016 for strategies baseline, 3, 6 and 11 at a) Cootamundra, and b) Walpeup. Rotation is either continuous wheat (CW), forage legume (FL) or long fallow (LF), and genotype is winter wheat with a long coleoptile (WW-LC).

3.3 Flowering date

Flowering dates were determined by genotype, establishment date and prevailing seasonal temperatures (Fig. 5). The mean flowering date of all strategies was 4 October in the HRZ, 26 September in the MRZ and 11 September in the LRZ. Strategies with WW had a greater mean flowering date stability index (0.68) and lower range in flowering dates (31 days), than strategies with spring wheat (stability index of 0.56, and a 39 day range in flowering dates). Spring cultivars with long coleoptiles (strategies FS-LC, FL-FS-LC, LF-FS-LC) flowered on average 5 days later than other strategies. Some sites had a less stable environment resulting in an overall greater range in flowering dates e.g. Waikerie (mean stability index of 0.45), Lameroo (mean stability index of 0.56). The most stable environments for flowering were Cootamundra (mean stability index of 0.75) and Temora (mean stability index of 0.67).

Chapter 5

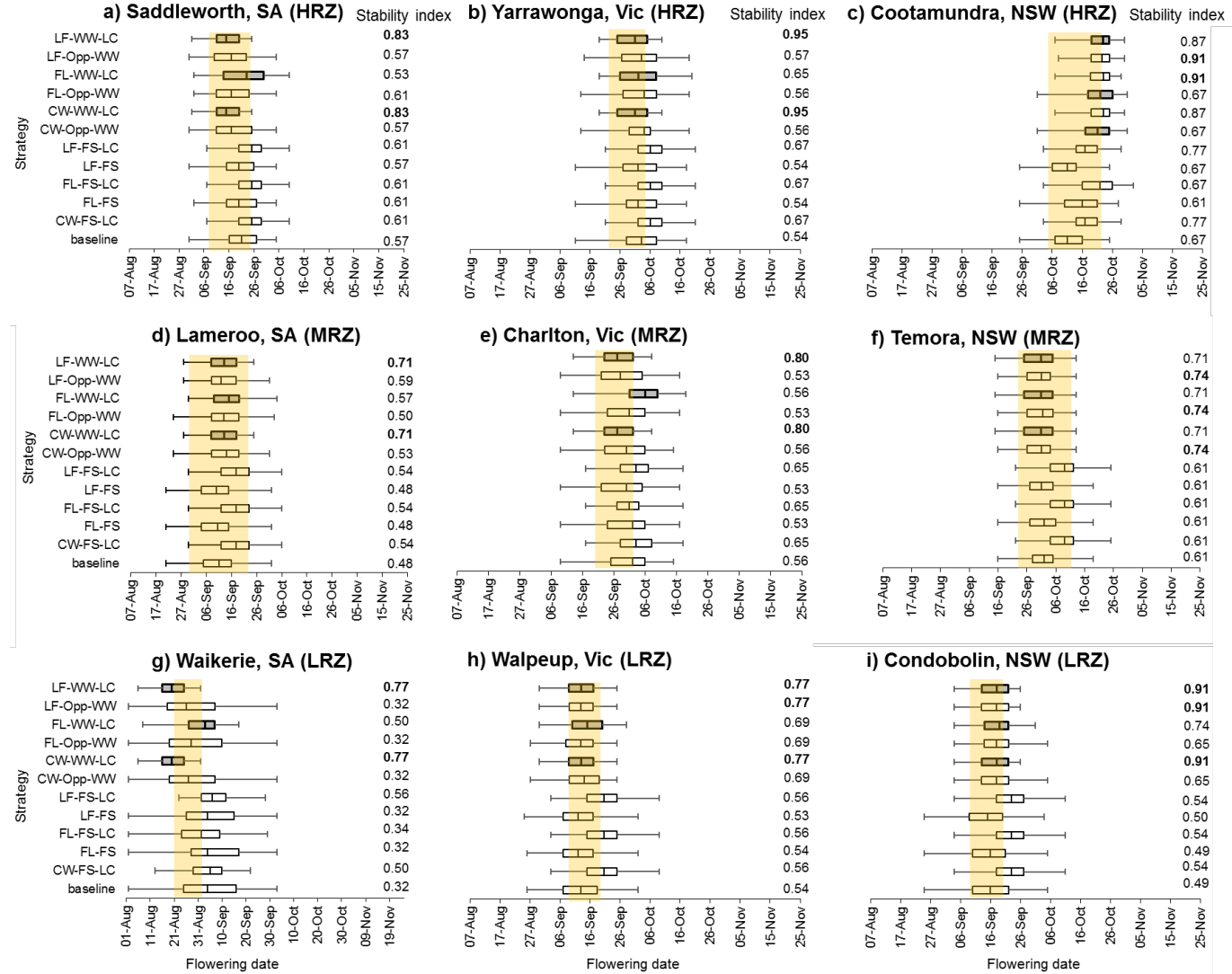


Figure 5. The distribution of simulated flowering dates for the total 20 day sowing program from 1990-2016 for the 12 genotype (winter vs. spring wheats and long vs. short coleoptile) x management (sowing date, fallow length and sowing depth) strategies. On the left hand side CW, FL and LF signify rotation of either continuous wheat, forage legume or long fallow, respectively, WW and FS signify winter wheat or spring wheat genotype and LC signifies a long coleoptile genotype. A higher stability index indicates a strategy that promotes greater flowering date stability over the whole farm and seasons, and bold text highlights the most stable strategy. Grey shaded box and whisker plots indicate strategies that sow a long coleoptile winter wheat genotype. Yellow shaded column represents the optimal flowering period for each site defined by Flohr *et al.* (2017b). Details of each strategy (baseline - 11) are in Table 3.

The effects of the different rotations on initial soil water are shown in Table 4. There was 18 mm more initial soil water on average following a forage legume rotation compared to continuous wheat. A long fallow rotation increased initial soil water by 44 mm.

Table 4: The mean initial plant available water (mm) at sowing (15 March) at each location in which a winter wheat genotype is established under different rotations.

Site	Rotation		
	Continuous wheat initial water (mm)	Forage legume initial water (mm)	Long fallow initial water (mm)
Saddleworth	45	65	87
Yarrowonga	75	75	99
Cootamundra	123	141	180
Lameroo	47	70	75
Charlton	34	44	65
Temora	68	84	94
Waikerie	48	64	73
Walpeup	54	80	126
Condoblin	100	132	189

4. Discussion

In the time period studied (1990-2016), our analysis predicts that novel G x M strategies can increase wheat yields (PY_w) at least partly by reducing reliance on autumn rainfall to establish crops, and stabilising flowering date on south-eastern Australian farms. The study period included the Millennium Drought (1996-2009 Verdon-Kidd *et al.* 2014), so that findings are influenced by a period that was drier than average. While a longer study period may have produced different findings, this period was chosen as it captures the recent trend of declining autumn rainfall. Depending on location and how interventions were combined, yield gain relative to continuous spring wheat ranged from -200 kg/ha to 3000 kg/ha (Fig. 3). Stacking genetic traits (i.e. development type + long coleoptile) with management (fallow, sowing date) generally had an additive effect on yield at most locations (greater mean yields and significant differences between the baseline and other strategies).

4.1 WW-LC for flowering date stability

Limited sowing opportunities and the lack of well adapted cultivars have restricted the adoption and possible PY_w gains associated with early-sown WW (Penrose 1993). Our results show the highest yielding G x M strategies in high, medium and low rainfall zones were those with WW-LC (Fig. 3). WW-LC genotypes provided an opportunity for a fixed and early establishment date. Long coleoptiles and rainfall carried over from the previous season using fallow management practices removed the reliance on autumn rainfall events to establish crops (Table 4). The response to low temperatures (vernalisation) of the WW growth habit ensured that development matched the growing season environment, such that flowering mostly occurred during the optimal flowering period (Fig. 5). WW-LC were critical to achieve maximum yield from the management strategies tested, particularly at LRZ sites (Fig. 3). In the LRZ, LF-WW-LC increased yield between 700-1700 kg/ha, or by 45-74%. This strategy mimics the PNW system, however yield increases modelled in the Australian context were less than those recorded in low rainfall zones of the PNW using the same strategy (Schillinger 2016). These differences may be related to different soil types in Australia, which tend to have lower plant available water capacity than PNW soils, the cooler spring temperatures in the PNW and the milder Australian winters that allow spring wheats to be sown in autumn rather than spring as in the PNW (Schillinger and Young 2014). A yield increase of 900 kg/ha was reported by Oliver *et al.* (2010) using a FS cultivar after long

fallow in Western Australia. Field data from elsewhere and our modelling both suggest that gains in PY_w from early establishment and slow development using long fallow systems would be beneficial in south-eastern Australia.

While coleoptile length varies between Australian cultivars, no cultivar currently exists that can be sown at the depths practiced in PNW at ~150 mm, nor at our simulated depth of 110 mm. Short coleoptiles are a consequence of the introduction of dwarfing (*Rht*) genes which reduced height and improved harvest index in modern cultivars (Richards 1992b). However, it is feasible to breed short stature, high harvest index cultivars with long coleoptiles (Rebetzke *et al.* 1999). Long coleoptiles have the added benefit of avoiding toxicity from soil applied pre-emergent herbicides (Lemerle *et al.* 1985), reduced removal of seed by birds and rodents (Brown *et al.* 2003) and improved establishment in unfavourable seedbed conditions (Rebetzke *et al.* 1999). In this simulation, the model assumes the same established plant density of deep sown wheat. However, some field studies have shown a trade-off between emergence and deeper sowing (Rebetzke *et al.* 2007b). To counter this, higher seeding rates may be required. Breeding companies should be encouraged to select for WW-LC cultivars, and until these cultivars are available, the full value of WW and fallow is unlikely to be realised in the Australian context. Australian wheat breeders have shown an interest in selecting for long coleoptile winter wheats, but given that winter wheat genotypes are still relatively novel in south-eastern Australian farming systems, combining appropriate winteriness with long coleoptiles is still in the early stages of development. There is an opportunity to extend these findings (vernalisation requirement and long coleoptile/hypocotyl) and lift PY_w of other crops which also have optimal flowering periods, and where early establishment would also be beneficial e.g. Lilley *et al.* (2017). In medium-low rainfall environments, it will be important that WW-LC cultivars have adaptation to the local constraints e.g. cereal cyst nematode, boron toxicity, acidity and salinity (Hunt 2017).

Long coleoptiles mostly had either no effect or decreased yield in the absence of winter habit or increased stored soil water. The highest yield increase achieved from the FS-LC genotype was when combined with long fallow in low rainfall environments (LF-FS-LC, 600 kg/ha or 27% yield gain), but this yield gain was less than the yield increase achieved from LF-WW-LC (1300 kg/ha or 58% yield). In strategies 1, 5 and 9 the wheat shoot took longer to emerge from depth (~6 days longer than baseline), delaying

development and flowering outside the optimal period (Fig. 5). Yield reduction can be associated at least partly with a smaller proportion of the crop flowering within the optimal flowering period, highlighting the importance of correctly matching genotypic traits with management. French and Schultz (1984) showed that each 1-day delay in germination resulted in between 0.3 and 0.4 days delay to flowering. It is likely that FS-LC cultivars should be planted earlier than the recommended sowing date for the current FS cultivars to account for the delayed emergence.

The extreme minimum and maximum yield values shown in Figure 3 can be related to the impact of growing season rainfall, and number and timing of frost and heat events on yield. For example, large yields (Fig. 3) were achieved at Condobolin in 2016, with 498 mm growing season rainfall (long term average is 249 mm) resulting in large PY_w indicated by the large maximum kg/ha obtained in strategies CW-Opp-WW, CW-WW-LC, FL-Opp-WW, FL-WW-LC, LF-Opp-WW and LF-WW-LC. While the optimal flowering period represents the period where combined heat, frost and drought stress is lowest in an environment, the frost and heat rules applied as per Bell *et al.* (2015) can result in large yield penalties or crop failures in particularly frosty or dry seasons, as demonstrated by the low minimum values in Figure 3. In proposing novel strategies in risky environments, it is important to be aware of the impacts of temperature extremes and while further refinement of the model may be required, improvements in prediction of yield have been demonstrated in other crops (Kirkegaard *et al.* 2016).

4.2 Optimal phenology and rotation in the LRZ

WW phenology extended the sowing window (opening on the 15 March rather than early-May for a FS cultivar), while maintaining the reliability of flowering within the optimal period (Fig. 5). Aside from CW-Opp-WW at Walpeup, no other site showed a yield reduction using a WW genotype (Fig. 3). A fast-winter genotype was simulated at sites with shorter growing season (Waikerie, Saddleworth, Lameroo, Walpeup and Condobolin). In the LRZ, a WW cultivar achieved a mean ~23% (500 kg/ha) yield increase in a continuous wheat rotation, ~33% (900 kg/ha) in a forage legume rotation and ~58% (1300 kg/ha) yield increase in the long fallow rotation. Consistent with the findings of Flohr *et al.* (2017c), there is a significant opportunity for well-adapted, fast WW genotypes in non-traditional regions of Australia e.g. Lameroo and Condobolin. The initial findings of Flohr *et al.* (2017c) have been extended here by simulation with a

cultivar of similar development speed which has identified additional suitable sites and sowing dates for novel WW cultivars.

In the LRZ, there was a relatively small yield advantage (170 kg/ha) from a CW-Opp-WW strategy relative to other strategies and sites. With the exception of Waikerie, the yield increase (460 kg/ha) from CW-WW-LC was likely associated with a greater portion of crop flowering within the optimal period, as shown by the increase in stability index of this strategy (Fig. 5). Seasons of nil or minor yield gain from WW establishment are likely due to greater vegetative biomass accumulation and pre-flowering water use of WW in high vapour pressure deficit environments, reducing harvest index and water use efficiency (Gomez-Macpherson and Richards 1995). It is possible that more stringent sowing rules to ensure more available soil water prior to sowing will result in greater yield gains in continuous WW rotations in the LRZ.

Autumn rainfall decline, increasingly variable growing season rainfall, and greater interest in WW cultivars has prompted the re-evaluation of long fallow to increase establishment opportunities in south-eastern Australia. Long fallow was once common practice in southern Australia, but has been in decline since the 1980s following the development of no-till farming systems and adapted break crops e.g. lentils, chickpeas, field peas and canola that replaced the role of long fallow as a disease and weed break (Ridge 1986). Our results align with studies that have shown that long fallow cannot double crop production in a single year to compensate for a year of no production (Hatfield and Karlen 1993). However, yield of the crop following long fallow does not necessarily need to double to be economically viable; income from yield only needs to be double minus the cost of production of the second wheat crop (Schillinger *et al.* 2007). To estimate the potential value of long fallow rotation over common practice (baseline strategy), the following scenario based in Condobolin has been conceived. Assuming the annual cost of production per wheat crop is \$150 per ha (Hudson and Krause 2013; Oliver and Sands 2013), the annual cost of fallow is \$60 per ha (Oliver and Sands 2013), the value of wheat is \$200/t (ABARES 2017) and that the baseline strategy yielded 2300 kg/ha, the fallow-wheat rotation will provide economic advantage if wheat yield exceeds 4150 kg/ha. The average yield of LF-WW-LC in Condobolin was 4000 kg/ha, which is near the point to be economically viable.

The benefits of long fallow will mainly be realised at the long-term whole-farm scale, and for improved management of financial risk by providing year-to-year yield stability

(Oliver *et al.* 2010). Soil water accumulated from the previous crop rotation (Table 4) can be used to buffer against seasonal and annual rainfall variability and the risk of crop failure in dry seasons. By carrying water over from the previous crop, long fallow reduces risk through an overall reduction in inputs and by overriding the risk of crop failure in seasonal drought, thus providing a buffer against economic loss caused by commodity price fluctuation and seasonal yield variability (Oliver *et al.* 2010).

Inoculum of important soil-borne diseases for cereal production in southern Australia (take-all, cereal cyst nematode) can also decline under long fallows, provided they are kept free of grasses for a sufficient length of time (Sims *et al.* 1961; Meagher and Rooney 1966). Disease control has on occasion been cited as the primary cause of yield response to long fallows, and Tuohey *et al.* (1972) quotes Fisher (1962) as reporting that yield responses to long fallow in WA were very small except where 'root rot fungi' were very prevalent.

Decisions to fallow are complex and dependent on a number of biophysical, economic and social factors which differ from business to business (French 1978). French (1978) found greatest yield increase from fallow on fine textured soils, and Oliver *et al.* (2010) identified that fallow is of most value to subsequent crops in environments where fallow rainfall makes up a greater proportion of annual rainfall, and in environments where rainfall is more variable. As our simulation is continuous for the whole period (1990-2016), the legacy effects following a higher yielding wheat crop are accounted for i.e. drier soil. This also provides an explanation as to why continuous wheat strategies performed better in environments with higher annual rainfall, and fallow rotations performed better in environments with lower annual rainfall (Fig. 4). Sites that have both higher plant available water content and unreliable growing season rainfall are likely to benefit most from fallow, e.g. Walpeup and Condobolin. In our simulations, only one soil type has been used at each site and in environments with variable soil types, results may differ across total farm area. The strategy is also suited to farm managers who do not want to risk significant financial losses in poor seasons. This study demonstrates that WW-LC can boost wheat yield following long fallow, and close the gap between profitability of continuous cropping sequences by capturing the benefits of early and timely sowing, thus further contributing to managing seasonal rainfall variability.

4.3 Optimal phenology and rotation in the M and HRZ

Yield gain from continuous cropping WW was highest in high and medium rainfall zones where higher yield potential of slow developing wheat cultivars can be expressed, and where annual rainfall is more reliable i.e. Saddleworth, Yarrawonga, Temora and Cootamundra. In continuous wheat strategies (CW-Opp-WW and CW-WW-LC) in medium and high rainfall zones, the mean increase in yield between short and long coleoptile WW favoured WW-LC by 14% or 400 kg/ha. For rotations between forage legume and WW, the long coleoptile type also outperformed the short coleoptile type (15% or 500 kg/ha). This suggests that long coleoptiles are not only an important trait in LRZ when combined with long fallow, but also in HRZ and MRZ. Yield increases observed in early sown WW rotations may be attributed to the combination of deeper roots and increased subsoil water extraction (Incerti and O'Leary 1990; Lilley and Kirkegaard 2016), reduced evaporation (Eastham *et al.* 1999), higher transpiration efficiencies (Gomez-Macpherson and Richards 1995) and a longer spike development phase (Hunt *et al.* 2012).

Over the time period simulated (1990-2016), the area sown to wheat has increased by 26% or by ~3 million ha in Australia (ABARES 2017). Crop diversity has also increased, signalling a period of intensification and expansion into less favourable environments in Australian dryland cropping systems (Kirkegaard *et al.* 2014; Anderson *et al.* 2016; ABARES 2017). Reduced sheep numbers, access to N fertiliser and greater herbicide selection has supported continuous wheat cropping sequences in recent decades (Kirkegaard *et al.* 2011). However, disease carry-over from the stubble of previous crops and herbicide resistant weeds mean that eventually a break crop is necessary to control these factors (Seymour *et al.* 2012); otherwise, the benefits of no-till may not be fully realised (Patrignani *et al.* 2012). It is also well documented that cereals yield more when grown after a different species rather than grown as consecutive wheat crops (Seymour *et al.* 2012; Angus *et al.* 2015). In locations of higher land value and more reliable rainfall, it is unlikely that a farm manager will justify an area of long fallow. Therefore profitable break-crops, which maintain some of the benefits of long fallow are better suited. Our simulations show that yield gain is very similar in both long fallow and forage legume rotations in high yielding environments, with the best break-crop rotation being FL-WW-LC. This finding supports Angus *et al.* (2015) who identified that long fallow increased yield more in low yield environments

than break crops, but break crops had a greater effect in high yielding environments. This also aligns with international findings (Holman *et al.* 2018). We have used a forage legume as an example of a break crop in our simulations. However, depending on location and environmental constraints, other break crop options could include oaten hay, lentils or canola (Angus *et al.* 2015). Simulation experiments to test other break crop options would be insightful. Depending on the water requirement of the break crop and date of desiccation or maturity, residual soil water available for the following wheat crop will vary. Generally residual soil water is higher following a legume break crop than an oilseed break crop (Kirkegaard *et al.* 2008). A 10-year study in the Canadian Prairies found less residual water for a subsequent WW crop following canola (45 mm) than lentils (74 mm) (Larney and Lindwall 1995). Given that oaten hay is cut at flowering, it could be expected to result in a greater accumulation of soil water than canola and lentils.

5. Conclusions

This study has identified G x M strategies that can stabilise flowering time and increase PY_w in high, medium and low rainfall sites of the south-eastern Australian wheat belt. At all sites the highest yielding strategies established WW-LC cultivars early on stored sub-soil moisture from the previous rotation. In the LRZ long fallow in rotation with WW-LC can provide a buffer against rainfall variability. In MRZ and HRZ, where land is of higher value and rainfall more reliable, profitable break crops such as forage legume did not reduce subsequent WW-LC wheat yield compared to long fallow. The most promising G x M strategies identified in this study should be verified in field experiments. There is strong evidence that the benefits of early established, slow developing cultivars and fallow are not likely to be realised until the release of cultivars with long coleoptiles that can be sown at a greater depth than existing Australian cultivars.

6. Supplementary material

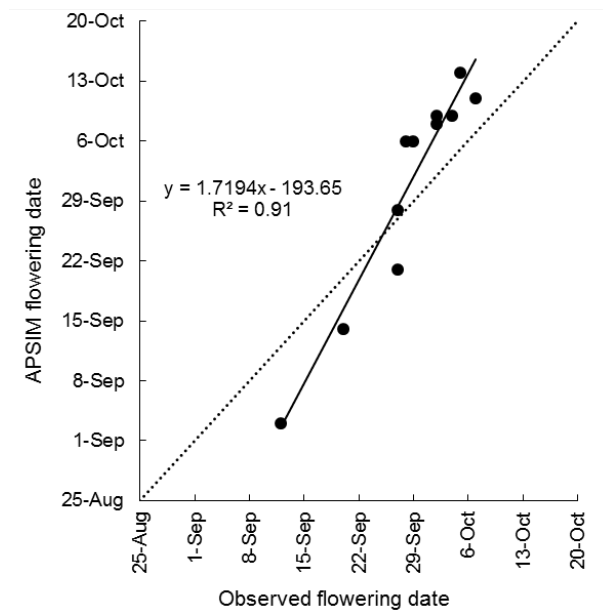


Figure S1. Validation of flowering time for APSIM cultivar V4-P1 used in simulations at locations Saddleworth, Lameroo, Waikerie, Walpeup and Condobolin. Observed flowering dates were recorded in Temora, New South Wales in 2015 and 2016 and Minnipa, South Australia in 2015. Flowering dates were simulated using the same sowing dates and under the same seasonal conditions as field experiments from Flohr *et al.* (2017c).

Chapter 5

Table S1. P-values of two-tailed t-test between yield of the baseline strategy vs. yield of strategies 1 to 11, and slope of the linear function for deviation of yield from the environmental mean and the environmental mean (mean of all strategies at a particular location). Bold text highlights significant differences, a slope closer to zero suggest the strategy is equally stable as the environmental mean, a positive slope indicates that the strategy is more stable than the environmental mean, and a negative slope indicates the strategy is less stable as per Eberhart and Russell (1966).

Strategy	CW-FS-LC		FL-FS		FL-FS-LC		LF-FS		LF-FS-LC		CW-Opp-WW		CW-WW-LC		FL-Opp-WW		FL-WW-LC		LF-Opp-WW		LF-WW-LC	
	1	2	3	4	5	6	7	8	9	10	11	1	2	3	4	5	6	7	8	9	10	11
Site	P-value	Slope	P-value	Slope	P-value	Slope	P-value	Slope	P-value	Slope	P-value	Slope	P-value	Slope	P-value	Slope	P-value	Slope	P-value	Slope	P-value	Slope
Charlton	0.22	-	0.10	-	0.00	-	0.00	-	0.00	-	0.00	0.08	0.00	0.23	0.00	0.10	0.00	0.13	0.00	0.21	0.00	0.24
Condobolin	0.27	-	0.02	-	0.00	-0.28	0.00	-0.4	0.00	-	0.00	0.19	0.00	0.30	0.00	0.24	0.00	0.36	0.00	0.47	0.00	0.48
Cootamundra	0.95	-	0.19	-	0.35	-	0.23	-	0.49	-	0.00	0.31	0.00	0.25	0.00	0.32	0.00	0.24	0.00	0.28	0.00	0.23
Lameroo	0.04	-	0.22	-	0.49	-	0.04	-	0.72	-	0.00	0.42	0.00	0.39	0.00	0.29	0.00	0.36	0.00	0.27	0.00	0.32
Saddleworth	0.32	-	0.12	-	0.87	-	0.00	-	0.34	-	0.00	0.37	0.00	0.43	0.00	0.34	0.00	0.43	0.00	0.32	0.00	0.31
Temora	0.37	-	0.25	-	0.18	-	0.40	-	0.81	-	0.00	0.19	0.00	0.19	0.02	0.16	0.00	0.21	0.00	0.26	0.00	0.21
Waikerie	0.02	-	0.47	-	0.00	-	0.14	-	0.00	-	0.00	0.16	0.00	0.18	0.06	0.00	0.00	0.18	0.00	0.16	0.00	0.24
Walpeup	0.01	-	0.00	-	0.28	-0.16	0.00	-	0.00	-	0.51	0.18	0.00	0.21	0.00	0.28	0.00	0.38	0.00	0.31	0.00	0.33
Yarrawonga	0.32	-	0.36	-	0.04	-	0.10	-	0.00	-	0.53	0.13	0.00	0.18	0.01	0.21	0.00	0.20	0.04	0.08	0.00	0.14

Chapter 6

Overview of the thesis



Image 6: Aerial image of field experimental plots at Temora, NSW, September 2015. The red box highlights plots where data was collected and presented in this thesis.

Contribution of the thesis

In south-eastern Australia, the most successful wheat cultivars are those that have their development aligned to the optimal flowering period, where the possibilities of drought, frost and heat stress are least likely to impact yield. Today, after more than a century of breeding, the most popular cultivars in SEA are those with fast-spring development with little photoperiod or vernalisation sensitivity. The combination of declining autumn rainfall (Cai and Cowan 2013), increasing farm size (Fletcher *et al.* 2016) and more frequent spring heat events and drought (Kirkegaard and Hunt 2010) is placing pressure on the traditional wheat production system in SEA. Alongside challenging environmental conditions, is concern about farm-level profitability. As a result of the increasing costs of production and greater competition from global wheat producers, Australian growers need to produce higher yields using the same or fewer resources. This situation has prompted a re-evaluation of wheat breeding objectives and management options available to wheat producers in SEA. The findings in this thesis provide significant insight on strategies that breeders, agronomists and growers can use to overcome these challenges, and lift PY_w and FY by stabilising the flowering time of wheat. In the following sections, I highlight the main findings from the field and simulation experiments, and their implications for farm practice and for future research.

6.1 Water and temperature stress define optimal flowering periods

In all environments, an optimal flowering period exists. Despite the critical importance of the optimal flowering period, prior to this research, optimal flowering periods had not been comprehensively defined. By using potential yield predictions from model simulation to integrate the effects of temperature, radiation and water supply and demand, this research extends the work of Zheng *et al.* (2012) who used only air temperature records to identify optimal flowering periods. Simulations found that optimal flowering periods varied with site and season, and were driven by the combined effects of seasonal water supply and demand, and extremes of temperature during critical periods of development. In addition to optimal flowering periods, the study identified the optimal sowing window for widely grown fast developing spring genotypes so that they flower during the optimal period (Table 1). This enables further refinement of existing state department recommendations. Quantifying optimal flowering periods is the first vital step to target G x M combinations that maximise yield to particular environments. This is particularly useful in the context of recent and predicted regional climate shifts, such as the decline in autumn rainfall.

Future research or limitations:

Our methodology used simulations with weekly spaced sowing dates. In retrospect, running daily simulations would deliver a more refined flowering period and this could be considered in future research, though would require a longer computing time. APSIMs ability to predict flowering date could be refined by verifying variability in thermal time between cultivars of different development in the field, and determining if development can be predicted from the development alleles.

The frost and heat rules applied to grain yield in simulation chapters (2 and 5) are limited in their ability to accurately capture frost and heat effects. The rules applied to grain yield are based on expert opinion, and have not been comprehensively evaluated in the field, or in controlled environment facilities. First, the rules only simulate the effects of frost and heat between Zadock growth stages 60-79, when in fact wheat is susceptible to frost when the spike emerges at Zadock 49 (Single 1964) and sensitivity increases thereafter (Livingston and Swinbank 1950; Single 1964 ; Afanasev 1966; Paulsen and Heyne 1983). Second, as discussed by Zheng *et al.* (2015) the historic weather data used in this study uses minimum temperatures that are recorded in Stevenson screens, and temperatures measured in this way have been found to not

accurately reflect canopy temperature and damage caused by frost (Hayman *et al.* 2007; Frederiks *et al.* 2012). Temperatures measured in this way may underestimate yield loss caused by radiant frosts, and overestimate frost damaged based on temperature above the canopy when there may actually be air movement or partial cloud cover (Zheng *et al.* 2015). Improvement in the models ability to predict frost and heat stress would be beneficial for yield predictions, and could be achieved through controlled environment experiments. Having said this, the flowering dates of the highest yielding genotype*sowing date treatments at four sites in Chapter 4 (Temora, Berriwillock, Minnipa and Cunderdin) occurred within the OFP defined using our approach.

The methodology is applicable to other Australian crops where yield is also dependant on flowering during an optimal period (e.g. barley, canola, grain legumes). Since the publication of this chapter in the journal *Field Crops Research*, there has been interest from colleagues about extending this method into Western Australia and to other crops such as canola e.g. Lilley *et al.* (2017). Pending access to reliable rainfall, temperature records, and satisfactory soil characterisation, this methodology can be applied to other environments also with distinct optimal flowering periods e.g. the Middle East, northern Africa and west Asia.

6.2.1 Development duration and partitioning are de-coupled

Previous authors have attributed some of the observed yield gain in Australia and around the world to faster development and earlier flowering (Perry and D'Antuono 1989; Siddique *et al.* 1989a; Siddique *et al.* 1989b; Richards 1991). The novel aspect of this work is that we tested this hypothesis using two sets of data, whilst also addressing the knowledge gap of yield gain for NSW cultivars. The two data sets were controlled by synchronised flowering time, or by a common sowing date. The novel first approach allowed us to control for the large differences in life cycle duration common in previous historic cultivar comparisons. To our knowledge, no previous study in this field has attempted this.

In both the 2015 and 2016 growing seasons, yield gain was not associated with changes in flowering time, in agreement with the study by Sadras and Lawson (2011). However, we found chronological differences in phenology leading up to flowering. Our data indicate that yield gain of NSW cultivars was associated with reduced duration of vegetative growth brought about by faster development. However this may not be causal and may have occurred through selection for both yield and faster development.

Data collected on the newly released FW cultivar Longsword provides some clarity on the two possible hypotheses. Superior partitioning occurred in cultivars with both slow (e.g. Longsword) and fast (e.g. Condo) development, indicating that improved partitioning is not necessarily linked to a shorter duration of pre-flowering growth. Therefore, longer growth duration can potentially be used as a means to increase dry-matter production and thereby increase yield. We suggest that future yield increases may be achieved by combining longer durations with modern cultivar canopy characteristics (erect leaves with high chlorophyll content delivering greater radiation use efficiency) and superior partitioning (provided that development duration and partitioning are de-coupled), theoretically resulting in greater partitioning of assimilates to the spike. The benefits are likely to be three-fold: (i) greater assimilate capture during the growing season, (ii) increased transpiration efficiency (Fletcher and Chenu 2015)(iii) greater partitioning to the spike and (iv) stabilised flowering time delivering increased sowing opportunities to growers.

Future research and limitations:

This research showed that superior partitioning can occur in cultivars with both slow and fast development, suggesting that development duration and partitioning are de-coupled. This needs to be confirmed independent of “genetic noise” by comparing the growth and development characteristics of near-isogenic lines, which differ only in flowering time (*Vrn* and *Ppd* genes) but are otherwise genetically similar.

There are other useful aspects that could be investigated using data collected in this experiment to further guide breeding programs, particularly around increases in radiation use efficiency in modern cultivar canopies. Using biomass collected at flowering and maturity, photosynthetically active radiation (PAR) measurements and normalised different vegetation index (NDVI) recordings, the interaction between irradiance, thermal time, growth and development can be studied. Dry-matter samples from flowering have been sent for water-soluble carbohydrate and nitrogen lab analysis. These data could be used to complement reported cases of greater photosynthetic rates being associated with higher leaf nitrogen around flowering (Fischer *et al.* 2014), with similar questions investigated as South Australian studies by Sadras and Lawson (2013) and Sadras *et al.* (2012). A possible future research question could be, do modern NSW cultivars produce biomass more efficiently, and what traits enable this?

Secondly, in both 2015 and 2016, CSIRO colleagues extracted soil cores from the historic wheat experiment in Temora to study rooting depth variation between cultivars released between 1901 and 2014. When analysis is complete, this may provide useful information regarding the interaction and possible benefits of enhanced rooting depth due to the longer vegetative phase in early sown, slow-developing wheat.

6.2.2 PYw gain of NSW cultivars released between 1901 and 2014 is 26 kg/ha p.a. (or 0.4% p.a.)

The quantification of yield improvement under current agronomy and climate provides insight into associated changes in physiology and can assist with future improvement (Sadras and Lawson 2011). Previous studies have documented chronological changes in physiology associated with yield gain of local cultivars in Western Australia (Perry and D'Antuono 1989; Siddique *et al.* 1989a; Siddique *et al.* 1989b) and South Australia (Black *et al.* 2008; Saunders 2008; Sadras and Lawson 2011), but no published studies had considered cultivars adapted to the important grain producing region in southern New South Wales.

Results showed that yield gain of NSW wheat cultivars released between 1901 and 2014 can be explained by a sigmoid curve. A logistic function fitted to the relationship between yield and year of release showed superior fit in comparison to a linear function. Yield gain was slow for the first three decades, followed by a greater rate of genetic gain during the middle of the century (approximately 1940s to 1980s), with slow improvements thereafter. Similar sigmoid curves can be seen in data presented by Austin *et al.* (1980) in the UK, Cox *et al.* (1988) in the US and Perry and D'Antuono (1989) in WA, with the greatest period of yield gain associated with the introduction of semi-dwarf cultivars. A plateau in PYw in recent decades has also been observed in experiments from Mediterranean Spain (Acreche *et al.* 2008; Sanchez-Garcia *et al.* 2013) and in the Yaqui Valley, Mexico (Fischer and Edmeades 2010).

In both seasons, yield increased with year of cultivar release at a rate of 26 kg/ha per annum or 0.4% p.a., regardless of whether common sowing or common flowering date was used to analyse data. The annual rate of yield progress is close to the 0.6% p.a. reported by Anthony and Brennan (1987) and 0.4% p.a. estimated by Sadras and Lawson (2011). Given that there was no difference in rate of yield progress between data balanced by common flowering or common sowing dates, yield increases were not associated with earlier flowering, but with an interplay between greater grain

number/m² and greater grain weight which was the result of increased partitioning of assimilates to spikes, and greater number of grains per unit spike weight (fruiting efficiency). These results concur with the findings of a similar study based in South Australia by Sadras and Lawson (2011).

Future research or limitations:

This historic wheat experiment used one genotype per decade, and cultivars were chosen based on historic popularity. Use of a small number of genotypes may restrict or overlook valuable findings regarding trait development over year of release, and as with previous historic wheat experiments, there is the possibility that observed trends may be subject to cultivar number and choice. However given limited resources and time, the cultivar choice was deemed appropriate.

An alternative approach to analysing trait vs. year of release regressions would be to plot non-continuous fits according to important historic dates in relation to genetic yield gain e.g. the advent of semi-dwarves. This may shift inflection points in the data. For instance, the statistical analysis found inflection points during the 1940s and 1980s, whereas semi-dwarfs were introduced to Australia in the 1970s which may have been a more logical date to split the data. Regardless how the data is analysed, data showed increases in PY_w have stalled in NSW cultivars since the ~1980s. Therefore the need to identify avenues to increase PY_w (such as longer durations outlined in 6.2.1) for global food security is urgent, especially under an increasingly variable climate.

Wheat breeders are unable to select for yield alone and must also maintain grain quality and disease resistance. One explanation for the yield stall observed in NSW cultivars since the 1980s may be that there has been a greater emphasis on breeding for grain quality and disease resistance, at the expense of yield gain. An interesting future investigation could determine how much the focus on grain quality and disease resistance reduces progress in yield gain. We began this consideration in Hunt et al. (2017).

6.3 Early sowing combined with fast-winter genotype stabilises flowering time and yield in diverse environments

Chapter 4 shows that farmers in southern Australia are sowing progressively earlier. Analysis of sowing date records from the Yield Prophet[®] database indicate a shift of around 1.5 days/year over a 10 year period in the southern wheat belt of Australia. To match the new sowing dates being practiced by growers, new genotypes are required to align flowering to the optimal flowering period and maximise yield.

The suitability of the fast-winter cultivar Longsword was investigated further in Chapter 4 in a wider set of environments. Sowing the fast-winter genotype early could increase yields by 10-20% compared to current cultivars sown in the current window. The results indicated that in cooler temperate environments (optimal flowering period from late September to mid-October), flowering stability occurred across a broader range of sowing dates for a fast-winter line compared to spring or slower developing winter wheats. In Mediterranean type environments (optimal flowering periods from late August to mid-September), it is likely that fast-winter genotypes will augment current mid and fast developing spring types by further opening the sowing window available to growers. However, it is unlikely to replace them wherever later sowing dates are practised, as the fast-winter wheat is inappropriate as it will flower after the optimal flowering period. By extending the sowing window, fast-winter cultivars will contribute to timeliness of the sowing program to maximise whole farm yield by allowing a greater area of wheat to flower at the optimal time.

Future research and limitations:

In this study a limited number of genotypes and allelic combinations were tested, and factors other than phenology may have contributed to the yield differences observed. Further research with a wider range of allelic combinations beyond the environments studied here is required before the optimal allelic combination for different environments can be determined. With the use of modelling, our findings could be extrapolated into a wider range of environments.

Our findings provide strong evidence that well-adapted winter wheat cultivars have a place in Australian sowing programs. In early 2018, AGT announced that the cultivar Longsword failed to receive a milling quality classification from the Wheat Quality Australian Classification Panel, and can only be delivered as Feed quality. However the

fast-winter cultivar Longsword is the first winter wheat released to show adaptation for the whole of southern Australia, and is likely to provide further impetus for other breeding companies to release winter cultivars.

The early sown fast-winter genotype offers a novel way to increase PY_w and maximise resource use. Given that yield = light intercepted x radiation use efficiency x harvest index, early sowing and slow development allows greater integrated light interception which can be translated into greater yield (provided superior partitioning occurs in slower-developing genotypes). In chapter 3 we found decreasing trends in thermal time from double ridge to terminal spikelet and flowering in modern cultivars and in the novel FW genotype, in addition to a greater spike weight. This suggests that improved partitioning can also occur in vernalisation sensitive cultivars.

Given that a fast-winter genotype in combination with early sowing has not been common practice in SA, WA and Vic, optimal management needs to be considered in these areas. This includes optimal sowing density and canopy management to avoid excessive crop canopy growth (unless grazed), weed control, disease and pest management i.e. barley yellow dwarf virus (Hunt *et al.* 2015b), take- all (Penrose 1993), *Septoria tritici* blotch (Penrose 1993), wheat streak mosaic virus (Hunt *et al.* 2015b) and Russian wheat aphid (Umina *et al.* 2017).

There may be potential for vernalisation to stabilise flowering and yield of other Australian crops such as barley and canola. Aside from Australia, there are other regions around the world where earlier planting could raise yield and maximise resource use such as other Mediterranean and temperate environments in North Africa, West Asia and the Middle East, which also have distinct optimal flowering periods and where such genotypes have not yet been utilised (Hoshino and Tahir, 1987).

6.4 Long coleoptile winter wheat and fallow rotation reduces reliability on autumn rainfall

Chapters 3 and 4 have clearly demonstrated the potential yield gains attainable from early sown winter wheat genotypes. However establishment of wheat in dry-land wheat production in southern Australia is reliant on autumn rainfall to provide seed-bed moisture to germinate seed and allow emergence. If rains do not fall during the optimal establishment time, crops flower too late and yield is reduced by drought and heat.

While our results show great promise for winter wheat cultivars in Australian sowing programs, to exploit the FY and PY_w gains demonstrated by early establishment and winter growth habit, we need to overcome the reliance on irregular rainfall events in late summer/ early autumn to establish crops. International studies have shown that reliance on irregular rainfall can be reduced, and early establishment opportunities increased, by sowing deeper into stored sub-soil moisture accumulated during fallow periods (Schillinger 2016). In order to allow establishment on stored soil water, cultivars with long coleoptiles that can be safely sown at a greater depth are required (Rebetzke *et al.* 2007a). This chapter describes simulation studies to investigate the effect of manipulating genotype (winter vs. spring wheats and long vs. short coleoptile) and management (sowing date, fallow length and sowing depth) interventions on yield and flowering date in high, medium and low rainfall zones. At all sites, the highest yielding strategies established winter wheats with long coleoptiles (LCWW) on stored moisture from the previous rotation, and achieved a mean yield increase of 42% (1.2 t/ha) compared to the baseline strategy. The PY_w gain demonstrated by early establishment and winter growth habit in Chapters 3 and 4 is not likely to be realised until the release of cultivars with a long coleoptile that allow deeper sowing. Alternatively, management can adopt innovative technology that allows access to stored soil moisture without the need of a long coleoptile, such as the modified cultivator allowing deep seed placement for chickpeas recently shown in Queensland (Wells 2017).

Future research and limitations:

A recent simulation study by Cann and Hunt (2018) showed an average yield increase of 1.5 t/ha for wheat grown after fallow compared to wheat grown after wheat, and in the field, the average yield response to fallow in Australia is 0.9 t/ha (Oliver *et al.* 2010; Angus *et al.* 2015). Similar to these previous studies, long fallow strategies in Chapter 5 are contributing to the observed yield increases in our G x M strategies. However the

novel aspect of Chapter 5 was combining fallow with optimal sowing dates and novel genetic traits to promote establishment opportunities under seasonal rainfall variability. The sites that had greatest yield gain from fallow-wheat vs. continuous wheat were sites that had combined medium-low rainfall and soil with high water holding capacity such as Walpeup, Charlton and Condobolin (discussed in Chapter 5, section 4.3). At these sites the yield increase from fallow alone was ~ 0.7 t/ha. When long fallow was combined with early sowing, long coleoptile and winter genotype, there was an additional yield increase of an average of 0.9 t/ha at these sites. This is a similar yield increase as found in the Kirkegaard and Hunt (2010), thus suggesting that long coleoptile and winter wheat contribute partly to the improved yield when combined with optimal management.

Characterisation of soils in APSOIL are commonly poorly parameterised for soil evaporation. Given that top layers were critical for establishment date in this study it is possible that dates do not reflect what would occur in the field. Therefore the findings from this study should be validated in field experiments. However this pre-experimental simulation indicates that long coleoptile winter wheats are a breeding objective worth pursuing. The next step of this research could include testing potential breeding lines, rotations and sowing equipment in field experiments in high, medium and low rainfall environments.

6.5 Recommendations

The overarching objective of the thesis was to identify G x M strategies that stabilise flowering and maximise yield in SEA. Several potential strategies have emerged from the work. They are usefully considered in relation to two main environmental types in SEA: temperate and Mediterranean.

Temperate environments generally have higher and more reliable rainfall and milder spring temperatures. This includes high rainfall zones of the wheat belt where growing seasons are longer, such as southern NSW and southern Victoria. In Chapter 2, an optimal flowering period was identified in these environments from late September to early-October, and fast spring genotypes are best suited to mid- to late-May sowing dates. In temperate environments, a fast-winter genotype can flower during the optimal flowering period from a wide sowing window starting early-April to mid-May (Chapter 3 & 4). In medium and high rainfall sites, long coleoptile winter wheat cultivars sown in mid-March in a continuous wheat rotation (mean 40% yield increase) and in rotation

with legume hay (mean 43% yield increase) have potential to both extend the appropriate sowing windows due to their stabilised flowering and increase yield (Chapter 5).

Mediterranean environments tend to have medium-low rainfall, and hotter and drier springs. This includes medium-low rainfall zones of the wheat belt where growing seasons are shorter e.g. South Australia, northern Victoria, and low-rainfall locations in NSW and Western Australia. Optimal flowering periods identified for these environments were in late August to mid-September, and fast spring genotypes were best suited to sowing from late-April to mid-May. In Mediterranean environments, a combination of fast-spring and fast-winter genotypes should be used to lengthen the sowing window and achieve optimal flowering. A novel fast-winter genotype can achieve the optimal flowering period with early sowing opportunities from April- early May, but cannot from later sowing times. Therefore growers in these areas should switch cultivars to fast-spring types at the opening of the sowing window for a fast-spring cultivar (Chapter 2 & 4). Long coleoptile winter wheat genotypes sown after a long fallow increased yield on average by 58% in low rainfall zones, with the best 2-yr crop rotation in low rainfall zones being forage legume followed by long coleoptile winter wheat.

6.6 Concluding remarks

Stabilising the flowering time of wheat can lift whole-farm yield and PYw by ensuring a greater area of crop is flowering at the optimal time, and through lengthening the period available for sowing whilst still flowering at the optimal time in regions of SEA affected by autumn rainfall decline. This thesis has analysed flowering time of wheat from a detailed plant physiological perspective, a crop-level simulation perspective, and a whole farm system perspective. The thesis has defined optimal flowering periods, quantified yield gain under common flowering dates, and provided direction for breeding programs by identifying a novel genotype which offers flowering date and yield stability at sowing dates being practiced by Australian wheat producers. Simulation revealed that these winter wheats with long coleoptiles could be managed with novel agronomy (crop rotation to reduce the reliance on irregular autumn rainfall by allowing the earlier establishment of wheat crops). Table 1 summarises the main key findings from this thesis. The findings have potential to be extended to different crops and regions of Australia and overseas not included in this study. It is possible that novel

genotypes (winter growth habit, long coleoptile) and management (early sowing, augmenting cultivars and crop rotation) will be applicable to environments with similar climatic constraints such as North Africa and West Asia.

The implementation of these findings relies on continued interaction between wheat breeders, agronomists and farmers. Firstly, breeders need to identify germplasm with appropriate winter habit and long coleoptiles suited to different season lengths in the Australian wheat belt. Secondly, agronomists need to test the novel cultivars to identify the optimal management in different environments. The best practice may require machinery alteration, which will also need to be tested. Perhaps most importantly, the findings need to be adopted by farmers such that FY is increased, therefore the communication and fitting of novel technologies into farming systems is paramount.

Table 1: A map of research questions pursued in the thesis, and the main outcomes.

Overarching thesis objective: Identify novel G x M to achieve flowering date stability		
Chapter, topic and journal	Research question	Outcome
<p>Chapter 2</p> <p><u>Topic:</u> Optimal flowering periods</p> <p><u>Journal:</u> <i>Published, Field Crops Research</i></p>	<ol style="list-style-type: none"> 1. What are the optimal flowering periods in the SEA cropping zone as defined by temperature and water supply and demand? 2. What sowing dates are required for widely grown mid-fast developing cultivars to flower during the optimal period? 	<p>Frost, heat, average temperature and water supply and demand plays an important role in defining optimal flowering periods. G x M can now be aligned accordingly in different environments.</p> <p>The optimal establishment date for mid-fast cultivars targeting optimal flowering periods in this study, align with period of rainfall decline. Sowing date ranges were consistently of shorter duration than those currently recommended by state departments of agriculture. Whilst state recommendations appear to correctly estimate the start of the sowing period, they greatly overestimate the end of the optimal period.</p>
<p>Chapter 3</p> <p><u>Topic:</u> Change in yield potential & growth and development traits of popular wheat cultivars released in southern New South Wales between 1901-2014</p> <p><u>Journal:</u> <i>Published, European Journal of Agronomy</i></p>	<ol style="list-style-type: none"> 3. How much observed yield gain is associated with: (i) earlier flowering, (ii) reduced duration to flowering, (iii) inherently better partitioning to grain? 	<p>There was no difference in yield gain when comparing flowering date vs. sowing date balanced data in our two-year field experiment. Therefore, change in flowering date has not contributed to yield gain for southern NSW cultivars.</p> <p>Yield increases in modern cultivars were associated with increased grain number/spikelet, reduced</p>

	<p>4. What is the genetic yield gain of New South Wales wheat cultivars released between 1901 and 2014?</p>	<p>spike number (tillers), increased spike weight, and reduced dry-matter at flowering.</p> <p>Only when cultivars were balanced by flowering date was it revealed that breeding has reduced thermal time from double ridge to terminal spikelet, and thermal time from double ridge to flowering in modern cultivars. This has consequently contributed to improving partitioning of assimilates to the head in modern cultivars.</p> <p>Sowing to flowering duration and partitioning appear to be de-coupled. Therefore longer duration can potentially be used as a means to increase dry-matter production and thereby increase yield.</p> <p>The annual rate of yield progress in our collection of historic wheats was 26 kg/ha p.a., or when presented as relative to the mean yield of the most recently released cultivar (Condo, 6 t/ha), progress is ~ 0.4% p.a. (2014 release).</p>
<p>Chapter 4</p> <p><u>Topic</u>: Novel fast-winter genotype</p> <p><u>Journal</u>: <i>Published, Field Crops Research</i></p>	<p>1. What sowing dates are farmers currently practicing?</p> <p>2. Can a fast-winter wheat genotype stabilise flowering across the early</p>	<p>Analysis of sowing date records indicate a shift of around 1.5 days/year earlier over a 10 year period.</p> <p>In cooler environments, the fast-winter wheat exhibited a more stable flowering time across a broader range of</p>

	sowing dates being practiced by farmers in southern Australia?	sowing dates compared to spring or slower developing winter cultivars. The optimal sowing window was shorter in warmer environments for the fast-winter. The fast-winter genotype sown early could increase yields by 10-20% compared to current cultivars.
<p>Chapter 5</p> <p><u>Topic:</u> Novel G x M strategies</p> <p><u>Journal:</u> <i>Published, Crop and Pasture Science</i></p>	1. Can novel genotype x management strategies reduce reliance on autumn rainfall for establishment and increase PY_w by allowing a greater portion of wheat to flower during the optimal period?	Our simulation experiments predict that winter wheats with long coleoptiles sown after long fallow allow for early crop establishment using stored soil water to optimise flowering and maximise yield.

References

References

- ABARES, 2017. Agricultural Commodity Statistics 2017. Commonwealth of Australia, Canberra, ACT.
- Abbate, PE, Andrade, FH, Lazaro, L, Bariffi, JH, Berardocco, HG, Inza, VH, Marturano, F (1998) Grain yield increase in recent argentine wheat cultivars. *Crop Science* **38**, 1203-1209.
- ACAS (2007) 'National Variety Trials.' Available at <http://www.nvtonline.com.au> [Accessed 12 May 2015].
- Acreche, MM, Briceno-Felix, G, Sanchez, JAM, Slafer, GA (2008) Physiological bases of genetic gains in Mediterranean bread wheat yield in Spain. *European Journal of Agronomy* **28**, 162-170.
- AEGIC (2016a) AEGIC Annual Report 2015-2016. Department of Agriculture and Food Western Australia, Grains Research and Development Corporation.
- AEGIC (2016b) Russia's wheat industry: implications for Australia. Australian Export Grains Innovation Centre (AEGIC).
- AEGIC (2017) 'Wheat.' Available at <http://aegic.org.au> [Accessed 13 November 2017].
- Afanasev, M (1966) Frost injury in wheat. *Plant Disease Reporter* **50**,
- An-Vo, DA, Mushtaq, S, Zheng, BY, Christopher, JT, Chapman, SC, Chenu, K (2018) Direct and Indirect Costs of Frost in the Australian Wheatbelt. *Ecological Economics* **150**, 122-136.
- Anderson, W, Smith, W (1990) Yield advantage of two semi-dwarf compared with two tall wheats depends on sowing time. *Australian Journal of Agricultural Research* **41**, 811-826.
- Anderson, WK, Garlinge, JR (2000) Crop management In 'The wheat book- principles and practice.' Vol. 4443 pp. 131-164. (Department of Agriculture and Food: Western Australia, Perth)
- Anderson, WK, Heinrich, A, Abbotts, R (1996) Long-season wheats extend sowing opportunities in the central wheat belt of Western Australia. *Australian Journal of Experimental Agriculture* **36**, 203-208.
- Anderson, WK, Stephens, D, Siddique, KHM (2016) Dryland Agriculture in Australia: Experiences and Innovations. In 'Innovations in Dryland Agriculture.' (Eds M Farooq, KHM Siddique.) pp. 299-319. (Springer International Publishing: Cham)
- Angus, JF, Kirkegaard, JA, Hunt, JR, Ryan, MH, Ohlander, L, Peoples, MB (2015) Break crops and rotations for wheat. *Crop & Pasture Science* **66**, 523-552.
- Anthony, G, Brennan, JP, 1987. Progress in yield potential and in bread-making characteristics in wheat in NSW. Ag. Econ. Bull. . NSW Dept. of Agriculture, 1925–26 to 1984–85.
- Archontoulis, SV, Miguez, FE (2015) Nonlinear Regression Models and Applications in Agricultural Research. *Agronomy Journal* **107**, 786-798.
- Asseng, S, Pannell, DJ (2013) Adapting dryland agriculture to climate change: Farming implications and research and development needs in Western Australia. *Climatic Change* **118**, 167-181.
- Asseng, S, Turner, NC, Keating, BA (2001) Analysis of water- and nitrogen-use efficiency of wheat in a Mediterranean climate. *Plant and Soil* **233**, 127-143.
- Austin, RB, Bingham, J, Blackwell, RD, Evans, LT, Ford, MA, Morgan, CL, Taylor, M (1980) Genetic improvements in winter-wheat yields since 1900 and associated physiological-changes. *Journal of Agricultural Science* **94**, 675-689.
- Australian Government, BoM (2017) 'Climate Data Online.' Available at <http://www.bom.gov.au/climate/data/> [Accessed 1 June].
- Barlow, KM, Christy, BP, O'Leary, GJ, Riffkin, PA, Nuttall, JG (2015) Simulating the impact of extreme heat and frost events on wheat crop production: A review. *Field Crops Research* **171**, 109-119.

References

- Batten, G, Khan, M (1987) Effect of time of sowing on grain yield, and nutrient uptake of wheats with contrasting phenology. *Australian Journal of Experimental Agriculture* **27**, 881-887.
- Bell, LW, Lilley, JM, Hunt, JR, Kirkegaard, JA (2015) Optimising grain yield and grazing potential of crops across Australia's high-rainfall zone: a simulation analysis. 1. Wheat. *Crop & Pasture Science* **66**, 332-348.
- Black, I, Dyson, C, Hayman, P, Alexander, B (2008) The determinants of South Australian yield increase. In 'Proceedings of 14th Australian Agronomy Conference. Adelaide, South Australia', 21- 25 September. Available at www.agronomyaustralia.org
- Bodner, G, Nakhforoosh, A, Kaul, H-P (2015) Management of crop water under drought: a review. *Agronomy for Sustainable Development*
- Boer, R, Campbell, LC, Fletcher, DJ (1993) Characteristics of frost in a major wheat-growing region of Australia. *Australian Journal of Agricultural Research* **44**, 1731-1743.
- Brennan, JP, Bialowas, A (2001) Changes in Characteristics of NSW Wheat Varieties, 1965-1997: Economic Research Report No. 8. NSW Agriculture, Wagga Wagga.
- Brown, HE, Huth, NI, Holzworth, DP, Teixeira, EI, Zyskowski, RF, Hargreaves, JNG, Moot, DJ (2014) Plant Modelling Framework: Software for building and running crop models on the APSIM platform. *Environmental Modelling & Software* **62**, 385-398.
- Brown, P, Singleton, G, Tann, C, Mock, I (2003) 'Increasing sowing depth to reduce mouse damage to winter crops.'
- Bushuk, W (1998) Wheat breeding for end-product use (Reprinted from Wheat: Prospects for global improvement, 1998). *Euphytica* **100**, 137-145.
- Cai, W, Cowan, T (2013) Southeast Australia Autumn Rainfall Reduction: A Climate-Change-Induced Poleward Shift of Ocean-Atmosphere Circulation. *Journal of Climate* **26**, 189-205.
- Cai, W, Cowan, T, Thatcher, M (2012) Rainfall reductions over Southern Hemisphere semi-arid regions: the role of subtropical dry zone expansion. *Scientific Reports* **2**, 702.
- Calderini, DF, Dreccer, MF, Slafer, GA (1995) Genetic-improvement in wheat yield and associated traits - a reexamination of previous results and the latest trends. *Plant Breeding* **114**, 108-112.
- Calderini, DF, Slafer, GA (1999) Has yield stability changed with genetic improvement of wheat yield? *Euphytica* **107**, 51-59.
- Cane, K, Eagles, HA, Laurie, DA, Trevaskis, B, Vallance, N, Eastwood, RF, Gororo, NN, Kuchel, H, Martin, PJ (2013) Ppd-B1 and Ppd-D1 and their effects in southern Australian wheat. *Crop & Pasture Science* **64**, 100-114.
- Cann, D, Hunt, J (2018) Long fallows maintain whole-farm profit and reduce risk in the Mallee. In 'GRDC Update 18/07/2018. Walpeup'. (Grains Research and Development Corporation:
- Carberry, PS, Hochman, Z, Hunt, JR, Dalgliesh, NP, McCown, RL, Whish, JPM, Robertson, MJ, Foale, MA, Poulton, PL, van Rees, H (2009) Re-inventing model-based decision support with Australian dryland farmers. 3. Relevance of APSIM to commercial crops. *Crop & Pasture Science* **60**, 1044-1056.
- Chenu, K, Dehifard, R, Chapman, SC (2013) Large-scale characterization of drought pattern: a continent-wide modelling approach applied to the Australian wheatbelt spatial and temporal trends. *New Phytologist* **198**, 801-820.
- Cockram, J, Jones, H, Leigh, FJ, O'Sullivan, D, Powell, W, Laurie, DA, Greenland, AJ (2007) Control of flowering time in temperate cereals: genes, domestication, and sustainable productivity. *J Exp Bot* **58**, 1231-44.
- Commonwealth of Australia, 2013. Principal Agricultural Commodities, Australia, 2012-2013. Canberra. cat. no. 7111.0:
- Coombes, NE (2002) The Reactive Tabu Search for efficient correlated experimental designs. PhD thesis, John Moores University
- Coventry, DR, Reeves, TG, Brooke, HD, Cann, DK (1993) Influence of genotype, sowing date, and seeding rate on wheat development and yield. *Australian Journal of Experimental Agriculture* **33**, 751-757.

References

- Cox, TS, Shroyer, JP, Ben-Hui, L, Sears, RG, Martin, TJ (1988) Genetic Improvement in Agronomic Traits of Hard Red Winter Wheat Cultivars 1919 to 1987. *Crop Science* **28**, 756-760.
- Crimp, S, Bakar, KS, Kokic, P, Jin, HD, Nicholls, N, Howden, M (2015) Bayesian space-time model to analyse frost risk for agriculture in Southeast Australia. *International Journal of Climatology* **35**, 2092-2108.
- CSIRO, Bureau of Meteorology (2015) Climate Change in Australia Information for Australia's Natural Resource Management Regions. Australia. Available at https://www.climatechangeinaustralia.gov.au/media/ccia/2.1.6/cms_page_media/168/CIA_2015_NRM_TechnicalReport_WEB.pdf.
- Dalglish, NP, Foale, MA, McCown, RL (2009) Re-inventing model-based decision support with Australian dryland farmers. 2. Pragmatic provision of soil information for paddock-specific simulation and farmer decision making. *Crop & Pasture Science* **60**, 1031-1043.
- Davidson, JL, Christian, KR, Jones, DB, Bremner, PM (1985) Responses of wheat to vernalization and photoperiod. *Australian Journal of Agricultural Research* **36**, 347-359.
- del Moral, LFG, Rharrabti, Y, Villegas, D, Royo, C (2003) Evaluation of grain yield and its components in durum wheat under Mediterranean conditions: An ontogenic approach. *Agronomy Journal* **95**, 266-274.
- Department of Economic Development Jobs Transport and Resources, GRDC (2015) National Variety Trials. [Accessed 1/09/2015].
- Doyle, AD, Fischer, RA (1979) Dry-matter accumulation and water-use relationships in wheat crops. *Australian Journal of Agricultural Research* **30**, 815-829.
- Eagles, HA, Cane, K, Kuchel, H, Hollamby, GJ, Vallance, N, Eastwood, RF, Gororo, NN, Martin, PJ (2010) Photoperiod and vernalization gene effects in southern Australian wheat. *Crop & Pasture Science* **61**, 721-730.
- Eagles, HA, Cane, K, Vallance, N (2009) The flow of alleles of important photoperiod and vernalisation genes through Australian wheat. *Crop & Pasture Science* **60**, 646-657.
- Eastham, J, Gregory, PJ, Williamson, DR, Watson, GD (1999) The influence of early sowing of wheat and lupin crops on evapotranspiration and evaporation from the soil surface in a Mediterranean climate. *Agricultural Water Management* **42**, 205-218.
- Eberhart, SA, Russell, WA (1966) Stability Parameters for Comparing Varieties I. *Crop Science* **6**, 36-40.
- Edwards, J, Umbers, A, Wentworth, S (2012) Farm Practices Survey Report 2012. Grains Research and Development Corporation Available at <https://grdc.com.au/resources-and-publications/all-publications/publications/2012/11/farmpractices> (accessed 17 May 2017).
- Ferris, R, Ellis, RH, Wheeler, TR, Hadley, P (1998) Effect of high temperature stress at anthesis on grain yield and biomass of field-grown crops of wheat. *Annals of Botany* **82**, 631-639.
- Fettell, N, Brill, R, Hunt, J (2011) Matching wheat varieties and sowing time - the impacts of water stress and frost risk. In 'GRDC Grains Research Update. Dubbo, NSW', 25 March pp. 84- 91.
- Fischer, R, Kohn, G (1966) The relationship of grain yield to vegetative growth and post-flowering leaf area in the wheat crop under conditions of limited soil moisture. *Australian Journal of Agricultural Research* **17**, 281-295.
- Fischer, RA (1979) Growth and water limitation to dryland wheat yield in Australia: a physiological framework.
- Fischer, RA (1984) Wheat. In 'In 'Proceedings of symposium on potential productivity of field crops under different environments' September 1980.' (Ed. SB Eds WH Smith.) pp. pp. 129-154. IRRI: Los Baños, Philippines)
- Fischer, RA (1985) Number of kernels in wheat crops and the influence of solar-radiation and temperature. *Journal of Agricultural Science* **105**, 447-461.

References

- Fischer, RA (2009) Farming systems of Australia, exploiting the synergy between genetic improvement and agronomy. In 'Applied Crop Physiology: Boundaries with genetic improvement and agronomy.' (Eds V Sadras, D Calderini.) pp. 23-54 (Elsevier Inc. :
- Fischer, RA (2011) Wheat physiology: a review of recent developments. *Crop & Pasture Science* **62**, 95-114.
- Fischer, RA (2015) Definitions and determination of crop yield, yield gaps, and of rates of change. *Field Crops Research* **182**, 9-18.
- Fischer, RA (2016) The effect of duration of the vegetative phase in irrigated semi-dwarf spring wheat on phenology, growth and potential yield across sowing dates at low latitude. *Field Crops Research* **198**, 188-199.
- Fischer, RA, Armstrong, JS (1990) 'Simulation of soil water storage and sowing day probabilities with fallow and no-fallow in southern New South Wales: II. Stochasticity and management tactics.'
- Fischer, RAT, Edmeades, GO (2010) Breeding and Cereal Yield Progress. *Crop Science* **50**, S85-S98.
- Fischer, T, Byerlee, D, Edmeades, GO (2014) Crop yields and global food security: will yield increase continue to feed the world? *ACIAR Monograph No. 158* xxii + 634pp.
- Fisher, H (1962) Farming without fallow. *Journal of Agriculture, Western Australia (4th series)* **3**, 172.
- Fitzsimmons, RW (1991) 'Wheat Variety Statistics NSW 1925-1990 Areas of All Wheat Varieties Planted - NSW by Local Government Areas.' (Australian Institute of Agricultural Science: Wairoa, NSW)
- Fletcher, A, Chenu, K (2015) Change in biomass partitioning and transpiration efficiency in Australian wheat varieties over the last decades. In '17th Australian Agronomy Conference. Hobart, Australia'.
- Fletcher, A, Lawes, R, Weeks, C (2016) Crop area increases drive earlier and dry sowing in Western Australia: implications for farming systems. *Crop and Pasture Science* **67**, 1268-1280.
- Flohr, B, Hunt, J, Kirkegaard, J, Evans, J, 2017a. Stabilising wheat flowering time and yield under drought in Australia. InterDrought-V. Hyderabad, India.
- Flohr, BM, Hunt, JR, Kirkegaard, JA, Evans, JR (2017b) Water and temperature stress define the optimal flowering period for wheat in south-eastern Australia. *Field Crops Research* **209**, 108-119.
- Flohr, BM, Hunt, JR, Kirkegaard, JA, Evans, JR (2017c) Winter is coming: the potential for a fast winter wheat to stabilise flowering and maximise yield in southern and Western Australia. In 'Proceedings of the 18th Agronomy Australia Conference. Ballarat, Australia', 24 – 28 September 2017. Available at www.agronomyconference.com
- Flohr, BM, Hunt, JR, Kirkegaard, JA, Evans, JR, Swan, A, Rheinheimer, B (2018) Genetic gains in NSW wheat cultivars from 1901 to 2014 as revealed from synchronous flowering during the optimum period. *European Journal of Agronomy* **98**, 1-13.
- Fondy, BR, Geiger, DR (1980) Effect of Rapid Changes in Sink-Source Ratio on Export and Distribution of Products of Photosynthesis in Leaves of *Beta vulgaris* L. and *Phaseolus vulgaris* L. *Plant Physiology* **66**, 945-949.
- Frederiks, TM, Christopher, JT, Harvey, GL, Sutherland, MW, Borrell, AK (2012) Current and emerging screening methods to identify post-head-emergence frost adaptation in wheat and barley. *J Exp Bot* **63**, 5405-5416.
- French, R (1978) The effect of fallowing on the yield of wheat. II. The effect on grain yield. *Australian Journal of Agricultural Research* **29**, 669-684.
- French, R, Schultz, J (1984) Water use efficiency of wheat in a Mediterranean-type environment. I. The relation between yield, water use and climate. *Australian Journal of Agricultural Research* **35**, 743-764.
- Frischke, AJ, Hunt, JR, McMillan, DK, Browne, CJ (2015) Forage and grain yield of grazed or defoliated spring and winter cereals in a winter-dominant, low-rainfall environment. *Crop & Pasture Science* **66**, 308-317.
- Fujita, M, Kawada, N, Tahir, M (1992) Relationship between cold resistance, heading traits and ear primordia development of wheat cultivars. *Euphytica* **64**, 123-130.

References

- Fuller, MP, Fuller, AM, Kaniouras, S, Christophers, J, Fredericks, T (2007) The freezing characteristics of wheat at ear emergence. *European Journal of Agronomy* **26**, 435-441.
- Giunta, F, Motzo, R, Deidda, M (1993) Effect of drought on yield and yield components of durum-wheat and triticale in a mediterranean environment. *Field Crops Research* **33**, 399-409.
- Giunta, F, Motzo, R, Pruneddu, G (2007) Trends since 1900 in the yield potential of Italian-bred durum wheat cultivars. *European Journal of Agronomy* **27**, 12-24.
- Gomez-Macpherson, H, Richards, RA (1995) Effect of sowing time on yield and agronomic characteristics of wheat in south-eastern australia. *Australian Journal of Agricultural Research* **46**, 1381-1399.
- González, FG, Slafer, GA, Miralles, DJ (2005) Pre-anthesis development and number of fertile florets in wheat as affected by photoperiod sensitivity genes Ppd-D1 and Ppd-B1. *Euphytica* **146**, 253-269.
- GrainCorp (2014) GrainCorp Australian Crop Report 2013/14. GrainCorp, Sydney. Available at [www.graincorp.com.au/literature/158567/2013 - 2014 GrainCorp Crop Report](http://www.graincorp.com.au/literature/158567/2013-2014_GrainCorp_Crop_Report).
- GrainCorp (2016) GrainCorp Australian Crop Report 2015/16. GrainCorp, Sydney. Available at <http://www.graincorp.com.au/storage-and-logistics/technical-services/graincorp-australian-crop-report-2015-16>.
- GRDC, 2017. Sowing time delivers competitive edge on weeds. Ground Cover. Barton, ACT.
- Harris, F, Koetz, R, Menz, I (2017a) The effect of sowing date on phenology and grain yield of wheat in southern NSW 2016. In 'GRDC Grains Research Update. Wagga Wagga, NSW', 14-15 February Available at <https://grdc.com.au/Research-and-Development/GRDC-Update-Papers/2017/02/The-effect-of-sowing-date-on-phenology-and-grain-yield-of-wheat-in-southern-NSW-2016>
- Harris, FAJ, Eagles, HA, Virgona, JM, Martin, PJ, Condon, JR, Angus, JF (2017b) Effect of VRN1 and PPD1 genes on anthesis date and wheat growth. *Crop & Pasture Science* **68**, 195-201.
- Harrison, MT, Evans, JR, Dove, H, Moore, AD (2011) Recovery dynamics of rainfed winter wheat after livestock grazing 1. Growth rates, grain yields, soil water use and water-use efficiency. *Crop and Pasture Science* **62**, 947-959.
- Harrison, MT, Evans, JR, Moore, AD (2012) Using a mathematical framework to examine physiological changes in winter wheat after livestock grazing: 2. Model validation and effects of grazing management. *Field Crops Research* **136**, 127-137.
- Hatfield, J, Karlen, D (1993) 'Sustainable Agricultural Systems.' (Lewis Publishers: Boca Raton, Florida)
- Hayman, P, Alexander, B, Knell, G, Rebbeck, M (2007) 'The balancing act of managing frost risk.' (South Australian Research and Development Institute and Grains Research and Development Corporation)
- Hochman, Z, Dang, YP, Schwenke, GD, Dalgliesh, NP, Routley, R, McDonald, M, Daniells, IG, Manning, W, Poulton, PL (2007) Simulating the effects of saline and sodic subsols on wheat crops growing on Vertosols. *Australian Journal of Agricultural Research* **58**, 802-810.
- Hochman, Z, Gobbett, DL, Horan, H (2017) Climate trends account for stalled wheat yields in Australia since 1990. *Glob Chang Biol* **23**, 2071-2081.
- Hochman, Z, Holzworth, D, Hunt, JR (2009a) Potential to improve on-farm wheat yield and WUE in Australia. *Crop & Pasture Science* **60**, 708-716.
- Hochman, Z, van Rees, H, Carberry, PS, Hunt, JR, McCown, RL, Gartmann, A, Holzworth, D, van Rees, S, Dalgliesh, NP, Long, W, Peake, AS, Poulton, PL, McClelland, T (2009b) Re-inventing model-based decision support with Australian dryland farmers. 4. Yield Prophet (R) helps farmers monitor and manage crops in a variable climate. *Crop & Pasture Science* **60**, 1057-1070.
- Holman, JD, Arnet, K, Dille, J, Maxwell, S, Obour, A, Roberts, T, Roozeboom, K, Schlegel, A (2018) Can Cover or Forage Crops Replace Fallow in the Semiarid Central Great Plains? *Crop Science* **58**, 1-13.
- Holzworth, DP, Huth, NI, Devoil, PG, Zurcher, EJ, Herrmann, NI, McLean, G, Chenu, K, van Oosterom, EJ, Snow, V, Murphy, C, Moore, AD, Brown, H, Whish, JPM, Verrall, S,

References

- Fainges, J, Bell, LW, Peake, AS, Poulton, PL, Hochman, Z, Thorburn, PJ, Gaydon, DS, Dalglish, NP, Rodriguez, D, Cox, H, Chapman, S, Doherty, A, Teixeira, E, Sharp, J, Cichota, R, Vogeler, I, Li, FY, Wang, EL, Hammer, GL, Robertson, MJ, Dimes, JP, Whitbread, AM, Hunt, J, van Rees, H, McClelland, T, Carberry, PS, Hargreaves, JNG, MacLeod, N, McDonald, C, Harsdorf, J, Wedgwood, S, Keating, BA (2014) APSIM - Evolution towards a new generation of agricultural systems simulation. *Environmental Modelling & Software* **62**, 327-350.
- Hoshino, T, Tahir, M (1987) Relationship between ear primordia development and growth attributes of wheat cultivars in dry areas of North Africa and West Asia. *Japan Agricultural Research Quarterly* **21**, 226-232.
- Hudson, T, Krause, M, 2013. Cost of production. GRDC, Canberra, ACT.
- Hunt, J, Fettell, N, Midwood, J, Breust, P, Peries, R, Gill, J, Paridaen, A (2012) 'Optimising flowering time, phase duration, HI and yield of milling wheat in different rainfall zones of southern Australia, Capturing Opportunities and Overcoming Obstacles in Australian Agronomy: 16th Australian Society of Agronomy Conference. Armidale, Australia.' Armidale, Australia. (Australian Society of Agronomy. Available at <http://www.regional.org.au> [Accessed 22 May 2017].
- Hunt, JR (2017) Winter wheat cultivars in Australian farming systems: a review. *Crop and Pasture Science* **68**, 501-515.
- Hunt, JR, Browne, C, McBeath, TM, Verburg, K, Craig, S, Whitbread, AM (2013) Summer fallow weed control and residue management impacts on winter crop yield though soil water and N accumulation in a winter-dominant, low rainfall region of southern Australia. *Crop and Pasture Science* **64**, 922.
- Hunt, JR, Flohr, BM, Fettell, N, Stear, M, Swan, A, Rheinheimer, B, Haskins, B, J.A., K (2017) Genetic yield progress in popular southern NSW bread wheat cultivars from 1901-2014. In 'Proceedings of the 18th Agronomy Australia Conference. Ballarat, Australia', 24-28 September 2017. Available at www.agronomyaustraliaproceedings.org/
- Hunt, JR, Kirkegaard, JA (2011) Re-evaluating the contribution of summer fallow rain to wheat yield in southern Australia. *Crop & Pasture Science* **62**, 915-929.
- Hunt, JR, Kirkegaard, JA, Lilley, JM, Trevaskis, B, Sprague, S, Swan, T, Rheinheimer, B (2014) Strategies and tactics to extend whole-farm water-use efficiency - sow on-time or early! In 'GRDC Grains Research Update. Adelaide, SA', 25-26 February. Available at <https://grdc.com.au/Research-and-Development/GRDC-Update-Papers/2014/02/Strategies-and-tactics-to-extend-whole-farm-water-use-efficiency-NSW>
- Hunt, JR, Rheinheimer, B, Swan, A, Goward, L, Wheeler, R, Ware, A, Davis, L, Nairn, J, Pearce, A, Ludwig, I, Noack, S, Hooper, P, Faulkner, M, Braun, J, Flohr, L (2016) 'Early sowing in SA – results from 2015 and a summary of two years of trials.' Available at Available at <https://grdc.com.au> [Accessed May 2017].
- Hunt, JR, Rheinheimer, B, Swan, T, Goward, L, Fettell, N, Haskins, B, Whitworth, R, Ryan, MH, Pratt, T (2015a) 'Early sowing in 2014 – how did it go?' Available at Available at <https://grdc.com.au> [Accessed May 2017].
- Hunt, JR, Swan, A, Rheinheimer, B, Goward, L, Kirkegaard, JA, Poole, N, Wylie, T, Kreeck, G, Paridaen, A, Breust, P, Midwood, J (2015b) 'Mud, weeds, frost, sheep and disease - managing the risks of early-sown wheat in South West Victoria.' Available at Available at <https://grdc.com.au> [Accessed May 2017].
- Incerti, M, O'Leary, G (1990) Rooting depth of wheat in the Victorian Mallee. *Australian Journal of Experimental Agriculture* **30**, 817-824.
- IPCC (2013) 'Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.' (Cambridge University Press: Cambridge, United Kingdom and New York, NY, USA)
- Jeffrey, SJ, Carter, JO, Moodie, KB, Beswick, AR (2001) Using spatial interpolation to construct a comprehensive archive of Australian climate data. *Environmental Modelling & Software* **16**, 309-330.
- Kamran, A, Iqbal, M, Spaner, D (2014) Flowering time in wheat (*Triticum aestivum* L.): a key factor for global adaptability. *Euphytica* **197**, 1-26.

References

- Keating, BA, Carberry, PS, Hammer, GL, Probert, ME, Robertson, MJ, Holzworth, D, Huth, NI, Hargreaves, JNG, Meinke, H, Hochman, Z, McLean, G, Verburg, K, Snow, V, Dimes, JP, Silburn, M, Wang, E, Brown, S, Bristow, KL, Asseng, S, Chapman, S, McCown, RL, Freebairn, DM, Smith, CJ (2003) An overview of APSIM, a model designed for farming systems simulation. *European Journal of Agronomy* **18**, 267-288.
- Kerr, N, Siddique, K, Delane, R (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.
- Kirby, EJM, Appleyard, M (Ed. NA Centre (1981) 'Cereal Development Guide.' Cereal Unit, National Agriculture Centre, Stoneleigh, England)
- Kirby, EJM, Siddique, KHM, Perry, MW, Kaesehagen, D, Stern, WR (1989) Variation in skikelet initiation and ear development of old and modern Australian wheat varieties. *Field Crops Research* **20**, 113-128.
- Kirkegaard, J, Christen, O, Krupinsky, J, Layzell, D (2008) Break crop benefits in temperate wheat production. *Field Crops Research* **107**, 185-195.
- Kirkegaard, J, Peoples, M, Angus, J, Unkovich, M (2011) Diversity and evolution of rainfed farming systems in southern Australia. In 'In 'Rainfed farming systems.' (Ed. IC Eds P Tow, I Patridge, C Birch.) pp. 715-754. (Springer: Springer: Dordrecht, Netherlands)
- Kirkegaard, JA, Hunt, JR (2010) Increasing productivity by matching farming system management and genotype in water-limited environments. *J Exp Bot* **61**, 4129-43.
- Kirkegaard, JA, Hunt, JR, McBeath, TM, Lilley, JM, Moore, A, Verburg, K, Robertson, M, Oliver, Y, Ward, PR, Milroy, S, Whitbread, AM (2014) Improving water productivity in the Australian Grains industry-a nationally coordinated approach. *Crop & Pasture Science* **65**, 583-601.
- Kirkegaard, JA, Lilley, JM, Hunt, JR, Sprague, SJ, Ytting, NK, Rasmussen, IS, Graham, JM (2015) Effect of defoliation by grazing or shoot removal on the root growth of field-grown wheat (*Triticum aestivum* L.). *Crop and Pasture Science* **66**, 249-259.
- Kirkegaard, JA, Lilley, JM, Morrison, MJ (2016) Drivers of trends in Australian canola productivity and future prospects. *Crop and Pasture Science* **67**, i-ix.
- Kitonyo, OM, Sadras, VO, Zhou, Y, Denton, MD (2017) Evaluation of historic Australian wheat varieties reveals increased grain yield and changes in senescence patterns but limited adaptation to tillage systems. *Field Crops Research* **206**, 65-73.
- Larney, FJ, Lindwall, CW (1995) Rotation and tillage effects on available soil water for winter wheat in a semi-arid environment. *Soil and Tillage Research* **36**, 111-127.
- Lemerle, D, Leys, AR, Hinkley, RB, Fisher, JA (1985) Tolerances of wheat cultivars to pre-emergence herbicides. *Aust. J. Exp. Agric.* **25**, 922-926.
- Lesk, C, Rowhani, P, Ramankutty, N (2016) Influence of extreme weather disasters on global crop production. *Nature* **529**, 84-87.
- Lilley, J, Flohr, B, Whish, J, JA., K (2017) Optimal flowering periods for canola in eastern Australia In '18th Australian Agronomy Conference Ballarat, Australia', 25-28 September 2017.
- Lilley, J, Kirkegaard, J, Robertson, M, Probert, M, Angus, J, Howe, G (2003) Simulating crop and soil processes in crop sequences in southern NSW. In 'Solutions for a Better Environment: 11th Australian Agronomy Conference'. 2-6 February 2003, Geelong (Eds M Unkovich, GJ O'Leary)
- Lilley, JM, Kirkegaard, JA (2007) Seasonal variation in the value of subsoil water to wheat: simulation studies in southern New South Wales. *Australian Journal of Agricultural Research* **58**, 1115-1128.
- Lilley, JM, Kirkegaard, JA (2016) Farming system context drives the value of deep wheat roots in semi-arid environments. *J Exp Bot* **67**, 3665-3681.
- Livingston, JE, Swinbank, JC (1950) Some factors influencing the injury to winter wheat heads by low temperatures. *Agronomy Journal* **42**, 153-57.
- Loss, SP, Siddique, KHM (1994) Morphological and physiological traits associated with wheat yield increases in mediterranean environments. *Advances in Agronomy, Vol 52* **52**, 229-276.

References

- Ludwig, F, Asseng, S (2010) Potential benefits of early vigor and changes in phenology in wheat to adapt to warmer and drier climates. *Agricultural Systems* **103**, 127-136.
- Mac-Indoe, SL (1937) An Australian 'winter' wheat. *Journal Australian Institute Agricultural Science* **3**, 219-224.
- Martin, RH (1981) In Farrer's footsteps: Farrer memorial oration 1980. *Journal of the Australian Institute of Agricultural Science* **47**, 123-131.
- Matthews, P, McCaffery, D, Jenkins, L, 2015. Winter crop variety sowing guide 2015. NSW Department of Primary Industries,
- Meagher, J, Rooney, D (1966) The effect of crop rotations in the Victorian Wimmera on the cereal cyst nematode. *Australian Journal of Experimental Agriculture* **6**, 425-431.
- Miller, P, Gan, Y, McConkey, BG, McDonald, C (2003) 'Pulse Crops for the Northern Great Plains.'
- Miralles, DJ, Richards, RA (2000) Responses of Leaf and Tiller Emergence and Primordium Initiation in Wheat and Barley to Interchanged Photoperiod. *Annals of Botany* **85**, 655-663.
- Monteith, JL (1972) Solar-radiation and productivity in tropical ecosystems. *Journal of Applied Ecology* **9**, 747-766.
- Moore, AD (2009) Opportunities and trade-offs in dual-purpose cereals across the southern Australian mixed-farming zone: a modelling study. *Animal Production Science* **49**, 759-768.
- Murphy, BF, Timbal, B (2008) A review of recent climate variability and climate change in southeastern Australia. *International Journal of Climatology* **28**, 859-879.
- Oliver, Y, Sands, R (2013) 'Yield, soil water and economic benefits of long fallow.' Available at <https://grdc.com.au/resources-and-publications/grdc-update-papers/tab-content/grdc-update-papers/2013/03/research-update> [Accessed January 2018].
- Oliver, YM, Robertson, MJ, Weeks, C (2010) A new look at an old practice: Benefits from soil water accumulation in long fallows under Mediterranean conditions. *Agricultural Water Management* **98**, 291-300.
- Ortiz, R, Sayre, KD, Govaerts, B, Gupta, R, Subbarao, GV, Ban, T, Hodson, D, Dixon, JA, Ortiz-Monasterio, JI, Reynolds, M (2008) Climate change: Can wheat beat the heat? *Agriculture Ecosystems & Environment* **126**, 46-58.
- Passioura, JB (1977) Grain-yield, harvest index, and water-use of wheat. *Journal of the Australian Institute of Agricultural Science* **43**, 117-120.
- Patrignani, A, Godsey, CB, Ochsner, TE, Edwards, JT (2012) Soil Water Dynamics of Conventional and No-Till Wheat in the Southern Great Plains. *Soil Science Society of America Journal* **76**, 1768-1775.
- Paulsen, GM, Heyne, EG (1983) GRAIN PRODUCTION OF WINTER-WHEAT AFTER SPRING FREEZE INJURY. *Agronomy Journal* **75**, 705-707.
- Penrose, L (1993) Yield of early dryland sowing of wheat with winter and spring habit in southern and central New South Wales. *Australian Journal of Experimental Agriculture* **33**, 601-608.
- Penrose, L (1997) Prediction of ear emergence in winter wheats grown at Temora, New South Wales. *Australian Journal of Agricultural Research* **48**, 433-445.
- Penrose, LDJ, Martin, RH (1997) Comparison of winter habit and photoperiod sensitivity in delaying development in early-sown wheat at a site in New South Wales. *Australian Journal of Experimental Agriculture* **37**, 181-190.
- Perry, M, D'Antuono, M (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.
- Piggin, C, Haddad, A, Khalil, Y, Loss, S, Pala, M (2015) 'Effects of tillage and time of sowing on bread wheat, chickpea, barley and lentil grown in rotation in rainfed systems in Syria.'
- Pook, M, Lisson, S, Risbey, J, Ummenhofer, CC, McIntosh, P, Rebeck, M (2009) The autumn break for cropping in southeast Australia: trends, synoptic influences and impacts on wheat yield. *International Journal of Climatology* **29**, 2012-2026.

References

- Porter, JR, Gawith, M (1999) Temperatures and the growth and development of wheat: a review. *European Journal of Agronomy* **10**, 23-36.
- Potgieter, AB, Hammer, GL, Butler, D (2002) Spatial and temporal patterns in Australian wheat yield and their relationship with ENSO. *Australian Journal of Agricultural Research* **53**, 77-89.
- Pugsley, AT (1983) The impact of plant physiology on Australian wheat breeding. *Euphytica* **32**, 743-748.
- Randall, PJ, Moss, HJ (1990) Some effects of temperature regime during grain filling on wheat quality. *Australian Journal of Agricultural Research* **41**, 603-617.
- Raun, WR, Barreto, HJ, Westerman, RL (1993) Use of Stability Analysis for Long-Term Soil Fertility Experiments. *Agronomy Journal* **85**, 159-167.
- Rebetzke, GJ, Ellis, MH, Bonnett, DG, Richards, RA (2007a) Molecular mapping of genes for coleoptile growth in bread wheat (*Triticum aestivum* L.). *Theoretical and Applied Genetics* **114**, 1173-1183.
- Rebetzke, GJ, Richards, RA, Fettell, NA, Long, M, Condon, AG, Forrester, RI, Botwright, TL (2007b) Genotypic increases in coleoptile length improves stand establishment, vigour and grain yield of deep-sown wheat. *Field Crops Research* **100**, 10-23.
- Rebetzke, GJ, Richards, RA, Fischer, VM, Mickelson, BJ (1999) Breeding long coleoptile, reduced height wheats. *Euphytica* **106**, 159-168.
- Reinheimer, JL, Barr, AR, Eglinton, JK (2004) QTL mapping of chromosomal regions conferring reproductive frost tolerance in barley (*Hordeum vulgare* L.). *Theor Appl Genet* **109**, 1267-74.
- Reithmuller, GP (1990) Machinery for improved crop establishment in Western Australia. In 'Agricultural Engineering Conference 1990. pp. pp. 40-45. (Institute of Engineers, Australia:
- Reynolds, M, Foulkes, J, Furbank, R, Griffiths, S, King, J, Murchie, E, Parry, M, Slafer, G (2012) Achieving yield gains in wheat. *Plant Cell and Environment* **35**, 1799-1823.
- Richards, RA (1991) Crop improvement for temperate Australia: Future opportunities. *Field Crops Research* **26**, 141-169.
- Richards, RA (1992a) The effect of dwarfing genes in spring wheat in dry environments .1. Agronomic characteristics. *Australian Journal of Agricultural Research* **43**, 517-527.
- Richards, RA (1992b) The effect of dwarfing genes in spring wheat in dry environments .2. Growth, water-use and water-use efficiency. *Australian Journal of Agricultural Research* **43**, 529-539.
- Richards, RA, Hunt, JR, Kirkegaard, JA, Passioura, JB (2014) Yield improvement and adaptation of wheat to water-limited environments in Australia-a case study. *Crop & Pasture Science* **65**, 676-689.
- Ridge, PE (1986) A review of long fallows for dryland wheat production in southern australia. *Journal of the Australian Institute of Agricultural Science* **52**, 37-44.
- Ritchie, JT (1991) Wheat Phasic Development. In 'Modeling plant and soil systems.' (Eds J Hanks, JT Ritchie.) pp. 31-54. Madison, Wisconsin USA)
- Sadras, VO, Lawson, C (2011) Genetic gain in yield and associated changes in phenotype, trait plasticity and competitive ability of South Australian wheat varieties released between 1958 and 2007. *Crop & Pasture Science* **62**, 533-549.
- Sadras, VO, Lawson, C (2013) Nitrogen and water-use efficiency of Australian wheat varieties released between 1958 and 2007. *European Journal of Agronomy* **46**, 34-41.
- Sadras, VO, Lawson, C, Montoro, A (2012) Photosynthetic traits in Australian wheat varieties released between 1958 and 2007. *Field Crops Research* **134**, 19-29.
- Sadras, VO, Roget, DK (2004) Production and environmental aspects of cropping intensification in a semiarid environment of southeastern Australia. *Agronomy Journal* **96**, 236-246.
- Sanchez-Garcia, M, Royo, C, Aparicio, N, Martin-Sanchez, JA, Alvaro, F (2013) Genetic improvement of bread wheat yield and associated traits in Spain during the 20th century. *J Agric Sci* **151**, 105-118.

References

- Saunders, R (2008) Grain yield of heritage wheat varieties in South Australian Mallee. In 'Proceeding of 14th Australian Agronomy Conference. Adelaide, South Australia', 21-25 September. Available at www.agronomyaustralia.org
- Schillinger, WF (2016) Seven rainfed wheat rotation systems in a drought-prone Mediterranean climate. *Field Crops Research* **191**, 123-130.
- Schillinger, WF, Kennedy, AC, Young, DL (2007) Eight years of annual no-till cropping in Washington's winter wheat-summer fallow region. *Agriculture, Ecosystems & Environment* **120**, 345-358.
- Schillinger, WF, Young, DL (2014) Best Management Practices for Summer Fallow in the World's Driest Rainfed Wheat Region. *Soil Science Society of America Journal* **78**, 1707-1715.
- Schultz, JE (1971) 'Soil water changes under fallow-crop treatments in relation to soil type, rainfall and yield of wheat.'
- Scott, B, Martin, P, Riethmuller, G (2013) 'Row spacing of winter crops in broad scale agriculture in southern Australia.' (NSW DPI: Orange)
- Seymour, M, Kirkegaard, JA, Peoples, MB, White, PF, French, RJ (2012) Break-crop benefits to wheat in Western Australia - insights from over three decades of research. *Crop & Pasture Science* **63**, 1-16.
- Shearman, VJ, Sylvester-Bradley, R, Scott, RK, Foulkes, MJ (2005) Physiological processes associated with wheat yield progress in the UK. *Crop Science* **45**, 175-185.
- Shpiler, L, Blum, A (1990) Heat tolerance for yield and its components in different wheat cultivars *Euphytica* **51**, 257-263.
- Siddique, K, Belford, R, Perry, M, 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, KHM, Belford, RK, 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, KHM, Kirby, EJM, Perry, MW (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, KHM, Tennant, D, Perry, MW, Belford, RK (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.
- Sims, H, Meagher, J, Millikan, C (1961) Deadheads in wheat-field studies in Victoria. *Australian Journal of Experimental Agriculture* **1**, 99-108.
- Single, WV (1964) Studies on frost injury to wheat .2. Ice formation within plant. *Australian Journal of Agricultural Research* **15**, 869-&.
- Slafer, GA, Andrade, FH (1989) Genetic improvement in bread wheat (*Triticum aestivum*) yield in Argentina. *Field Crops Research* **21**, 289-296.
- Slafer, GA, Andrade, FH (1991) Changes in physiological attributes of the dry-matter economy of bread wheat (*triticum-aestivum*) through genetic-improvement of grain-yield potential at different regions of the world - a review. *Euphytica* **58**, 37-49.
- Slafer, GA, Andrade, FH (1993) Physiological attributes related to the generation of grain-yield in bread wheat cultivars released at different eras. *Field Crops Research* **31**, 351-367.
- Slafer, GA, Elia, M, Savin, R, García, GA, Terrile, II, Ferrante, A, Miralles, DJ, González, FG (2015a) Fruiting efficiency: an alternative trait to further rise wheat yield. *Food and Energy Security* **4**, 92-109.
- Slafer, GA, Kantolic, AG, Appendino, ML, Tranquilli, G, Miralles, DJ, Savin, R (2015b) Genetic and environmental effects on crop development determining adaption and yield. In 'Crop Physiology: Applications for Genetic Improvement and Agronomy.' (Eds V Sadras, D Calderini.) pp. 285-319. (Elsevier Inc.:
- Slafer, GA, Rawson, HM (1994) Sensitivity of wheat phasic development to major environmental-factors - a reexamination of some assumptions made by physiologists and modelers. *Australian Journal of Plant Physiology* **21**, 393-426.
- Slafer, GA, Rawson, HM (1995a) Photoperiod X temperature interactions in contrasting wheat genotypes: Time to heading and final leaf number. *Field Crops Research* **44**, 73-83.

References

- Slafer, GA, Rawson, HM (1995b) Rates and cardinal temperatures for processes of development in wheat: Effects of temperature and thermal amplitude. *Australian Journal of Plant Physiology* **22**, 913-926.
- Slafer, GA, Rawson, HM (1996) Responses to photoperiod change with phenophase and temperature during wheat development. *Field Crops Research* **46**, 1-13.
- Stapper, M, Harris, HC (1989) Assessing the productivity of wheat genotypes in a Mediterranean climate, using a crop-simulation model. *Field Crops Research* **20**, 129-152.
- Steinfart, U, Fukai, S, Trevaskis, B, Glassop, D, Chan, A, Dreccer, MF (2017) Vernalisation and photoperiod sensitivity in wheat: The response of floret fertility and grain number is affected by vernalisation status. *Field Crops Research* **203**, 243-255.
- Stelmakh, AF (1998) Genetic systems regulating flowering response in wheat. *Euphytica* **100**, 359-369.
- Stephens, DJ, Lyons, TJ (1998) Variability and trends in sowing dates across the Australian wheatbelt. *Australian Journal of Agricultural Research* **49**, 1111-1118.
- Stone, PJ, Nicolas, ME (1995) Effect of timing of heat stress during grain filling on two wheat varieties differing in heat tolerance. 1. Grain growth. *Australian Journal of Plant Physiology* **22**, 927-934.
- Sukumaran, S, Lopes, MS, Dreisigacker, S, Dixon, LE, Zikhali, M, Griffiths, S, Zheng, BY, Chapman, S, Reynolds, MP (2016) Identification of Earliness Per Se Flowering Time Locus in Spring Wheat through a Genome-Wide Association Study. *Crop Science* **56**, 2962-2972.
- Tashiro, T, Wardlaw, IF (1990) The response to high-temperature shock and humidity changes prior to and during the early stages of grain development in wheat. *Australian Journal of Plant Physiology* **17**, 551-561.
- Tilman, D, Cassman, KG, Matson, PA, Naylor, R, Polasky, S (2002) Agricultural sustainability and intensive production practices. *Nature* **418**, 671-677.
- Trevaskis, B (2010) The central role of the VERNALIZATION1 gene in the vernalization response of cereals. *Functional Plant Biology* **37**, 479-487.
- Tuohey, C, Robson, A, Rooney, D (1972) Moisture and nitrate conservation and responses to following after medic ley in the Wimmera. *Australian Journal of Experimental Agriculture* **12**, 414-419.
- Turner, NC (2004) Agronomic options for improving rainfall-use efficiency of crops in dryland farming systems. *J Exp Bot* **55**, 2413-25.
- Umina, P, Severi, J, McDonald, G (2017) What we know about Russian wheat aphid including lessons learnt from 2016. In. Available at <https://grdc.com.au/resources-and-publications/grdc-update-papers/tab-content/grdc-update-papers/2017/02/what-we-know-about-russian-wheat-aphid-including-lessons-learnt-from-2016>
- van Ittersum, MK, Cassman, KG, Grassini, P, Wolf, J, Tittonell, P, Hochman, Z (2013) Yield gap analysis with local to global relevance—A review. *Field Crops Research* **143**, 4-17.
- van Rees, H, McClelland, T, Hochman, Z, Carberry, P, Hunt, J, Huth, N, Holzworth, D (2014) Leading farmers in South East Australia have closed the exploitable wheat yield gap: Prospects for further improvement. *Field Crops Research* **164**, 1-11.
- Verburg, K, Bond, WJ, Hunt, JR (2012) Fallow management in dryland agriculture: Explaining soil water accumulation using a pulse paradigm. *Field Crops Research* **130**, 68-79.
- Verdon-Kidd, DC, Kiem, AS, Moran, R (2014) Links between the Big Dry in Australia and hemispheric multi-decadal climate variability - implications for water resource management. *Hydrology and Earth System Sciences* **18**, 2235-2256.
- Voss-Fels, KP, Robinson, H, Mudge, SR, Richard, C, Newman, S, Wittkop, B, Stahl, A, Friedt, W, Frisch, M, Gabur, I, Miller-Cooper, A, Campbell, BC, Kelly, A, Fox, G, Christopher, J, Christopher, M, Chenu, K, Franckowiak, J, Mace, ES, Borrell, AK, Eagles, H, Jordan, DR, Botella, JR, Hammer, G, Godwin, ID, Trevaskis, B, Snowdon, RJ, Hickey, LT (2018) VERNALIZATION1 Modulates Root System Architecture in Wheat and Barley. *Mol Plant* **11**, 226-229.
- VSN International (2013) 'GenStat for Windows 18th Edition.' Available at GenStat.co.uk

References

- Waddington, S, Cartwright, P, Wall, P (1982) A Quantitative Scale of Spike Initial and Pistil Development in Barley and Wheat. *Annals of Botany* **51**, 119-130
- Watanabe, N, Evans, JR, Chow, WS (1994) Changes in the photosynthetic properties of Australian wheat cultivars over the last century. *Australian Journal of Plant Physiology* **21**, 169-183.
- Watson, J, Zheng, BY, Chapman, S, Chenu, K (2017) Projected impact of future climate on water-stress patterns across the Australian wheatbelt. *J Exp Bot* **68**, 5907-5921.
- Wells, L, 2017. Planter innovation helps chase deeper moisture. GroundCover™. GRDC, Canberra, ACT.
- Whitechurch, EM, Slafer, GA (2002) Contrasting Ppd Alleles in Wheat: Effects on Sensitivity to Photoperiod in Different Phases. *Field Crops Research* **73**, 95-105.
- Worland, AJ (1996) The influence of flowering time genes on environmental adaptability in European wheats. *Euphytica* **89**, 49-57.
- Yang, YM, Liu, DL, Anwar, MR, Zuo, HP, Yang, YH (2014) Impact of future climate change on wheat production in relation to plant-available water capacity in a semiarid environment. *Theoretical and Applied Climatology* **115**, 391-410.
- Yunusa, IAM, Siddique, KHM, Belford, RK, Karimi, MM (1993) 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, JC, Chang, TT, Konzak, CF (1974) A decimal code for the growth stages of cereals. *Weed Research* **14**, 415-421.
- Zelege, KT, Nendel, C (2016) Analysis of options for increasing wheat (*Triticum aestivum* L.) yield in south-eastern Australia: The role of irrigation, cultivar choice and time of sowing. *Agricultural Water Management* **166**, 139-148.
- Zheng, B, Chenu, K, Doherty, A, Chapman, S (2014) 'The APSIM-Wheat Module (7.5 R3008).' Available at <http://www.apsim.info/Portals/0/Documentation/Crops/WheatDocumentation.pdf> [Accessed March 2017].
- Zheng, BY, Biddulph, B, Li, DR, Kuchel, H, Chapman, S (2013) Quantification of the effects of VRN1 and Ppd-D1 to predict spring wheat (*Triticum aestivum*) heading time across diverse environments. *J Exp Bot* **64**, 3747-3761.
- Zheng, BY, Chapman, SC, Christopher, JT, Frederiks, TM, Chenu, K (2015) Frost trends and their estimated impact on yield in the Australian wheatbelt. *J Exp Bot* **66**, 3611-3623.
- Zheng, BY, Chenu, K, Dreccer, MF, Chapman, SC (2012) Breeding for the future: what are the potential impacts of future frost and heat events on sowing and flowering time requirements for Australian bread wheat (*Triticum aestivum*) varieties? *Glob Chang Biol* **18**, 2899-2914.

Appendix

1. Experiment layout

1.1 Example of block layout for Temora experiments in 2015 and 2016 growing seasons

		Block 1																																					
		Rows																																					
		1	2	3	4																																		
		1	2	3	4	B1	v1	v2	v3	v4	v5	B2	B3	v6	v7	v8	v9	v10	B4	B5	v11	v12	v13	v14	v15	B6	B7	v16	v17	v18	v19	v20	B8						
Sowing date																																							
	KEY																																						
		27-Apr																																					
		27-Apr																																					
		27-Apr																																					
		27-Apr																																					
		27-Apr																																					
		15-May																																					
		15-May																																					
		15-May																																					
		15-May																																					
		15-May																																					
		7-May																																					
		7-May																																					
		7-May																																					
		7-May																																					
		7-May																																					
		17-Apr																																					
		17-Apr																																					
		17-Apr																																					
		17-Apr																																					
		17-Apr																																					

2. Dissemination of thesis results to the industry

- 09/15 Flohr, B.M., Hunt, J.R., Kirkegaard J.A., Evans J.R., Identifying the optimal flowering period for wheat in south eastern Australia: A simulation study. *Proceedings of the 17th Australian Agronomy Conference*, 20-24 September 2015, Hobart, Australia. Australian Society of Agronomy.
- 02/16 Flohr B.M., Sustainable Agriculture Forum, Paruna, South Australian Mallee.
- 02/16 Flohr B.M., Mallee Sustainable Farming Updates in Renmark, South Australia
- 02/16 Flohr B.M., Mallee Sustainable Farming Updates in Managatang, Victoria
- 03/16 Flohr B.M., National GRDC Frost Initiative meeting, Canberra
- 02/ 17 Flohr B.M., 2017 GRDC Updates, Wagga Wagga, New South Wales
- 03/17 Flohr BM, Hunt JR, Kirkegaard JA, Evans JR, Stabilising wheat flowering time and yield under drought in Australia, *InterDrought V Conference*, 21-25 February 2017, Hyderabad, India.
- 08/17 Baxter, N. 2017. Study shows a need for new fast winter wheats. *Ground Cover Issue 130*, September-October 2017, pg 34-35
- 09/17 Early sown winter wheats, Hart Field Day 2017
- 09/17 Flohr, B.M., Hunt, J.R., Kirkegaard J.A., Evans J.R., 2017, Winter is coming: the potential for a fast winter wheat to stabilise flowering and maximise yield in southern and Western Australia. *Proceedings of the 18th Australian Agronomy Conference 24 – 28 September 2017*, Ballarat, Australia