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

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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 times 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, 2016). 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., 2017). 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

Abbreviations: FW, Fast-winter; VSS, very-slow spring; MS, mid-fast spring; FS, fast-spring; MW, mid-winter; OFP, optimal flowering period; TOS, time of sowing; VD, vernal days

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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., 2017). Flohr et al. (2017) 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 (response to low temperatures, Trevaskis, 2010), photoperiod (response to day length, Slafer and Rawson, 1995) and earliness *per se* (temperature accumulation, 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 (Fig. 1, Kirby and Appleyard, 1981). Penrose (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.

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 (Vic, 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., 2009). 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

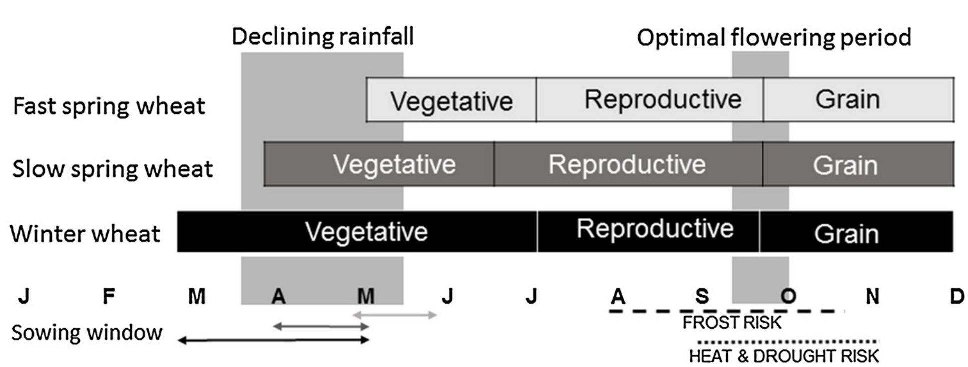

Fig. 1. Duration and timing of the different development phases of winter wheat, fast and slow developing spring wheat in relation to the months of the year, typical optimal sowing windows and flowering period for southern Australia (Flohr et al., 2017) and the autumn period during which rainfall has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

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.

Flowering date (Z65, 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 m^2 (two 0.83×1.2 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 (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). 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 (Z89, 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. $TT = \Sigma\ ((T_{min} + T_{max})/2) - T_{base}$ 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 $T_{base} = 0$ °C, $T_{optimal} = 23$ °C and $T_{max} = 37$ °C as per Porter and Gawith (1999). Using the same method, vernal days (VD) were calculated using $T_{base} = -1.3$ °C, $T_{optimal} = 4.9$ °C and $T_{max} = 15.7$ °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. (2017) the OFP for Berriwillock (not included in Flohr et al., 2017) was determined and found to be 15–25 September. All other OFP referred to are from Flohr et al. (2017). 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).

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 also 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).

3.2. Seasonal conditions

The monthly TT accumulation (°C) in the year of experiment for

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	Plot size (m), row spacing (cm)	Targeted plant density (plants /m2)	Mean growing season rainfall (mm)	Growing season rainfall in year of experiment (mm)	TOS	Cultivars grown	Development type
Temora -34.397, 147.539	2015	12 x 1.8, 31	120	262	276	17 April 27 April 07 May 15 May	Condo Gregory Longsword Eaglehawk Wedgetail Sunstate-FS Sunstate-VSS Sunstate- FW Sunstate-MW	FS MS FW VSS FW FS VSS FW MW
Temora -34.397, 147.539	2016	10 x 1.8, 31	140	262	591	15 April* 27 April* 06 May 15 May	Condo Gregory Longsword Eaglehawk Wedgetail Sunstate-FS Sunstate-VSS Sunstate- FW Sunstate-MW	FS MS FW VSS FW FS VSS FW MW
Berriwillock -35.640, 142.996	2015	12 x 1.8, 30	150	178	139	09 April* 08 May	Scout Kiora Longsword Bolac Wedgetail	FS MS FW VSS MW
Minnipa -32.834, 135.151	2015	10 x 1.4, 23	120	205	249	13 April 29 April 13 May	Mace Cutlass Longsword Eaglehawk Wedgetail Sunstate-FS Sunstate-VSS Sunstate- FW Sunstate-MW	FS MS FW VSS MW FS VSS FW MW
Cunderdin -31.345, 117.144	2015	10 x 1.5, 25	150	228	188	14 April 28 April 22 May	Mace Magenta Longsword Eaglehawk Wedgetail Sunstate-FS Sunstate-VSS Sunstate- FW Sunstate-MW	FS MS FW VSS MW FS VSS FW MW

*treatment irrigated a small amount to ensure germination.

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

each site is summarised in Fig. 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 °C, when many treatments were flowering. 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. In Minnipa in 2015, temperature was close to long-term average and rainfall was slightly above average. In Cunderdin in 2015 there were two frost events, −0.5 °C and −0.1 °C on October 2 and 4 and below average rainfall.

3.3. Field experiments comparing cultivar response to time of sowing

3.3.1. 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., 2017). Grain yields were largely related to the effect of time of sowing on date of flowering (Fig. 5 and 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 >

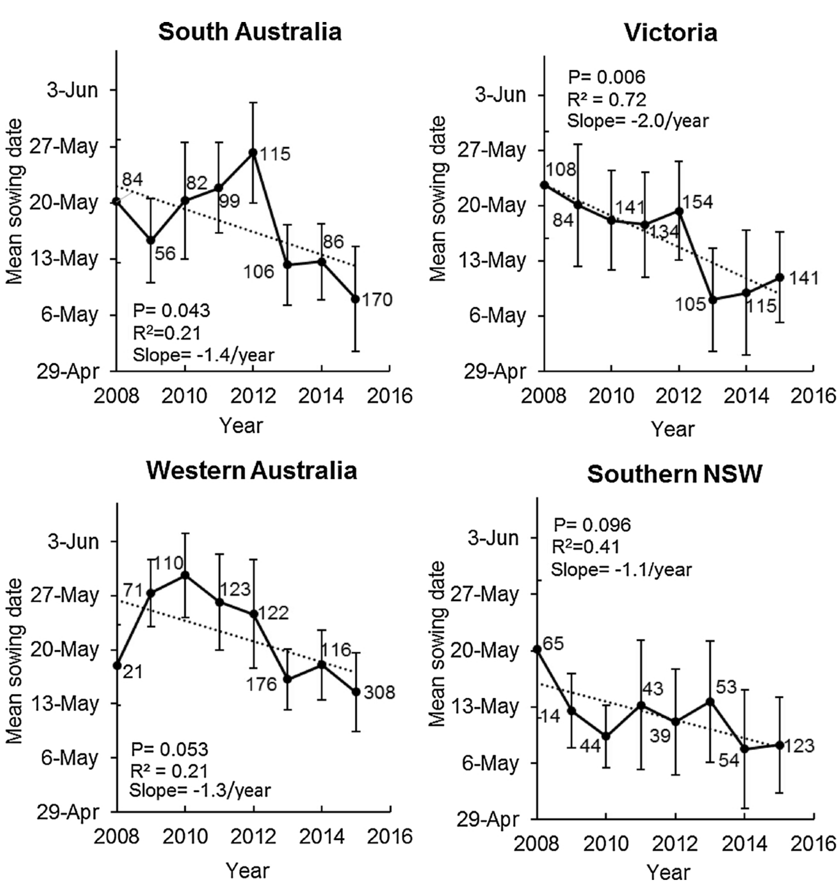

Fig. 2. Mean sowing date for different regions from 2008 to 2015 from the Yield Prophet® data base, and P-value, R^2 and the slope of the linear function fitted to the data. The number next to marker is the number of fields included in the mean sowing date for each year. Error bars are the standard deviation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

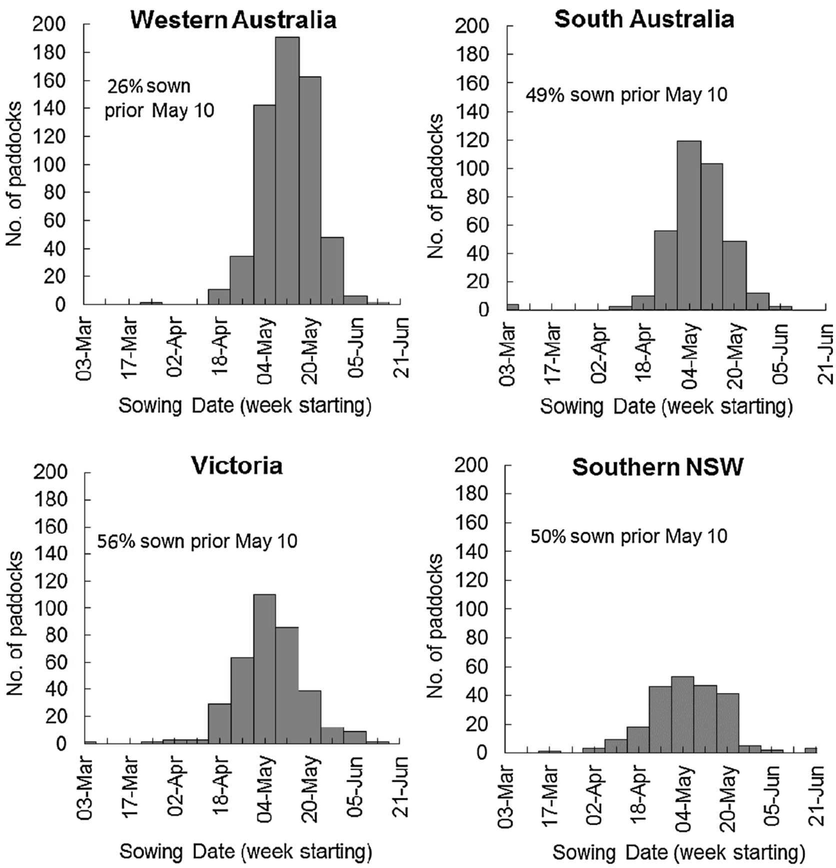

Fig. 3. Number of fields sown at weekly time intervals for wheat growing regions in Western Australia (total fields 600, median sowing date 15 May), South Australia (total fields 359, median sowing date 10 May), Victoria (total fields 358, median sowing date 9 May), southern New South Wales where (total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

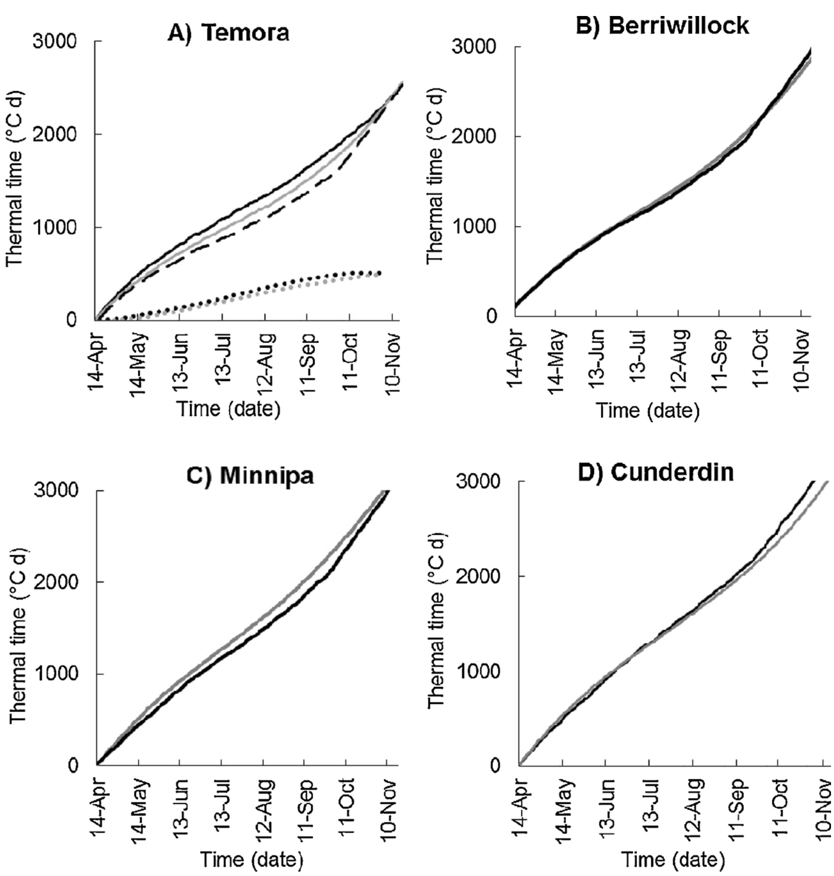

Fig. 4. Cumulative thermal time (°C d) for A) Temora, NSW black line 2016, broken black line 2015, grey line average of years 2005–2016, and adjusted vernal days (●●●● 2015 and ●●● 2016) B) Berriwillock in 2015 vs. mean 1997–2016 C) Minnipa in 2015 vs mean 1998–2016 and D) Cunderdin in 2015 vs mean 1990–2016.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

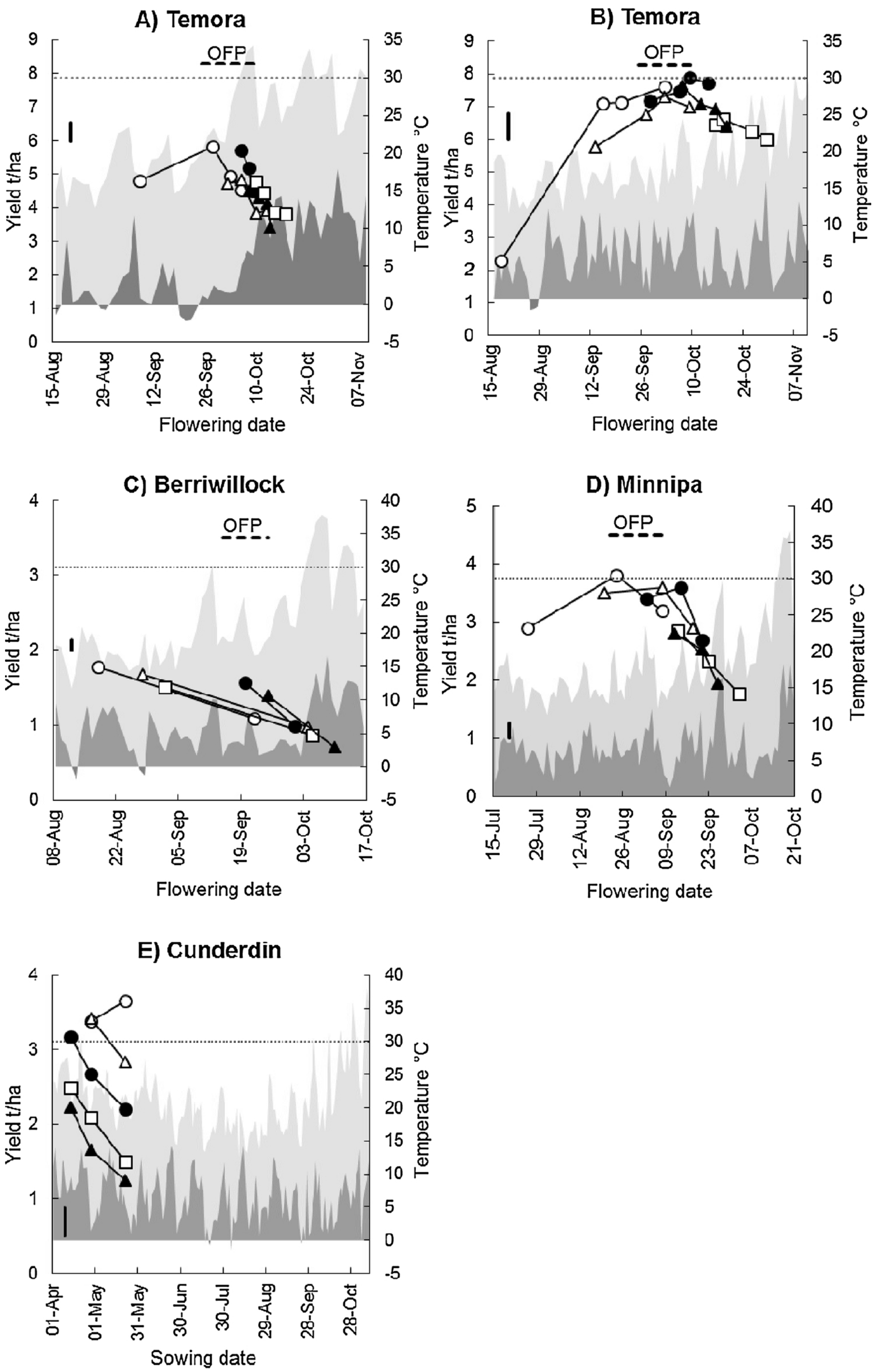

Fig. 5. Mean grain yield (t/ha) of a fast developing spring wheat (○), mid-fast developing spring wheat (Δ), very-slow spring wheat (□), fast developing winter wheat (Longsword, ●), and mid-winter wheat (▲) plotted against flowering date and minimum (°C, dark grey shading) and maximum temperatures (°C, 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. 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.

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).

3.3.2. 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–E). The average yield advantage of FW sown early vs. FS sown late (current practice) in these environments was 7%.

In 2015 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),

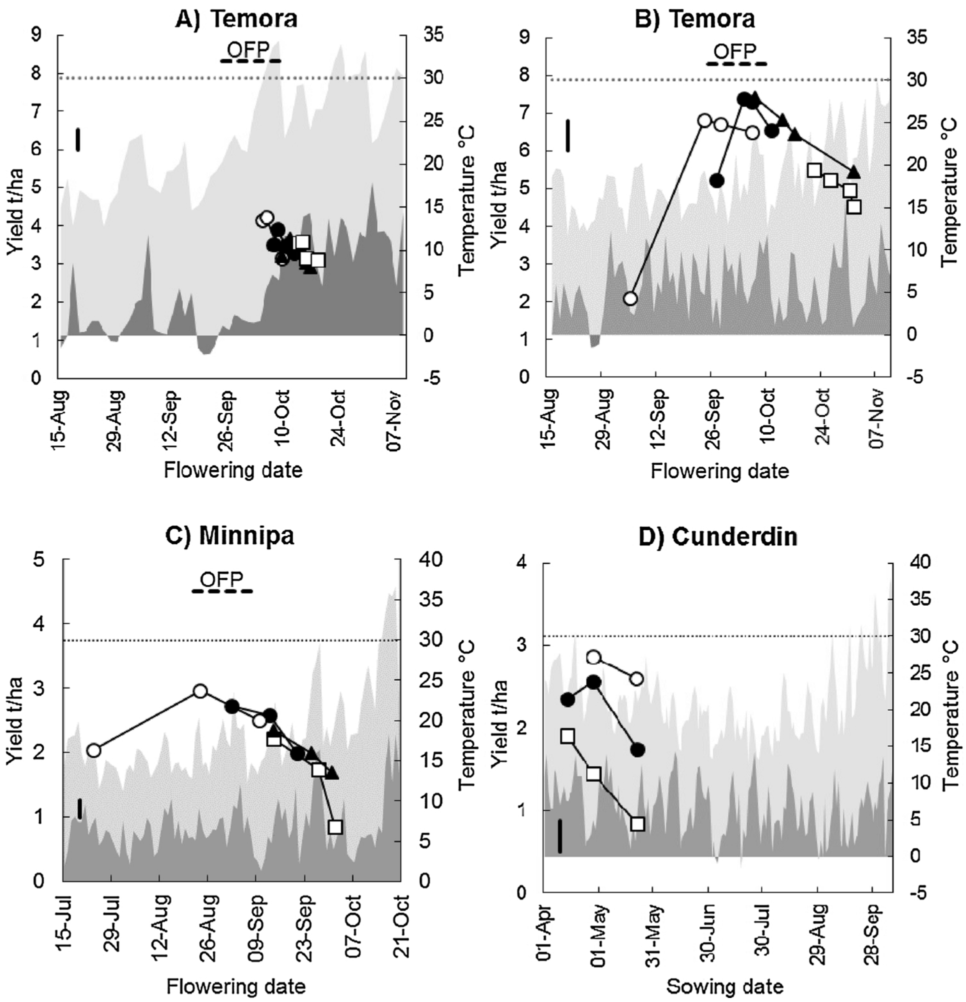

Fig. 6. Mean grain yield (t/ha) of near-isogenic lines with development patterns representing a fast developing winter wheat (●), fast developing spring wheat (○), very-slow spring wheat (□) and mid-winter wheat (▲) plotted against flowering date and minimum (°C, dark grey shading) and maximum temperatures (°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.

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.

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 to 29 April TOS, and

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.**

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.

3.4. 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.

3.5. Development

Environmental influences on key developmental stages affected cultivars grown in Temora. Fig. 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 Fig. 7 and 8 by calculating a flowering date stability index (Table 3). The winter cultivars remained vegetative from early sowings longer than spring cultivars (Fig. 7 and 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 required a mean of 249 VD to reach DR (SD ± 41 VD), Longsword 229 VD (SD ± 37 VD), EGA Eaglehawk 226 VD (SD ± 45 VD), Gregory 182 VD (SD ± 63 VD), Condo 136 VD (SD ± 48 VD), Sunstate-MW 249 (SD ± 42), Sunstate-FW 221 (SD ± 55), Sunstate-VSS 216 (SD ± 50) and Sunstate-FS 156 (SD ± 67).

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 for WA). 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., 2017). 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., 2017).

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 agreeance with Fischer and Kohn (1966), grain yield in these trials was 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 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

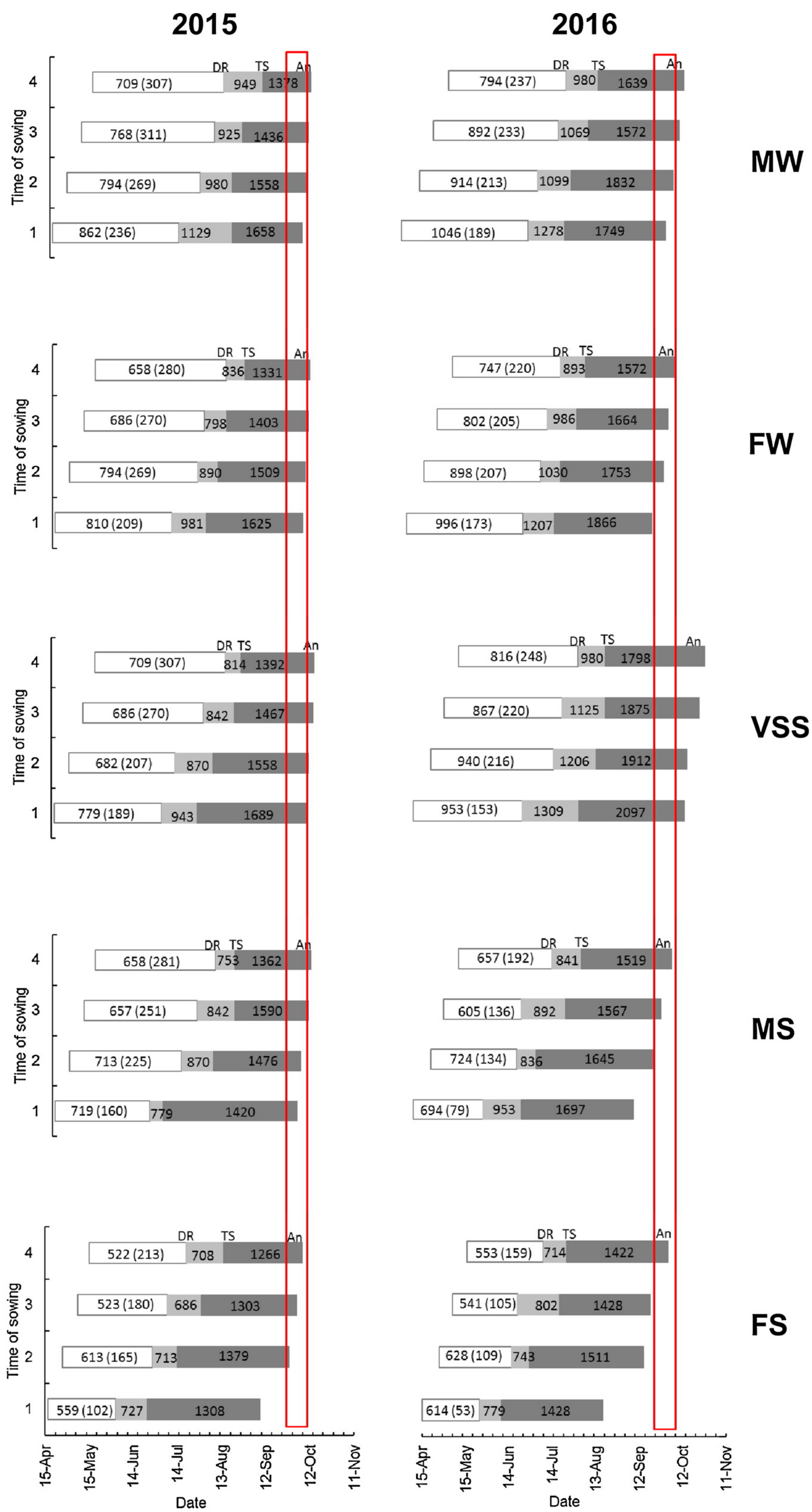

Fig. 7. Developmental patterns of mid-winter (MW), fast-winter (FW, Longsword), very-slow spring (VSS), mid-spring (MS) and fast-spring (FS) cultivars sown in Temora, NSW in 2015 and 2016. In 2015 time of sowing (TOS) were 17 April, 27 April, 7 May and 15 May and in 2016 TOS were 17 April, 27 April, 6 May and 15 May. White area is calendar days from sowing to double ridge (DR), light grey area 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 °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).

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 index (0.09 vs. 0.52). Condo had low stability in both 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

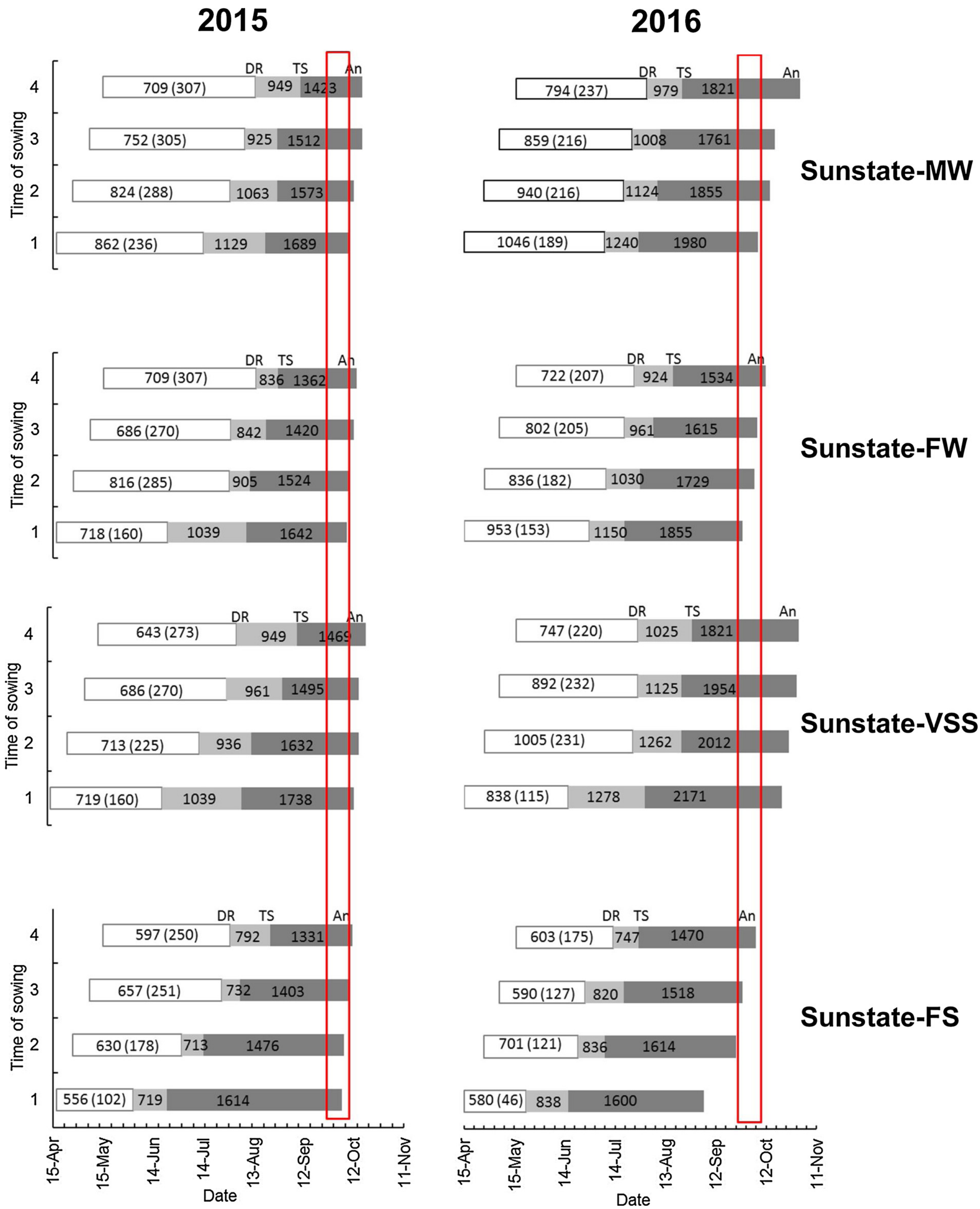

Fig. 8. Developmental patterns of Sunstate-MW, Sunstate-FW, Sunstate-VSS and Sunstate-FS near isogenic lines sown in Temora, NSW in 2015 and 2016. In 2015 time of sowing (TOS) were 17 April, 27 April, 7 May and 15 May and in 2016 TOS were 17 April, 27 April, 6 May and 15 May, and. White area is calendar days from sowing to double ridge (DR), light grey area 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).

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; Slafer and Rawson, 1996; Whitechurch and Slafer, 2002; González et al., 2005). Steinfort et al. (2017) conclude that the utilisation of sensitivity to 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. 5–8, 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 NSW, only a few MW varieties have been released in the last 15 years (Whistler, 1998; Wylah, 1999; EGA Wedgetail, 2002; Kittyhawk, 2016; 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 Figs. 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., 2017). This helps resolve the logistical issue of increased farm size described by Fletcher et al. (2016) and securing a greater area of crop flowering within the OFP to maximise yield.

4.5. Implications for agronomy and genotype by management interactions

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 adaption 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.

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, 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.

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 × M strategies to minimise water and temperature stress at flowering and maximise yield. A novel 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.

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