Field Crops Research 246 (2020) 107697

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Using a novel PLS approach for envirotyping of barley phenology and adaptation

K. Porker[a,b,*], S. Coventry[a], NA Fettell[c], D. Cozzolino[d], J. Eglinton[e]

[a] School of Agriculture, Food and Wine, Faculty of Sciences, The University of Adelaide, Waite Campus, Glen Osmond SA, Adelaide 5064, Australia
[b] South Australian Research and Development Institute, Waite Campus, Australia
[c] School of Science, RMIT University, Melbourne, VIC 3000, Australia
[d] School of Science, RMIT University, Melbourne, VIC 3000, Australia
[e] Sugar Research Australia, Bruce Highway, Gordonvale, Qld 4865, Australia

ARTICLE INFO

Keywords:
Phenology
Crop model
Adaptation
Barley
Anthesis
Photoperiod
Crop development
Envirotyping

ABSTRACT

Improving grain yield and adaptation is achieved by synchronising crop phenology with the environment. Phenology research is complex and encounters analytical challenges in characterising genotype x environment (GxE) interactions. This paper presents a simple approach that helps to explain the environmental drivers of phenology. Photoperiod and temperature are major environmental cues for expression of crop developmental genes, and sensitivity to photoperiod is thought to be the major cause of maturity differences among Australian spring barley varieties. However, temperature and photoperiod show similar seasonal trends and strong auto-correlation makes it difficult to distinguish their relative importance in crop development. Partial Least Squares regression (PLS) was developed to handle large data sets with many correlated explanatory variables and only one dependent variable. Across 35 environments encompassing a wide range of temperature and photoperiod regimes in southern Australia, a PLS model described more than 90 % of the phenotypic variation in time to anthesis of three adapted barley cultivars. The PLS outputs defined the critical periods when photoperiod and temperature were most influential, and revealed that temperature effects are of equal or greater importance than photoperiod in determining anthesis date, which is a new finding for genotypes adapted to Australian environments. Insight into the previously elusive differential responses to changes in daily average, maximum, and minimum temperatures will assist in developing flowering models for growers that are more accurate, and assist breeders in the genetic dissection of phenology for target environments.

1. Introduction

Understanding GxE interaction is a critical aspect of plant breeding. Improving grain yield and adaptation is achieved by synchronising crop phenology phases with resource availability and favourable climate conditions to maximize crop growth (Richards, 1991). Yield has been significantly improved through direct selection for grain yield in low rainfall Mediterranean environments, such as those located in southern Australia, Consequently this has led to indirect selection for phenology allele combinations that facilitate anthesis during the most desirable period to minimise frost, heat, and water stress. Despite yield improvement, understanding of the interaction of major phenology genes with different environmental controls of phenology is poor. The characterization of environmental factors affecting plant growth and development have recently been defined using the concept of "envirotyping" (Cooper et al., 2014; Xu, 2016). Envirotyping complements genotyping and phenotyping allowing better characterization of genotype (and QTL) × environment interaction. Such site-specific characterization and prediction of plant performance will likely be coupled with phenomics, crop growth modelling, and genome-wide prediction (Cooper et al., 2014). Improved characterisation of GxE for barley phenology will facilitate selection of favourable phenology gene combinations in concert with sowing dates that ensure anthesis occurs during the optimal period. It is thought that the major control of spring barley phenology in Australia is photoperiod sensitivity (Boyd et al., 2003), while importance of the sensitivity to vernalising and non-vernalising temperatures is less understood (Ren et al., 2010). There is limited information describing the photoperiodic and temperature environment types and phenology responses in barley cultivars adapted to Australian conditions. Robust characterisation of the genetic responses to thermal and photoperiod regimes are needed to determine annual and inter-annual variations in crop phenology across environments.

* Corresponding author.
E-mail address: kenton.porker@sa.gov.au (K. Porker).

https://doi.org/10.1016/j.fcr.2019.107697
Received 10 November 2019; Accepted 27 November 2019
Available online 14 December 2019

The main phenology phases of barley are the vegetative, early reproductive, late reproductive and grain filling phases (Appleyard et al., 1982). Genes that regulate the plant's response to environmental cues control the timing and duration of these phases. The major phenology genes include the photoperiod (*Ppd*), vernalisation (*Vrn*), and earliness *per se* (*Eps or Eam*) genes (Cockram et al., 2007). Allelic variation exists in these genes, enabling commercial production in winter and summer, in regions outside of barley's Mediterranean centre of origin, which differ in temperature, altitude and latitude to those found in southern Australia (Cockram et al., 2007). Both photoperiod and vernalisation affect the rate of crop development. In barley, increased photoperiod shortens the time to heading up to an optimum photoperiod, beyond which the time to heading is constant provided vernalisation requirements have been satisfied. Temperature may affect time from sowing to anthesis in two main ways. Firstly, there may be a vernalisation requirement for exposure to low temperature before floral initiation proceeds. The temperature ranges for vernalisation reported in the literature are from -5 to 16 °C, with a maximum effect generally between 0 and 8 °C (Roberts et al., 1988), and from 3 to 12 °C with an optimum of 7 °C (Trione and Metzger, 1970). Secondly, temperature *per se* affects all phases constitutively from sowing to maturity and can be characterised in thermal time units with a base temp of 0 °C (Kirby and Appleyard, 1987b; Holzworth et al., 2014). Over a wide range of temperatures the rate of progress towards anthesis increases with an increase in temperature to an optimum temperature at which anthesis is most rapid (Bonhomme, 2000). At supra-optimal temperatures, flowering is progressively delayed as temperatures get warmer (Roberts et al., 1988). Researchers have always encountered difficulty when trying to identify the temperature measurements and the types of interaction with daylength that best predict the timing of developmental events (Atkinson and Porter, 1996).

Under field conditions, sowing date and location determine the temperatures and photoperiods under which a crop develops. In Mediterranean environments such as southern Australia, spring barley is typically sown in late autumn or early winter, grown through spring, and harvested in early summer. Temperatures are relatively warm along with photoperiods of up to 12.5 h around early sowing in April. Temperatures decrease thereafter until late winter, after which they increase during spring towards anthesis. Photoperiod follows a similar pattern decreasing after sowing until the shortest photoperiod in June (around 9.5 h) then increasing through the period of stem elongation back to 12 − 13 hours by anthesis in September to October. Delayed sowing in southern Australian environments is typically associated with increased photoperiod and temperature during the stem elongation phase, reducing the duration of the emergence to heading phase (Hay and Elliss, 1998).

Controlled experiments have attempted to dissect phenology in several Australian barley genotypes using above optimum photoperiod (up to 18 h) and constant temperature regimes (Kernich et al., 1996; Miralles and Richards, 2000), while most other factors are held constant or their effects ignored (Karsai et al., 2008). While this may be a valid approach, it could be argued that controlled experiments may not be representative of target growing environments in southern Australia and could infer relatively simple relationships between photoperiod and temperature. Karsai et al. (2008) demonstrated a delay in anthesis with minor temperature fluctuations in the order of 2 °C, compared to a constant temperature regime within a day. Spring genotypes were the least affected, and facultative genotypes the most affected. These results highlight the need for rigorous characterization of all environmental cues in flowering time experiments.

1.1. Phenology analysis models

Models are often used to support theoretical research, yield predictions and decision making in agriculture. Photoperiodic and temperature regression models have been used to describe phasic development in field crops for many years (Angus et al., 1981) particularly in wheat (Perry et al., 1987; Loss et al., 1990), and in fact empirical thermal models of flowering time date back to before the 20th century (Wang, 1960). Using a simple linear regression model based on photoperiod and temperature, (Alzueta et al., 2014) predicted barley heading time with an accuracy of +/- four days in cultivars not requiring vernalisation. Other crop process based simulation models such as APSIM (Manschadi et al., 2006; Holzworth et al., 2014), CERES-Barley (Otter-Nacke et al., 1991) and QBAR (Goyne et al., 1996) are powerful tools for predicting phenology. These models use mathematical algorithms that describe variations in the rate of development over time in response to temperature and photoperiod.

In quantitative genetics, the mean performance of genotypes has traditionally been used to measure the value of that environment. In the simplest form, the Finlay-Wilkinson Regression approach has been a popular method to describe GxE interactions (Finlay and Wilkinson, 1963). This is limited since only the phenotype is used to describe the environment, which masks some GxE effects. Uncertainty about the environmental means is ignored, and there is no clear way of incorporating other environmental indicators, pedigree, or molecular marker information when estimating the intercepts and slopes of the regression lines.

Analysing genotype–phenotype relationships requires more robust crop models than those for other agricultural applications. This is possible using a combination of ecophysiological or phenological modelling and QTL analysis (Yin et al., 2005a, b; Chapman, 2008; Hammer et al., 2010) and more than 90 % of the variation in flowering time was accounted for by Yin et al. (2005b). More recently, genome-wide models have helped overcome some of the limitations of classical QTL based approaches, which may ignore the effects of QTL with small effects (Uptmoor et al., 2016). Precise estimation of allelic marker effects in response to environmental regulators is required; however, even in current state-of-the-art models, accounting for complex environmental interactions remains a challenge, and at present, best results are obtained with relatively simple models comprising few parameters (Uptmoor et al., 2016). The key to improving crop adaptation will be to understand the cumulative effect of the environmental factors from sowing that trigger the complex biological processors that control flowering time. Traditional analysis of phenology often does not consider this dynamic nature of GxE making it difficult to derive any significant biological understanding. Robust envirotyping or improved characterisation of phenological environments according to different variables would be more biologically meaningful (Xu, 2016).

1.2. Partial least squares regression

An alternative approach for environmental characterisation is Partial Least Squares regression (PLS), a statistical analysis tool developed to handle large datasets and widely used in chemometrics and hyperspectral remote sensing with many auto-correlated variables. Similar challenges exist when analysing phenology data because the environmental input variables influencing phenology are often highly auto-correlated and not distributed evenly. For example, the photoperiods of two consecutive days are more closely correlated than the photoperiods of any other day in the year and the seasonal changes in photoperiod and temperature are highly correlated. Other problems are likely to arise when analysing phenology because the number of independent data variables exceeds the number of dependent variables (i.e. flowering time), particularly if high-resolution weather records are used. Multiple linear regression could be used to handle complex datasets, however, with a large number of factors this can lead to overfitted models that fail to predict new data well (Wold et al., 2001). In such cases, there may be only a few underlying or latent factors that account for most of the variation in the response.

Wold (1966) introduced the basic statistics of PLS that first construct latent quantitative factor variables forming an X matrix (similar

to principal components) from the independent data (e.g. daily temperatures and photoperiod) and then uses these components in regressing a variable Y. The contribution of each individual variable to the PLS model is then evaluated by the standardized model coefficients, with the outputs indicating the direction and magnitude of the effect. If coefficients are positive and high, there is a strong positive correlation between the respective independent variable and the dependent variable (e.g. between temperature and the timing of a phenological stage) (Luedeling et al., 2013; Guo et al., 2015).

Further advancements have led to optimisation techniques where the number of variables to be included in each latent variable matrix can be chosen empirically based on the strength and significance of the regression component to facilitate biological interpretation. Luedeling and Gassner (2012) proposed that PLS is effective for analysing the effect of climatic variables on the variation of biological phenomena, in a standardized procedure, which has been difficult with other methods used to date. PLS regression analysis was used to identify the chilling and forcing periods of temperate fruit trees in Mediterranean climates, and more recently to determine the effects of warming temperatures in walnuts and apricots (Luedeling and Gassner, 2012; Luedeling et al., 2013; Guo et al., 2015) and olives (Aguilera et al., 2015). PLS was used for guiding experimental research in walnuts by identifying critical periods of the season that were important for the timing of key developmental stages, such as budburst. A similar approach in cereals may help to describe phenological environments and identify key periods during the growing season where thermal and photoperiodic regimes influence crop phenology. More recently PLS is finding application in genomic selection where whole genome markers are used to predict and describe a phenotype (Burstin et al., 2015). The advantage of PLS over other approaches is that it identifies only relevant predictor variables, while other linear models require pre-selection of potential predictor variables prior to regression analysis. There are no current studies where PLS has been applied to understand the environmental influences on cereal phenology.

The objectives of this study are: (i) to characterize crop phenology of Australian barley cultivars in response to thermal and photoperiodic environments to identify key phenological environments, and (ii) to assess the application of PLS for its utility in explaining and identifying the phenological responses. The criteria applied for building the model can be applied to other cultivars, crops, and regions to assist in developing a method to dissect the GxE interaction for complex phenotypic traits.

2. Materials and methods

2.1. Source of data

Experiments were conducted in South Australia in 2014 and 2015 at the Loxton Research Station, Waite Campus (Urrbrae), Strathalbyn (Charlick Research farm) and Roseworthy Agricultural College (Table 1). Each experiment consisted of three to eight sowing dates in 2014 and 2015 using cultivars and unreleased breeding lines adapted to south-eastern Australia. Only the fast – medium developing cultivars Compass, Commander, and Fathom will be discussed as they are the highest yielding varieties in these regions (Porker, 2017).

The experiments were split-plot randomised complete block designs with two to five replicates, sowing dates where randomly distributed as the whole plots and varieties randomly allocated within each sowing date. All sites had a seeding density of 150 seeds/m^2 and plot sizes of 2 m x 0.66 m (3 rows × 22 cm) at Loxton, 3 m × 0.66 m (3 rows × 22 cm) at Waite and 3.8 m × 1.28 m (6 rows × 22 cm) at Strathalbyn and Roseworthy. Fertiliser application and weed and disease control matched conventional district practices, and no nutritional or biotic stresses were observed.

2.2. Phenology data

Phenology data was collected from 2 weeks after sowing until anthesis at 2–14 day intervals depending on location and growth stage. Assessments were more frequent around anthesis. A minimum of three plants per genotype was randomly sampled from each plot and development was described using Zadoks growth stages (Zadoks et al., 1974). Three main stems were dissected to observe the apical meristem (Kirby and Appleyard, 1987a, b), and the developmental stage was recorded using the scale of Waddington et al. (1983). The time of anthesis was defined as when 50 % of florets within a main stem spike had flowered. The duration from sowing to anthesis was measured in days and thermal time units (TT; °Cd, growing degree days) using 0 °C as a base temperature (Kirby and Appleyard, 1987b; Holzworth et al., 2014). Days and thermal time to anthesis were determined for each genotype in each environment by fitting a linear or polynomial regression of the Waddington developmental scores against days and accumulated degree days from sowing using GraphPad Prism version 7.00.

2.3. Environmental data

Daily maximum and minimum air temperature, rainfall, and other meteorological data were recorded hourly with meteorological stations at the Roseworthy and Loxton sites. Waite and Strathalbyn daily temperature, rainfall and other meteorological data were obtained from the patched point dataset described by (Jeffrey et al., 2001) derived from weather stations 1.8 km away at Strathalbyn and 6.5 km to Waite. Daylength including civil twilight was calculated using the formulae of Forsythe et al. (1995).

2.4. Statistical analysis

2.4.1. Data pre-processing

For every environment, the daily minimum and maximum temperatures were averaged to obtain daily mean temperature. A 10-day running mean of daily minimum, maximum, and mean temperatures was used to improve PLS modelling by smoothing out the high day-to-day variability in temperatures which can result in poor autocorrelation as reported by (Luedeling and Gassner, 2012). The temperature began smoothing from 5 days before sowing to 5 days after sowing. Temperature data for analysis using this approach was generated for each environment for the period up until 115 days after sowing.

Table 1
Description of the experimental sites, showing latitude, longitude, season, sowing date range and the sowing day of the year for each experiment.

Study Location	Coordinates	Year	Sowing date range	Sowing days of year
Loxton	34°26′21.4″S 140°35′55.3″E	2014	15 Apr–10 Jun	106, 113, 119, 127, 134, 148, 162
		2015	15 Apr–15 Jun	106, 119, 126, 140, 146, 153, 160, 127
Urrbrae	34°57′56.6″S 138°38′00.2″E	2014	21 Apr–1 Jul	112, 125, 132, 147, 162, 183
		2015	19 Apr–29 Jun	110, 124, 138, 152, 181
Strathalbyn	35°19′19.9″S 138°53′02.5″E	2014	27 Apr–20 Jun	118, 140, 172
		2015	27 Apr–21 Jun	118, 145, 173
Roseworthy	34°28′51.1″S 138°40′26.9″E	2015	26 Apr–3 Jul	117, 144, 185

Table 2
Descriptive statistics for thermal time and days to anthesis in Compass, Commander and Fathom, indicating range, median, mean and standard deviation across the 35 environments.

	Thermal time to anthesis (°Cd)			Days to anthesis (days)		
	Compass	Commander	Fathom	Compass	Commander	Fathom
Min–Max	1045–1439	980–1608	1009–1615	93–121	89–131	89–130
Median	1251	1325	1287	108	118	114
Mean	1237	1315	1278	108	115	111
Std Deviation	102.4	165.5	155.5	7.7	11.7	11.34

This time period was chosen as it is the median flower time for all experiments and captures the majority of temperatures and photoperiod leading up to flowering in each experiment. Photoperiod variables started from 10 days after sowing to reflect emergence and the phase in which the plant begins to respond to the inductive signals of photoperiod which is supported by other crop models such as APSIM

2.4.1.1. Full partial least regression (PLS) model 1. For the PLS analysis, the dependent variable of interest was thermal time to anthesis. Separate analyses were used for Compass, Commander, and Fathom. The x latent variables comprised a matrix of 460 environmental variables for each of the 35 flowering time observations The 460 variables were made up 4 by 115 day measurements of the independent environment variables ; daily photoperiod, smoothed daily mean, and minimum and maximum temperatures.

The PLS analysis was conducted using the Unscrambler software (version 10.3, CAMO, Norway) and the NIPALS algorithm, where the data was standardised based on the mean and standard deviation. The dependent and independent variables were centred and scaled to allow comparison between different variables, with respect to their influence in the model. Optimal PLS models were developed with full cross-validation using leave-one-out cross-validation which identifies significant variables contributing to the best fit of the model (Martens and Martens, 2000). The weighted regression coefficients were significant at $P < 0.05$ and the direction and strength of the effect of each variable in the model were generated. The optimal models reported were identified by the optimum number of terms in the PLS calibration models, as determined by the lowest number of factors giving the minimum value of the predicted residual error sum of squares. The coefficient of determination in calibration and cross-validation (R^2), and the root-mean-square error (RMSE) was calculated for the prediction or validation samples (RMSEV) and the calibration samples (RMSECV) to test the predictive ability of the models developed. The regression coefficient profile was obtained by plotting the model coefficients of the standardised data against the predictor variables.

2.4.1.2. Simplified PLS model 2. The statistical approach to Model 2 was dependent on the outputs from Model 1 that identified the periods and environmental variables significantly influencing the time to anthesis. Significant variables from Model 1 were used to create six simplified mean environmental variables. The six variables were used for a simplified (lower resolution) PLS model using the same method as described in Model 1. The accuracy of each model was compared using a correlation analysis.

2.4.2. Genotypic comparison

Simple statistics and ANOVA of flowering time were conducted using GenStat VSN International, Version 15. Finlay–Wilkinson regression (Finlay and Wilkinson, 1963) was used to assess the stability of varieties across different environments by regressing the time to anthesis of each genotype against the environmental means of all three varieties. From the PLS analysis the strength and direction of the variables of importance (weighted regression coefficients) were used to compare the influence of the environment on the time to flower between genotypes for PLS model 1 and 2. Differences in genotype sensitivity to environmental variables were further tested by comparison of partial regression coefficients using a *t*-test of difference between the significant standardized partial regression coefficients (β) identified from Model 1 during the significant periods.

2.4.3. Identifying phenological environments

PLS models are similar to principal component analysis which results in scores and loadings that may be visualized in a score-loading plot (biplot). Scores and loadings from the optimised PLS Model 2 analysis were used to group and characterise the environments accounting for most of the variation in time to anthesis. Score plots were used for interpreting relationships among observation sites, and loadings plots were used to interpret relations among environmental variables within each grouping.

2.4.4. APSIM simulation

Simulations to estimate the anthesis date of Commander across all environments were conducted using APSIM version 7.6 (Holzworth et al., 2014). Soil characterization was obtained from the APSoil database (Dalgliesh et al., 2009) and meteorological weather data as described in the methods. Manschadi et al. (2006) present a full description of the approach to modelling barley phenology in APSIM. The daily thermal time in APSIM is calculated as crown temperature, and is adjusted by predetermined genetic and environmental factors in APSIM. Therefore, the simulated days to anthesis were compared with observed days to anthesis in a linear regression and predictive statistics are reported.

3. Results

Table 2 shows the mean, range and standard deviation of thermal time and days to anthesis for three genotypes across 35 environments. Further information about anthesis dates can be found in Supplementary Table 1. There was a wide range of days to anthesis (92–131) and thermal time to anthesis (980 − 1615 °Cd) which suggests a strong influence of genotypes and environmental conditions resulting from sowing date and location. The data set was therefore considered appropriate to test the robustness of PLS models to characterise phenology. Compared to Compass, Commander flowered 78 °C.d later and Fathom 41 °C.d later (Table 2).

A multi-site analysis revealed significant GxE (results not shown) for anthesis date. Using the slope in the Finlay-Wilkinson plot as a measure of environmental responsiveness and the GxE interaction. Compass was the least responsive variety with a slope of 0.72 compared to 1.10 in Fathom and 1.18 in Commander for thermal days to anthesis (Fig. 1). Parameters and estimates from the regression for days to anthesis can be found in Supplementary Table 2 and Supplementary Fig. 1.

3.1. Full PLS model 1

Calibration and validation statistics for the observations of thermal time to anthesis in Compass, Commander, and Fathom using the full environmental PLS model 1, and Simplified PLS Model 2 in all 35 environments are shown in Table 3. For thermal time to anthesis the coefficient of determination in cross-validation (R^2) and the RMSECV

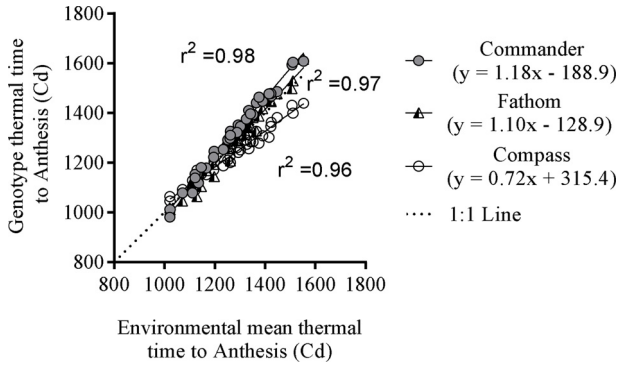

Fig. 1. Relationship between the environmental mean of thermal time to anthesis of cultivars, Compass, Commander, and Fathom from 35 growing utilising a combination of site x year x sowing date.

were 0.92 (RMSECV = 27.9 °C.d) in Compass, 0.95 (RMSECV = 36.5 °C.d in Commander, and 0.89 (RMSECV = 52.1 °C.d) in Fathom. For days to anthesis, the R^2 ranged from 0.79 in Compass to 0.92 in Commander, and the RMSECV were 3.3 in Commander and 4.6 in Fathom, respectively. The optimised PLS models developed using the full environmental matrix explained more than 90 % of the variability in thermal time to flower in all genotypes. Thermal time to flower will be used in subsequent modelling, as the R^2 of cross-validation was more accurate than predicting days to anthesis; however, the number of days to flower model will be used to compare with APSIM phenology predictions. The calibration and validation statistics for the full environmental PLS model 1 for days to anthesis in all environments can be found in Supplementary Table 3. The number of PLS factors are derived by the full cross-validation method where the optimum number of terms are determined by the lowest number of factors giving the minimum value of the prediction residual error sum of squares; adding more PLS factors beyond this would not significantly improve the percentage variance explained by the model.

The most significant weighted regression coefficients are determined by the uncertainty test and show the direction and strength of the impact of each variable in the PLS model. Fig. 2 shows the optimal loadings derived from the PLS calibration.

Examination of the loadings (or weighted regression coefficients) is important to identify specific periods and the most important environmental variables related to the thermal time to anthesis. Based on the output demonstrated in Fig. 2 seven environmental variables were identified as significantly influencing thermal time to anthesis both negatively and positively at different time periods after sowing and are defined in Table 4.

3.1.1. Genotypic comparisons

The weighted regression coefficients show the direction and strength of the effect of each variable; differences in genotypic sensitivity to the environmental variables can be visualized in the full PLS model for Compass, Commander, and Fathom (Fig. 2). The response patterns to the environmental variables were similar for all genotypes, although the strengths of the environmental effects differed. The most noticeable difference is the lack of significant effect of maximum temperatures in the period 27–38 days after sowing in Compass, compared to a significant effect in Fathom and Commander. Differences in genotype sensitivity to environmental variables were further tested by ANOVA on the significant regression coefficients (β) identified from the full PLS Model 1 during the seven critical periods and corrected for multiple comparisons using a Tukey test (Table 5). Compass always had significantly smaller mean regression coefficient values than Commander and Fathom, suggesting it was less influenced by environmental stimuli (Fig. 3). Compass behaved differently to Fathom across all environmental variables whereas Commander and Fathom only differed in responses to Early_Ppd, Late_Ppd, and Early_MinT and Late_MaxT. Compass and Commander differed in response to all variables apart from Early_Ppd. According to the regression coefficients, in all varieties early minimum temperatures had the largest positive influence on the thermal time to anthesis in the model whereas late maximum temperature had the highest negative influence. Early photoperiods had the largest influence on Fathom, while Commander was more sensitive to late photoperiod, early minimum and late maximum temperatures than Fathom and Compass, and Compass was the least sensitive to all seven environmental variables.

3.2. Simplified PLS model 2

The simplified PLS model 2 utilised only the mean environmental variables derived from the seven significant periods identified in Table 4, resulting in a low-resolution matrix of environmental information but capturing the most critical periods of the year controlling the thermal time to anthesis.

Calibration and validation statistics using the simplified environmental PLS model are presented in Table 3 for the thermal time to anthesis in Compass, Commander, and Fathom. Despite an effect in the full environmental model 1, the Early_MaxT did not significantly influence thermal time to anthesis in any genotype in the simplified model so was removed from the final model. The coefficient of determination in cross-validation (R^2) and the RMSECV were 0.92 (RMSECV = 26.9 °C.d) v in Compass, 0.94 (RMSECV = 39.3 °C.d) in Commander, and 0.87 (RMSECV = 54 °C.d) in Fathom

3.3. Comparison of models

Similar trends were observed when the variables of importance (weighted regression coefficients) were compared with the simplified PLS model 2 (Supplementary Fig. 2). The R^2 and RMSECV of cross calibration in the simplified model are similar to that of the full environmental model (Table 3) in all genotypes. Importantly, more than 90 % of the variability in thermal time to anthesis in all genotypes can be explained by each PLS model. This suggests PLS has excellent application for characterisation of phenology in these environments and the simplified PLS model is an appropriate method to be utilised for easier to interpret environmental characterisation instead of the full environmental matrix used in PLS model 1.

Table 3
Calibration and validation statistics for the observations of thermal time to anthesis in Compass, Commander, and Fathom using the full environmental PLS model 1, and Simplified PLS Model 2 in all 35 environments.

	Full PLS Model 1			Simplified PLS Model 2		
	Compass	Commander	Fathom	Compass	Commander	Fathom
R^2 Calibration	0.95	0.96	0.92	0.93	0.95	0.90
R^2 Cross-validation	0.92	0.95	0.90	0.92	0.94	0.87
RMSEC	22.5	29.4	42.9	25.8	33.3	46
RMSECV	27.9	36.5	52.1	26.9	39.3	54
No. of PLS factors	2	2	2	2	2	2

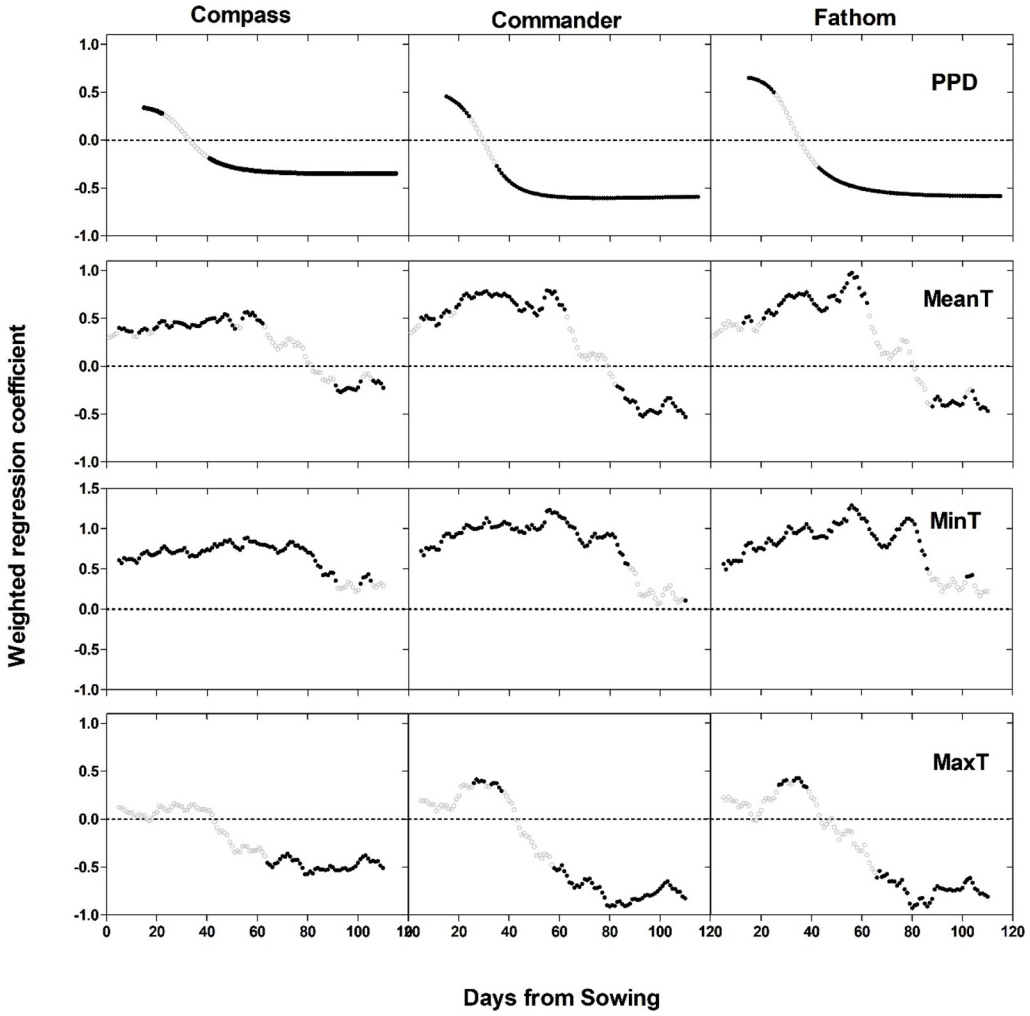

Fig. 2. The model weighted regression coefficients from PLS model 1 analysis for the growing degree days to anthesis in cultivars (from left to right) Compass, Commander, and Fathom. The four panels from top to bottom display the model coefficients of the centred and scaled data for each cultivar using daily photoperiod (Ppd) and smoothed mean (MeanT), minimum (MinT) and maximum (MaxT) temperatures as independent input variables. The black closed symbols represent the coefficient as a significant variable and the open grey symbols represent a non-significant variation not included in optimised models.

Table 4
Descriptions of the significant latent x environmental variables contributing to the thermal time to anthesis derived from key periods identified in PLS model1.

Early_Ppd	Mean daylength (hrs) during the period 15–25 days after sowing
Late_Ppd	Mean daylength (hrs) during the period 40–115 days after sowing
Early_MeanT	Mean temperature during the period 5–60 days after sowing
Late_MeanT	Mean temperature during the period 90–110 days after sowing
Early_MinT	Mean minimum temperatures during the period 1–70 after sowing
Early_MaxT*	Mean maximum temperatures for the period 27–38 days after sowing
Late_MaxT	Mean maximum temperatures for the period 55–110 days after sowing

* removed from final simplified model.

3.4. Environmental characterisation

Scores and loadings plots for Commander (from the simplified PLS Model 2 analysis only) were used to group and characterise the key phenological environments to help describe phenology responses. Commander was selected to characterise the environments because it is the current benchmark genotype for adaptation to Australian environments and represented the greatest response to all environmental variables in this dataset. The scores plot revealed relationships among observational sites and identified six key environment groupings in the first two factors, named ENV1 - 6. The loading plot reveals relationships among environmental variables within each grouping (Fig. 4).

PLS shows clear patterns in the antagonistic effects of early and late temperatures, and early and late photoperiod in factor 1. For example,

Table 5
Summary of Tukey multiple comparisons test between Compass, Commander, Fathom for mean regression coefficients over seven environmental sensitive variables and time periods., not significant (ns), ** < 0.01, *** < 0.001, **** < 0.0001.

	Early_Ppd	Late_Ppd	Early_MeanT	Late_MeanT	Early_MinT	Early_MaxT	Late_MaxT
No of β values	10	75	55	20	70	11	55
Compass vs. Commander	ns	****	****	****	****	****	****
Compass vs. Fathom	****	****	****	****	****	****	****
Commander vs. Fathom	****	***	ns	ns	****	Ns	**

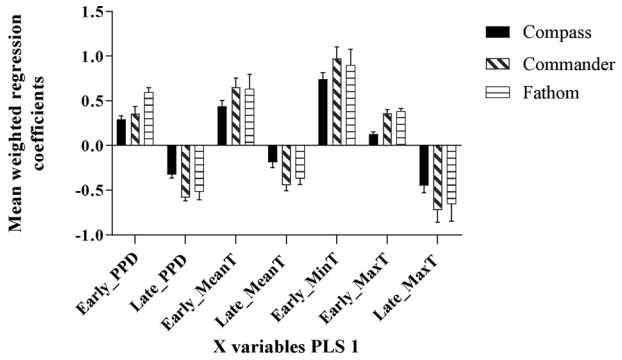

Fig. 3. The mean weighted regression coefficients (variables of importance) from the PLS model 1 for thermal time to flower in cultivars Compass, Commander, and Fathom using the x latent variables Early_Ppd, Late_Ppd, Early_MeanT, Late_MeanT, Early_MinT, Early MaxT and Late_MaxT across 35 growing environments, error bars indicate the standard deviation of the weighted regression coefficients.

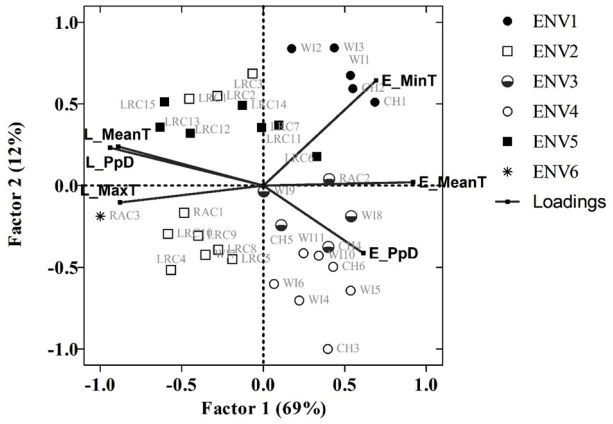

Fig. 4. PLS scores and loading plot derived from the simplified PLS model 2 of Commander for the first two factors used to identify groups of environments to discriminate phenology based on phenotypic and environmental data. Loadings show the x variables contributing to the PLS phenological environments in Factor 1 and 2. Early_Ppd (E_PpD), Late_Ppd (L_PpD) and temperature (°C) for variables defined previously Early_MeanT (E_MeanT), Late_MeanT (L_MeanT), Early_MinT (E_MinT), and Late_MaxT (L_MaxT).

sites within ENV1recorded 4 °C higher mean and minimum early temperatures compared to ENV 5 and ENV6. The key environmental patterns for each group as defined by the PLS model are summarised in the boxplot diagram (Fig. 5) and description in Table 6.

3.5. Genotype by environment responses

On average across all genotypes, anthesis was delayed in environment types ENV1 to ENV6 in descending order. However, within and between environment types, there were significant changes in the genotypic rankings. In ENV1 and ENV2, Compass was 150 °C.d earlier to anthesis than Commander and 100 °C.d earlier than Fathom. In the intermediate environment type ENV3, Compass flowered 100 °C.d earlier than both Commander and Fathom, which were similar. There was no significant difference between genotypes in ENV4 and ENV5, although Compass flowered 37 °C.d earlier, Commander 115 °C.d earlier and Fathom 80 °C.d earlier than their respective means. Fathom and Commander flowered significantly earlier in environment type ENV6 but not Compass; in this instance, Commander flowered similar to Fathom but 70 °C.d earlier than Compass (Fig. 6).

3.6. APSIM comparison

A comparison of APSIM simulated anthesis dates to the observed dates for Commander provides a relatively robust prediction when anthesis occurred after September 5 (day of year 250). However, APSIM predicted earlier flowering dates in situations where flowering occurred before this date by between 2 and 35 days earlier than the observed anthesis day of year. (Fig. 7). This also corresponds to earlier planting dates and ENV1-3 which are defined by higher mean and minimum temperatures early in the growing season. This suggests the current APSIM model for Commander may not be accounting for the temperature influences observed in the experimental dataset.

4. Discussion

This study has demonstrated that PLS is a novel and robust method of handling complex cereal phenology and climatic data. The approach developed has provided a methodology to identify the most relevant environmental variables that regulate crop development and helped to define phenology envirotypes in southern Australia. Outcomes from this research provide new insight into GxE interactions, and the temperature and photoperiodic responses that contribute to the adaptation of high yielding barley lines across commercially relevant sowing times.

4.1. PLS phenology model

In phenology studies, information on the response of genotypes to the environment is critical for breeders in developing new cultivars and for growers to match planting time with a variety's maturity to achieve an appropriate anthesis date. Crop developmental research encounters analytical challenges in characterising the GxE interactions, largely due to the fact there are many highly auto correlated climate variables, such as photoperiod and temperature that act as cues for crop developmental genes. Using PLS it was possible to fit a complex and simplified model that described more than 90 % of the variation in thermal time to anthesis in the three elite genotypes, Compass, Commander, and Fathom, in 35 environments with an accuracy of between 22 and 47 °C.d, which equated to 3–4 days, similar to the model used in (Alzueta et al., 2014). This confirms PLS and the methodology used in this study has application for robust characterisation of phenology in these environments, and is in agreement with other studies utilising PLS for phenology for example chilling periods in walnuts (Luedeling and Gassner, 2012) and phenology in apricots (Guo et al., 2015). While the GxE responses can be quantified using traditional approaches such as Finlay and Wilkinson (Finlay and Wilkinson, 1963), measures of trait plasticity (Sadras et al., 2009; Sadras and Slafer, 2012) and linear models (Perry et al., 1987), they rarely provide insight into the environmental factors that interact with the genotype beyond univariate observations.

4.2. Towards improved biological understanding

Establishing a meaningful relationship between environmental variables and crop development has been the objective of many studies. Statistical modelling approaches such as PLS allow for greater biological understanding and can inform experimental research by first pinpointing the key environmental variables of interest (Luedeling and Gassner, 2012; Luedeling et al., 2013), test hypotheses, and provide new insight into biological processes. PLS identifies only relevant predictor variables, while other linear models require pre-selection of potential predictor variables prior regression analysis.

Using the outputs and interpretation of the significant regression coefficients from the full optimised PLS, it was possible to define critical periods in the plant's life cycle (days after sowing) where the effects of photoperiod and temperature were most influential outlined in Table 4. The six key environmental variables could then be utilised in the simplified lower resolution model and it was possible to identify six key

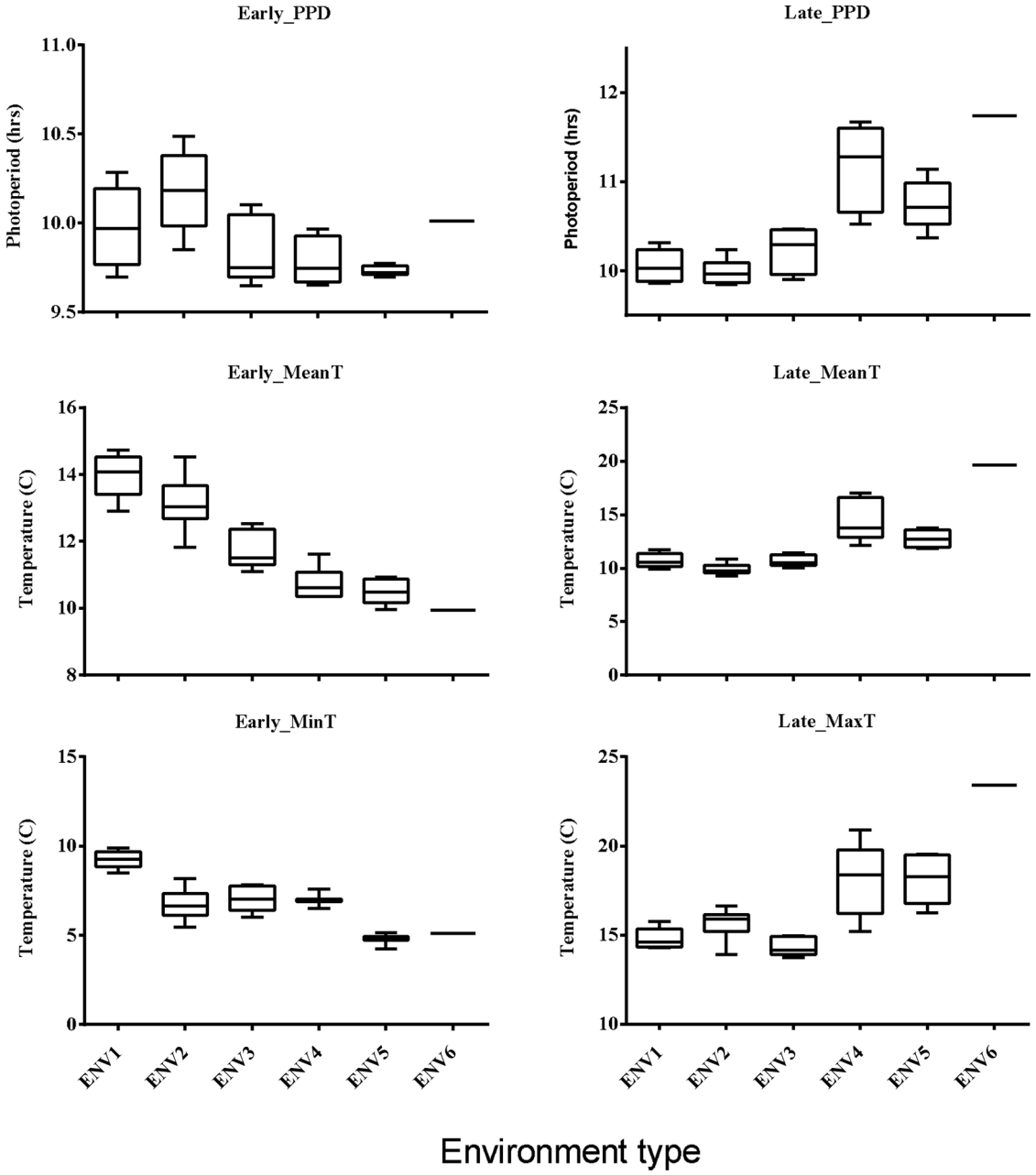

Fig. 5. Box plots representative of photoperiod (hrs) for defined variables; Early_Ppd, Late_Ppd and temperature (C) for variables defined previously Early_MeanT, Late_MeanT, Early_MinT, and Late_MaxT in the different environmental types; the boundaries of the box indicate the 25th and 75th percentiles; whiskers indicate the 10th and 90th percentiles. The horizontal line in the box corresponds to the median value. ENV1 (n = 5), ENV2 (n = 10), ENV3 (n = 5), ENV4 (n = 7), ENV5 (n = 7), ENV6 (n = 1).

Table 6
Description of phenological environment types identified in the PLS analysis.

Environment Type	Description of environment
Environment 1 (ENV1):	Higher mean and minimum temperatures early in the growing season linked to early sowing at Waite and Charlick where conditions are typically milder.
Environment 2 (ENV2):	Higher mean photoperiod and mean temperatures in the early part of the growing season and lower mean photoperiod in the later part of the season corresponding to pre-May planting dates at Loxton and Roseworthy.
Environment 3 (ENV3):	An intermediate environment with few extreme values and comprises approximately the median range for each environmental variable; these sites include typical May planting dates at Charlick, Waite, and Roseworthy
Environment 4 (ENV4):	Higher photoperiods combined with higher mean temperature and higher maximum temperature during the latter part of the growing season corresponding to post May-20 planting dates at Waite and Charlick
Environment 5 (ENV5):	Dominated by below average mean and minimum temperatures during the early part of the growing season and above average photoperiod and maximum temperatures in the late part of the season corresponding to later sowing dates at Loxton in both seasons
Environment 6 (ENV6):	One site sown on the 1st July at Roseworthy characterised by above average late maximum, mean temperature and photoperiod.

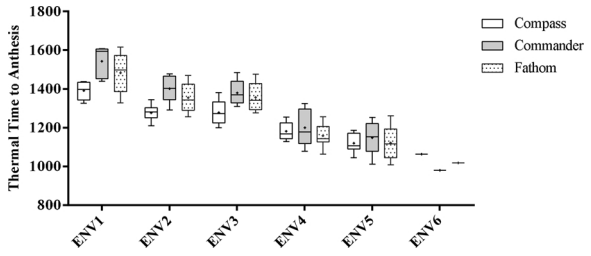

Fig. 6. Box plots representative of the thermal time to anthesis for cultivars Compass, Commander, and Fathom in the different environmental types based on outputs of PLS2; the boundaries of the box indicate the 25th and 75th percentiles; whiskers indicate the 90th and 10th percentiles. The horizontal line in the box corresponds to the median value and + indicates the mean.

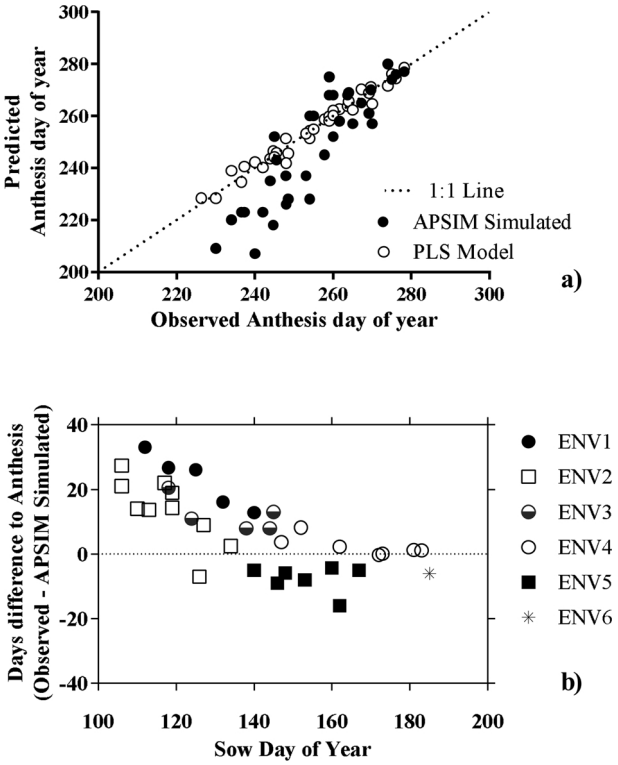

Fig. 7. a. Relationship between the observed anthesis day of the year and the predicted anthesis day of the year for Commander barley in 35 growing environments using the APSIM model and fitted PLS 2 model, dotted line indicates the 1:1 relationship. b) Relationship between the differences in observed anthesis days and predicted by APSIM compared to the sowing day of the year (from January 1) in each environment group type.

factorial eco-phenological environments for easier interpretation based on their climatic patterns (Table 6). Simplified models may be preferred in integrating phenotype and genetics in breeding programs, particularly as (Hammer et al., 2006) described successful models generally utilised a coarse level of granularity to capture system dynamics and much of the fine detail is not required.

There was significant GxE interaction for the thermal time to anthesis. The broadly adapted, higher yielding line Compass (Porker, 2017) had the shortest mean duration to anthesis but was also the most stable phenotype in this study recording the smallest variation in thermal time to anthesis across a wide range of environments. Sadras and Richards (2014) discussed possibilities of using phenotypic plasticity for breeding programs rather than direct selection for yield related traits. The stable phenotype of Compass suggests it has lower plasticity than Commander has, due to its lower sensitivity to environmental factors. Therefore, an increased focus on the reduced plasticity of anthesis time may be an important adaptive trait for Australian environments, in addition to a relatively short duration to anthesis. This is particularly relevant given there may be little scope for improving barley adaptability and yield by further adjustments in total time to anthesis and where GxE interaction is large (Boyd et al., 2003; Slafer et al., 2005). However, it must be noted anthesis date of the year rather than the plasticity of total time to anthesis should also be considered in the context of the farming system. Varieties that are not stable in flowering date may flower very early from earlier sowing times and be exposed to frost damage in Australian condtions.

The regions explored in this study represent important growing environments for barley in south-eastern Australia. The experiments were grown to determine the developmental response of high yielding barley lines to photoperiod and temperature regimes using different sowing dates and locations. The phenology drivers of well-adapted barley cultivars are poorly described in the literature, it has long been recognised the best-adapted barley cultivars for Australian low-medium rainfall environments are early-maturing spring types, which exhibit a relatively high photoperiod response to achieve a short duration to heading (Boyd et al., 2003; Read et al., 2003). However, in a new finding for Australian environments, these results using PLS analysis show that, under field conditions, Compass was less responsive to photoperiod and has a shorter time to anthesis than the current benchmark Commander and Fathom. This suggests other genetic and environmental factors that previously have not usually been considered for Australian studies may be equally or more important in regulating anthesis time.

The influence of other environmental factors is highlighted by the fact that thermal time to anthesis varied among genotypes and between environments of similar planting and photoperiod. The differences in development between these environments could be explained by the temperatures experienced in the period between sowing and anthesis. Higher minimum and mean temperatures during the first seventy days delayed anthesis by a maximum of 200 °C.d, which suggests there is a significant effect of minimum temperatures having a vernalisation-like response. This is noticeable in environment types ENV2 – 6 (Fig. 5), where early minimum temperatures are within the range for maximum vernalisation effect between 0 and 8 °C (Roberts et al., 1988) whereas environment one was warmer and resulted in longer times to anthesis. This is an important finding given that all previous literature describing most adapted Australian cultivars and spring types introduced from Europe, Canada, and Japan have either no or a very minimal vernalisation requirement. While there are some exceptions with the cultivar's Ulandra, Urambie and Yambla; these cultivars are not widely grown but maybe useful for very early sowing (Boyd et al., 2003).

The other period sensitive to temperature occurred just prior to anthesis, where high maximum temperatures reduced the thermal time to anthesis. This was particularly pronounced in Commander grown at Roseworthy in 2015 and environment six where delayed sowing resulting in the crop being exposed to significantly higher temperatures during this period. These findings provide further evidence that differences in anthesis time among varieties exist for reasons other than photoperiod. This should not come as a surprise, however, quantifying the responses to temperature in the field have remained relatively elusive. Ren et al. (2010) noted large differences in heading dates among genotypes between Australian and Southeast Asian environments, despite similar latitudes. These studies indicated there were genes conditioned by temperature differences between the locations, and suggested that variation in duration to heading existed for reasons other than vernalisation and photoperiod. This may be an important adaptive trait for Australian cultivars. Temperature effects could be equal to or even greater than some of the most extreme responses recorded for vernalisation or photoperiod (Read et al., 2003) when grown under milder winter growing conditions. However, it must be noted that all varieties were responsive to photoperiod and it remains an important trait for Australian environments.

In the context of phenology, PLS provides new insight into the previously elusive differential responses to the subtle changes in average, maximum and minimum temperatures and provides evidence for the need to include differential effects of temperature during different seasons into explanatory models of the effects of temperature on phenology. APSIM-Barley has proven to be robust in simulating the response of barley crops to management and environmental conditions at experimental sites and in farmers' fields (Manschadi et al., 2006). However, the model's capacity to simulate crop phenology reliably in some environments creates challenges for current APSIM users. Comparison with APSIM drawn in these experiments suggests that the current APSIM model used for Commander may not be accounting for the temperature influences previously discussed particularly at earlier sowing dates.

In the case of other crop models, photoperiods are often extended artificially to determine photoperiod coefficient factors and temperature studies have frequently been studied in controlled growth rooms (Ellis et al., 1988; Kernich et al., 1995, 1996; Karsai et al., 2008). The generation of model coefficients in this way inherently assumes that the genotypic temperature and photoperiod sensitivity factors are fixed in all environments, whereas in fact there may be genes that differ in their sensitivity depending on the level of environmental stimulus. The use of PLS as an analytical tool has helped to investigate these relationships in barley under field conditions, without the need for systematic manipulation of the growing environment. It allows exploration of a wide range of environmental conditions similar to those experienced by the barley crop in field conditions and at the crop level of organisation.

One of the limitations of PLS for use as a predictive model lies in the fact that it is only valid for the particular conditions under which observed data was obtained. Thus, it could be argued that they are not directly useful for predicting biological processes outside the climatic domain of the observations (i.e. at different locations or for climate change scenarios). We acknowledge the model is unlikely to be reliable in environments outside those in which it is parameterised in. Therefore the findings should be used to direct research interpreting relationships with phenology and climate data to assist in updating current predictive models like APSIM. Although the experiment to obtain the variables to build the model was carried out over two growing seasons and three sites, the fact that cultivars were sown in a wide range of sowing dates ensured that the different genotypes explored a wide range of environments with different temperatures and photoperiods.

4.3. Future applications

More generally, the PLS method used has application for characterisation of phenology in these environments. This model will now be used as a method to analyse other phenological data collected to assist in the understanding of pre-anthesis development, such as the critical period when the number of grains is determined (Arisnabarreta and Miralles, 2008) or stages such as double ridge when barley transitions from the vegetative to reproductive phase. An extended approach could help develop criteria to be applied to other cultivars or crops and to other regions. This method could be useful for explaining quantitative variation in biological events or the outcomes of biological processes through analysis of full-season records of temperature, precipitation or other environmental variables. Crop models have previously been used to study impacts of extreme climate, as they allow correction for the effect of multiple environmental factors and allow testing of multiple genotype-environment-management combinations (e.g. sowing date × variety) (Hammer et al., 2006). PLS analysis of environmental parameters could find application in various contexts, e.g. for explaining crop yields or for characterizing the vulnerability of farming systems to climate variability during certain phases of crop growth.

The examination of the differences between genotypic environmental loadings (regression coefficients) provide insights into aspects of crop phenology that can be used for genetic dissection. Phenotype by genotype prediction based on eco-physiological models, which account for allelic gene, QTL, or marker effects, have many possible applications in plant breeding programs. (Uptmoor et al., 2016) suggested that, in order for such models to become more applicable, a precise estimation of allelic marker effects in response to environmental regulators is required for improving models predicting phenotype by genotype. Using PLS crop models in the genomic prediction of heading date may be of practical importance if there is a large variation in heading date in target environments of commercial cultivars. The next obvious step is to combine a PLS approach using environmental parameters identification outlined in this research with genomic data using a wider range of cultivars to determine the functional effects of key crop developmental genes on crop phenology. Hammer et al. (2006) suggested novel modelling approaches are needed to predict gene-to-phenotype associations, and to assist with the complexity and scales of biological organization for breeding improved crop plants. There are a number of alternative pathways in the literature, which will all enable an increased understanding of gene-to-phenotype systems for complex traits.

5. Conclusion

Using the framework of phenology as a proof of concept for a complex trait, this study has shown that PLS is a robust method to extract meaningful biological explanations from large data sets. It was possible to define critical periods where the effects of photoperiod and temperature were most influential in Australian barley cultivars. This has helped quantify the effect of subtle changes in temperature on barley, providing new evidence that the effect of temperature may be of equal or greater importance than photoperiod in determining the total thermal time to anthesis. Not only should these effects be considered in future crop models but integrated with genomic data to investigate aspects of crop phenology that can be used for genetic dissection and the design of new ideotypes adapted to Australian environments. PLS has proven its usefulness for envirotyping and paves the way for development of a four-dimensional profile of crop science involving genotype (G), phenotype (P), envirotype (E) and time (T) (developmental stage) as proposed by (Xu, 2016).

Funding

Thanks to the Grains Research and Development Corporation Australia (GRS10690), the Playford Trust/Thyne Reid foundation PhD scholarship (South Australia), and the University of Adelaide who supported this work as part of a PhD.

Acknowledgments

Members of the Adelaide University barley research group for field trial management, and Michael Laws for collection of plants.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fcr.2019.107697.

References

Aguilera, F., Fornaciari, M., Ruiz-Valenzuela, L., Galán, C., Msallem, M., Dhiab, A.B., la Guardia, C.D.-d, del Mar Trigo, M., Bonofiglio, T., Orlandi, F., 2015. Phenological models to predict the main flowering phases of olive (Olea europaea L.) along a latitudinal and longitudinal gradient across the Mediterranean region. Int. J. Biometeorol. 59, 629–641.

Alzueta, I., Arisnabarreta, S., Abeledo, L.G., Miralles, D.J., 2014. A simple model to predict phenology in malting barley based on cultivar thermo-photoperiodic response. Comput. Electron. Agric. 107, 8–19.

Angus, J.F., Mackenzie, D.H., Morton, R., Schafer, C.A., 1981. Phasic development in field crops II. Thermal and photoperiodic responses of spring wheat. Field Crops Res. 4,

269–283.
Appleyard, M., Kirby, E.J.M., Fellowes, G., 1982. Relationships between the duration of phases in the pre-anthesis life cycle of spring barley. Aust. J. Agric. Res. 33, 917–925.
Arisnabarreta, S., Miralles, D.J., 2008. Critical period for grain number establishment of near isogenic lines of two- and six-rowed barley. Field Crops Res. 107, 196–202.
Atkinson, D., Porter, J.R., 1996. Temperature, plant development and crop yields. Trends Plant Sci. 1, 119–124.
Bonhomme, R., 2000. Beware of comparing RUE values calculated from PAR vs solar radiation or absorbed vs intercepted radiation. Field Crops Res. 68, 247–252.
Boyd, W.J.R., Li, C.D., Grime, C.R., Cakir, M., Potipibool, S., Kaveeta, L., Men, S., Kamali, M.R.J., Barr, A.R., Moody, D.B., Lance, R.C.M., Logue, S.J., Raman, H., Readj, B.J., 2003. Conventional and molecular genetic analysis of factors contributing to variation in the timing of heading among spring barley (Hordeum vulgare L.) genotypes grown over a mild winter growing season. Aust. J. Agric. Res. 54, 1277–1301.
Burstin, J., Salloignon, P., Chabert-Martinello, M., Magnin-Robert, J.-B., Siol, M., Jacquin, F., Chauveau, A., Pont, C., Aubert, G., Delaitre, C., Truntzer, C., Duc, G., 2015. Genetic diversity and trait genomic prediction in a pea diversity panel. BMC Genomics 16, 105.
Chapman, S.C., 2008. Use of crop models to understand genotype by environment interactions for drought in real-world and simulated plant breeding trials. Euphytica 161, 195–208.
Cockram, J., Jones, H., Leigh, F.J., O'Sullivan, D., Powell, W., Laurie, D.A., Greenland, A.J., 2007. Control of flowering time in temperate cereals: genes, domestication, and sustainable productivity. J. Exp. Bot. 58, 1231–1244.
Cooper, M., Messina, C.D., Podlich, D., Totir, L.R., Baumgarten, A., Hausmann, N.J., Wright, D., Graham, G., 2014. Predicting the future of plant breeding: complementing empirical evaluation with genetic prediction. Crop Pasture Sci. 65, 311–336.
Dalgliesh, N.P., Foale, M.A., McCown, R.L., 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 Sci. 60, 1031–1043.
Ellis, R.H., Roberts, E.H., Summerfield, R.J., Cooper, J.P., 1988. Environmental control of flowering in barley (Hordeum vulgare L.). II. Rate of developement as a function of temperature and photoperiod and its modification by low-temperature vernalization. Ann. Bot. 62, 145–158.
Finlay, K., Wilkinson, G., 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14, 742–754.
Forsythe, W.C., Rykiel, E.J., Stahl, R.S., Wu, H.-i, Schoolfield, R.M., 1995. A model comparison for daylength as a function of latitude and day of year. Ecol. Modell. 80, 87–95.
Goyne, P., Meinke, H., Milroy, S., Hammer, G., Hare, J., 1996. Development and use of a barley crop simulation model to evaluate production management strategies in north-eastern Australia. Crop Pasture Sci. 47, 997–1015.
Guo, L., Dai, J., Wang, M., Xu, J., Luedeling, E., 2015. Responses of spring phenology in temperate zone trees to climate warming: a case study of apricot flowering in China. Agric. For. Meteorol. 201, 1–7.
Hammer, G., Cooper, M., Tardieu, F., Welch, S., Walsh, B., van Eeuwijk, F., Chapman, S., Podlich, D., 2006. Models for navigating biological complexity in breeding improved crop plants. Trends Plant Sci. 11, 587–593.
Hammer, G.L., Van Oosterom, E., McLean, G., Chapman, S.C., Broad, I., Harland, P., Muchow, R.C., 2010. Adapting APSIM to model the physiology and genetics of complex adaptive traits in field crops. J. Exp. Bot. 61, 2185–2202.
Hay, R.K.M., Elliss, R.P., 1998. The control of flowering in wheat and barley: what recent advances in molecular genetics can reveal. Ann. Bot. 82, 541–554.
Holzworth, D.P., Huth, N.I., deVoil, P.G., Zurcher, E.J., Herrmann, N.I., McLean, G., Chenu, K., van Oosterom, E.J., Snow, V., Murphy, C., Moore, A.D., Brown, H., Whish, J.P.M., Verrall, S., Fainges, J., Bell, L.W., Peake, A.S., Poulton, P.L., Hochman, Z., Thorburn, P.J., Gaydon, D.S., Dalgliesh, N.P., Rodriguez, D., Cox, H., Chapman, S., Doherty, A., Teixeira, E., Sharp, J., Cichota, R., Vogeler, I., Li, F.Y., Wang, E., Hammer, G.L., Robertson, M.J., Dimes, J.P., Whitbread, A.M., Hunt, J., van Rees, H., McClelland, T., Carberry, P.S., Hargreaves, J.N.G., MacLeod, N., McDonald, C., Harsdorf, J., Wedgwood, S., Keating, B.A., 2014. APSIM - Evolution towards a new generation of agricultural systems simulation. Environ. Model. Softw. 62, 327–350.
Jeffrey, S.J., Carter, J.O., Moodie, K.B., Beswick, A.R., 2001. Using spatial interpolation to construct a comprehensive archive of Australian climate data. Environ. Model. Softw. 16, 309–330.
Karsai, I., Szűcs, P., Kőszegi, B., Hayes, P.M., Casas, A., Bedő, Z., Veisz, O., 2008. Effects of photo and thermo cycles on flowering time in barley: a genetical phenomics approach. J. Exp. Bot. 59, 2707–2715.
Kernich, G.C., Halloran, G.M., Flood, R.G., 1996. Constant and interchanged photoperiod effects on the rate of development in barley (Hordeum vulgare). Aust. J. Plant Physiol. 23, 489–496.
Kernich, G.C., Slafer, G.A., Halloran, G.M., 1995. Barley development as affected by rate of change of photoperiod. J. Agric. Sci. 124, 379–388.
Kirby, E., Appleyard, M., 1987a. Cereal Development Guide. NAC Cereal Unit, Stoneleigh, UK.
Kirby, E.J.M., Appleyard, M., 1987b. Cereal development guide. Arable Unit, National Agricultural Centre, Kenilworth, England.
Loss, S., Perry, M., Anderson, W., 1990. Flowering times of wheats in south-western Australia: a modelling approach. Aust. J. Agric. Res. 41, 213–223.
Luedeling, E., Gassner, A., 2012. Partial least squares regression for analyzing walnut phenology in California. Agric. For. Meteorol. 158–159, 43–52.
Luedeling, E., Kunz, A., Blanke, M.M., 2013. Identification of chilling and heat requirements of cherry trees—a statistical approach. Int. J. Biometeorol. 57, 679–689.
Manschadi, A., Hochman, Z., Mclean, G., DeVoil, P., Holzworth, D., Meinke, H., 2006. In: APSIM-Barley Model–Adaptation of a Wheat Model to Simulate Barley Growth and Development, 13th Australian Agronomy Conference. Perth, Western Australia.
Martens, H., Martens, M., 2000. Modified Jack-knife estimation of parameter uncertainty in bilinear modelling by partial least squares regression (PLSR). Food Qual. Prefer. 11, 5–16.
Miralles, D.J., Richards, R.A., 2000. Responses of leaf and tiller emergence and primordium initiation in wheat and barley to interchanged photoperiod. Ann. Bot. 85, 655–663.
Otter-Nacke, S., Ritchie, J., Godwin, D., Singh, U., 1991. A Users Guide to CERES Barley v. 2.10. International Fertilizer Development Center, Muscle Shoals, AL.
Perry, M., Siddique, K., Wallace, J., 1987. Predicting phenological development for Australian wheats. Aust. J. Agric. Res. 38, 809–819.
Porker, K., 2017. Barley Variety Sowing Guide. 2017. Available at. https://grdc.com.au/SA-SowingGuide2017.
Read, B.J., Raman, H., McMichael, G., Chalmers, K.J., Ablett, G.A., Platz, G.J., Raman, R., Genger, R.K., Boyd, W.J.R., Li, C.D., Grime, C.R., Park, R.F., Wallwork, H., Prangnell, R., Lance, R.C.M., 2003. Mapping and QTL analysis of the barley population Sloop × Halcyon. Aust. J. Agric. Res. 54, 1145–1153.
Ren, X.F., Li, C.D., Boyd, W.J.R., Westcott, S., Grime, C.R., Sun, D.F., Lance, R., 2010. QTLs and their interaction determining different heading dates of barley in Australia and China. Crop Pasture Sci. 61, 145–152.
Richards, R.A., 1991. Crop improvement for temperate australia - future opportunities. Field Crops Res. 26, 141–169.
Roberts, E.H., Summerfield, R.J., Cooper, J.P., Ellis, R.H., 1988. Environmental-control of flowering in barley (hordeum-vulgare-l) .1. Photoperiod limits to long-day responses, photoperiod-insensitive phases and effects of low-temperature and short-day vernalization. Ann. Bot. 62, 127–144.
Sadras, V., Reynolds, M., De la Vega, A., Petrie, P., Robinson, R., 2009. Phenotypic plasticity of yield and phenology in wheat, sunflower and grapevine. Field Crops Res. 110, 242–250.
Sadras, V.O., Richards, R.A., 2014. Improvement of crop yield in dry environments: benchmarks, levels of organisation and the role of nitrogen. J. Exp. Bot. 65, 1981–1995.
Sadras, V.O., Slafer, G.A., 2012. Environmental modulation of yield components in cereals: heritabilities reveal a hierarchy of phenotypic plasticities. Field Crops Res. 127, 215–224.
Slafer, G.A., Araus, J.L., Royo, C., Del Moral, L.F.G., 2005. Promising eco-physiological traits for genetic improvement of cereal yields in Mediterranean environments. Ann. Appl. Biol. 146, 61–70.
Trione, E.J., Metzger, R.J., 1970. Wheat and barley vernalization in a precise temperature Gradient1. Crop Sci. 10, 390–392.
Uptmoor, R., Pillen, K., Matschegewski, C., 2016. Combining genome-wide prediction and a phenology model to simulate heading date in spring barley. Field Crops Res.
Waddington, S.R., Cartwright, P.M., Wall, P.C., 1983. A quantitative scale of spike initial and pistil development in barley and wheat. Ann. Bot. 51, 119–130.
Wang, J.Y., 1960. A critique of the heat unit approach to plant response studies. Ecology 41, 785–790.
Wold, H., 1966. In: Krishnaiaah, P.R. (Ed.), Estimation of Principal Components and Related Models by Iterative Least Squares. Multivariate Analysis. Academic Press, New York 1966.
Wold, S., Sjöström, M., Eriksson, L., 2001. PLS-regression: a basic tool of chemometrics. Chemom. Intell. Lab. Syst. 58, 109–130.
Xu, Y., 2016. Envirotyping for deciphering environmental impacts on crop plants. Theor. Appl. Genet. 129, 653–673.
Yin, X., Struik, P.C., Tang, J., Qi, C., Liu, T., 2005a. Model analysis of flowering phenology in recombinant inbred lines of barley. J. Exp. Bot. 56, 959–965.
Yin, X., Struik, P.C., van Eeuwijk, F.A., Stam, P., Tang, J., 2005b. QTL analysis and QTL-based prediction of flowering phenology in recombinant inbred lines of barley. J. Exp. Bot. 56, 967–976.
Zadoks, J.C., Chang, T.T., Konzak, C.F., 1974. A decimal code for the growth stages of cereals. Weed Res. 14, 415–421.