Using a crop model to characterise the developmental phenotype of different wheat varieties.

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Abstract

Correct characterisation of vernalisation and photoperiod sensitivity is necessary for accurately quantifying the developmental phenotype of wheat varieties. In this paper the APSIM wheat models phenology routines were used as a framework to quantify the development phenotype of common New Zealand and Australian wheat varieties. Flowering data from 39 sowing dates over 10 years (between March and December) was used to determine vernalisation and photoperiod sensitivity coefficients (*VS* and *PPS*, respectively) that control the duration from sowing to flowering. Firstly, each variety was assigned a value for *VS*; 0 for spring type wheats that flowered regardless of sowing date, 5 for winter types that showed no signs of stem elongation when sown later than the 1 August and, 3 for intermediate types that showed no signs of stem elongation following a 1 October sowing. Then optimisation was used (with assigned *VS* values) to determine *PPS* values that gave the best fit with observed flowering dates. This gave *PPS* values ranging from 3 – 5. The procedure gave good agreement between observed and predicted flowering dates for all 52 varieties. However, analysis of the thermal time from flag leaf to flowering showed a clear photoperiod response in this phase. Photoperiod sensitivity in APSIM wheat ends at terminal spikelet which precedes flag leaf. So although APSIM was able to give accurate estimations of flowering date the mechanism for producing these estimates was not entirely correct. The analysis also gave *VS* and *PPS* values for Australian varieties that differed substantially from those currently used in APSIM suggesting there is a need to assess the generic relevance of the mechanisms underlying this flowering model.

Key Words
APSIM, Flowering, Photoperiod, Vernalisation, Wheat.

Introduction
Simulation models are useful tools for analysing farm systems, identifying and demonstrating improved management practices and providing a framework for understanding genotype by environment interactions of specific crop types. To be useful in such applications the mechanism of the models prediction must accurately represent reality and model coefficients must be easily quantifiable. Flowering date predictions are important to all simulation models as it determines the environmental conditions that grain growth occurs in and so has a large effect on predictions of yield. This paper focuses on the prediction of flowering date in wheat using the APSIM wheat model. The APSIM model (http://www.apsim.info/Wiki/Wheat.ashx) is based on the CERES wheat model with development characterised by a series of stages; Sowing, Germination, Emergence, Terminal Spikelet, Flowering, Start of Grainfill and End of Grainfill. The time from sowing to germination is dependent on soil moisture and time from germination to emergence depends on soil temperature and sowing depth. Subsequent phases are fixed thermal time (*Tt*) targets so their duration is dependent on temperature. *Tt* increases linearly with temperature between base (0 °C) and optimal (25 °C) temperatures and then decreases linearly from optimal to maximum temperature (35 °C). The stage from Emergence to Terminal Spikelet is 400 °Cd but, vernalisation and photoperiod (*PP*) influence the rate of Tt accumulation by multiplying daily Tt by the minimum of a vernalisation and photoperiod effect (*VernEff* and *PPeff*, respectively). *VernEff* is calculated from accumulated vernal days (*ΣVD*) and a variety specific vernalisation sensitivity (*VS*) coefficient (Equation 1).

Equation 1. $VernEff = 1 - VS \times (50 - \Sigma VD)$

Where 50 is the maximum vernalisation requirement and *VD* is calculated daily from crown temperatures. No *VD* is accumulated at temperatures below 0 °C or above 15 °C. Within this temperature range One *VD* will be accumulated each day if crown temperature is 2 °C and this decreases linearly to 0 at 0 and 15 °C. *PPeff* is calculated daily from *PP* and a variety specific *PP* sensitivity (*PPS*) coefficient (Equation 2).

Equation 2. $PPEff = 1 - PPS \times 0.002 \times (20 - PP)^2$

Where 20 is a maximum photoperiod, beyond which no further response occurs. Values of *VS* and *PPS* range from 0 – 5. Varieties with a *VS* and *PPS* of 0 will simply take 400 °Cd to reach terminal spikelet and

as *VS* and *PPS* values are increased, the *Tt* required to reach will increase whenever *PP* is less than 20 and crown temperature is not 2 °C. Therefore the accuracy of the prediction of flowering time is dependent on assigning appropriate values of *VS* and *PPS* for different varieties. The Objective of this paper is to quantify values of *VS* and *PPS* for common New Zealand and Australian wheat varieties and determine the accuracy of the APSIM wheat model to predict flowering dates in New Zealand.

Methods
Wheat material and Flowering data
Each year from 2002 to 2012 a range of wheat varieties planted in autumn (March or April), winter (May or June), early spring (September) and late spring (November) at Lincoln New Zealand. Each year varieties 'Amarok', 'Claire' and 'Otane' were sown on each sowing date as reference varieties along with new varieties and breeding lines. Each new variety is included in the phenology trials for at least 3 consecutive years. Flowering and Flag leaf ligule appearance dates are observed and recorded for each sowing date. Recently a number of common Australian varieties have also been included in the trials.
Quantifying VS and PPS coefficients
Although the model enables the setting of non-integer *VS* values anywhere between 0 and 5 the density of data for most varieties was not sufficient to enable fine separation of *VS* so varieties were separated into three groups; Spring type's where those that flowered regardless of their time of sowing (see Figure 1a for examples). Intermediate types were those that did not flower for planting dates later that 1 October (an arbitrary date chosen to enable separation). Winter types were those that did not flower for sowing dates after the 1 August. A *VS* value of 0, 3 and 5 was assigned to each of these groups respectively.
An optimisation procedure was then used to quantify the *PPS* for each variety. Different hypothetical varieties representing the complete combination of *VS* (0, 3 and 5) and *PPS* (0, 1, 2, 3, 4, 5) were run for each sowing date. A spread sheet was set up to compare observed flowering dates for each variety with those predicted for the different hypothetical varieties. The appropriate *VS* value determined from the procedure outlined above was given for each variety and then the *PPS* coefficient was changed to determine which value gave the best agreement between observed and predicted flowering dates. While this was a manual process it worked very well and the appropriate value for *PPS* was always clear (e.g. Figure lb).
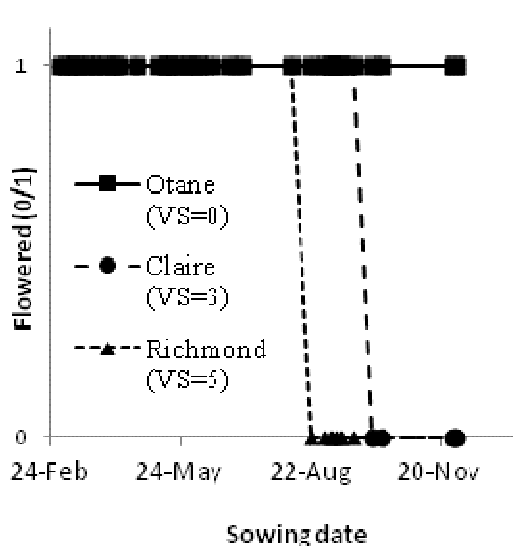

Figure 1a. Plot of Flowering (0 = no Flowering, 1 = Flowering) against sowing date for three varieties of differing vernalisation sensitivities (*VS*).
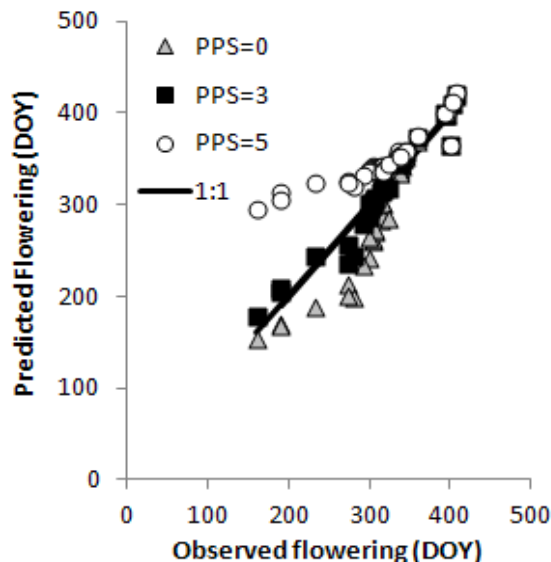
Figure 1b. Plot of observed vs predicted Flowering dates for Otane wheat with photoperiod sensitivities (*PPS*) of 0, 3 and 5)

Results
In general the agreement between observed flowering date and that predicted following the procedure to quantify *VS* and *PPS* was good with R^2 values for regressions of observed Vs predicted ranging from 0.79 to 0.99. In the majority of cases these regressions had a slope close to 1 and an intercept close to zero. However, in some instances there was a non-zero intercept suggesting there may be some varietal variation

in either the *Tt* target from Emergence to Terminal Spikelet or from Terminal Spikelet to Flowering. Other varieties had both a non-zero intercept and a slope that differed from 1 suggesting finer separation was required in the *VS* values used or some deficiency in the models mechanism. Of the 63 varieties analysed, similar numbers were assigned to each of the three *VS* groupings and *PPS* values fitted to these varieties ranged from 3 – 5 (Table 1).

Table 1. Number of flowering date observations (Obs No) and fitted photoperiod sensitivities (*PPS*) for each variety. Varieties are separated into 3 groups depending on the vernalisation sensitivities (*VS*) assigned. Varieties marked with * are Australian. 1 = Spring Isoline, 2 = Winter Isoline.

| | *VS* = 0 | | | *VS* = 3 | | | *VS* = 5 | |
Variety	Obs No	PPS	Variety	Obs No	PPS	Variety	Obs No	PPS
Otane	35	3	Saracen	12	5	Aspiring	15	3
Janz*	8	4	Mackellar*	8	4	Richmond	12	3
Lang*	8	4	Amarok	43	4	KWW-31	10	3
Sunco*	8	4	Morph	8	4	Solstice	13	3
Rubric	8	4	Alberic	12	4	Einstein	11	3
H45*	8	4	Macro	10	4	Regency	14	4
Tribute	14	4	Vanquish	8	5	Centaur	13	4
Yitpi*	8	4	Robigus	12	5	Marshall	8	4
Raffles	7	4	Option	12	5	Hilton	11	4
Kohika	8	4	Claire	42	5	Equinox	12	4
Monad	9	4	KWW-7	8	5	Savanah	12	4
Torlesse	8	4	KWW-34	8	5	Wakanui	12	4
Commando	6	4	KWW-38	8	5	Weston	13	4
Conquest	16	4	2000116	12	5	KWW-29	7	4
Bakker Gold	7	4	Oakley	8	5	CFR03-195	10	4
Domino	9	5	Batten[2]	8	5	CFR03-196	10	4
Batten[1]	8	5	Buster	7	5	Exceed	12	4
Sage	11	5				Pennant	13	4
Endeavour	7	5				Genghis	8	4
Majestic	8	5				Consort	9	4
McCubbin*	8	5				Tanker	12	5

The *Tt* accumulated between flag leaf appearance and flowering (*Tt_FL-F*) ranged from 150 – 600 °Cd and there was a clear pattern between *Tt_FL-F* and the *PP* on the day of flag leaf appearance. An example of this relationship is shown for some vernalisation insensitive varieties in Figure 2a. Otane was the only variety that flowered at *PP* below 11 h and at these photoperiods the *Tt_FL-F* was 200 °Cd. This showed a sudden increase to 500 °Cd at 11 h *PP* and then a linear decrease to 200 again at 16 h *PP* (Figure 2a). Regression analysis showed a linear reduction ($p<0.001$) in *Tt_FL-F* as photoperiod increased and that there was no difference ($p=0.483$) in the slope of this relationship between varieties. There was variation in the intercept of the regression with varieties with a higher *PPS* having a higher intercept.

Discussion
The APSIM wheat model could be parameterized to predict flowering date with reasonable accuracy. The *VS* and *PPS* coefficients presented for the New Zealand varieties in Table 1 are included in APSIM 7.4 and can be used for predicting the performance of wheat crops in New Zealand. The method used proved suitable for quantifying developmental coefficients and the wide range of sowing dates over which observations were recorded enabled good estimates of these coefficients. Although the model could be fitted to work with adequate accuracy in NZ this exercise raised some issues that question how well the models mechanism represent the actual response of wheat development to environment. In particular the model only accounts for the effects of photoperiod during the development phase from Emergence to Terminal Spikelet. However, the results presented (Figure 2a) show there was substantial photoperiod response in *Tt_FL-F*. APSIM wheat does not predict the time from flag leaf to flowering explicitly, rather it is part of the phase

from "Terminal Spikelet to Flowering. However, flag leaf appearance occurs approximately 3 phyllochrons after terminal spikelet (Jamieson et al. 2007) so the duration from Terminal Spikelet to Flowering will be $Tt\_FL\text{-}F + 300\,°Cd$ and would show the same photoperiod response as $Tt\_FL\text{-}F$ (Figure 2b). Thus, it is not strictly correct to fit all of the crops flowering response to photoperiod into the phase preceding Terminal Spikelet when some of it is actually happening in the subsequent phase.
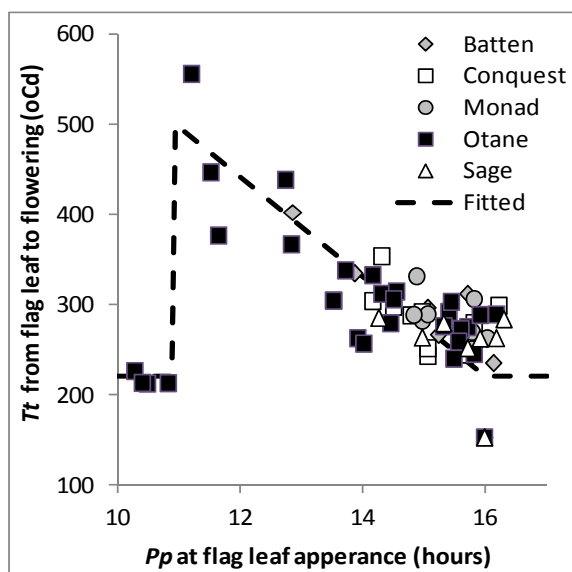

Figure 2a. Thermal time accumulated between the time of flag leaf appearance and Flowering in relation to photoperiod on the day of flag leaf appearance.
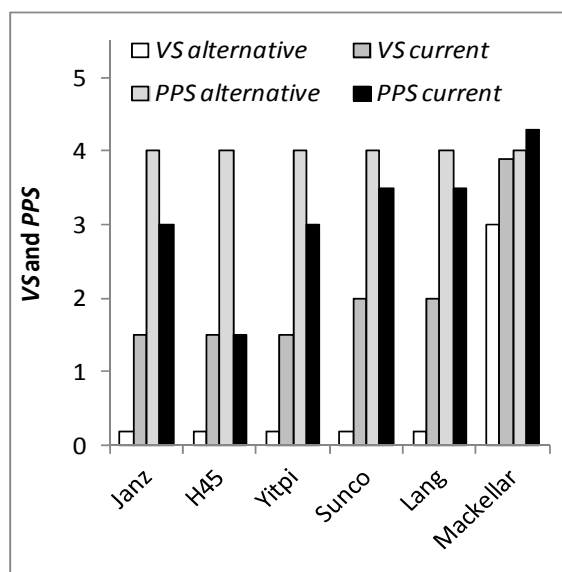
Figure 2b. Vernalisation (*VS*) and Photoperiod (*PPS*) sensitivity coefficients for Australian wheat varieties both currently used in APSIM and the alternative values determined by the fitting exercise detailed in this paper.

Furthermore, the *VS* and *PPS* coefficients determined for Australian wheat varieties were different to those values currently assigned to those varieties in APSIM (Table 2). When the current APSIM coefficients were used for these varieties there was poor agreement between observed and predicted values. The disagreement between the incumbent coefficient values and those quantified in this paper could be due to two reasons. 1. Incumbent coefficients were quantified with data from a narrow range of photoperiod and temperature conditions and did provide a robust quantification of coefficient values. 2. That the models mechanisms are not generically applicable so different coefficient values are obtained when they are quantified in different environments. We could not determine the cause of the difference between the two sets of coefficients but this highlights some important considerations in the use of a model to quantify phenology of a crop. To have confidence that model coefficients provide a suitable representation of a varieties developmental phenotype firstly we need to have a suitable process and a sufficiently broad set of observed data to determine model coefficients with a high level of confidence. Secondly, to have confidence in the generic applicability of these coefficients the underlying model must also be generically applicable. To achieve this, the model must be based on sound principals and be tested and verified with detailed developmental data from a wide range of situations. The results presented here suggest if APSIM wheat is to be used as a framework for studying the development of wheat and provide coefficients for linking to genotype data the models mechanisms should be reviewed.

Conclusion
The procedure used to quantify *VS* and *PPS* gave good agreement between observed and predicted flowering dates. However, further analysis showed *PP* response in phases following Terminal Spikelet and also showed *VS* and *PPS* values for Australian varieties that differed substantially from those currently used in APSIM suggesting there is a need to review this phenology model.

Reference
Jamieson P D, Brooking I R, Semenov M A, McMaster G S, White J W and Porter J R 2007 Reconciling alternative models of phenological development in winter wheat. Field Crops Research 103, 36-41.