Modeling Final Leaf Number and Anthesis Date in the Wheat Simulation Model *SiriusQuality*2

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Responding to environmental factors the apical meristem of the wheat shoot switches from a vegetative phase where it produces leaf primordia to a reproductive phase where it produces floral primordia. The successive appearance of leaves on the main-stem and tillers is the expression of the vegetative development, while anthesis is a particular stage in the reproductive development of wheat plants. Vegetative and reproductive development are coordinated and overlap in time (Kirby, 1990; Hay & Kirby, 1991), so that much of the reproductive development occurs early in unison with vegetative development. This means that, as far as timing of events is concerned, vegetative and reproductive processes are not independent. Within this framework, in the phenology model proposed by (Jamieson *et al.*, 1998), the variations associated with vernalization requirement and daylength sensitivity are described in terms of primordium initiation, leaf production, and final main-stem leaf number. The duration of three developmental phases are simulated. First, the pre-emergence phase (sowing to emergence) is simulated as a fixed duration in thermal time which may differ between cultivars (Dse; parameter definitions and values are given in Table 1; Weir *et al.*, 1984). Second, the leaf production phase from crop emergence to flag leaf appearance integrates the effects of vernalization and photoperiod. Third, the duration of the flag leaf ligule appearance-anthesis phase is proportional to the phyllochron ($t_{\text{flag}}^{\text{anth}}$) (Brooking *et al.*, 1995). The equations describing the leaf production phase implemented in *Siriusquality*2 (Martre *et al.*, 2006; Martre *et al.*, 2008) are described below.

The leaf production phase is modeled based on two independently controlled processes, leaf initiation (primordia formation) and emergence (leaf tip appearance) rates and organ identity defining the fate of the apex primordia whether vegetative or floral. The interaction between these processes leads to the determination of the final number of leaves (LN_f) that will be produced on the main-stem. Thermal time since emergence (T_t) is calculated with a base temperature of 0°C. Initially the controlling temperature (apex temperature) is assumed to be that of the near soil surface (0-2 cm), and then that of the canopy after Haun stage 4 ($L_{\text{max}}^{\text{soil}}$). Sirius calculates near soil surface temperature and canopy temperature based on the surface energy balance as described by (Jamieson *et al.*, 1995).

Leaf production follows a segmented linear model in thermal time (Boone *et al.*, 1990; Jamieson *et al.*, 1995; Slafer & Rawson, 1997; González *et al.*, 2002). The first two leaves appear more rapidly than the next six, and then leaf appearance slows again for the subsequent leaves independently of the total number of leaves produced:

$$\mathrm{LN} = \begin{cases} \mathrm{Phyll}_{\mathrm{decr}} \times \mathrm{Phyll}_{\mathrm{SD}} \times T_{\mathrm{t}}, & \mathrm{LN} < L_{\mathrm{decr}} \\ \mathrm{Phyll}_{\mathrm{SD}} \times T_{\mathrm{t}}, & L_{\mathrm{decr}} \le \mathrm{LN} < L_{\mathrm{incr}} \\ \mathrm{Phyll}_{\mathrm{incr}} \times \mathrm{Phyll}_{\mathrm{SD}} \times T_{\mathrm{t}}, & \mathrm{LN} \ge L_{\mathrm{incr}} \end{cases} \tag{1}$$

where LN is the actual number of visible leaves on the main-stem (equivalent to the Haun stage); T_{t} is the thermal time accumulated by the apex since emergence; $\mathrm{Phyll}_{\mathrm{SD}}$ is the phyllochron from Haun stages 2 to 8 modified for the sowing date; $\mathrm{Phyll}_{\mathrm{decr}}$ is a factor decreasing the phyllochron for leaf number less than L_{decr}; $\mathrm{Phyll}_{\mathrm{decr}}$ is a factor increasing the phyllochron for leaf number higher than or equal to L_{incr}; L_{decr} is the Haun stage up to which Phyll is decreased by $\mathrm{Phyll}_{\mathrm{decr}}$; and L_{incr} is the Haun stage above which Phyll is increased by $\mathrm{Phyll}_{\mathrm{incr}}$. Many studies have shown that phyllochron depends on the sowing date, several authors have discussed putative physiological causes of theses variations (Slafer & Rawson, 1997; McMaster *et al.*, 2003); while others have shown that most of the observed variations in phyllochron are due to apex-air temperature differences (Vinocur & Ritchie, 2001; Jamieson *et al.*, 2008). In Sirius, as a surrogate for the apex-air temperature correction, for a winter sowing (day of the year 1 to 90 for the Northern hemisphere), the phyllochron decreases linearly with the sowing date and is minimum until mid-July for the Northern hemisphere (day of the year 200):

$$\mathrm{Phyll}_{\mathrm{SD}} = \begin{cases} \mathrm{Phyll} \times \left(1 - R_{\mathrm{P}} \times \min\left(\mathrm{SD}, \mathrm{SD}_{\mathrm{W/S}}\right)\right), & \mathrm{SD} > \mathrm{SD}_{\mathrm{S/A}} \\ \mathrm{Phyll}, & 1 \le \mathrm{SD} \le \mathrm{SD}_{\mathrm{S/A}} \end{cases} \tag{2}$$

where SD is the sowing date in day of the year; Phyll is a varietal parameter defining the phyllochron for autumn sowing; R_{P} is the rate of decrease of $\mathrm{Phyll}_{\mathrm{SD}}$ for winter sowing; $\mathrm{SD}_{\mathrm{W/S}}$ and $\mathrm{SD}_{\mathrm{S/A}}$ are the sowing dates for which P_{SD} is minimum and maximum, respectively.

At any time during vegetative development apex primordia number (PN) is calculated through a simple metric relationship with leaf number (Kirby, 1990) under the assumption that the apex contains four primordia at emergence and that they accumulate at twice the rate of leaf emergence (Brooking *et al.*, 1995; Jamieson *et al.*, 1995):

$$\mathrm{PN} = 2 \times \mathrm{LN} + 4 \tag{3}$$

Concomitant processes governing apical progress towards a reproductive state and defining LN_{f} (i.e. vernalization requirements and photoperiodic responses) are modeled sequentially. Vernalization commences once the seed has imbibed water. The daily vernalization rate (V_{rate}) increases at a constant rate (VAI) with daily mean soil or canopy temperature from its value (VBEE) at the minimum vernalizing temperature ($T_{\mathrm{min}}^{\mathrm{ver}}$) to a maximum for an intermediate temperature ($T_{\mathrm{int}}^{\mathrm{ver}}$). Above this temperature V_{rate} reduces to zero at the maximum vernalizing temperature ($T_{\max}^{\text{ver}}$).

Previous work indicates that the vernalization requirement of some winter wheat genotypes can be eliminated or greatly reduced by a prolonged exposure to short photoperiods (Evans, 1987; Dubcovsky *et al.*, 2006), a process referred in the literature as short day vernalization. The vernalizing effect of short days was introduced in *SiriusQuality*2. The photoperiodic effect on the vernalization rate is likely to involve a quantitative interaction with temperature rather than a complete replacement of the vernalization requirement (Brooking & Jamieson, 2002; Allard *et al.*, 2012). It is modelled following Sirius vernalization framework, with the assumption that the effectiveness of short days decreases progressively as photoperiods increases from $\mathrm{DL}_{\min}^{\text{ver}}$ (set at 8 h) to $\mathrm{DL}_{\max}^{\text{ver}}$ (set at 15 h):

$$V_{\text{rate}} = \times\begin{cases} \mathrm{VAI}\times T_{\text{t}} + \mathrm{VBEE}, & T_{\min}^{\text{ver}} \le T_{\text{t}} \le T_{\text{int}}^{\text{ver}} \\ \max\left(\begin{matrix} 0,\left(\mathrm{VAI}\times T_{\text{int}}^{\text{ver}} + \mathrm{VBEE}\right) \\ \times\left(1+\dfrac{\left(T_{\text{int}}^{\text{ver}} - T_{\text{t}}\right)}{\left(T_{\max}^{\text{ver}} - T_{\text{int}}^{\text{ver}}\right)}\times\dfrac{\left(\mathrm{DL}_{\text{eff}}^{\text{ver}} - \mathrm{DL}_{\min}^{\text{ver}}\right)}{\left(\mathrm{DL}_{\max}^{\text{ver}} - \mathrm{DL}_{\min}^{\text{ver}}\right)}\right)\end{matrix}\right), & T_{\text{int}}^{\text{ver}} < T_{\text{t}} \le T_{\max}^{\text{ver}} \end{cases} \tag{4}$$

where

$$\mathrm{DL}_{\text{eff}}^{\text{vern}} = \max\left(\mathrm{DL}_{\min}^{\text{vern}}, \min\left(\mathrm{DL}_{\max}^{\text{vern}}, \mathrm{DL}\right)\right) \tag{5}$$

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The photoperiodic effect on the vernalization rate is likely to involve a quantitative interaction with temperature rather than a complete replacement of the vernalization requirement (Brooking & Jamieson, 2002; Allard *et al.*, 2012). It is modelled following Sirius vernalization framework, with the assumption that the effectiveness of short days decreases progressively as photoperiods increases from $\mathrm{DL}_{\min}^{\text{ver}}$ (set at 8 h) to $\mathrm{DL}_{\max}^{\text{ver}}$ (set at 15 h):

where VAI and VBEE are two varietal parameters (Table 1). The progress toward full vernalization (V_{prog}) is simulated as a time integral:

$$V_{\text{prog}} = \sum_{\text{day}=1}^{n} V_{\text{rate}}, \quad \text{with} \quad V_{\text{prog}} \in [0,1] \tag{6}$$

Two varietal parameters define the minimum ($L_{\text{min}}^{\text{abs}}$) and maximum ($L_{\text{max}}^{\text{abs}}$) number of leaves that can emerge on the main-stem. The model assumes that plants start their lives with a high potential leaf number (LN_{pot} set to an initial value of $L_{\text{max}}^{\text{abs}}$) which decreases with vernalization progress:

$$\text{LN}_{\text{pot}} = L_{\text{max}}^{\text{abs}} - \left(L_{\text{max}}^{\text{abs}} - L_{\text{min}}^{\text{abs}}\right) \times V_{\text{prog}} \tag{7}$$

Vernalization is completed when one of three conditions is met. Either V_{prog} has reached a value of 1, LN_{pot} has reached a value that equals $L_{\text{min}}^{\text{abs}}$, or LN_{pot} has reduced to PN. These primordia are all assumed to produce leaves.

The crop responds to daylength (DL) only once vernalization is complete (or at emergence for a spring cultivar for which the vernalization routine is skipped). It is assumed that DL sensitivity leads to an increase in the number of leaf primordia resulting from the vernalization routine. DL is calculated following the treatment of Sellers (1965) with a correction for atmospheric refraction equivalent to 50'. If DL of the day when vernalization is completed exceeds a given value (DL_{sat}), then LN_f is set to the value calculated at the end of the vernalization routine (Brooking *et al.*, 1995). For DL shorter than DL_{sat}, Brooking *et al.* (1995) have shown that LN_f is determined by DL at the stage of two leaves after the flag leaf primordium has formed. This creates the need for an iterative calculation of an approximate final leaf number (LN_{app}) that stops when the required leaf stage is reached:

$$\text{LN}_{\text{app}} = \max\left(\text{LN}_{\text{pot}}, \text{LN}_{\text{pot}} + \text{SLDL} \times \left(\text{DL}_{\text{sat}} - \text{DL}\right)\right) \tag{8}$$

where SLDL is a varietal parameter defining the daylength response as a linear function of DL. The attainment of the stage “two leaves after flag leaf primordium” is reached when half of leaves have emerged (Brooking *et al.*, 1995):

$$\text{if} \;\; 0.5 \times \text{LN}_{\text{app}} \le \text{LN}, \quad \text{then} \;\; \text{LN}_{\text{f}} = \text{LN}_{\text{app}} \tag{9}$$

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Table 1
Name, symbol, definition, nominal, minimal, and maximal value and unit of the non-varietal and varietal parameters of Sirius phenology sub-model.

Name	Symbol	Definition	Value			Unit
			Nominal	Min	Max	
Non-varietal parameters						
MaxDL	DL_{sat}	Saturating photoperiod above which final leaf number is not influenced by daylength	15	_	_	h
MaxDL	DL_{max}^{ver}	Threshold daylength above which it does influence vernalization rate	15	_	_	h
MinDL	DL_{min}^{ver}	Threshold daylength below which it does influence vernalization rate	8	_	_	h
MaxLeafSoil	L_{max}^{soil}	Haun stage up to which thermal time is calculated based on soil temperature (0-2 cm deep)	4	_	_	leaf
Ldecr	L_{decr}	Haun stage up to which Phyll is decreased by $Phyll_{decr}$	2	_	_	leaf
Lincr	L_{incr}	Haun stage above which Phyll is increased by $Phyll_{incr}$	8	_	_	leaf
Pdecr	$Phyll_{decr}$	Factor decreasing the phyllochron for leaf number less than L_{decr}	0.75	_	_	dimensionless
Pincr	$Phyll_{incr}$	Factor increasing the phyllochron for leaf number higher than or equal to L_{incr}	1.25	_	_	dimensionless
Rp	R_P	Rate of decrease of the P_{SD} for winter sowing	0.003	_	_	°Cd d^{-1}
PFLLAnth	t_{flag}^{anth}	Phyllochronic duration of the period between flag leaf ligule appearance and anthesis	1.39	_	_	phyllochron
SDWS	$SD_{W/S}$	Sowing date for which P_{SD} is minimum	90	-	-	day of the year
SDSA	$SD_{S/A}$	Sowing date for which P_{SD} is maximum	200	-	-	day of the year
IntTvern	T_{int}^{ver}	Intermediate temperature for vernalization to occur	8	_	_	°C
MaxTvern	T_{max}^{ver}	Maximum temperature for vernalization to occur	17	_	_	°C

MinTvern	T_{min}^{ver}	Minimum temperature for vernalization to occur	0	_	_	°C
Varietal parameters						
Dse	D_{se}	Thermal time from sowing to emergence	175	100	250	°Cd

Table 1. (cont.)

AMXLFNO	L_{max}^{abs}	Absolute maximum leaf number	24	13	28	leaf
AMNLFNO	L_{min}^{abs}	Absolute minimum possible leaf number	5.5	4	11	leaf
Phyll	Phyll	Phyllochron	100	70	150	°Cd
SLDL	SLDL	Daylength response of leaf production	0.15	0	3	leaf h^{-1} (daylength)
VAI	VAI	Response of vernalization rate to temperature	0.001	0	0.01	d^{-1} °C^{-1}
VBEE	VBEE	Vernalization rate at temperature equal to T_{min}^{ver}	0.01	0	2	d^{-1}