Modeling Final Leaf Number and Anthesis Date in the Wheat Simulation Model *SiriusQuality2*

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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 *SiriusQuality2* (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 ($T_{\text{max}}^{\text{min}}$). 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:

$$\begin{align*}
\text{LN} &= \begin{cases} 
\text{Phyll}_{\text{decr}} \times \text{Phyll}_{\text{SD}} \times T_t, & \text{LN} < L_{\text{decr}} \\
\text{Phyll}_{\text{SD}} \times T_t, & L_{\text{decr}} \leq \text{LN} < L_{\text{incr}} \\
\text{Phyll}_{\text{incr}} \times \text{Phyll}_{\text{SD}} \times T_t, & \text{LN} \geq L_{\text{incr}}
\end{cases}
\end{align*}$$

(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; Phyll$_{\text{SD}}$ is the phyllochron from Haun stages 2 to 8 modified for the sowing date; Phyll$_{\text{decr}}$ is a factor decreasing the phyllochron for leaf number less than $L_{\text{decr}}$; Phyll$_{\text{incr}}$ is a factor increasing the phyllochron for leaf number higher than or equal to $L_{\text{incr}}$; $L_{\text{decr}}$ is the Haun stage up to which Phyll is decreased by Phyll$_{\text{decr}}$; and $L_{\text{incr}}$ is the Haun stage above which Phyll is increased by Phyll$_{\text{incr}}$. Many studies have shown that phyllochron depends on the sowing date, several authors have discussed putative physiological causes of these 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):

$$\text{PN} = 2 \times \text{LN} + 4$$

(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 ($V_{\text{rate}}$) increases at a constant rate (VAI) with daily mean soil or canopy temperature from its value (VBEE) at the minimum vernalizing temperature ($T_{\text{ver}}^{\text{min}}$) to a maximum for an intermediate temperature ($T_{\text{ver}}^{\text{int}}$). Above
this temperature \( V_{\text{rate}} \) reduces to zero at the maximum vernalizing temperature \( T_{\text{max}}^{\text{ver}} \).

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 \( DL_{\text{min}}^{\text{ver}} \) (set at 8 h) to \( DL_{\text{max}}^{\text{ver}} \) (set at 15 h):

\[
V_{\text{rate}} = \begin{cases} 
V_{\text{AI}} \times T_{i} + V_{\text{BEE}}, & \text{if } T_{\text{min}}^{\text{ver}} \leq T_{i} \leq T_{\text{int}}^{\text{ver}} \\
\max \left( 0, \left( V_{\text{AI}} \times T_{\text{int}}^{\text{ver}} + V_{\text{BEE}} \right) \right) \times \left( 1 + \frac{T_{\text{int}}^{\text{ver}} - T_{i}}{T_{\text{max}}^{\text{ver}} - T_{\text{int}}^{\text{ver}}} \right) \times \frac{DL_{\text{eff}}^{\text{ver}} - DL_{\text{min}}^{\text{ver}}}{DL_{\text{max}}^{\text{ver}} - DL_{\text{min}}^{\text{ver}}} & \text{if } T_{\text{int}}^{\text{ver}} < T_{i} \leq T_{\text{max}}^{\text{ver}}
\end{cases}
\]  

\[ (4) \]

where

\[
DL_{\text{eff}}^{\text{ver}} = \max \left( DL_{\text{min}}^{\text{ver}}, \min \left( DL_{\text{max}}^{\text{ver}}, DL \right) \right)
\]  

\[ (5) \]

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* V2.0 to improve the simulation of anthesis date in the hot-serial-cereal experiment (White et al., 2011).

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 \( DL_{\text{min}}^{\text{ver}} \) (set at 8 h) to \( DL_{\text{max}}^{\text{ver}} \) (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:

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

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 ($L_{pot}^{\text{abs}}$ set to an initial value of $L_{max}^{\text{abs}}$) which decreases with vernalization progress:

$$L_{pot} = L_{\text{max}}^{\text{abs}} - (L_{\text{max}}^{\text{abs}} - L_{\text{min}}^{\text{abs}}) \times V_{prog} \quad (7)$$

Vernalization is completed when one of three conditions is met. Either $V_{prog}$ has reached a value of 1, $L_{pot}^{\text{abs}}$ has reached a value that equals $L_{\text{min}}^{\text{abs}}$, or $L_{pot}^{\text{abs}}$ 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$_{\text{sat}}$), 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$_{\text{sat}}$, 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:

$$LN_{app} = \max \left( LN_{pot}, LN_{pot} + SLDL \times (DL_{\text{sat}} - DL) \right) \quad (8)$$

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):

if $0.5 \times LN_{app} \leq LN$, then $LN_{f} = LN_{app} \quad (9)$

References


Brooking IR, Jamieson PD. 2002. Temperature and photoperiod response of


**Sellers WD. 1965.** *Physical Climatology*. Chicago, USA: University of Chicago Press.


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

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

### Varietal parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$D_{\text{se}}$</td>
<td>Thermal time from sowing to emergence</td>
<td>°Cd</td>
</tr>
<tr>
<td>$L_{\text{max}}$</td>
<td>Absolute maximum leaf number</td>
<td>leaf</td>
</tr>
<tr>
<td>$L_{\text{min}}$</td>
<td>Absolute minimum possible leaf number</td>
<td>leaf</td>
</tr>
<tr>
<td>Phyll</td>
<td>Phyllochron</td>
<td>°Cd</td>
</tr>
<tr>
<td>SLDL</td>
<td>Daylength response of leaf production</td>
<td>leaf h$^{-1}$ day$^{-1}$</td>
</tr>
<tr>
<td>VAI</td>
<td>Response of vernalization rate to temperature</td>
<td>d$^{-1}$ °C$^{-1}$</td>
</tr>
<tr>
<td>VBEE</td>
<td>Vernalization rate at temperature equal to $T_{\text{ver}}^{\text{min}}$</td>
<td>d$^{-1}$</td>
</tr>
</tbody>
</table>

Table 1. (cont.)