



SQ-Phenology: BioMA-SiriusQuality component of wheat LAI

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Summary

This document describes the procedure used in the *SQ-WheatLAI* crop model component to predict the leaf area development under normal conditions (potential leaf area) and conditions of limited resources (*Martre et al 2018*). The phytomer state (Growing, Mature, Senescing or Dead) is determined, as well. The model is integrated in the wheat crop model *SiriusQuality3* (*Brooking et al 1995; Jamieson et al 1995b; Jamieson et al 1995a; Jamieson et al 1998b*) as an independent component. This component is developed in the public domain software framework *BioMA* (Biophysical Model Applications). BioMA is developed using Microsoft C# language in .Net framework (version 4.5). The component was coded using the development environment Microsoft Visual Studio 2013. A console application is available to enlighten the practical use of the component.



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1. Theoretical background

In (Martre et al 2018), growth coordination rules between wheat plant organs are deciphered to model the dynamics of canopy development. The BioMa component described above is an encapsulation of the key part of *SiriusQuality3* crop model which was used for the study.

In cereal crops, the development of the canopy takes place through the sequential production of leaves on the mainstem and its axillary tillers. There is a strong coordination between the mainstem and its tillers, and between the different leaves depending on their position along the stem and leaf development is dependent on the development of the previous leaf, either on the same tiller or on the mainstem (Bos and Neuteboom, 1998; Tivet et al., 2001; Zhu et al., 2015). Each leaf is composed of a lamina and a sheath enclosing an internode, which with an axillary bud constitute a phytomer. The emergence of the collar (the junction of sheath and lamina) is coordinated with the development of the lamina and internode (Andrieu et al., 2006). Leaf growth is also tightly related to changes in the apical meristem, and thus to flowering time (Brooking and Jamieson, 2002). Therefore, vegetative and reproductive developments are not independent since floral initiation occurs during leaf development and is strongly related to the final number of leaves on the mainstem through a reduction of the duration of the phase of leaf primordia production (Brown et al., 2013) and has a large impact on final leaf size (Borrill, 1959). The precise coordination between the mainstem and its tillers and between successive leaves on an axis have to be considered to model leaf expansive growth at the whole plant level.

The *SQ-WheatLAI* component relies on a unique relationship between lamina area and leaf rank for the mainstem and its tillers. Robust relationships between lamina and sheath areas are also used, highlighting the tight control of organ growth within and between phytomers. While these relationships are identified at the phytomer scale, leaf area dynamics is integrated at the canopy level by mean of cohorts (or leaf layers). The model accurately predicts leaf area dynamics under different scenarios of nitrogen and water limitations (Martre et al 2018).

2. Overview of the calculation procedure

Figure 1 shows the flowchart of the *SQ-WheatLAI* component. It is composed of eight simple strategies and a composite one. Each time a leaf layer appears:

- It is determined if it corresponds to a small phytomer (the phytomers closest to the soil which die first, *Is Small Phytomer*);
- The thermal time duration of expansion of the newly created lamina is calculated (*Laminae Expansion Thermal Time*);
- The thermal time duration of the maturity period of the new phytomer is assessed (*Maturity Thermal Time*);



- The thermal time duration of the phytomer senescence period is fixed (Senescence Thermal Time).

Each day drought stress factors for expansion and senescence are calculated (*Leaf Expansion Drought Factor*), the potential final leaf area index (the surface area of green leaf laminae per unit ground area, *LAI*) is evaluated (*Maximum Potential Final LAI*) and the actual expansion or senescence rates of laminae and sheaths are estimated under drought stress conditions (*Water Limited Leaf expansion*). The state of the leaf layers (Growing, Mature, Senescing, Dead) is also settled. Then the outputs of the component are exported via the composite class to the *SiriusQuality3* core where carbon and nitrogen economics are balanced. When done, another simple strategy is called (*Update Leaf Area*) which updates the *LAI* taking into account the eventual stress caused by nitrogen lake in case of leaf growth. In what follows each section refers to one of the strategies described above.

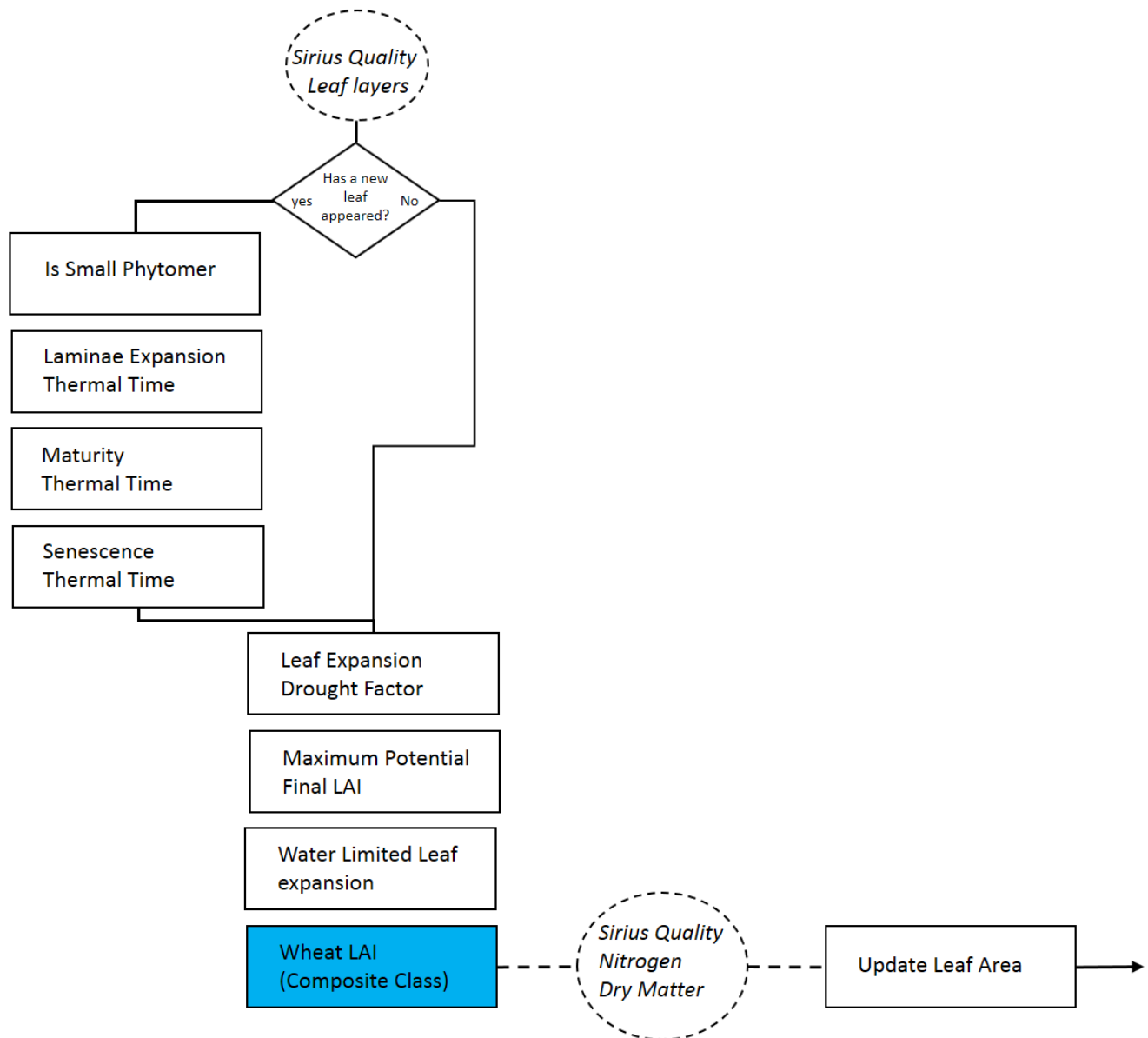


Figure 1. Shema of the BioMA-*SiriusQuality* SQ-WheatLAI component.

3. Determination of small phytomers

Small (or juvenile) phytomers are located at the bottom of the canopy. They are the first to senesce, are supposed to have a constant potential final area (i.e. in the absence of biotic or abiotic limitations) and their allometry is described by a particular set of parameters. A leaf is considered as juvenile when it is produced before floral initiation. The number of leaves produced after floral initiation (larger leaves) is $NLL=6$. Juvenile leaves are located



below the *NLL* first leaves counted basipetally (from the top of the mainstem to the base of the plant).

4. Thermal time duration of the lamina expansion

According to Gallagher (1979), the phyllochronic duration of lamina expansion is constant and closed to 1.1. Based on this result, a unique phyllochronic duration of lamina expansion is considered to model the expansive growth of the laminae of the different leaf ranks and tiller orders. The phyllochronic duration is converted into thermal time (*TTGroLamina*), as follows:

$$TTGroLamina = Phyll_{Layer} \times Pexpl \quad (1)$$

Where $Phyll_{Layer}$ is the plant phyllochron (i.e. the thermal time requirement for the appearance of successive leaf tips on mainstem) when the leaf layer has just appeared. Phyllochron is calculated in the BioMa *SQ-Phenology* component. The *Pexpl* parameter is the number of phyllochron between the appearance of the tip and the collar of leaf *n* above the collar of leaf *n* – 1 (counted from the top to the base of the plant).

5. Thermal time duration of the leaf layer maturity period

As for the duration of the expansive growth period, the potential durations of the period during which the green area of a leaf is unchanged (mature period) is assumed to be constant in phyllochronic time. The duration (in phyllochronic time) of the mature period is longer for large leaves than for juvenile (small) leaves. Phyllochronic durations are converted in thermal time (*TTmat*) as described in the previous section:

$$TTmat = Phyll_{Layer} \times PlagSL \quad (2)$$

With *PlagSL* the phyllochronic duration for small (juvenile) leaves, or:

$$TTmat = Phyll_{Layer} \times PlagLL \quad (3)$$

With *PlagLL* the phyllochronic duration for larger leaves.

6. Thermal time duration of the leaf layer senescence period

The period during which the leaf layer green area regresses due to senescence is assumed to be constant in phyllochronic time. Then the thermal time duration of senescence (*TTsen*) is:

$$TTsen = Phyll_{Layer} \times PsenSL \quad (4)$$

or



$$TT_{sen} = Phyll_{Layer} \times PsenLL \quad (5)$$

Where $PsenLL$, the duration (in phyllochronic time) of the senescence period for the last $NLL=6$ leaves on top of the plant, is larger than $PsenLL$, that of juvenile (small) leaves.

7. Drought stress factors for expansion and senescence periods

In order to account for drought stress on deceleration of leaf expansion or acceleration of leaf senescence, two choking functions are used: DEF for expansion and DSF for senescence. Even if, most of the time, soil available water content drives drought stress effects DEF and DSF factors include also the impact of the Vapor Pressure Deficit (VPD).

7.1. Stress factor for expansion (DEF)

For most crops species, leaf expansion decreases linearly as the fraction of available soil water ($FPAW$, dimensionless) decreases below a threshold value (Meyer and Green, 1981; Robertson and Giunta, 1994; Sadras and Milroy, 1996). Therefore, the soil available water effect (DEF^{FPAW}) is modeled using a bi-linear function:

$$DEF^{FPAW} = \begin{cases} 1 & FPAW > FPAW_{upper}^{exp} \\ \frac{FPAW - FPAW_{lower}^{exp}}{FPAW_{upper}^{exp} - FPAW_{lower}^{exp}} & FPAW_{upper}^{exp} \geq FPAW \geq FPAW_{lower}^{exp} \\ 0 & FPAW < FPAW_{lower}^{exp} \end{cases} \quad (6)$$

It is assumed that the VPD effect can be modeled this way:

$$DF^{VPD} = \frac{\overline{VPD} - VPD_{upper}}{VPD_{lower} - VPD_{upper}} \times \frac{DL}{24} + \left(1 - \frac{DL}{24}\right) \quad (7)$$

With $FPAW_{upper}^{exp}$ (VPD_{upper}) the threshold $FPAW$ (VPD) value at which the stress is minimum, $FPAW_{lower}^{exp}$ (VPD_{lower}) the $FPAW$ (VPD) value at which the stress is maximum and \overline{VPD} the diurnal average of Vapor Pressure deficit. Finally, DEF is obtained by multiplying the two contributions:

$$DEF = DEF^{FPAW} \times DF^{VPD} \quad (8)$$

The potential (i.e. in the absence of biotic or abiotic limitations) daily increase in leaf area index is multiplied by DEF when assessing the actual expansion rate (see section 9). In well-watered condition $DEF=1$ and leaves expand at the maximum allowed by their potential rate. When stress increases, DEF decreases and the elongation is slowed down.



7.2. Stress factor for senescence (*DSF*)

In wheat, heat stress significantly accelerates the rate of leaf ageing and senescence (Wollenweber *et al.*, 2003; Tewolde *et al.*, 2006; Zhao *et al.*, 2007; Eyshi Rezaei *et al.*, 2015; Asseng *et al.*, 2011). In our model this effect was considered by multiplying the daily contribution to the senescence cumulative thermal time (see section 9) by the *DSF* stress factor (Semenov *et al.*, 2009).

$$DSF = \max DF + (1 - \max DF) \times DSF^{FPAW} \quad (9)$$

Where DSF^{FPAW} have the same expression than DEF^{FPAW} , but where $FPAW_{upper}^{exp}$ and $FPAW_{lower}^{exp}$ parameters are replaced by those for senescence: $FPAW_{upper}^{sen}$ and $FPAW_{lower}^{sen}$. The trend of *DSF* is the opposite of that of *DEF*. It is maximum ($\max DF$) under pronounced stress conditions, then, thermal time runs quicker and senescence is accelerated. In the contrary, in well-watered conditions $DSF=1$, leaving the thermal time flow unchanged.

8. Maximum potential final Leaf Area Index

The final area of leaf laminae and light exposed sheaths of the mainstem and axillary tillers in absence of stresses (potential) can be calculated with only five parameters.

8.1. Maximum potential final Lamina Area Index

Observations in (Martre *et al* 2018), have allowed determining a relationship between the lamina area and leaf rank for all the tillers. It is suggested that this relationship may be unique, whatever the sowing date or density and was used to model the potential final lamina area for the different phytomer numbers and tillers (A_L^{pot}). It is assumed that A_L^{pot} of the juvenile leaves (see section 3) is constant ($A_{L_{juv}}^{pot}$, cm²). Then, A_L^{pot} of the different phytomers and tillers was modeled as:

$$A_L^{pot}(i, j) = \begin{cases} A_{L_{juv}}^{pot} & i < N - (NLL - 1) \\ A_{L_{N-1}}^{pot} \times \left(1 - \frac{1}{NLL-1} \times (N - i - 1 + s(j))\right) & N - (NLL - 1) \leq i < N \\ \alpha_{L_N/L_{N-1}} \times A_{L_{N-1}}^{pot} \times \left(s(j) \times \left(1 - \frac{1}{NLL-1}\right)\right) & i = N \end{cases} \quad (10)$$

where i is the phytomer number counted from the base of the plant, j is the tiller order, $A_{L_{N-1}}^{pot}$ (cm²) is the potential final lamina area of the mainstem penultimate leaf, $\alpha_{L_N/L_{N-1}}$ (dimensionless) is the ratio of the



mainstem flag-to-penultimate laminae area and N (leaf) is the final leaf number. In order to account for the increasing delay between the emergence of successive tillers (*Fournier et al., 2003*), the phytomer numbers of axillary tillers have to be shifted by a decimal number (*Evers et al., 2005*). The s function returns the number of phytomers by which the phytomer number of the different tiller order is shifted:

$$s(j) = \begin{cases} 0 & j = 1 \\ 0.35 & j = 2 \\ 0.75 & 2 < j \leq 5 \\ 1.0 & j > 5 \end{cases} \quad (11)$$

8.2. Maximum potential final Exposed Sheath Area Index

To model light interception by leaf sheaths one has to model the area of sheaths between successive leaf collars, which corresponds to the exposed area of the pseudostem (A_{ExpS}^{pot} , cm²) or exposed sheath. This requires modeling the length of the sheaths and internodes for the last leaves with expanded internodes. The area A_{ExpS}^{pot} increases with the phytomer number and a unique relationship links A_{ExpS}^{pot} normalized by $A_{L_{N-1}}^{pot}$ and s . This relationship provides a direct way to model A_{ExpS}^{pot} . In wheat, the beginning of stem extension occurs after floral initiation, approximately at the terminal spikelet stage of development (*Hay, 1978; Hay and Kirby, 1991*) and the final number of elongated internodes is closely related to the number of leaf emerged after the terminal spikelet stage (*Giunta et al., 2001*). This explains why the sheaths area starts to increase approximately one phytomer after that of the laminae:

$$A_{ExpS}^{pot}(i, j) = \begin{cases} A_{S_1}^{pot} & i = 1 \\ 0 & 1 < i \leq N - (NLL - 2) \\ \alpha_{L_N/L_{N-1}} \times A_{L_{N-1}}^{pot} \times \left(s(j) \times \left(1 - \frac{1}{NLL-1} \right) \right) & N - (NLL - 2) < i \leq N \end{cases} \quad (12)$$

where $A_{S_1}^{pot}$ (cm²) is the potential final exposed sheath area of the first leaf. This leaf corresponds to a juvenile phytomer. Others juvenile phytomers have no exposed sheath.

The areas A_L^{pot} and A_{ExpS}^{pot} (in cm²) are further converted in area index (number of square meters of leaf covering one square meter of ground,



$\text{m}^2(\text{leaf})/\text{m}^2(\text{ground})$) by multiplying the surface area (in m^2) of each individual leaf fraction (lamina or exposed sheath) by the density of shoot (mainstem or tillers, shoot/ m^2) bearing the leaf. The contribution of each tiller is then summed up to obtain distinctly the lamina area index or the exposed sheath area index of single phytomers (or leaf layers). In what follows we will consider only final potential area index at the leaf layer level which will be noted $\text{AI}_L^{\text{pot}}(\text{i})$ and $\text{AI}_{\text{ExpS}}^{\text{pot}}(\text{i})$ for lamina and exposed sheath, respectively.

9. Leaf layer state and water limited leaf expansion rates

9.1. Leaf layer state succession

Leaf layers composing the canopy grow, senesce and die. The succession of the states a leaf layer can be in is essentially determined by the thermal time it has accumulated and its actual Green Area Index (*GAI*). The *GAI* corresponds to the area index of the part of the phytomer intercepting radiation. It is the actual lamina area index added to the actual exposed sheath area index.

9.1.1. Thermal times

Thermal time is accumulated by the canopy (*cumulTTShoot*) either during the growth period or the senescence one. *cumulTTShoot* is the sum of the daily integral of thermal time from the sowing day to the current date. This daily integral is defined for developmental and expansive growth ($\Delta T_{t,\text{exp}}^{\text{canopy}}$, °Cday) or for leaf ageing and senescence ($\Delta T_{t,\text{sen}}^{\text{canopy}}$, °Cdays). One or the other of these quantities enters in the *cumulTTShoot* calculation depending on the state of the leaf layer. Both $\Delta T_{t,\text{exp}}^{\text{canopy}}$ and $\Delta T_{t,\text{sen}}^{\text{canopy}}$ are outputs fromd.

9.1.1.1. Physiological thermal time for developmental and expansive growth

The daily integral of thermal time for developmental and expansive growth ($\Delta T_{t,\text{exp}}^{\text{canopy}}$, °Cday) is obtained from the daily minimum ($T_{\text{min}}^{\text{canopy}}$) and maximum ($T_{\text{max}}^{\text{canopy}}$) canopy temperatures which are calculated using an energy balance (see forthcoming BioMa SQ-*EnergyBalance* component) assuming neutral atmospheric stability approach (Jamieson et al., 1995). Each day, eight contributions of a cosinusoidal variation between $T_{\text{min}}^{\text{canopy}}$ and $T_{\text{max}}^{\text{canopy}}$ modified from (Weir et al., 1984) are summed leading to $\Delta T_{t,\text{exp}}^{\text{canopy}}$ value:

$$\Delta T_{t,\text{exp}}^{\text{canopy}} = \frac{1}{8} \sum_{r=1}^{r=8} (T_{\text{opt}} \times f(T_h^{\text{canopy}})) \quad (13)$$

where

$$T_h^{canopy} = \max(T_{min}, T_{min}^{canopy} + f_r(r) \times (T_{max}^{canopy} - T_{min}^{canopy})) \quad (14)$$

and

$$f_r(r) = \frac{1}{2} \left(1 + \cos \left(\frac{90}{8} \right) \times (2 \times r - 1) \right) \quad (15)$$

where T_{min} and T_{opt} (°C) are the minimum (base) and optimum temperatures for leaf development and expansive growth, $f(T)$ (dimensionless) is the temperature response function for leaf development and expansive growth, T_h^{canopy} (°C) is the calculated 3-hourly canopy temperature contribution to estimated daily mean canopy temperature, and f_r (dimensionless) is the fraction that each 3-h period during the day contributes to the thermal time for that day, r is the array index of the item.

Recent studies showed that all developmental and expansive growth processes follow a common curvilinear response to temperature after normalization by a common reference temperature (*Parent et al., 2010; Parent and Tardieu, 2012; Wang et al., 2017*). To model the temperature response of leaf growth we use the non-linear temperature function proposed by (*Wang and Engel, 1998*):

$$f(T) = \begin{cases} \frac{2 \times (T_h^{canopy}(r) - T_{min})^\alpha \times (T_{opt} - T_{min})^\alpha - (T_h^{canopy}(r) - T_{min})^{2\alpha}}{(T_{opt} - T_{min})^{2\alpha}} & T_h^{canopy}(r) < T_{max} \\ 0 & T_h^{canopy}(r) \geq T_{max} \end{cases} \quad (16)$$

where

$$\alpha = \frac{\ln(2)}{\ln \left(\frac{T_{max} - T_{min}}{T_{opt} - T_{min}} \right)} \quad (17)$$

where T_{max} (°C) is the maximum canopy temperature for leaf development and expansive growth. Equation (9-10) simulates the effect [0-1] of temperature between T_{min} and T_{max} and is used with the same cardinal temperature values to model the duration of expansion and the rate of leaf appearance.



9.1.1.2. Physiological thermal time for ageing and senescence processes

The daily integral of thermal time for leaf ageing and senescence ($\Delta T_{t, \text{sen}}^{\text{canopy}}$, °Cdays) accounts for the shortening of the mature and senescence phases caused by heat. The 3-hourly canopy temperatures used to calculate the duration of these two leaf ontogenic phases are multiplied by an accelerated leaf senescence factor (R_i^L , dimensionless) which increases linearly from 1 when T_h^{canopy} exceeds a threshold temperature (T^L , °C) (Stratonovitch and Semenov, 2015):

$$\Delta T_{t, \text{sen}}^{\text{canopy}} = \frac{1}{8} \sum_{r=1}^{r=8} (R^L(r) \times T_h^{\text{canopy}}(r) - T_{\text{min}}) \quad (18)$$

$$R^L(r) = (1 + \max(0, T_h^{\text{canopy}}(r) - T^L) \times S^L) \quad (19)$$

where S^L (°C⁻¹) is the slope of the senescence acceleration per unit of canopy temperature above T^L .

9.1.1.3. Thermal time at the layer level

Physiological thermal time is defined at the layer level as follows:

- The thermal time accumulated by the canopy (*cumulTTShoot*) since the mainstem emergence is assigned to each leaf layer at its creation (*TTem*);
- The thermal time accumulated by a single leaf layer (*TT*) corresponds to the sum of $\Delta T_{t, \text{exp}}^{\text{canopy}}$, or $\Delta T_{t, \text{exp}}^{\text{canopy}}$ (depending on the leaf's state) values from the layer emergence date to the current date;

In addition, assuming that the relative rate of expansion with thermal time is the same for the laminae and the sheaths, the duration of sheath expansion above the collar of the preceding leaf is calculated as a fraction of that of the lamina (see section 4), the fraction being the ratio of maximum potential final area indexes (see section 8.2):

$$\text{TTgroSheath}(i) = \text{TTgroLamina}(i) \times \frac{\text{AI}_{\text{ExpS}}^{\text{pot}}(i)}{\text{AI}_L^{\text{pot}}(i)} \quad (20)$$



The total growth duration (in thermal time) for a particular leaf layer is then:

$$TT_{gro}(i) = TT_{groLamina}(i) + TT_{groSheath}(i) \quad (21)$$

9.1.2. Leaf layer states

A leaf layer can successively be in four states:

- It is expanding (*GAI* increases) while the thermal time accumulated by the layer has not exceeded the leaf growth duration (see section 4):

$$TT \leq TT_{gro} + TT_{em} \quad (22)$$

- It is mature (*GAI* remains constant) while the thermal time accumulated by the layer has not exceeded the maturity duration (see section 5):

$$TT_{gro} + TT_{em} < TT < TT_{gro} + TT_{em} + TT_{mat} \quad (23)$$

- It is senescing (*GAI* decreases) from the end of the maturity phase until the end of the senescence period (see section 6):

$$TT_{gro} + TT_{em} + TT_{mat} \leq TT < TT_{gro} + TT_{em} + TT_{mat} + TT_{sen} \quad (24)$$

If the lamina content in photosynthetically active nitrogen (g/m^2) is lower than the minimum amount (SLN_{min} , g/m^2) at which the plant photosynthesis stops (null Light Use Efficiency), the leaf is considered as prematurely dying and the start of its senescence period is triggered.

- A leaf layer is dead once its Green Area Index (*GAI*) becomes equal to zero.

In addition, the case when the lamina is growing is disentangle from the case the exposed sheath is doing. The priority is given to the lamina which is expanding when:

$$TT \leq TT_{groLamina} + TT_{em} \quad (25)$$

The exposed sheath starts only to expand when the lamina growth has stopped and continues until the end of its own expansion period:

$$TT_{groLamina} + TT_{em} < TT \leq TT_{groSheath} + TT_{em} \quad (26)$$



9.2. Expansion and senescence rates under drought stress

The length of wheat leaf laminae increases (expansion) almost linearly after emergence of the tip of the leaf above the whorl of subtending leaves until the appearance of the leaf collar, after which it decreases rapidly (senescence) (Gallagher, 1979; Fournier et al., 2005). When normalized by their mature length and plotted against phyllochronic time centered on the time of leaf tip emergence, a unique kinetic of leaf expansion is observed for all the leaf and tiller ranks (Fournier et al., 2005). The daily expansion and senescence rates ($\Delta AI^{exp}(i)$, $\Delta AI^{sen}(i)$, $m^2(\text{leaf})/(m^2(\text{ground})\text{day})$) can thus be calculated layer by layer as follows:

- The daily lamina expansion rate is proportional to its potential final area index (AI_L^{pot}). The area index fraction corresponds to the daily increase in growth thermal time ($\Delta T_{t,exp}^{canopy}$) to the duration of the expanding period ($TT_{groLamina}$) ratio. The rate is calculated for each phytomer (leaf layer) identified by a number of appeared tips on the mainstem (i):

$$\Delta AI^{exp}(i) = AI_L^{pot}(i) \times \frac{\Delta T_{t,exp}^{canopy}}{TT_{groLamina}(i)} \quad (27)$$

- Similarly, the daily expansion rate of the exposed sheath is:

$$\Delta AI^{exp}(i) = AI_{ExpS}^{pot}(i) \times \frac{\Delta T_{t,exp}^{canopy}}{TT_{groSheath}(i)} \quad (28)$$

Expansion rates are limited in a way the daily increase in area index cannot exceed the potential final area index.

- The daily decrease in area index follows the same proportionality rules in relative daily thermal time increase. But, the senescence period is now considered and it is assumed that the area index loss ranges between the actual green area index of the day (GAI) and the largest GAI achieved so far ($maxGAI$):

$$\Delta AI^{sen}(i) = -\max(maxGAI(i) \times \frac{\Delta T_{t,sen}^{canopy} \times DSF}{TT_{sen}(i)}, GAI(i)) \quad (29)$$

Where the senescence stress factor DSF is described in section 7.2.

The expansion rate is integrated daily at the canopy level (ΔAI_{pot}^{exp}) by summing the contribution of each leaf layer for:



$$\Delta AI_{pot}^{exp} = \sum_i \Delta AI^{exp}(i) \quad (30)$$

The expansion rate ΔAI^{exp} can either be that of lamina or that of exposed sheaths depending of which part of the leaf is growing (lamina growth first, then exposed sheaths, see section 9.1.2)

The effect of drought stress is then applied to obtained the water-stressed change in area index at the canopy level (ΔAI_w^{exp}):

$$\Delta AI_w^{exp} = DEF \times \Delta AI_{pot}^{exp} \quad (31)$$

With the expansion stress factor, DEF , described in section 7.1.

10. Leaf area index update

10.1. Actual expansion under nitrogen limitation

Expanding grass leaves require a minimum nitrogen content and do not store nitrogen during their growth period (*Gastal and Lemaire, 2002*), and it was shown that the area-based leaf nitrogen mass of light exposed part of expanding leaves is constant and independent of the N status of the crop (*van Oosterom et al., 2010*). Based on these results, in our model leaf expansion is reduced if there is not enough nitrogen available in the plant to maintain a critical area-based leaf nitrogen mass (N_{cri}^{LA} , g N cm⁻² leaf). The water and nitrogen limited daily increase in green area index at the canopy level (ΔAI , m² leaf m⁻² ground) is thus calculated as:

$$\Delta AI = \min \left(\Delta AI_w^{exp}, \frac{N_{plant}^{av}}{N_{cri}^{LA}} \right) \quad (32)$$

where N_{plant}^{ava} (g N m⁻² ground) is the mass of labile (remobilizable) N in the crop. The mass of labile N is calculated as the total mass of N in the crop minus the mass of structural N and plus N taken from the soil. The concentration of structural N is constant and is different for internodes (3×10^{-3} g N g⁻¹ DM) and leaves (5×10^{-3} g N g⁻¹ DM; *Martre et al., 2006*).

Finally, the water and nitrogen limited daily rate of expansion of each growing leaf lamina (ΔA_L) and sheath (ΔA_{ExpS}) is calculated according to their potential expansion rate and the water and nitrogen limited rate of expansion of the whole canopy:

$$\Delta AI_L(i) = \frac{\Delta AI}{\Delta AI_{pot}^{exp}} \times AI_L^{pot}(i) \quad (33)$$

and



$$\Delta AI_{ExpS}(i) = \frac{\Delta AI_{exp}}{\Delta AI_{pot}} \times AI_{ExpS}^{pot}(i) \quad (34)$$

10.2. Actual area index decrease due to senescence

The loss in area index for a given lamina or exposed sheath is obtained by multiplying the leaf variation $\Delta AI^{sen}(i)$ (see section 9.2) by the ratio of the actual Lamina Area Index ($LAI(i)$) or Exposed Sheath Area Index ($ESAI(i)$) to the total Green Area Index of the layer ($GAI(i)$):

$$\Delta AI_L^{sen}(i) = \frac{LAI(i)}{GAI(i)} \times \Delta AI^{sen}(i) \quad (35)$$

and

$$\Delta AI_{ExpS}^{sen}(i) = \frac{ESAI(i)}{GAI(i)} \times \Delta AI^{sen}(i) \quad (36)$$

The last step of the calculation before moving to the next day, is to update the Lamina Area Index and Exposed Sheath Area Index of each layer accordingly to the daily variations estimated above (expansion or senescence) and to calculate the GAI and $maxGAI$ layer by layer or at the canopy level.

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12. Appendix

Table A1. List of variables used in *SQ-WheatLAI* component.

Symbol	Name in the code	Unit	Description	Equation	Strategy
$TT_{groLamina}$	TTGroLamina	°Cd	Thermal time duration of the leaf layer expansion phase	(1)(20)(21)(25)(27)	<i>LaminaExpansionThermalTime</i> <i>WaterLimitedLeafExpansion</i>
$Phyll_{layer}$	Phyllochron	Leaf/°Cd	Phyllochron of the leaf layer	(1)(2)(3)(4)(5)	<i>LaminaExpansionThermalTime</i> <i>MaturityThermalTime</i> <i>SenescenceThermalTime</i>
TT_{mat}	TTmat	°Cd	Thermal time duration between the expansion and the senescence phase for a leaf layer	(2)(3)(23)(24)	<i>MaturityThermalTime</i> <i>WaterLimitedLeafExpansion</i>
TT_{sen}	TTsen	°Cd	Thermal time duration of the leaf layer senescence phase	(4)(5)(24)(29)	<i>SenescenceThermalTime</i> <i>WaterLimitedLeafExpansion</i>
DEF^{FPAW}	-	-	Choking function for soil available water effect stress on leaf expansion	(6)(8)	<i>LeafExpansionDroughtFactor</i>
DF^{VPD}	-	-	Choking function for Vapor Pressure Deficit effect stress on leaf expansion and senescence	(7)(8)	<i>LeafExpansionDroughtFactor</i>



SQ-WheatLAI

\overline{VPD}	avHourVPDDay	kPa	Diurnal average of Vapor Pressure Deficit	(7)	LeafExpansionDroughtFactor
DL	dayLength	h	Number of hour during the diurnal period	(7)	LeafExpansionDroughtFactor
DEF	DEF	-	Chocking function for drought stress effect on leaf expansion	(8)(31)	LeafExpansionDroughtFactor WaterLimitedLeafExpansion
DSF	DSF	-	Chocking function for drought stress effect on leaf senescence	(9)(29)	LeafExpansionDroughtFactor WaterLimitedLeafExpansion
VPD	VPDairCanopy	hPa	Vapor Pressure Deficit between air and canopy	(7)	LeafExpansionDroughtFactor
$FPAW$	FPAW	-	Fraction of soil Available Water	(6)	LeafExpansionDroughtFactor
N	roundedFinalLeafNumber	leaf	Final leaf number	(10)(12)	MaximumPotentialFinalLAI
i	PhytoNum	—	Number of leaf tips emerged on mainstem	(10)(11)(12) (20)(21)(27) (28)(29)(30) (33)(34)(35) (36)	MaximumPotentialFinalLAI
j	tillerIndex	—	Tiller order	(10)(11)(12)	MaximumPotentialFinalLAI
A_L^{pot}	-	cm ²	Lamina final potential area	(10)	MaximumPotentialFinalLAI
A_{ExpS}^{pot}	-	cm ²	Exposed sheath final potential area	(12)	MaximumPotentialFinalLAI



SQ-WheatLAI

$\Delta T_{t,exp}^{canopy}$	deltaTTShoot	$^{\circ}\text{Cd}$	Daily integral of physiological thermal time for canopy growth	(13)(27)(28)	<i>WaterLimitedLeafExpansion</i>
T_h^{canopy}	-	$^{\circ}\text{C}$	Calculated 3-hourly canopy temperature contribution to estimated daily mean canopy temperature	(13)(14)(16) (18)(19)	-
f	-	-	Temperature response of leaf growth	(13)(16)	-
T_{min}^{canopy}	-	$^{\circ}\text{C}$	Daily minimum canopy temperature	(14)	-
T_{max}^{canopy}	-	$^{\circ}\text{C}$	Daily maximum canopy temperature	(14)	-
f_r	-	-	Fraction that each 3-h period during the day contributes to the thermal time for that day	(14)(15)	-
$\Delta T_{t,sen}^{canopy}$	deltaTTSenescence	$^{\circ}\text{Cd}$	Daily integral of physiological thermal time for canopy senescence	(18)(29)	<i>WaterLimitedLeafExpansion</i>
R^L	-	-	Factor for leaf senescence acceleration	(18)(19)	-
$TTem$	TTem	$^{\circ}\text{Cd}$	Cummul of physiological thermal time from sowing to a leaf layer emergence	(22)(23)(24) (25)(26)	<i>WaterLimitedLeafExpansion</i>
TT	TT	Cd	Cummul of physiological thermal time from a leaf layer emergence to the current date	(22)(23)(24) (25)(26)	<i>WaterLimitedLeafExpansion</i>
$TTgroSheath$	TTgroSheathList	$^{\circ}\text{Cd}$	Thermal time duration of a exposed sheath expansion	(20)(21)(26) (28)	<i>WaterLimitedLeafExpansion</i>
$TTgro$	TTgro	$^{\circ}\text{Cd}$	Thermal time duration of a leaf layer expansion	(21)(22)(23) (24)	<i>WaterLimitedLeafExpansion</i>



SQ-WheatLAI

AI_L^{pot}	MaximumPotentialLaminaeAI	$m^2(leaf)/m^2(ground)$	Maximum final potential area index of lamina	(20)(27)(33)	MaximumPotentialFinalLAI WaterLimitedLeafExpansion
AI_{ExpS}^{pot}	MaximumPotentialSheathAI	$m^2(leaf)/m^2(ground)$	Maximum final potential area index of exposed sheaths	(20)(28)(34)	MaximumPotentialFinalLAI WaterLimitedLeafExpansion
ΔAI^{exp}	WaterLimitedPotDeltaAIList	$m^2(leaf)/m^2(ground)/d$	Daily area index expansion rate of lamina or exposed sheaths	(27)(28)(30)	WaterLimitedLeafExpansion
ΔAI^{sen}	WaterLimitedPotDeltaAIList	$m^2(leaf)/m^2(ground)/d$	Daily area index senescence rate of the leaf	(29)(35)(36)	WaterLimitedLeafExpansion
$maxGAI$	MaxAI	$m^2(leaf)/m^2(ground)$	Maximum leaf Green Area Index Achieve the current since leaf emergence to the current day	(29)	WaterLimitedLeafExpansion UpdateLeafArea
GAI		$m^2(leaf)/m^2(ground)$	Leaf Green Area Index of the day		WaterLimitedLeafExpansion UpdateLeafArea
ΔAI_{pot}^{exp}	potentialIncDeltaArea	$m^2(leaf)/m^2(ground)$	Daily potential expansion rate at the canopy level	(30)(31)(33)(34)	WaterLimitedLeafExpansion UpdateLeafArea
ΔAI_w^{exp}	incDeltaAreaLimitSF	$m^2(leaf)/m^2(ground)$	Daily expansion rate at the canopy level under drought stress	(31)(32)	WaterLimitedLeafExpansion UpdateLeafArea
ΔAI		$m^2(leaf)/m^2(ground)$	Daily actual canopy expansion rate (under drought and nitrogen lake stresses)	(32)(33)(34)	UpdateLeafArea



SQ-WheatLAI

N_{plant}^{av}	availableN	g N cm ⁻² leaf	Daily plant labile nitrogen (remobilizable) content	(32)	UpdateLeafArea
ΔAI_L	deltaAI	m ² (leaf)/m ² (ground)	Daily actual lamina expansion rate (at the leaf level and under drought and nitrogen lake stresses)	(33)	UpdateLeafArea
ΔAI_{ExpS}	deltaAI	m ² (leaf)/m ² (ground)	Daily actual exposed sheath expansion rate (at the leaf level and under drought and nitrogen lake stresses)	(34)	UpdateLeafArea
ΔAI_L^{sen}	leafLaminaeDec	m ² (leaf)/m ² (ground)	Daily actual lamina senescence rate (at the leaf level and under drought)	(35)	UpdateLeafArea
ΔAI_{ExpS}^{sen}	exposedSheathDec	m ² (leaf)/m ² (ground)	Daily actual exposed sheath senescence rate (at the leaf level and under drought stress)	(36)	UpdateLeafArea
GAI	GAI	m ² (leaf)/m ² (ground)	Green Area Index at the leaf level	(29)(35)(36)	UpdateLeafArea
LAI	LaminaAI	m ² (leaf)/m ² (ground)	Lamina Area Index at the leaf level	(35)	UpdateLeafArea
ESAI	SheathAI	m ² (leaf)/m ² (ground)	Exposed Sheath Area Index at the leaf level	(36)	UpdateLeafArea



Table A2: List of parameters and constants used in the *SQ-WheatLAI* component. Parameter values are given for winter wheat and Soisson variety. When nothing is indicated, a Non-varietal parameter is considered.

Symbol	Name in the code	Nominal value	Unit	Description	Equation	Reference
<i>Pexpl</i>	Pexpl	1.1	Phyllochron	Phyllochronic duration of lamina expansion (varietal)	(1)	Gallagher et al. (1979)
<i>PlagSL</i>	PlagSL	4	Phyllochron	Phyllochronic duration between the end of expansion and the beginning of senescence for the juvenile leaves (varietal)	(2)	Lawless et al. (2005)
<i>PlagLL</i>	PlagLL	8.5	Phyllochron	Phyllochronic duration between the end of expansion and the beginning of senescence for the mature leaves (varietal)	(3)	Bogard et al. (2011); Gaju et al. (2014)
<i>PsenSL</i>	PsenSL	3.3	Phyllochron	Phyllochronic duration of the senescence period for the juvenile leaves (varietal)	(4)	Lawless et al. (2005)
<i>PsenLL</i>	PsenLL	4.5	Phyllochron	Phyllochronic duration of the senescence period for the mature leaves (varietal)	(5)	Bogard et al. (2011); Gaju et al. (2014)
<i>FPAW^{exp}_{upper}</i>	UpperFPAWexp	0.55	-	Threshold fraction of soil available water (FPAW) value at which the rate of leaf expansion starts to decrease (Varietal)	(9)	Robertson and Giunta (1994)



SQ-WheatLAI

$FPAW_{upper}^{sen}$	UpperFPAWsen	0.5	-	Threshold FPAW value at which the rate of leaf senescence is accelerated		Mitchell et al. (2001); Semenov et al. (2009)
$FPAW_{lower}^{exp}$	LowerFPAWexp	0.1	-	FPAW value at which the rate of leaf expansion equals to zero (varietal)	(6)	Robertson and Giunta (1994)
$FPAW_{lower}^{sen}$	LowerFPAWsen	0.1	-	FPAW value at which the maximum value of leaf senescence acceleration (DSF_{max}) is reached	(9)	Semenov et al. (2009)
VPD_{upper}	UpperVPD	45	-	Threshold fraction of Vapor Pressure Deficit (VPD) value at which the rate of leaf expansion starts to decrease or the rate of leaf senescence starts to increase	(7)	-
VPD_{lower}	LowerVPD	15	-	VPD value at which the rate of leaf expansion equals to zero or where no effect is observed on senescence	(7)	-
$maxDF$	MaxDSF	3.4	-	Maximum value of the drought stress factor for leaf senescence	(9)	Martre et al. (2015)
NLL	NLL	4.5	leaf	x-intercept of the final lamina areas to ($N - i$) relationship for the mainstem mature leaves (varietal)	(10)(12)	Martre et al (2018)
$A_{L_{N-1}}^{pot}$	AreaPL	30	cm ² /leaf	Potential final lamina area of the mainstem penultimate leaf (varietal)	(10)(12)	Martre et al (2018)
$A_{L_{juv}}^{pot}$	AreaSL	2.5	cm ² /leaf	Potential final lamina area of the mainstem juvenile leaves (varietal)	(10)	Martre et al (2018)
$A_{S_s}^{pot}$	AreaSS	1.83	leaf	Potential final sheath area of the mainstem juvenile (varietal)	(12)	Martre et al (2018)



SQ-WheatLAI

s	ShiftTiller	See Eq.11	Phytomer	Phytomer shifts for primary tillers	(10)(11)(12)	Martre et al (2018)
$\alpha_{L_N/L_{N-1}}$	RatioFLPL	1.0	-	Ratio of the mainstem flag-to-penultimate laminae area (varietal)	(10)(12)	Martre et al (2018)
T_{opt}	-	27.5	°C	Optimum temperature for leaf development and expansive growth	(13)(16)(17)	Parent and Tardieu (2012); Wang et al. (2017)
T_{min}	-	0	°C	Minimum temperature for leaf development and expansive growth	(14)(16)(17)(18)	Parent and Tardieu (2012); Wang et al. (2017)
T_{max}	-	40	°C	Maximum temperature for leaf development and expansive growth	(16)(17)	Parent and Tardieu (2012); Wang et al. (2017)
S^L	-	0.11	1/°C	The slope of the senescence acceleration per unit of canopy temperature above T^L	(19)	Stratonovitch and Semenov (2015)
T^L	-	30	°Cd	Threshold of canopy temperature at which leaf ageing and senescence is acceleration	(19)	Eyshi Rezaei et al. (2015); Maiorano et al. (2017)
N_{cri}^{LA}	SLNcri	1.5	g N m ⁻² leaf	Critical area-based nitrogen mass for leaf expansion	(32)	Bertheloot et al. (2012); Moreau et al. (2012)