



Sirius Quality: BioMa Maize LAI Component

**Loïc Manceau, Sébastien Lacube, Boris Parent,
François Tardieu**

LEPSE, Univ. Montpellier, INRA, Montpellier SupAgro, Montpellier, France
(loic.manceau@inra.fr; <http://www1.clermont.inra.fr/siriusquality/>)

Documentation version	component version	Last modified on	Component status	Licence
1.0	1.0	17/05/2018	Release	MIT (X11)

How to cite: Manceau L, Lacube S, Parent B, Tardieu F (2019) SQ-MaizeLAI: BioMA-SiriusQuality component of maize LAI. [doi:10.5281/zenodo.3569347](https://doi.org/10.5281/zenodo.3569347).

Summary

This document describes the procedure used in the *SQ-MaizeLAI* crop model component to predict the leaf area development of individual leaves, adapted to a large range of maize hybrids in contrasted fields. The model describes the several phases of individual leaf development, potential expansion rate (elongation and widening) and responses to environmental conditions based on genetic parameters which can be determined in phenotyping platforms. 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.



Contents

Summary	1
1. Theoretical background.....	3
2. Overview of the calculation procedure.....	4
3. Decimal fraction of the haun-stage for final leaf number.....	6
4. Leaf expansion rate of leaf six.....	6
5. Rank scaling coefficient of expansion rate	7
6. Thermal time when leaf tips emerge	8
7. Thermal time when leaf ligules appear	8
8. Thermal time at floral initiation	9
9. Thermal time when expansion starts.....	9
10. Thermal time when leaves are fully expanded.....	10
11. Base width of leaves (without radiation effect)	10
12. Thermal time when enlargement of leaves starts.....	11
13. Thermal time when enlargement of leaves stops	11
14. Leaf state and expansion in Leaf Area Index	11
14.1. Leaf state	11
14.2. Leaf Area Index.....	11
14.3. Increase in Leaf Area Index	14
15. Leaf area index update (Actual expansion under nitrogen limitation).....	14
16. References.....	15
17. Appendix.....	17



1. Theoretical background

This new model of leaf development and expansion was developed for hundreds of genotypes in a large range of environmental scenarios, and provides novel ways for integrating the effect of the genetic variability of flowering time on the progression of leaf area. It can be considered that the model is based on a considerable amount of data for both establishment and test. This model allows one to simulate the leaf dimensions of all leaves of a wide range of genotypes under contrasting environmental conditions (Lacube et al. 2019).

The model is based on ten genetic parameters (genotype-dependent) that can be measured at high throughput in a phenotyping platform.

Progress thru development phases of all leaves were formalized based on destructive measurements in the field (Lacube et al. 2019) with a special effort for linking all phases which are not directly observable non-destructively (e.g. beginning of elongation ...) to those easily observable (e.g. leaf tip appearance). First, the thermal time when leaves begin to elongate is linked to that of leaf tip appearance. In the same way, the end of leaf elongation is related to the thermal time at ligule appearance. The time course of leaf elongation follows similar patterns for all leaves with linear increase between beginning and end of elongation. Therefore, the time courses are approximated by three-domain linear curves. Leaf length is considered as null in a first domain, as equal to the maximum leaf length in the third domain, and to follow a linear increase in the intermediate domain. This linear increase is consistent with the constant leaf elongation rate measured in a phenotyping platform (Dignat et al., 2013) and with the anatomy of the elongating zone in maize leaves (Tardieu et al., 2000).

The reference profiles of leaf elongation rate, is dependent on genotype and leaf rank. The profile is formalized by a beta function with parameters depending on final leaf number (which is a genotypic parameter) and a genotype-specific effect considered via the leaf 6 reference.

The environmental controls of elongation rate of monocotyledon leaves have been extensively studied (Tardieu et al., 2018) together with the effect of temperature (Parent and Tardieu, 2012) and circadian rhythms (Caldeira et al., 2014). However, the resulting model (Tardieu et al., 2015) cannot be used here because of its number of parameters and the complexity of their measurements which make difficult the description of a large number of hybrids, what is the purpose of the present model.



Hence, it is considered that leaf elongation rate is globally impacted by temperature, evaporative demand and soil water potential, as considered by meta-analysis of different experiments for hundreds of genotypes (Welcker et al., 2011). Notably, neither incident light nor carbon availability for growth were taken into account (Lacube et al., 2017; Salah and Tardieu, 1996). During the period of elongation, the elongation rate of any growing leaf during the day is then calculated from that of leaf 6, the profile of normalized leaf elongation rate and the effects of evaporative demand and soil water potential.

The timing of leaf widening is closely related to that of elongation. Leaves begin to enlarge when elongation starts but stop before their maximum length has been reached (Lacube et al., 2017). As for elongation rate, the reference profile of leaf width is dependent on genotype and leaf rank via a beta function. The model considered only two genotypic parameters to calculate the width of individual leaves, namely, the final leaf number and the reference width of leaf 6. The environmental effects are taken into account via a sensitivity to intercepted light which is a genotype-dependent parameter. The two last parameters values can be inferred from measurements of one leaf in two conditions of light.

The width and the length of the leaves are finally used to calculate a Leaf Area Index (*LAI*). Nitrogen availability effects are applied separately and integrated to the process which describes the dynamics of the *LAI*. Leaf Area Index calculation and application of nitrogen limitation are specific to *SiriusQuality*.

2. Overview of the calculation procedure

Figure 1 shows the flowchart of the *SQ-MaizeLAI* component. It is composed of fourteen simple strategies and a composite one. The inputs are first imported from the core of *SiriusQuality* to the component. Then state variables for leaf development and expansion are processed.

The final leaf number fraction is first calculated (*calcFracPopn*), then the elongation rate of the leaf 6 (*calcLER*) and the scaling coefficient which is used to calculate elongation rate at other ranks (*calcLERCoeff*). Thermal times of development phases are then calculated: thermal time at leaf tip appearance (*calcTipTT*), ligule appearance (*calcLiguleTT*), floral initiation (*calcInitTT*), beginning of elongation (*calcStartExpTT*) and end (*calcFullyExpTT*).



Next step concerns processes related to leaf widening: base width of the leaves (*calcBaseWidth*, ie. leaf width at base intercepted radiation), thermal time when widening starts (*calcStartEnlargeTT*) and stops (*calcStopEnlargeTT*). Finally, leaf state (growing or mature) and daily increase in Leaf Area Index (*DeltaLAIMaize*) are obtained.

Outputs of the component are exported via the composite class to the *SiriusQuality* core where carbon and nitrogen economics are balanced. Then, another simple strategy is called (*Update Leaf Area*) which updates the Leaf Area Index taking into account the eventual stress caused by lack of nitrogen. In what follows, each section refers to one of the strategies described above.

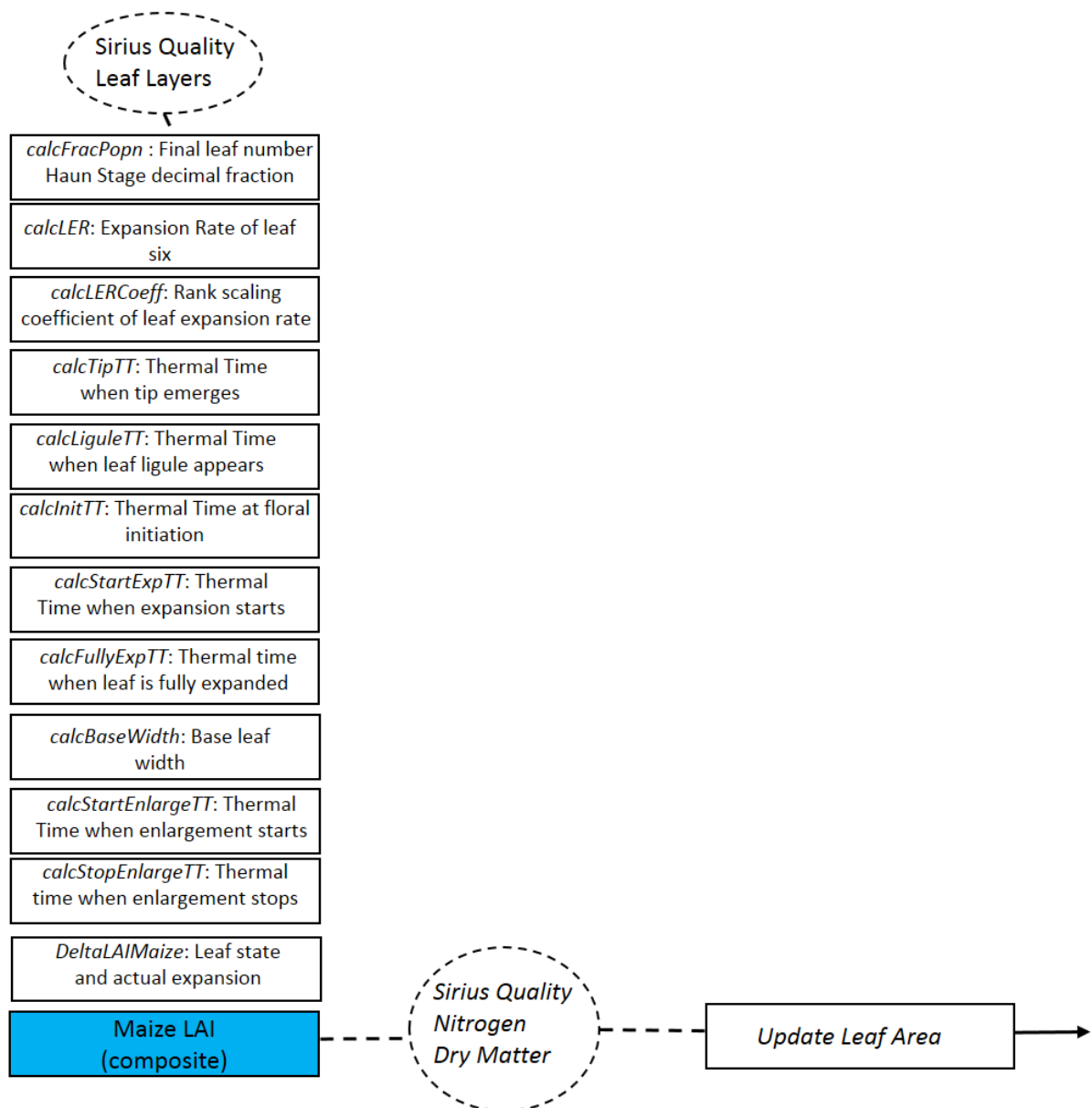




Figure 1. Shema of the BioMA-SiriusQuality SQ-MaizeLAI component. Strategy names are in italic style.

3. Decimal fraction of the haun-stage for final leaf number

Each time a new leaf emerges, a fraction ($f_h(n)$) is assigned to it. If its rank is lower than the final leaf number, then this fraction is equal to 1. If its rank is above the final leaf number (which can be decimal), then the fraction value corresponds to the decimal part of the final leaf number.

4. Leaf expansion rate of leaf six

The model calculates an elongation rate for leaf 6 (counted acropetally) every day by taking into account the environmental conditions. Hourly expansion rate is first calculated:

$$LER_h^6 = (a_6 + b \times VPD_h + c \times \psi) \times \Delta tt_h \quad (1)$$

With parameter a_6 the maximum leaf elongation rate of leaf 6 (in mm/°Cd), parameter b the sensitivity of leaf elongation rate to vapour pressure (in mm/°Cd kPa), parameter c the sensitivity to soil water deficit (in mm/°Cd bars), VPD the hourly vapour pressure deficit air-leaf (kPa) which is calculated in the energy balance BioMa component, ψ the value of soil water potential (MPa) and Δtt_h the hourly increase in thermal time.

Soil water potential (ψ , in bars) is related to the fraction of soil available water ($FPAW$) by a function involving two parameters and limited by a minimum value of -1.5 bars when water is not available in the soil profile ($FPAW < 0.001$):

$$\psi = \begin{cases} -1.5 & FPAW \leq 0.001 \\ \text{Min}(-0.1, -0.0578 + 0.246 \times \ln(FPAW)) & FPAW > 0.001 \end{cases} \quad (2)$$

The hourly increase in thermal time is obtained by correcting the hourly canopy temperature T_{maize} (calculated in the BioMa energy balance component) by the maize physiological response function:

$$\Delta tt_h = \begin{cases} \frac{10}{18} \times T_{maize} & 0 < T_{maize} \leq 18 \\ T_{maize} - 8.0 & 18 < T_{maize} \leq 34 \\ -2.6 \times T_{maize} + 114.4 & 34 < T_{maize} \leq 44 \end{cases} \quad (3)$$

For negative canopy temperatures or temperatures larger than 44°C there is no thermal time increment. Equation (2) can be used to calculate daily increase in thermal time by replacing T_{maize} by its average on 24 hours.

The Leaf expansion rate of the day for leaf 6 (LER^6) is the average of LER_h^6 on 24 hours.

5. Rank scaling coefficient of expansion rate

Leaf number largely affects individual leaf lengths and thus elongation rates. For leaves with rank $n+1$ different of six, the model calculates the coefficient ($LER_{norm}(n)$) representing the ratio of the elongation rate of the considered leaf and elongation rate of leaf 6. $LER_{norm}(n)$ is related to leaf rank with a two-parameter beta function. The two parameters β_L and σ_L (both relative to the maximum leaf number) represent the relative rank of the leaf with the highest growth and the curvature of the function, respectively. The leaf expansion rate is normalized to leaf 6 via the θ_L coefficient.

$$LER_{norm}(n) = \theta_L \times e^{-\frac{(n+1-B_L)^2}{2 \times G_L^2}} \quad (4)$$

With

$$\theta_L = e^{-\frac{(6-B)^2}{2 \times G_L^2}} \quad (5)$$

$$B_L = \beta_L \times N_{final} \quad (6)$$

$$G_L = \sigma_L \times N_{final} \quad (7)$$

N_{final} being the final leaf number as genotypic parameter. $n+1$ represents the number of leaves emerged (counted acropetally from 1 to the final leaf number). In the component leaf rank is counted from 0 to $N_{final} - 1$. Usually, the maximum leaf length is reached at about half of the final leaf number rank.



6. Thermal time when leaf tips emerge

For a leaf of rank n , the physiological thermal time cumulated since sowing to tip appearance ($tt_{tip}(n)$) is calculated from three genotypic parameters. It depends on the phyllochron (thermal time between subsequent leaf tip appearances, a_{tip}), the thermal time of the appearance of the first leaf (b_{tip}) and the thermal time elapsed when plant emerge (Dse).

$$tt_{tip}(n) = \begin{cases} Dse & tt_{elapsed} \leq b_{tip} \\ a_{tip} \times (n + 1) + b_{tip} + Dse & tt_{elapsed} > b_{tip} \end{cases} \quad (8)$$

The variable $tt_{elapsed}$ is the thermal time cumulated since sowing date to the current day.

7. Thermal time when leaf ligules appear

Thermal time from sowing to leaf ligulation is simulated as a bi-linear function, with a breakpoint when N_{liml} leaves have emerged. This leaf rank depends on final leaf number. The first slope (a_{ll1}) is defined as a genotypic value, the second slope (a_{ll2}) is related to the first one with a proportionality factor independent of the genotype (k_{ll}). Both intercepts are calculated given a genotypic parameter (b_{ll1}) representing the thermal time of ligulation of the first leaf since appearance. This formalism simulates the acceleration in ligulation rate after the break point. The physiological thermal time cumulated since sowing to ligulation of the leaf of rank n is then calculated as below:

$$tt_{lig}(n) = \begin{cases} a_{ll1} \times (n + 1) + b_{ll1} + Dse & n + 1 \leq N_{liml} \\ a_{ll2} \times (n + 1) + b_{ll2} + Dse & n + 1 > N_{liml} \end{cases} \quad (9)$$

Where

$$N_{liml} = \alpha_{ll} \times N_{final} \quad (10)$$

Where α_{ll} is the transition parameter (non-genotypic) between the two linear functions relative to N_{final} . And:



$$a_{ll2} = a_{ll1} \times k_{ll} \quad (11)$$

$$b_{ll2} = a_{ll1} \times N_{limll} \times (1 - k_{ll}) + b_{ll1} \quad (12)$$

8. Thermal time at floral initiation

If the rank of the leaf is lower than a threshold parameter N_{emrg_init} , floral initiation occurs at the nominal thermal time from emergence ($tt_{initflo}$), if not, phytomer initiation rate (LIR) is considered:

$$tt_{ini}(n) = \begin{cases} tt_{initflo} & n < N_{emrg_init} \\ tt_{initflo} + \frac{1}{LIR} & n \geq N_{limll} \end{cases} \quad (13)$$

Thermal time at floral initiation is never used elsewhere in the calculation of leaf area, but this information can be useful for other purposes.

9. Thermal time when expansion starts

The beginning of linear elongation occurs simultaneously with leaf tip appearance in the first appeared leaves and then diverged at a common leaf rank (named N_{bl} hereafter, considered non-genotypic and equal to 6), i.e when the tips of the sixth leaf appeared in the whorl. The thermal time of expansion starting for leaf rank larger than N_{bl} is described by a linear function:

$$tt_{star_exp}(n) = \begin{cases} tt_{tip}(n) & n + 1 \leq N_{bl} \\ a_{bl} \times (n + 1) + b_{bl} + Dse & n + 1 > N_{bl} \end{cases} \quad (14)$$

With a slope proportional to the base phyllochron for tip appearance (a_{bl}):

$$a_{bl} = k_{bl} \times a_{tip} \quad (15)$$

and an intercept b_{bl} defined from the parameters described previously:

$$b_{bl} = N_{bl} \times a_{tip} \times (1 - k_{bl}) + b_{tip} \quad (16)$$



10. Thermal time when leaves are fully expanded

After ligule has appeared, a thermal time lag (lag) is applied to determine the cumulated thermal time (since sowing) when the linear elongation of maize leaf stops ($tt_{stop_exp}(n)$). The lag is proportional to the leaf number ($n+1$) via a parameter (a_{lag}):

$$lag = (n + 1) \times a_{lag} \quad (17)$$

The last two leaves (N_{last}) stop elongation simultaneously:

$$tt_{stop_exp}(n) = \begin{cases} tt_{lig}(n) - lag & n \leq N_{final} - N_{last} \\ tt_{stop_exp}(n - 1) & N_{final} - N_{last} < n \end{cases} \quad (18)$$

11. Base width of leaves (without radiation effect)

Leaf number largely affects individual leaf width. Leaf width is most often considered as a genotypic constant at a given leaf rank, and the profile of leaf width along the stem is deduced from that of leaf length. It is shown in (Lacube et al., 2017) that the genetic controls of leaf length and leaf width largely differ. Hence the profile of leaf width along the stem needs to be established for every genotype independently of that of leaf length.

In the same way as for leaf length, we considered a reference profile of leaf width ($W_{base}(n)$), which depends on genotype and leaf rank (n). The genotypic effect was taken into account via the width of leaf 6 (W_6 , in mm). The width profile (which can be considered as a stable trait of a given genotype) is formalized by a beta function, similar to that used for leaf elongation rate, with parameters depending on final leaf number and a genotype-specific effect considered via the reference width of leaf 6:

$$W_{base}(n) = W_6 * e^{\frac{-(n+1) - B_W}{2 * G_W^2}} \quad (19)$$

With

$$B_W = \beta_W * N_{final} \quad (20)$$

$$G_W = \sigma_W * N_{final} \quad (21)$$



Where β_w and G_w determine the rank of the leaf with maximum base width relative to final leaf number and that determining the skewness of the curve, respectively. Usually, the maximum width is located at a leaf rank slightly higher than that of leaf length.

12. Thermal time when enlargement of leaves starts

The time course of leaf widening is similar to that of elongation. It starts at the same time:

$$tt_{start_enl}(n) = tt_{start_exp}(n) \quad (22)$$

13. Thermal time when enlargement of leaves stops

Widening stops before elongation with a thermal time lag (lag_w in °Cd see Lacube et al., 2017):

$$tt_{stop_enl}(n) = tt_{stop_exp}(n) - lag_w \quad (23)$$

The lag is a non-genotypic parameter.

14. Leaf state and expansion in Leaf Area Index

14.1. Leaf state

Two leaf states are considered: Growing and Mature. First, all leaves are growing. They become mature when the thermal time cumulated since sowing date exceeds the thermal time when their individual ligule has appeared.

14.2. Leaf Area Index

As soon as the cumulated thermal time ($tt_{elapsed}$) has reached that of the individual start of leaf expansion ($tt_{start_exp}(n)$) and as long as it does not exceed that of the expansion end ($tt_{stop_exp}(n)$), the length, the width and the exposed area of the day is calculated for each leaf.

14.2.1. Length

Leaf elongation rate at a given time depends on a maximum rate, itself depending on the considered leaf rank and genotype. Environmental effects



(Lacube et al., 2017; Welcker et al., 2011) are included in the maximum leaf elongation rate of leaf 6 (LER^6) which is scaled by $LER_{norm}(n)$ to obtain the elongation rate of the leaf of rank n :

$$LER(n) = \frac{LER^6 \times LER_{norm}(n)}{\Delta tt} \quad (24)$$

With Δtt the thermal time increase of the day. Then the duration in thermal time for daily elongation of leaf of rank n is:

$$\Delta tt_{elong}(n) = \text{Min}(tt_{elapsed} + \Delta tt - tt_{start_exp}(n), tt_{stop_exp}(n) - tt_{elapsed}) \quad (25)$$

Finally, the length of each leaf ($length^{day}(n)$) is calculated from the length of the day before ($length^{day-1}(n)$):

$$length^{day}(n) = length^{day-1}(n) + \Delta length(n) \quad (26)$$

With $\Delta length(n)$ the length increase of the day, obtained by multiplying the elongation rate and the thermal time elapsed since the beginning of elongation:

$$\Delta length(n) = LER(n) \times \Delta tt_{elong}(n) \quad (27)$$

14.2.2. Width

Leaf widths are under environmental control, with a strong positive sensitivity to whole-plant intercepted light and no response to evaporative demand (Lacube et al., 2017). The amount of intercepted radiation (rad_{int} in MJ/day/m²(leaf)) is divided by the plant density (PD) to obtained the mean radiation intercepted by a single plant (rad_{int}^{plant} in MJ/day). The rad_{int}^{plant} contributes each day to the cumulative radiation intercepted (Σrad_{int}^{plant} in MJ). The mean intercepted radiation ($\overline{rad_{int}^{plant}}$ in MJ) is obtained by dividing Σrad_{int}^{plant} by the number of days that has passed since the beginning of expansion of the individual leaf. Mean intercepted radiation is further multiplied by the genotypic sensitivity of leaf widening to intercepted radiation (r_{RAD} in mm/MJ) to obtain the increase in width due to radiation (Δw_{rad}):



$$\Delta w_{rad} = \left(\overline{rad}_{int}^{plant} - RAD_{base} \right) \times r_{RAD} \quad (28)$$

With RAD_{base} the base value for radiation effect on leaf widening as a non-genotypic parameter. For each leaf of rank n the width is calculated as follow:

$$width_{rad}(n) = W_{base}(n) + \Delta w_{rad} \quad (29)$$

14.2.3. Exposed Area

The area of a leaf of rank n ($A(n)$) is:

$$A(n) = length^{day}(n) \times width_{rad}(n) \times Form(n) \quad (30)$$

With $Form(n)$ a form factor taking into account the fact that leaves are not square:

$$Form(n) = 0.5 + r_w(n) \times 0.25 \quad (31)$$

Where r_w^n account for the enlargement progression at a given day during the elongation phase:

$$r_w(n) = \frac{tt_{elapsed} - tt_{start_enl}(n)}{tt_{stop_enl}(n) - tt_{start_enl}(n)} \quad (32)$$

Between leaf tip appearance and ligule appearance, the leaves start to angle, thus exposing progressively their surface. Their exposed area ($A_{exp}(n)$) is:

$$A_{exp}(n) = A(n) \times F_{exp}(n) \quad (33)$$

Where the exposed fraction ($F_{exp}(n)$) is calculated as follow:

$$F_{exp}(n) = f_h(n) \times \frac{tt_{elapsed} + \Delta tt - tt_{tip}(n)}{tt_{lig}(n) - tt_{tip}(n)} \quad (34)$$



14.3. Increase in Leaf Area Index

The potential (without Nitrogen limitation) exposed area of each leaves ($A_{exp}(n)$ in mm^2) is converted into area index ($LAI_{pot}(n)$ in $\text{m}^2(\text{leaf})/\text{m}^2(\text{ground})$):

$$LAI_{pot}(n) = \frac{A_{exp}(n)}{10^6} \times PD \quad (35)$$

With PD the plant density in $\text{plant}/\text{m}^2(\text{ground})$. The coefficient 10^6 converts mm^2 into m^2 .

The total daily increase in Leaf Area Index ($\Delta LAI_{pot}(n)$) is the difference between the $LAI_{pot}(n)$ of the day and that of the day before. The daily variations $\Delta LAI_{pot}(n)$ are summed over each leaves to obtain the potential increase (without Nitrogen availability effects) in leaf area index at the canopy level ($\Delta LAI_{pot}^{canopy}$).

15. Leaf area index update (Actual expansion under nitrogen limitation)

Expanding grass leaves require a minimum Nitrogen (N) 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 *SiriusQuality*, 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 nitrogen limited daily increase in leaf area index at the canopy level (ΔLAI_N^{canopy} , $\text{m}^2 \text{ leaf m}^{-2} \text{ ground}$) is thus calculated as:

$$\Delta LAI_N^{canopy} = \min \left(\Delta LAI_{pot}^{canopy}, \frac{N_{plant}^{av}}{N_{cri}^{LA}} \right) \quad (36)$$

where N_{plant}^{ava} (g N m^{-2} ground) is the mass of labile (remobilizable) Nitrogen 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.

Finally, the drought and nitrogen limited daily rate of expansion of each growing leaf ($\Delta LAI(n)$) is calculated according to their potential expansion rate and the nitrogen limited rate of expansion of the whole canopy:



$$\Delta LAI(n) = \frac{\Delta LAI_N^{canopy}}{\Delta LAI_{pot}^{canopy}} \times \Delta LAI_{pot}(n) \quad (37)$$

The increase in Leaf Area Index is finally summed over the layers to obtain a that at the canopy level.

16. References

Caldeira C, Jeanguenin L, Chaumont F, Tardieu F. (2014). Circadian rhythms of hydraulic conductance and growth are enhanced by drought and improve plant performance. *Nat. Communications* **5**:5365.

Dignat G, Welcker C, Sawkins M, Ribaut JM, Tardieu F. (2013). The growths of leaves, shoots, roots and reproductive organs partly share their genetic control in maize plants. *Plant, Cell & Environment* **36**, 1105-1119.

457 Gouache D, Bogard

Jamieson PD, Brooking IR, Porter JR, Wilson DR (1995a). Prediction of leaf appearance in wheat: a question of temperature. *F Crop Res* 41:35–44. doi: 10.1016/0378-4290(94)00102-I.

Jamieson PD, Francis GS, Wilson DR, Martin RJ (1995b). Effects of water deficits on evapotranspiration from barley. *Agric For Meteorol* 76:41–58. doi: 10.1016/0168-1923(94)02214-5.

Jamieson PD, Porter JR, Goudriaan J, et al (1998a). A comparison of the models AFRCWHEAT2, CERES-Wheat, Sirius, SUCROS2 and SWHEAT with measurements from wheat grown under drought. *F Crop Res* 55:23–44. doi: 10.1016/S0378-4290(97)00060-9.

Jamieson PD, Semenov M a., Brooking IR, Francis GS (1998b). Sirius: a mechanistic model of wheat response to environmental variation. *Eur J Agron* 8:161–179. doi: 10.1016/S1161-0301(98)00020-3.

Gastal F, Lemaire G (2002). N uptake and distribution in crops : an agronomical and ecophysiological perspective. *J Exp Bot* **53**: 789-799

Lacube S, Fournier C, Palaffre C, Millet EJ, Tardieu F, Parent B. (2017). Distinct controls of leaf widening and elongation by light and evaporative demand in maize. *Plant Cell and Environment* **40**, 475 2017-2028.

Lacube S, Manceau L, Welcker C, Millet E, Palaffre K, Hammer G, Parent B, Tardieu F (2019). Simulating the effect of maize flowering time on individual leaf area in contrasting environmental scenarios. *J Exp Bot* **XX**: XXX-XXX.



Lizaso JI, Batchelor WD, Westgate ME. (2003). A leaf area model to simulate cultivar-specific expansion and senescence of maize leaves. *Field Crops Research* **80**, 1-17.

Parent B, Tardieu F. (2012). Temperature responses of developmental processes have not been affected by breeding in different ecological areas for 17 crop species. *New Phytologist* **194**, 760-774.

Salah HBH, Tardieu F. (1996). Quantitative analysis of the combined effects of temperature, evaporative demand and light on leaf elongation rate in well-watered field and laboratory-grown maize plants. *Journal of Experimental Botany* **47**, 1689-1698.

Sadok W, Naudin P, Boussuge B, Muller B, Welcker C, Tardieu F. (2007). Leaf growth rate per unit thermal time follows QTL-dependent daily patterns in hundreds of maize lines under naturally fluctuating conditions. *Plant, Cell & Environment* **30**, 135-146.

Tardieu F, Reymond M, Hamard P, Granier C, Muller B. (2000). Spatial distributions of expansion rate, cell division rate and cell size in maize leaves: a synthesis of the effects of soil water status, evaporative demand and temperature. *Journal of Experimental Botany* **51**, 1505-1514.

Tardieu F, Simonneau T, Muller B. (2018). The Physiological Basis of Drought Tolerance in Crop Plants: A Scenario-Dependent Probabilistic Approach. . *Annual Review of Plant Biology* **69**, 733-759.

Van Oosterom E, Borrell AK, Chapman SC, Broad IJ, Hammer GL (2010) Functional dynamics of leaf nitrogen balance of sorghum. I. N-balance during pre-anthesis. *Field Crops Res* **115**: 19-28.

Welcker C, Sadok W, Dignat G, Renault M, Salvi S, Charcosset A, Tardieu F. (2011). A Common Genetic Determinism for Sensitivities to Soil Water Deficit and Evaporative Demand: Meta-Analysis of Quantitative Trait Loci and Introgression Lines of Maize. *Plant Physiology* **157**, 718-729.



17. Appendix

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

Symbol	Name in the code	Unit	Description	Equation	Strategy
LER_h^6	hLER	$mm/^\circ Cd\ h$	Hourly leaf elongation rate of the sixth leaf	(1)	<i>calcLER</i>
VPD_h	VPDeq	kPa	Hourly Vapor Pressure Deficit	(1)	<i>calcLER</i>
$\Delta t t_h$	-	$^\circ Cd$	Hourly increase in thermal time	(1)(3)	<i>calcLER</i>
T_{maize}	TCanopyHourly	$^\circ C$	Hourly Canopy temperature	(3)	<i>calcLER</i>
ψ	CalcPsi	MPa	Soil water potential	(1)(2)	<i>calcLER</i>
$FPAW$	FPAW	-	Fraction of soil available water	(2)	<i>calcLER</i>
$LER_{norm}(n)$	coefLER	-	Ratio of the elongation rate of the considered leaf and leaf six elongation rate	(4)(24)	<i>calcLERCoeff</i> <i>DeltaLAIMAize</i>



n	index	-	Leaf rank counted acropetally from 0	(4)(5)(8)(9) (13)(14)(17) (18)	<i>calcFracPopn</i> <i>calcFullyExpTT</i> <i>calcInitTT</i> <i>calcLERCoeff</i> <i>calcLiguleTT</i> <i>calcPotentialWidth</i> <i>calcStartEnlargeTT</i> <i>calcStartExpTT</i> <i>calcStopEnlargeTT</i> <i>calcTipTT</i> <i>DeltaLAIMaize</i>
θ_L	A6	-	Normalization coefficient of LER_{norm}(n)	(4)(5)	<i>calcLERCoeff</i>
G_L	SIGMA	-	Leaf rank of the maximum elongation rate relative to maximum leaf number	(4)(5)(7)	<i>calcLERCoeff</i>
B_L	BETA	-	Distance in leaf number between inflexion points	(4)(5)(6)	<i>calcLERCoeff</i>
<i>tt_{tip}(n)</i>	tipTT	°Cd	Cumulative physiological thermal time from sowing to the time when the tip of the leaf of rank n is visible	(8)(14)(32)	<i>calcTipTT</i> <i>calcStartExpTT</i> <i>DeltaLAIMaize</i>



$tt_{lig}(n)$	liguleTT	°Cd	Cumulative physiological thermal time from sowing to ligulation for leaf of rank n	(9)(18)(34)	calcLiguleTT DeltaLAIMaize
N_{liml}	N_liml1	leaf	Leaf rank of transition between the two linear describing leaf ligulation with thermal time	(9)(10)(12)(13)	calcLiguleTT
b_{l2}	b_l12	leaf	Lump parameter corresponding to a the intercept of the second linear for the describing of the thermal time of ligulation	(9)(12)	calcLiguleTT calcFullyExpTT
a_{l2}	a_l12	°Cd/leaf	Lump coefficient corresponding to the second slope for the describing of the thermal time of ligulation	(9)(11)	calcLiguleTT calcFullyExpTT
$tt_{ini}(n)$	initialisationTT	°Cd	Physiological thermal time cumulated since sowing date to floral initiation for a phytomer of rank n	(13)	calcInitTT
$tt_{start_exp}(n)$	startExpTT	°Cd	Physiological thermal time cumulated since sowing date to the time when leaf of rank n starts expand	(14)(22)(25)	calcStartExpTT calcStartEnlargeTT DeltaLAIMaize
a_{bl}	abl	°Cd/leaf	Slope of the linear relation to describe $tt_{start_exp}(n)$ after N_{bl} leaves have emerged	(14)(15)	calcStartExpTT
b_{bl}	bb1	°Cd	Intercept of the linear relation to describe $tt_{start_exp}(n)$ after N_{bl} leaves have emerged	(14)(16)	calcStartExpTT



SQ-MaizeLAI

lag	lag	°Cd	Thermal time lag between start and stop of leaf expansion	(17)(18)	<i>calcFullyExpTT</i>
$tt_{stop_exp}(n)$	fullyExpTT	°Cd	Physiological thermal time cumulated since sowing date to the time expansion of the leaf of rank n stop	(18)(23)(25)	<i>calcFullyExpTT</i> <i>calcStopEnlargeTT</i> <i>DeltaLAIMaize</i>
$W_{base}(n)$	potentialWidth	mm	Base width of the leaf of rank n without effects due to intercepted radiation or drought stress	(19)(29)	<i>calcBaseWidth</i> <i>DeltaLAIMaize</i>
B_W	BW	leaf	Leaf with maximum base width	(19)(20)	<i>calcBaseWidth</i>
G_W	GW	leaf	Skewness of the curve of base width	(19)(21)	
$tt_{start_enl}(n)$	startEnlargeTT	°Cd	Physiological thermal time cumulated from sowing to the time enlargement of the leaf of rank n start	(22)(32)	<i>calcStartEnlargeTT</i> <i>DeltaLAIMaize</i>
$tt_{stop_enl}(n)$	stopEnlargeTT	°Cd	Physiological thermal time cumulated from sowing date to the time enlargement of the leaf of rank n stop	(23)(32)	<i>calcStopEnlargeTT</i> <i>DeltaLAIMaize</i>
VPD	VPDairCanopy	hPa	Vapor Pressure Deficit between air and canopy	(25)	<i>LeafExpansionDroughtFactor</i>
$LER(n)$	leaveLER	mm/°Cd	Elongation rate of the day for leaf of rank n	(24)(27)	<i>DeltaLAIMaize</i>
LER^6	LER	mm/°Cd	Elongation rate of the day for leaf six	(24)	<i>DeltaLAIMaize</i>
Δtt	dltTT	°Cd	Daily increase in physiological thermal time	(24)(25)(34)	<i>DeltaLAIMaize</i>



SQ-MaizeLAI

$tt_{elapsed}$	cumulTTPHenoMaize	°Cd	Physiological thermal cumulated since sowing date	(8)(25) (32)(34)	<i>DeltaLAIMaize</i>
$\Delta tt_{elong}(n)$	growthTT	°Cd	Duration in thermal time for daily elongation of leaf with rank n	(25)(27)	<i>DeltaLAIMaize</i>
$lenght^{day}(n)$	length	mm	Length of leaf of rank n	(26)(27)(29)	<i>DeltaLAIMaize</i>
$\Delta lenght(n)$	dltLength	mm	Daily elongation of leaf of rank n	(26)(27)	<i>DeltaLAIMaize</i>
Δw_{rad}	RADeffect	mm	Daily enlargement due to intercepted radiation	(28)(29)	<i>DeltaLAIMaize</i>
$\overline{rad}_{int}^{plant}$	RADmean	MJ	Radiation of the day intercepted by the plant	(28)	<i>DeltaLAIMaize</i>
$width_{rad}(n)$	width	mm	Width of the leaf of rank n after radiation absorption	(29)(30)	<i>DeltaLAIMaize</i>
$A(n)$	area	mm ²	Area of leaf of rank n	(30)(33)	<i>DeltaLAIMaize</i>
$Form(n)$	FormFactor	-	Form factor for area of leaf of rank n	(30)(31)	<i>DeltaLAIMaize</i>
$r_w(n)$	LeafWidthRatio	-	Coefficient for form factor	(31)(32)	<i>DeltaLAIMaize</i>
$A_{exp}(n)$	exposedArea	mm ²	Exposed area of leaf of rank n	(33)(35)	<i>DeltaLAIMaize</i>
$F_{exp}(n)$	exposedFraction	-	Exposed fraction of leaf n	(33)(34)	<i>DeltaLAIMaize</i>



SQ-MaizeLAI

$f_h(n)$	fracPopn	-	Decimal part of the haun stage for the last leaf. Unity for other leaves.	(34)	<i>DeltaLAIMaize</i>
$LAI_{pot}(n)$	ExposedLAI	m ² (leaf)/m ² (ground)	Potential Leaf Area Index (without nitorgen stress) of leaf of rank n	(35)	<i>DeltaLAIMaize</i> <i>UpdateLeafArea</i>
$\Delta LAI_{pot}(n)$	WaterLimitedPotDeltaA IList	m ² (leaf)/m ² (ground)	Potential increase (without nitrogen stress) of leaf area index during the day for leaf of rank n	(33)	
$\Delta LAI_{pot}^{canopy}$	potentialIncDeltaArea	m ² (leaf)/m ² (ground)	Potential increase (without nitrogen stress) of leaf area index during the day for the whole canopy	(37)	<i>DeltaLAIMaizev</i> <i>UpdateLeafArea</i>
$\Delta LAI_{drought}^{canopy}$	incDeltaAreaLimitSF	m ² (leaf)/m ² (ground)	Increase of leaf area index under drought stress during the day for the whole canopy	(36)(37)	<i>DeltaLAIMaize</i> <i>UpdateLeafArea</i>
ΔLAI_N^{canopy}	IncDeltaArea	m ² (leaf)/m ² (ground)	Increase of leaf area index under limited nitrogen resources stress during the day for the whole canopy	(36)(37)	<i>UpdateLeafArea</i>
$\Delta LAI(n)$	deltaAI	m ² (leaf)/m ² (ground)	Actual increase of leaf area index under limited nitrogen and water resources stress during the day for the whole canopy	(37)	<i>UpdateLeafArea</i>



Table A2: List of parameters and constants used in the *SQ-MaizeLAI* component. Values of genotypic parameters are given for hybrid *B73_H* (Lacube et al. 2019). When nothing is indicated, a non-varietal parameter is considered.

Symbol	Name in the code	Nominal value	Unit	Description	Equation
a_6	LERa	3.19	mm/°Cd	Maximum leaf elongation rate of leaf 6 (Genotypic)	(1)
b	LERb	-1.17	mm/°Cd kPa	Sensitivity of leaf elongation rate to vapour pressure deficit (Genotypic)	(1)
c	LERc	3.52	mm/°Cd bars	Sensitivity of leaf elongation rate to soil water deficit (Genotypic)	(1)
β_L	Beta	0.68	-	Coefficient determining the rank of the leaf with maximum growth relative to final leaf number	(6)
σ_L	Sigma	0.46	-	Coefficient determining the skewness of the curve of leaf growth relative to final leaf number	(7)
N_{final}	Nfinal	16	leaf	Maximum number of leaves (Genotypic)	(6)(7)(10) (18)(20)(21)
D_{se}	Dse	33	°Cd	Thermal time cumulated from sowing to emergence (Genotypic)	(8)(9)
b_{tip}	btip	-49	°Cd	Intercept of the regression of thermal time with tip appearance (Genotypic)	(8)(16)



SQ-MaizeLAI

a_{tip}	atip	51	°Cd/leaf	Slope of the regression of thermal time with tip appearance (ie: Phyllochron, thermal time between subsequent leaf tip appearances) (Genotypic)	(8)(15)(16)
α_{ll}	alpha_tr	0.52	-	Transition between the two linear describing leaf ligulation with thermal time relative to N_{final}	(9)
a_{ll1}	a_ll1	86	°Cd/leaf	Slope of the regression of thermal time with ligulation (ie: thermal time between subsequent leaf ligule appearances) (Genotypic)	(9)(10)(11)(12)
b_{ll1}	b_ll1	137	°Cd	Intercept of the regression of thermal time with tip appearance	(9)(11)(12)
k_{ll}	k_ll	0.454	-	Ratio between the two ligulation slopes with thermal time	(11)(12)
N_{emrg_init}	leafNoInitEmerg	6.59	leaf	Leaf number emerged at floral initiation	(13)
LIR	LIR	0.068	Leaf/°Cd	Leaf Initiation rate	(13)
$tt_{initflo}$	ttinitflo	28.9	°Cd	Thermal time of floral initiations of leaves created before emergence	(13)
k_{bl}	k_bl	0.708	-	Ratio between leaf appearance and linear of expansion for the last leaves	(15)(16)
N_{bl}	Nlim	6	leaf	Transition between first and last leaves for beginning of leaf linear expansion	(14)(16)
a_{lag}	Lagmax	5.4	°Cd/leaf	Relative thermal time difference per leaf between ligulation and end of expansion	(17)
N_{last}	Nlast	2	leaf	Number of last leaves that finish their expansion at the same thermal time	(18)



SQ-MaizeLAI

W_6	width6	41	mm	Base width of leaf six (Genotypic)	(19)
β_w	betaW	0.41	-	Coefficient determining the rank of the leaf with maximum base width relative to final leaf number	(20)
σ_w	sigmaW	0.69	-	Coefficient determining the skewness of the curve of base width relative to final leaf number	(21)
lag_w	lagStopWidthExpand	39	°Cd	Thermal time lag between end of expansion and end of leaf enlargement	(23)
Γ_{RAD}	SensiRad	34	mm/MJ	Sensitivity of leaf widening to intercepted radiation (Genotypic)	(28)
RAD_{base}	radBase	0.15	MJ	Base value for radiation effect on leaf widening	(28)
PD	plantDensity	7.5	(plant)/m ² (ground)	Plant density	(35)
N_{cri}^{LA}	SLNcri	1.0	g(N)/m ² (leaf)	Minimum nitrogen available in the plant to maintain a critical area-based leaf nitrogen mass	-