

HPP-23806 Crops, Physiology and Environment

HPP-21306 Quantitative Aspects of Crop production

Potential and water limited crop growth

In this course you will learn about crops and interactions between crops and the biophysical environment. These interactions are complex, but can be understood well when considering the most important processes only. To better study and understand these interactions, we use a summary type of model that computes the amount of biomass per unit of area, in this case per m² of soil. However you should also be able to use a “back-of-envelope” approach to calculate biomass production, yields and water requirements. To this end, some rules of thumb are provided that you need to learn by heart that will provide you with some tools to get a feel for range of values and magnitude of the numbers that are possible.

In comparison with more comprehensive models that include many detailed processes, the summary type of models include only the key processes and are relatively simple. The **Light Interception and Utilization (LINTUL)**¹ is such a model and is based on the radiation use efficiency concept as first described by Monteith (1977). It was first developed for potatoes (Spitters et al., 1990) to study how drought affects cultivars with different characteristics. Versions for cereals (maize, spring wheat) and perennial crops such as grass and cassava are now also available. All detailed processes that affect photosynthesis in the leaf chloroplasts, assimilation of carbohydrates and (growth and maintenance) respiration are summarised into one parameter value that allows to directly convert intercepted solar radiation into biomass. Although LINTUL cannot be used to study how the crop responds from hour to hour, it does allow to study how environmental factors influence crop growth during the season and yield at the end of the season.

The LINTUL model is developed to provide a reasonable estimate of crop biomass and yield at harvest under a wide range of environments. LINTUL is developed for a crop in the open field, representing many plant and ignores most processes that vary from day to day but are less important for a whole growing season. The process of maintenance respiration is such an example, although it is known to vary with daily temperatures. In comparison to the influence of maintenance respiration on yield, the influence of temperature on assimilation, crop development rates, evapotranspiration and hence drought is far more important. In LINTUL, many detailed processes are replaced by summary functions and parameters that combine and grasp key aspects of the more detailed processes operating on shorter time-scales, and smaller components. A second example of such ignored process is the amount of light arriving on an individual leaf that is used for assimilation during the day, which is partly used for maintenance respiration during the night and

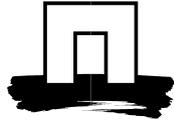
¹ Note that light interception here refers to the intercepted part of radiation that can be detected by the human eye that ranges from a wavelength of 400 to 700 nm, which is also the photosynthetically active component of radiation.

transferred to other plant organs to fuel growth processes. This is far too detailed for the purpose of simulating biomass and yield for a crop in the field for a range of years!

Due to its simplicity, LINTUL models require a minimum number of process parameters and other input variables, such as soil characteristics and daily values for weather data. The simplicity of the crop growth process in LINTUL is handy when considering the interactions between the crop and its environment. These interactions are important, yet sometimes difficult to grasp. The few model equations for crop growth allow to better understand these interactions. For example understanding how changes in crop growth rate affects leaf growth during early plant development can help to assess how a shortage of water in spring can impact light interception and hence growth rates on all later days in the season, even when rainfall ended the drought period.

The numbering of LINTUL models follows from the production situations (PS). PS1 reflects potential conditions, PS2 includes water limitations and PS3 nitrogen limitations. LINTUL1 therefore combines optimal management without water or nutrient limitations or reductions due to pests and diseases. LINTUL2 builds on LINTUL1 but includes a simple soil module and components to determine the evaporation and transpiration losses that allow to study how water-limitations reduce crop growth rates and yields. You will learn more about LINTUL2 in later in this course. N-limitations that are included in LINTUL3 and later versions including NPK limitations or rotations are not covered in this course.

The original text was written and edited by Dr M. van Oijen and Dr P. Leffelaar where details about the programming environment FST and the code of the implemented model have been removed for simplicity. The original source code of the LINTUL1 model for spring wheat as implemented in FST and R can be freely downloaded from models.pps.wur.nl. Versions for other crops are also available. LINTUL is now available in R and in Python, it is part of the Python Crop Simulation Environment. The description includes equations to adjust crop growth rates to ambient CO₂ levels, which is also present in the PCSE-LINTUL3 model but not in other versions.



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LINTUL1 A SIMPLE GENERAL CROP GROWTH MODEL FOR OPTIMAL GROWING CONDITIONS (EXAMPLE: SPRING WHEAT)

Introduction

LINTUL1 simulates potential growth of a crop, i.e. its dry matter accumulation under ample supply of water and nutrients in a pest-, disease- and weed-free environment, under the prevailing weather conditions. The rate of dry matter accumulation is a function of irradiation and crop characteristics. The model makes use of the common observation that the crop growth rate under favourable conditions is proportional to the amount of light intercepted (Monteith, 1977). Dry matter production is, therefore, modelled as the product of light interception and a constant light use efficiency. The dry matter produced is partitioned among the various plant organs, using partitioning factors defined as a function of the phenological development stage of the crop. The dry weights of the plant organs are obtained by integration of their growth rates over time.

LINTUL1 requires as input physiological properties of the crop (in this case for spring wheat) and the actual weather conditions at the site, characterized by its geographical latitude, i.e. daily maximum and minimum temperatures and irradiation for each day of the year.

The main model equations and functions of the program

LINTUL1 is based on a few mathematical equations and functions that describe the processes leading to dry matter production and grain yield. These equations and functions are described in this section. They can be used in a computer program that automatically computes crop dynamics throughout the season. For those who wish to understand the program implementation, the simulation program is fully explained after the description of the main model equations.

Light interception Radiation, more particularly the photosynthetically active radiation, provides the energy for the process of photosynthesis. The interception of radiation by the crop is thus essential. Assuming a homogeneous canopy, light exponentially decreases with the cumulative leaf area index, counted from the top of the canopy to the soil surface according to Lambert-Beer's law:

$$I = I_0 e^{-kL} \quad (1)$$

Where, I_0 is the incident radiation flux of photosynthetically active radiation (PAR^2 , $MJ\ m^{-2}d^{-1}$),

I the radiation flux that reaches the soil (PAR , $MJ\ m^{-2}d^{-1}$),

k the radiation extinction coefficient (K , $m^2\ (ground)\ m^{-2}\ (leaf)$),

L the leaf area index (LAI , $m^2\ (leaf)\ m^{-2}\ (ground)$).

The radiation extinction coefficient, k , depends on the leaf characteristics and the architecture of the crop: erect leaves intercept less radiation as compared to more horizontal leaves.

² Abbreviations inside brackets refer to the names in the LINTUL1-program. So, e.g. I_0 is similar to PAR .

The incident radiation flux of photosynthetically active radiation, I_0 , is about 50% of the daily total radiation (DTR), so $I_0 = 0.5 DTR$.

The amount of intercepted photosynthetically active radiation, I_{int} , is the difference between the incident radiation, I_0 , and the amount reaching the soil surface, I :

$$I_{int} = I_0 (1 - e^{-kL}) = 0.5 DTR (1 - e^{-kL}) \quad (2)$$

Both, DTR and L in Eq. (2) vary in time and thus also the amount of intercepted radiation. Daily total radiation is a measured quantity and is contained in the weather data that are needed. For the Light INTerception and Utilization model we use daily totals that are obtained by integrating a large number of measurements taken during the day. The (green) leaf area index, L , will increase with time due to growth of new leaves, but at a certain moment, leaf senescence will be stronger and the leaf area will decrease again. Leaf area dynamics will be discussed in a later section.

Combining the actual amount of intercepted photosynthetically active radiation with the radiation use efficiency enables us to calculate the daily growth rate of a crop.

Radiation or Light use efficiency Monteith (1977) showed that a graph of crop growth rate versus the cumulative amount of absorbed photosynthetically active radiation gives a straight line, Figure 1.

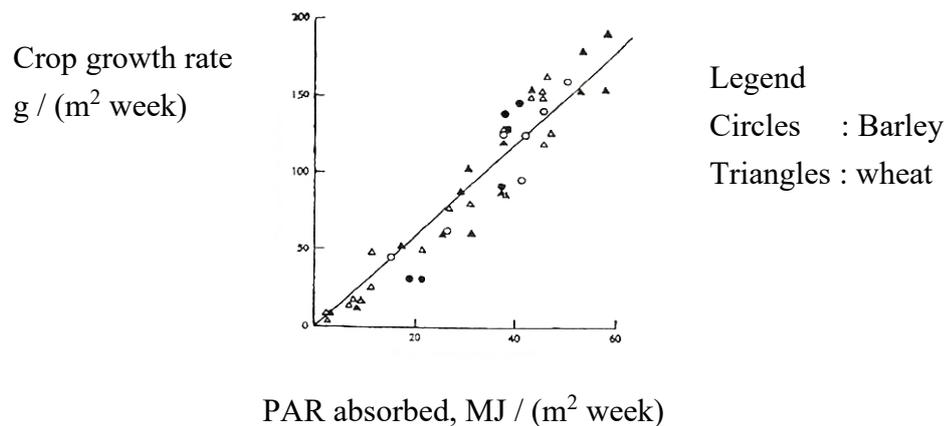


Figure 1. Crop growth rate versus the cumulative amount of absorbed photosynthetically active radiation (Gallagher and Biscoe, 1978).

The slope of this line gives an estimate of the radiation use efficiency (RUE) expressed in g dry matter per MJ of absorbed radiation. The meaning of the numerator (g dry matter) and the denominator (MJ of absorbed radiation) of this ratio is extensively discussed in the review article by Sinclair and Muchow (1999).

Crop growth rates are affected by CO_2 concentration, which is with temperature, radiation and genotype one of the defining factors in the concepts of production ecology. This means that with increasing ambient CO_2 concentrations in the outside air, also the conversion efficiency of intercepted light to dry matter increases. The following adjustment was made to account for these changes in RUE following the approach as described in Berghuijs et al. (2023):

$$RUE = RUE_{ref} \times fCO_2 \quad (3)$$

Where RUE_{ref} is defined as the RUE when the ambient CO_2 concentrations equals 350 parts per million (ppm). The adjustment factor for CO_2 (fCO_2) was determined using this equation (O'Leary et al. 2015):

$$fCO_2(y) = \frac{\frac{1.7}{350 \times (1-1.7)} \times C_a(y) \times 1.7}{\frac{1.7}{350 \times (1-1.7)} \times C_a(y) + 1.7} \quad (4)$$

Here, C_a refers to the ambient CO_2 concentration in ppm.

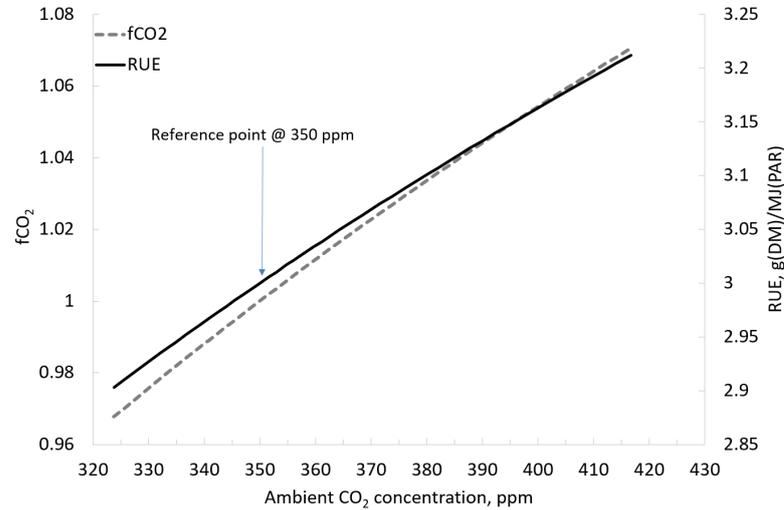


Figure 2. The fCO_2 value and resulting RUE value as function of ambient CO_2 concentration. Here, the RUE_{ref} parameter was set to 350 ppm.

Crop growth rate (dW/dt ; $GTOTAL$) can now be calculated as:

$$\frac{dW}{dt} = RUE I_{int} \quad (5)$$

with the unit g (dry matter) / (m² (ground) d). The crop weight is obtained by integrating Eq. (5) over time, usually a growing season:

$$W = \int_0^t \frac{dW}{dt} dt \quad (6)$$

We need to distinguish between growth and development. Growth is determined by the product of radiation interception and the efficiency by which this radiation is used to form crop assimilates (Eq. 5). Development is determined by physiological age as discussed in the following section.

Crop development Crops pass through a number of developmental stages (DVS) during their live cycle. These different stages control the partitioning of assimilates or dry matter. In general, temperature has the strongest effect on development. A problem in quantifying this effect is that it is not possible to measure *development rate* directly. Instead, it must be derived from the period of time elapsed between two distinct *development stages*. The rate of development, $dDist/dt$, can then be derived using the equation:

$$\left\{ \frac{dDist}{dt} = \frac{\text{distance between 2 stages}}{\text{time period between these 2 stages}} \right\}_{T_a} \quad (7)$$

where “distance between 2 stages” may, for example, be the distance between emergence and anthesis. Such a distance could be termed 1, or 100% or so, and does not have a unit. It appears from Eq. (8) that the “time period between these 2 stages”, the denominator, in days, must be assessed for a series of constant air temperatures, T_a . Development rate is found to be roughly linearly related to temperature over a wide range, although there is usually a maximum in the response curve above which the development rate will decrease again. A graph of $dDist/dt$ versus the temperature, T , is shown in Figure 2.

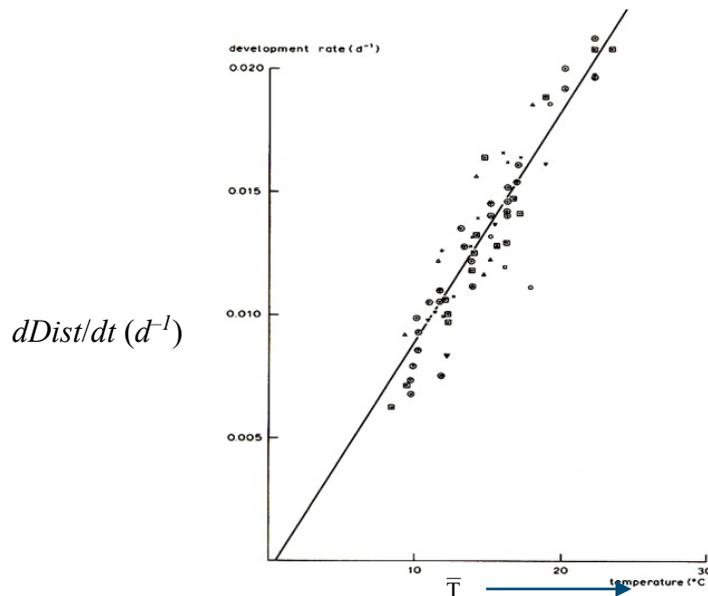


Figure 2. Development rate of spring wheat as a function of temperature from emergence till flowering (van Keulen and Seligman, 1987).

The extrapolation of the line to low temperatures yields an intercept with the temperature axis. This is often called the base temperature, T_b (*TBASE*), below which there is no or a hardly measurable development rate. Provided that air temperature, T_a (*DAVTMP*), lies between the base temperature, T_b , and the optimum temperature, beyond which the development starts to level off, the development rate is proportional to the integrated temperature

$$T_{sum} = \int (T_a - T_b) dt \quad (8)$$

From the slope of the line in Figure 2, the temperature sum, T_{sum} , to go from one development stage to the next can be calculated. The slope, α , will have the unit $1/(d \text{ } ^\circ\text{C})$, and thus $1/\alpha$ is the temperature sum.

The development rate, $dDist/dt$, is derived from experiments at constant air temperatures, T_a . In the field, however, temperatures are not constant. The temperature sum as a measure for physiological age or development stage nevertheless often works fine because of the instantaneous reaction of the crop to a change in temperature.

Allocation of assimilates In principle, photosynthesis yields assimilates that need to be partitioned over the different plant organs. In the radiation use efficiency approach, however, radiation is directly used to calculate the production of dry matter via the value of the RUE. Thus, dry matter is partitioned over the plant

organs: roots, stem, leaves and storage organs. The different developmental stages control the partitioning of assimilates or dry matter. Assessing the relationships between phenological development stages and the fractions of the dry matter that are partitioned towards the different organs is still only possible by empirical work. The relationships have been assessed for a number of important crops. Figure 3 shows the data points for spring wheat.

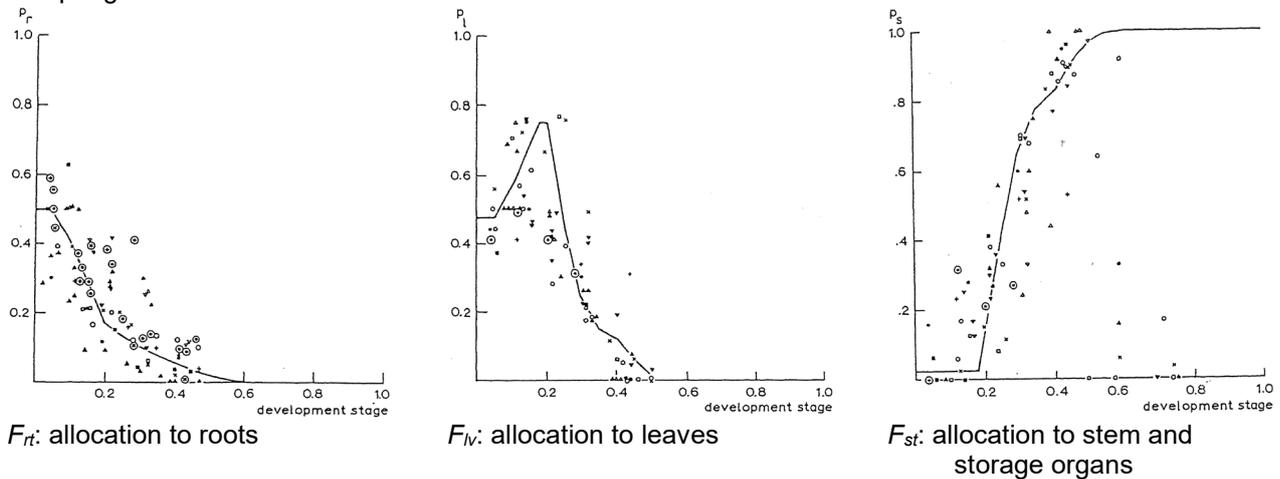


Figure 3. Allocation patterns for spring wheat (van Keulen and Seligman, 1987). Development stage one in the figures is equivalent to 2080 °Cd. Anthesis occurs at a development stage of 0.5.

It can be seen from the figure that in the beginning much dry matter is invested in the roots and the leaves, and that after flowering, when the development stage equals 0.5, root and leaf growth stop. It appears that after $DVS=0.5$ all the dry matter is invested in the stem, but in fact the allocation to the stem is also ceasing after $DVS=0.5$ and all the dry matter production is invested in the storage organs. Such empirical data can only be used through functions representing the partitioning fractions as a function of development stage, where the sum of the fractions should always be equal to 1.0.

The growth of each plant organ can now be calculated from Eq. (5) and the partitioning fractions depicted in Figure 3:

$$\frac{dW_i}{dt} = \frac{dW}{dt} F_i = RUE I_{int} F_i \tag{9}$$

where i represents the root (rt), stem (st), leaves (lv) or storage organ (so) of the plant, respectively. Since leaves partially senesce during the growing season, the equation for the net rate of change of green leaves, dW_{lv}/dt ($RWLVG$), is slightly different:

$$\frac{dW_{lv}}{dt} = \frac{dW_{lv}}{dt} - r_d W_{lv} = RUE I_{int} F_{lv} - r_d W_{lv} \tag{10}$$

where the leaf death rate is taken proportional to the green leaf weight, W_{lv} ($WLVG$, g DM m⁻²) and a relative senescence rate, r_d (RDR , d⁻¹). The relative death rate is further detailed in the section about *Leaf area senescence*. The senescence rate $r_d W_{lv}$ in Eq. (11) is similar to DLV in the LINTUL1 program. The other organs (root, stem, storage organs) are assumed to negligibly die during the season.

Describing crop growth and dry matter allocation according to Eq. (10) implies that it is assumed that all dry matter produced in a day is directly distributed over the plant organs, and thus no reserve pool of assimilates or dry matter is considered. Redistribution of dry matter at the end of the season to the storage organs is assumed negligible.

Leaf area growth Leaves are the major photosynthesizing organs, and the calculation of intercepted photosynthetically active radiation, *PAR*, is largely based on their surface area. Correct simulation of the time course of the leaf area index, *L* (*LAI*), is the first requirement for correct crop growth calculations. Roughly, two different situations exist with respect to the formation of new leaf area: its growth may be *sink-limited* or it may be *source-limited*.

During juvenile growth, temperature is the overriding factor, as the rate of leaf appearance and final leaf size are constrained by temperature through its effect on cell division and extension, rather than by the supply of assimilates. In these early, sink-limited stages, leaf area increases approximately exponentially over time, Eq. (11):

$$\frac{dL}{dt} = r_g L \quad (11)$$

with r_g the relative growth rate. This relative growth rate is the product of r_l (*RGRL*), the relative growth rate of leaf area during the juvenile exponential growth phase per degree centigrade in ($^{\circ}\text{Cd}$)⁻¹, and the effective temperature T_{eff} (*DTEFF*), which equals $(T_a - T_b)$ if $T_a \geq T_b$:

$$r_g = r_l T_{\text{eff}} \quad (12)$$

Integrating Eq. (11) and substituting Eq. (12) yields Eq. (13)³:

$$L = L_0 e^{(r_l T_{\text{eff}} t)} \quad (13)$$

Examination of unpublished field data suggests that a safe approximation is to restrict the exponential phase to the situation where $L < 0.75 \text{ m}^2 \text{ m}^{-2}$ and $T_{\text{SUM}} < 330 \text{ }^{\circ}\text{Cd}$.

In later development stages, leaf area expansion is increasingly restricted by assimilate supply (source-limited). Branching and tillering generate an increasing number of sites per plant where leaf initiation can take place and an increasing number of cells that can expand, while mutual shading of plants and leaves reduces the assimilate supply per growing point and per cell. During this stage ($L \geq 0.75 \text{ m}^2 \text{ m}^{-2}$ or $T_{\text{SUM}} \geq 330 \text{ }^{\circ}\text{Cd}$), the model calculates the growth of leaf area by multiplying the simulated rate of increase in leaf weight,

³ Eq. (13) can be used to derive the exact rate of leaf area development over e.g. daily time intervals. To this purpose Eq. (11) was rewritten as

$$L_{t+\Delta t} = L_t e^{(r_l T_{\text{eff}} \Delta t)} \quad (15)$$

with L_t and $L_{t+\Delta t}$ the current leaf area and the leaf area at the end of a time step Δt (*DEL T*, d), respectively. Subsequently, the slope of the exponential curve can be approximated by:

$$\frac{dL}{dt} = \frac{L_{t+\Delta t} - L_t}{\Delta t} = \frac{L_t e^{(r_l T_{\text{eff}} \Delta t)} - L_t}{\Delta t} = \frac{L_t (e^{(r_l T_{\text{eff}} \Delta t)} - 1)}{\Delta t} \quad (16)$$

Equation 16 is used in the LINTUL1 program, rather than Eq. (11), because Eq. (16) does not suffer from the accumulation of numerical integration errors and is a very accurate solution for the Euler integration method.

$dW/dt F_{lv}$ (GLV, g (leaf) m⁻² (soil) d⁻¹) by the specific leaf area of new leaves, S_{la} (SLA, m² (leaf) g⁻¹ (leaf)), Eq. (14):

$$\frac{dL}{dt} = \frac{dW}{dt} F_{lv} S_{la} \quad (14)$$

where dW/dt is defined by Eq. (5). The dynamics of S_{la} are not well understood yet. Therefore, it is assumed constant throughout the season.

Leaf area senescence The senescence rate of L ($DLAI$, d⁻¹), is described on the basis of a relative death rate, r_d (RDR , m² (leaf) m⁻² (soil) / (m² (leaf) m⁻² (soil) d) or just d⁻¹), Eq. (14)

$$\frac{dL}{dt} = -r_d L \quad (15)$$

where r_d is set to the maximum of either a relative death rate due to ageing, r_{d-ag} ($RDRDV$, d⁻¹), or one due to self-shading, r_{d-sh} ($RDRSH$, d⁻¹):

$$r_d = \max(r_{d-ag}, r_{d-sh}) \quad (16)$$

with $r_{d-ag} = f(T)$ and $r_{d-sh} = f(L)$.

The $r_{d-ag} = f(T)$ is specified by the following (x,y) pairs: (-10, 0.03), (10, 0.03), (15, 0.04), (30, 0.09), (50, 0.09), where -10, 10, 15, 30 and 50 are temperatures and the values 0.03, 0.04 and 0.09 are the corresponding relative death rates due to ageing. Death of leaves due to ageing only occurs after anthesis, as indicated by $T_{sum} \geq T_{sum-anthesis}$ ($TSUMAN$).

The $r_{d-sh} = f(L)$ equals zero for L smaller than a critical leaf area index, L_{cr} , which is set to 4 for spring wheat ($LAICR$, m² (leaf) m⁻² (soil)). For leaf area index values exceeding L_{cr} , r_{d-sh} increases linearly with increasing L until a maximum value, $r_{d-shmx} = 0.03$ ($RDRSHM$, d⁻¹) at $L = 8$.

Start conditions and environmental conditions Crop growth starts with emergence, which can be triggered either by an accumulation of heat units or just by reaching a pre-set date. In the first case one needs to have information about the sowing date and the temperature sum from sowing to emergence. In our case we did not have such information and therefore, a pre-set date is taken.

For an accurate description of the establishment of small plants, much information is needed. In the case of the light interception and utilization model we have chosen to initialize leaf area as if it appears at once: leaf area at emergence amounts to 0.012 m² (leaf) m⁻² (soil).

Quite some other parameters are needed too. These values were gathered from experimental data. Furthermore, weather data are needed. The models.pps.wur.nl website provides a large collection of daily weather data from the Netherlands, but also from a large number of other countries. For the potential growth model, we only need daily global radiation and minimum and maximum temperatures.

The model should stop making calculations at the end of the season, or when the temperature sum for maturity has been reached, ($TSUM = 2080$ for spring wheat).

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