

The uptake of N ($\text{g m}^{-2} \text{d}^{-1}$) in dependence of FNS is given in Figure 43.

$$\begin{aligned}\text{UPTAKE} &= \text{DEMAND} * \text{MXRCRS} \\ \text{DEMAND} &= \text{NOKER} * \text{PRPRA} * 1./5.95 \\ \text{PARAM PRPRA} &= 0.00013, \text{FNS} = 0.010 \\ \text{MXRCRS} &= \text{AFGEN}(\text{MXTB}, \text{FNS}) \\ \text{FUNCTION MXTB} &= 0.0035, 0.45, 0.006, 0.45, 0.01, 0.4, 0.014, 0.35, \dots \\ &\quad 0.08, 0.225 \\ \text{NG} &= \text{INTGRL}(0., \text{NAG})\end{aligned}$$

NG is the amount of N in the grains (g m^{-2}). NAG is the rate of N accumulation in the grains ($\text{g m}^{-2} \text{d}^{-1}$), which is a fraction ($\text{PRPRA}/(\text{PRCHA} * 5.95)$) of the actual growth rate of the grains. This fraction can be altered by the ratio of available N and available C: the reduction factor RED. Proteins are 5.95 times heavier than the N that they contain.

$$\begin{aligned}\text{NAG} &= \text{GGR} * 0.875 * \text{PRPRA}/(\text{PRCHA} * 5.95) * \text{RED} \\ \text{RED} &= \text{RED2}/\text{AMAX1}(0.5, \text{RED1})\end{aligned}$$

When the temperature is 16 °C the period between anthesis and maximum grain dry weight is 50 days.

Exercise 53

- Run the program (with RKSFX and DELT=1.) and study the results, in particular of the course of the factors that limit grain growth. What happens when the initial N concentration of the shoot is higher (0.015) or what if the standard rate of CO₂ assimilation is lower (25.)? Check the harvest index for dry matter (DHI) and for N (NHI) with those of Subsections 3.4.5 and 3.4.6.
 - What range of concentrations of N in the daily weight increment of grain is implied in this formulation of grain growth?
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Part III. A deterministic approach to modelling of organogenesis in wheat

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3.4.10 A preliminary model of organogenesis

The descriptive Equations 49 and 52 to calculate the number of grains per square metre are based on the weight of the crop at harvest and at anthesis, respectively. As a result of environmental conditions, among others, the constants in the equations are different for each new growing season. Although knowledge of the factors that govern kernel formation is still little developed, the pre-

liminary model on organogenesis presented below may clarify why a crop ends up in many cases with a number of kernels that matches more or less the carbohydrate supply in the post-anthesis phase. In the previous subsections attention is drawn to the fact that initiation and development of plant organs is governed by the interactive effects of genetic properties and environmental conditions. The necessary information is probably transmitted in the plant through hormonal levels. However, quantitative information on production and breakdown of plant hormones as affected by external and internal conditions, as well as on the influence of certain levels of these substances on relevant processes, is insufficient at the moment to keep track of such state variables in crop growth models. An alternative approach, which takes into account concepts outlined in foregoing subsections, was illustrated for tiller formation in Rhodes grass by Dayan et al. (1981). In this description the formation of new plant organs depends on the current supply of carbohydrates and the number of organs already present to utilize these assimilates, mimicking apical dominance. In basically the same way, this description is applied here to a wheat crop. The influence of a low availability of N is not considered, which implies that this preliminary model of organogenesis does not apply at levels of production where nutrient shortage is predominant.

First the number of tillers per ha is defined in an integral:

$$ANT = \text{INTGRL} (TLNI, RTF)$$

in which TLNI is the initial number of tillers per ha. The rate of tiller formation is described by:

$$RTF = (MXNT - ANT) / TCTF$$

in which TCTF is a time coefficient for tiller formation (d). MXNT, the maximum number of tillers per ha that could be supported at a particular moment, is obtained from:

$$MXNT = CHAVG / CHMPT$$

in which CHAVG is the carbohydrate supply for vegetative growth in $\text{kg ha}^{-1} \text{d}^{-1}$ and CHMPT the flux of carbohydrates that can be monopolized by one tiller in kilogram per tiller per day. The value of the latter variable is supposed to be related to the rate of development (DVR, defined as in Subsections 3.1.2 and 3.3.2) as follows:

$$CHMPT = CHMPTB / (DVR * 1.43)$$

in which CHMPTB is the 'basic' flux of carbohydrates that can be monopolized per tiller. CHMPTB is introduced in the model as a parameter and is cultivar specific, there being distinctions between prolific tillering varieties and those producing only limited numbers of tillers. It is as yet not possible to determine its value from independent measurements and it has to be derived from com-

parison between cultivars. This formulation ensures that final tiller number is mainly determined by assimilate supply and not by the length of the vegetative period for a given variety in accordance with experimental evidence.

In the present version of the model no distinction is yet made between tillers of different age in terms of assimilate supply or physiological characteristics.

During the period of ear initiation, which coincides partly with that for tiller formation, the rate at which ears are initiated is given by:

$$\text{REARI} = (\text{ANT} - \text{EARN}) / \text{TCEI} * \text{AFGEN}(\text{CHPTT}, \text{CHPT})$$

with EARN as the number of already initiated ears per ha, CHPT = CHAVG/ANT as the available carbohydrates per tiller per day and TCEI as time coefficient for ear initiation (d). The value of CHPTT varies between 1. and 0.

After anthesis, those tillers that fail to become reproductive gradually die off. Especially translocation of N to the remaining tissue may take place and this is taken into account. Redistribution of C compounds is not considered.

The rate of spikelet differentiation per ear in the next stage is described by:

$$\text{RSPLF} = \text{MXRSF} * \text{AFGEN}(\text{CHFPET}, \text{CHFPE})$$

in which MXRSF is the maximum rate of spikelet differentiation (number ear⁻¹ d⁻¹) and CHFPE = CHAVG/EARN, the value of CHFPET again varying between 1. and 0.

$$\text{SP} = \text{INTGRL}(0., \text{RSPLF})$$

$$\text{SPNR} = \text{SP} * \text{EARN}$$

in which SP is the number of spikelets per ear and SPNR the number of spikelets per hectare. The final spikelet number is thus affected both by the time available for initiation (high temperatures will shorten the development period available for spikelet formation) and by conditions governing assimilate supply (leaf area index, level of irradiance).

Spikelets may also be aborted – or cease further development – when the assimilate supply reaches very low levels. The carbohydrate ‘maintenance’ level for spikelets is set rather arbitrarily at one tenth of the value necessary for maximum development.

Finally the number of grains developing per spikelet (GN) is determined in dependence on the assimilate supply per spikelet (CHFPSP) during the appropriate development stage:

$$\text{GNPSP} = \text{GNMIN} + (\text{GNMAX} - \text{GNMIN}) * \text{AFGEN}(\text{CHFPST}, \dots \\ \text{CHFPSP})$$

$$\text{RFGF} = (\text{SPNR} * \text{GNPSP} - \text{FGNR}) / \text{TCT}$$

$$\text{FGNR} = \text{INTGRL}(0., \text{RFGF})$$

$$\text{GN} = \text{FGNR} / \text{SPNR}$$

in which RFGF is the rate of grain formation (number ha⁻¹ d⁻¹), GNPSP the maximum possible number of grains per spikelet determined by the supply of

assimilates per spikelet, GNMAX and GNMIN the maximum and minimum number of grains per spikelet, respectively, FGNR the total number of grains per hectare, and TCT the time coefficient for grain formation (d). $CHFPSP = CHAGG/SPNR$, CHFPST assumes a value between 1. and 0., CHAGG is the flux of carbohydrates available for grain growth, the flux of nitrogenous compounds is ignored for the time being. FGNR corresponds with N_g in Equation 49 and NOKER in the Subsections 3.4.7 and 3.4.9. The grain yield follows from the integrated value of CHAGG, and the weight per individual kernel can easily be calculated.

In this preliminary model the number of kernels per square metre is directly dependent on the carbohydrate supply during the last part of the vegetative phase. In many climates, the season proceeds in such a way that there is a good correlation between the carbohydrate supply in this period and that in the post-anthesis phase. This is why the number of kernels per square metre and the carbohydrate supply in the post-anthesis phase are often related, and how the crop ensures the formation of the number of kernels that it deserves. However, when there is a cool, overcast period during the end of the vegetative phase, or a dry spell followed by a bright period without water shortage, the number of kernels may be too low. Then, they reach their maximum individual weight before the vegetative parts are exhausted. When a bright period is followed by an overcast period, it may be the other way around, so that the weight of individual kernels is well below the maximum value. As stated earlier, this formulation is rather descriptive, but it accounts for the interaction between genetic properties and environmental conditions, while simulated results are in reasonable agreement with experimental data.

Exercise 54

a. Combine this modelling of the organogenesis in wheat with the model SUCROS and calculate ANT, EARN, SP, GN and FGNR. You need the following information:

INCON TLNI = 2.E6

PARAM TCTF = 2., TCEI = 2., TCT = 2.

PARAM GNMAX = 4., GNMIN = 1.

PARAM MXRSF = 0.3, CHMPTB = 2.E-7

FUNCTION CHPTT = (0., 0.), (1.E-5, 0.5), (2.5E-5,.8), ...
(3.E-5,.95), (3.5E-5,1.), (3.5E-4,1.)

FUNCTION CHFPET = (0., 0.),(1.E-6,.25), (2.5E-6, .5), (5.E-6,.9), ...
(1.E-5,1.), (1.E-4,1.)

FUNCTION CHFPST = (0.,0.), (1.0E-4, 1.), (1.0E-3,1.)

The tillers are initiated between $DVS = 0.$ and $DVS = 0.425$, the ears and spikelets between 0.35 and 0.425 and the grains between 1.00 and 1.05.

b. Simulate a growing season with a constant high light level and one with a

constant low light level (fixed FOV at 0.2 and 0.8, respectively), one with a bright period followed by an overcast period (FOV = 0.2 until anthesis, and FOV = 0.8 afterwards), and one with an overcast period followed by a bright period (FOV = 0.8 and 0.2, respectively). What about yield and kernel number?
c. Combine the statements of the Exercises 52, 53 and 54a and repeat the simulation. Omit the influence of temperature on the growth rates.
