tissue to the growing grains may be hampered, resulting in a lower N harvest index, thus decreasing the N use efficiency. This effect may become even stronger, when the moisture stress leads to accelerated senescence of the photosynthetic tissue. The developing grain cannot be properly filled so that at harvest kernels have a high protein content and a low dry weight, in extreme situations leading to shriveled grains.

With regular N supply to the plants, on average about 65% to 80% of the grain N was derived from the vegetative parts, the remainder originating from uptake by the roots after anthesis. Available N for relocation to the grains can be derived from N content of the crop at anthesis minus N residues in straw and chaff. The former amounts to about 150 kg ha^{-1} and the latter to about 60 kg ha^{-1} for an average wheat crop in the Netherlands. Mobile N for relocation to the grains is contributed by the leaves (40%), the stem and leaf sheaths (40%), and chaff (20%).

The rate of N accumulation in the grains is determined by dry matter growth rate and the N concentration of the grain. A growth rate of 200 kg ha^{-1} d^{-1} and a N concentration of 20 g kg^{-1} results in a N accumulation rate of 4 kg ha^{-1} d^{-1}. At low N levels the relation between grain yield and total N uptake in the grain is linear with a slope of about 60 kg kg^{-1}. At higher N supply levels the yield response curve deviates from the straight curve, reflecting an increase in the N content of the grains. The level of the plateau where increased N uptake does not result in higher grain yields is determined by other limiting factors (e.g. water shortage, diseases and pests) (cf. Subsection 1.2.3).

Increase in supply of N to grains cannot be obtained by further increasing the concentration of N in vegetative tissue, because this is strongly associated with the adverse effects of a too leafy wheat crop (risk of lodging and increased susceptibility to diseases). A substantial post-anthesis N uptake is therefore a prerequisite for achieving high grain yields.

Part II. Modelling of post-floral growth of wheat

J. Vos, E.M. Drees and F.W.T. Penning de Vries

3.4.7 Description of the model

This section deals with aspects of modelling post-floral growth of wheat. A detailed treatment of such a model is described by Vos (1981). The model describes and interrelates gross CO_2 assimilation, respiration, accumulation of carbohydrates (starch) and proteins in the grains, redistribution and additional uptake of N and leaf senescence. Structural growth of all organs except grains is assumed to have ceased at anthesis. Grain dry matter is assumed to consist of carbohydrates and protein only. The model is designed to run with time steps of one day. Besides crop characteristics at anthesis, daily records of irradiation and

mean temperature have to be given as input. Effects of pests, diseases and water stress are not accounted for.

Daily gross CO_2 assimilation is computed by a set of equations described by Goudriaan & van Laar (1978); these are also described in Subsection 3.2.4. Here it is relevant to note that a reduction of AMAX (photosynthetic capacity at saturating irradiation per unit green area) of remaining green area as a result of senescence appeared to be necessary. Based on only limited experimental evidence, AMAX is assumed to decline in proportion to the decline of the green area.

Due to senescence, the area of green photosynthesizing tissue decreases in the grain-filling period. In this model, the reduction is related almost proportionally to the fraction of N in the leaves at anthesis that is exported to the grains. To account for the contribution of stems and ears to canopy CO_2 assimilation, the total green area is assumed to be 2.2 times that of the leaf blades at any time. Growth respiration of grains is computed using the CO_2 production factors for synthesis of carbohydrates from glucose and proteins from amino acids, given by Penning de Vries (1975) (cf. Subsection 3.3.4). The application of constant factors for maintenance and transport processes (Penning de Vries, 1975; de Wit et al., 1978) appeared to lead to an unacceptable underestimation of measured respiration rates. Respiration of non-grain organs is therefore computed with empirical coefficients (decreasing the explanatory nature of this model). These coefficients are temperature dependent with a Q_{10} of 2.0.

The grain-filling period (Figure 42) can be subdivided into three consecutive stages. During the first 10 days, the grain growth rate is generally small (endosperm cell formation); this is called the lag period. During the second stage the grain growth rate is almost constant; it extends over most of the grain-filling period and it is often called the linear stage of grain filling. During the third or maturation stage the rate of dry matter accumulation can be small. At any day the accumulation rate of grain constituents (g m^{-2}) is given by the product of the number of kernels per square metre (NOKER) and the growth rate per kernel. The number of kernels is fixed at the beginning of grain filling: NOKER is estimated very satisfactorily by the equation:

$$\text{NOKER} = 3500.0 + 14.0 * \text{CRDWAN} \qquad (52)$$

where CRDWAN stands for the dry weight of the crop at anthesis (g m^{-2}).

Exponential growth is assumed during the lag period. The relative growth rate is 0.3 g g^{-1} d^{-1} at 16 °C, with a Q_{10} of 2.0. During the lag period the protein accumulation rate is fixed at 0.17 times the carbohydrate accumulation rate.

Exercise 51

Write statements describing the exponential growth during the lag period and account for the temperature dependency.

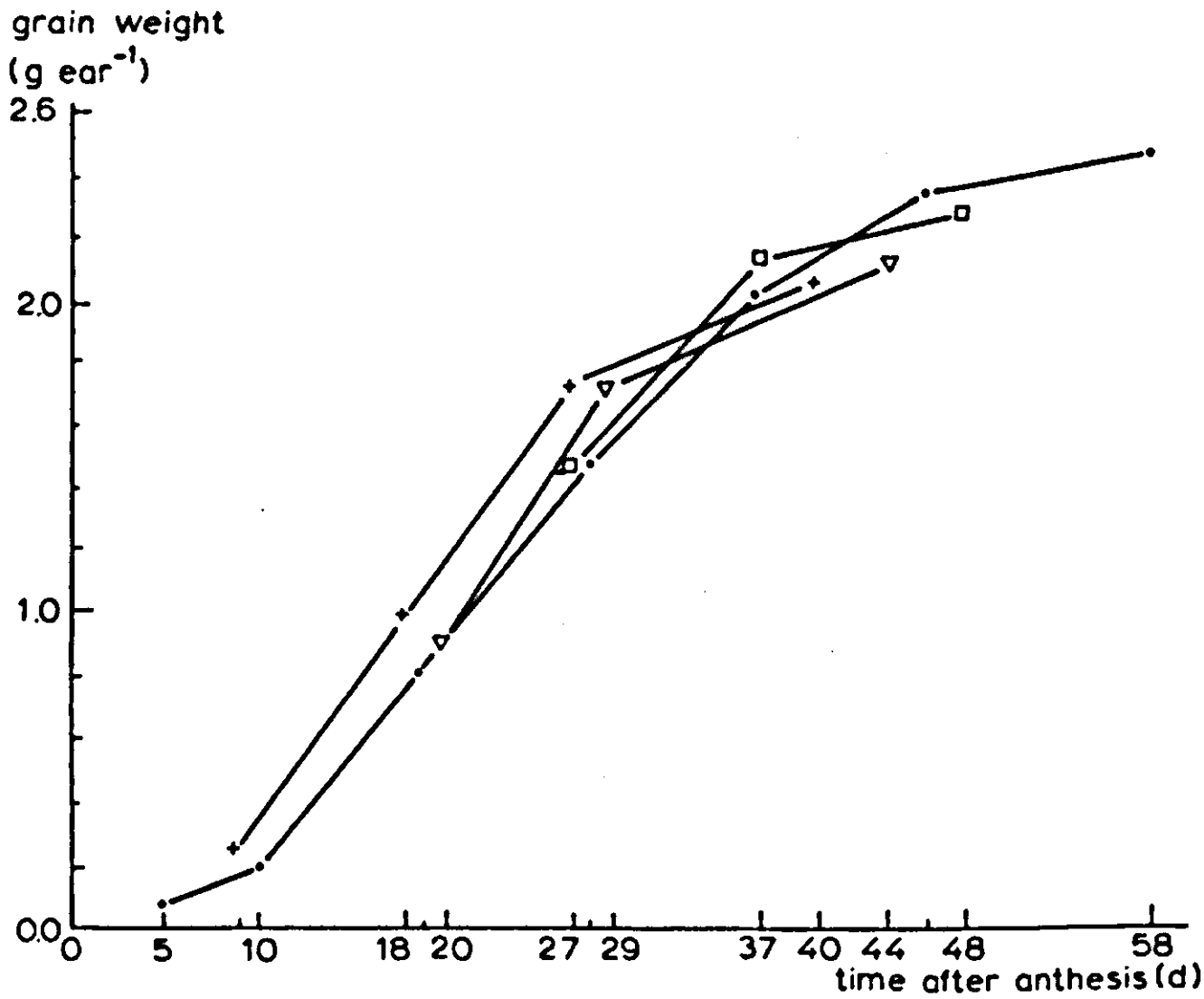

Figure 42. Change with time in grain dry weight as affected by air temperature. Data from Vos (1981). Treatments: • air temperature constant 16 °C; +, ∇ and □ transferred from 16 to 22 °C air temperature at 6, 17 and 24 days after anthesis, respectively. Root temperature 16 °C in all treatments.

Grain growth can be programmed to switch from exponential growth to linear growth when the exponential growth rate becomes equal to or larger than the (potential) growth rate during the linear stage. This last growth rate can be in the order of 25 g m^{-2} d^{-1} at 16 °C, with a Q_{10} of 1.5. The virtue of this approach is that it predicts an earlier transition from the lag period to the linear stage the higher the temperature (Figure 42).

Exercise 52
Which CSMP statements can be used for such transitions? Try this approach by simulation of the grain growth during the lag and linear period at high and low temperatures. Initial grain weight at 7.5 g m^{-2}.

The potential rates of accumulation of carbohydrates and proteins per grain (PRCHA and PRPRA, respectively) are taken to be constant during the linear stage and the maturation period at a reference temperature. As indicated before (Subsection 3.4.4) protein deposition in grains responds more to temperature (Q_{10} = 2.) than carbohydrate accumulation (Q_{10} = 1.5).

Gross CO_2 assimilation provides carbohydrates to the reserve pool (cf. Sub-

section 3.3.3), which is supposed to be situated in the stems only. Carbohydrates of this pool are consumed by accumulation of carbohydrates (starch) in the grain plus the associated growth respiration, growth respiration associated with protein deposition in grains, and respiration of non-grain organs. When daily gross carbohydrate production decreases and the supply of carbohydrate from the pool of reserves becomes smaller than the daily demand, carbohydrate accumulation in grains is the first process which is slowed down.

Daily 'demand' for protein by the grains is given by the product of the number of grains per square metre and the potential accumulation rate per grain. Sources of N for protein synthesis are additional uptake from the soil and removal from non-grain parts. Analyses of several experiments revealed a relationship between the contribution to final grain N yield by additional N uptake plus N removal from roots (treated as one variable, called MXRCRS: maximum relative contribution by roots and soil) and the initial N concentration in shoot dry matter at anthesis (Figure 43). This figure shows that the contribution to final N yield by uptake and removal from roots (calculated as the N content of grains that did not result from removal from aerial organs) decreases at higher initial shoot N concentrations. Furthermore, approximately similar relative distributions of shoot N (over ear structures, leaf blades and stems plus sheaths) were observed at the beginning and the end of the grain-filling period.

These feature allow modelling of the N regime of the reproductive wheat crop. The proportion of the daily N demand of grains to be supplied by additional uptake plus removal from roots (MXRCRS) is determined as displayed by Figure 43. The complementary fraction of the daily demand (= 1. − MXRCRS) is supplied by non-grain aerial parts, whilst the proportion of this fraction that is contributed by each of the various organs is equal to the proportion of shoot N initially present in these organs. (Note that this description is empirical, and may not apply in other situations of, for example, soil fertility.)

Export of N from non-grain shoot organs becomes reduced when the N concentration in the dry matter of these organs decreases below about 4 mg g^{-1}. When the minimum N concentration in the shoot (3.5 mg g^{-1}) is reached, protein accumulation in grains stops. The reduction of N supply from the roots is supposed to occur parallel to reduction from vegetative shoot organs.

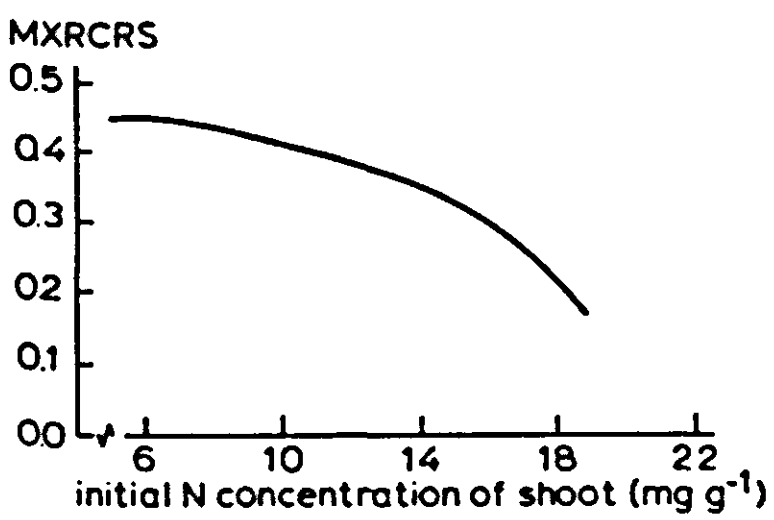

Figure 43. The relation between the relative contribution to final grain N yield by N uptake from the soil plus N removal from roots (= MXRCRS) and the initial concentration of N in shoot dry matter at anthesis.

The duration of the grain-filling phase can be limited by the availability of either carbohydrates or N, but there is also a physiological maximum to this phase. This maximum duration can be described reasonably well by the simple degree-day concept (cf. Subsection 3.3.2): the period between anthesis and maximum grain dry weight can be approximated by a heat sum (HSUM) above a minimum temperature (TMIN). The rate of development (DVR) during this phase was calculated from the mean daily temperature (TEMP) as follows:

$$DVR = (TEMP - TMIN)/HSUM$$

Appropriate values for TMIN and HSUM are 6 °C and about 500 degree-days, respectively. The stage of development, DVS, is assigned an initial value of 0. and is augmented daily by DVR. When DVS reaches the value 1.0 the grain-filling period is complete.

3.4.8 Validations and extrapolations

The model was cross-checked with results of several field experiments. In general good agreement between measured and simulated courses of grain growth and N (re)distribution could be obtained by adjustment of three parameters, viz. AMAXI (the initial value of the photosynthetic capacity per unit green area), and the potential accumulation rates of grain constituents, PRCHA and PRPRA. The range in grain yields of those crops was between 400 and 850 g m^{-2}. However, the range in values for AMAXI required to reach agreement between measured and simulated results seems too wide to be biologically realistic, viz. from 1.5 to more than 3.0 g m^{-2} h^{-1}. The reasons for this are not clear.

Ranges in required values for PRCHA and PRPRA were comparatively smaller. These rates are partly specific for each genotype. The ratio between PRCHA and PRPRA varies between about 7 and 9 at moderate temperatures.

With respect to carbohydrate consuming processes the following comments can be made. There are enough indications pointing at the validity of Penning de Vries' (1975) coefficients for growth respiration. However, growth respiration of grains constitutes at its maximum 30% of total plant respiration only. Respiration of non-grain organs was computed by empirical coefficients. This treatment gave rise to total plant respiration rates, which were likely to be in the correct order of magnitude, but erratic predictions of the rate of this major respiratory component might occur when the model is applied in a wider range of conditions. Furthermore, there might be another drain of assimilates which was not and cannot be treated in sufficient detail yet, viz. the flux of assimilates to the root or root medium. This aspect seems to require more study.

Assimilate partitioning is comparatively simple as there is only one site for growth, viz. the grains. Potential accumulation rates per unit land area for carbohydrates and proteins in grains cannot be derived accurately enough from the state of the crop at anthesis. Usually there is a direct relation between the number of grains per square metre and the shoot vegetative biomass, but the

parameters of the regression vary considerably between experiments (Equations 49 and 52) and genotypes (Vos, 1981). Potential accumulation rates per grain differ between cultivars and are possibly affected by environmental factors until the number of endosperm cells is fixed. In conclusion it can be stated that modelling of grain growth (at a reference temperature) per unit area (as composed of rate per grain times number of grains) requires further analysis. Subsection 3.4.10 shows an attempt to do so. So far, the description of the difference in temperature sensitivity between carbohydrate and protein accumulation in grains proved to be satisfactory.

The treatment of the N regime, which turned out to be fairly useful, is in fact based on a generalized observed pattern of redistribution, without giving much explanation. Adaptations will be required when other factors, like water stress and diseases, are introduced into the model.

Under otherwise similar conditions grain dry matter yield in the field was predicted (Vos, 1981) to be smaller by 30 to 40 g m^{-2} per 1 °C rise in temperature throughout the grain-filling period (Dutch climate and crop management). A concomitant increase in visible radiation by 130 to 180 J cm^{-2} d^{-1} could offset the adverse effect of such a rise of temperature. Model calculations showed little effects of temperature and irradiation on grain N yields. Saturation type of response curves were predicted for grain dry matter yield and final grain N concentration versus initial shoot N concentration (at a fixed crop dry weight at anthesis). Yield increases of about 15 to 20% were predicted when the initial N concentration of the shoot is increased from low (8 mg g^{-1}) to high values (about 16 mg g^{-1}); final N concentration in grain dry matter would increase from about 15 to more than 20 mg g^{-1}.

3.4.9 A simple model of the carbohydrate-nitrogen interaction

The modelling of the economy of carbohydrates and nitrogenous compounds has been described separately. In whole plants, however, both processes interact. To demonstrate this with a small program, a simplified though basically realistic approach to C and N availability during grain growth, is described. This simple model is somewhat different from the model described before. In addition the effect of temperature has been omitted, and the example is based on values for 16 °C.

The dry weight of the grains (GDW, g m^{-2}) is calculated from the actual growth rate of the grains (GGR, g m^{-2} d^{-1}). The potential growth rate (PGR) depends on the number of kernels and the potential rate of carbohydrate (as grain) accumulation (PRCHA, g $grain^{-1}$ d^{-1}). It is assumed that grains consist of 12.5% proteins in a standard situation, the rest of the biomass being carbohydrates. The actual growth rate is the minimum value of the potential growth rate and the growth rates determined by the availability of C (GRC) or of N (GRN) (for all abbreviations and constructions not explained here, one is referred to previous sections):

```
GDW     = INTGRL(0., GGR)
GGR     = AMIN1(PGR, GRC, GRN)
PGR     = NOKER*PRCHA/0.875
PARAM PRCHA = 0.00090
GRC     = PGR*RED1
RED1    = AFGEN(REDTB1, ACH/WVEG)
FUNCTION REDTB1 = 0., 0., 0.01, 0.0, 0.05, 1., 1., 1.
```

ACH is the available carbohydrates (g m^{-2}); WVEG is the dry weight of the vegetative mass (g m^{-2});

```
GRN     = PGR*RED2
RED2    = AFGEN(REDTB2, AN/WVEG)
FUNCTION REDTB2 = 0., 0., 0.0001, 0., 0.0005, 1., 0.1, 1.
```

AN is the available nitrogen (g m^{-2});

```
ACH     = INTGRL(ACHI, GPHOT-RNGO-CAG-MRG)
```

ACHI represents the available carbohydrates at flowering, GPHOT the actual photosynthesis (g m^{-2} d^{-1}), RNGO the respiration of non-grain organs (g m^{-2} d^{-1}), MRG the maintenance respiration of the grains (g m^{-2} d^{-1}) and CAG the carbohydrate accumulation in the grains (g m^{-2} d^{-1}).

```
CAG     = GGR/CVF
PARAM CVF = 0.73
MRG     = 0.005*GDW
RNGO    = WVEG*0.01
PARAM WVEG = 800., NOKER = 15000., ACHI = 160., GPHOTS = 30.
GPHOT = GPHOTS*AFGEN(REDTB3, ACH/WVEG)*...
            AFGEN (REDTB4, AN/WVEG)
```

GPHOTS is the standard rate of photosynthesis (g m^{-2} d^{-1}), RED3 is the reduction factor for photosynthesis as a consequence of too much available carbohydrates and RED4 represents senescence: it is the reduction factor of photosynthesis as a consequence of too little available N.

```
FUNCTION REDTB3 = 0., 1., 0.20, 1., 0.25, 0., 0.30, 0.
FUNCTION REDTB4 = 0., 0., 0.0001, 0., 0.001, 1., 0.01, 1.

AN      = INTGRL (ANI,UPTAKE-NAG)
```

The available N is the amount of N that can be translocated to the grains. The minimum level in the vegetative shoot, below which N is no more available, is 0.0035 g g^{-1}. FNS is the initial fraction of N in the shoot and determines the initial amount of N (ANI). ANI should be calculated in the intitial section.

```
ANI     = WVEG*(FNS-0.0035)
```

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

```
UPTAKE  = DEMAND*MXRCRS
DEMAND  = NOKER*PRPRA*1./5.95
PARAM PRPRA = 0.00013, FNS = 0.010
MXRCRS  = AFGEN(MXTB, FNS)
FUNCTION MXTB = 0.0035, 0.45, 0.006, 0.45, 0.01, 0.4, 0.014, 0.35, ...
                0.08, 0.225
NG      = INTGRL(0., NAG)
```

NG is the amount of N in the grains (g m^{-2}). NAG is the rate of N accumulation in the grains (g m^{-2} d^{-1}), which is a fraction (PRPRA/(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.

```
NAG     = GGR*0.875*PRPRA/(PRCHA*5.95)*RED
RED     = RED2/AMAX1(0.5, RED1)
```

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

Exercise 53

a. 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 CO_2 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.
b. What range of concentrations of N in the daily weight increment of grain is implied in this formulation of grain growth?

Part III. A deterministic approach to modelling of organogenesis in wheat

H. van Keulen

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-