MODELLING OF GROWTH PROCESSES IN PLANTS

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1. Introduction

Agricultural research on the wheat crop has a long tradition of field exper-
imentation, as may be illustrated by the prize essay of Edward Roberts Jun.,
that appeared in England in 1847, or a more or less casual look at the
reference section of fairly recent reviews on the crop (Fischer, 1983; Evans
et al., 1975) that easily contain over 100 references of which roughly 80
percent pertains to field experiments.

Since World War II this research has been complemented by an increasingly
intensive program of investigations under controlled conditions. Such inves-
tigations have the advantage that environmental conditions that in the field
are always unpredictable, often widely fluctuating and sometimes adverse, can
be maintained at reasonably constant levels. This provides the possibility to
study effects of well-defined factors within pre-determined ranges on speci-
fic plant properties or processes.

The development of powerful 'calculation machines' and their growing
accessibility at the beginning of the '70's, along with the development of
programming languages for these machines that were intended to combat their
major disadvantages with respect to the real world situation, they work
discrete and sequentially, provided an opportunity to apply the detailed
knowledge obtained, in an attempt to 'put things together again'.

These efforts have shown that the physiological, biochemical and physical machinery of a growing crop is of an enormous complexity. Claims that the relevant processes are well enough understood to develop explanatory and predictive models, applicable in all or most situations are certainly over-statements. However, that should not prevent one from embarking on those efforts, because a well-thought out whole crop model represents a coherent opinion about the functioning of such a system. Such an instrument is amen-able to testing, both under field and controlled conditions, it can be used to test the consequences of alternative hypotheses and it helps in for-mulating the right research questions. In this contribution such a whole-crop model is presented, using the wheat crop as an example

2. Elements of a whole-crop model

2.1 Gross CO_2 assimilation

The basis for organic matter production in any green plant is the process of CO_2 assimilation. The overall reaction, taught us probably already in high school, has not changed over the years, but that is only a very first step to quantitatively assess the amount of carbohydrates fixed by a canopy under field conditions. For that purpose, two major components of the system have to be described: the distribution of irradiance over the various chlorophyl-lous components of the crop system and the response in CO_2 assimilation of these components to increasing energy availability. Detailed mathematical descriptions of the former have been developed, using sun path, crop geometry and leaf optical properties as inputs (cf. Goudriaan, 1977). The degree of accuracy of these descriptions can be doubted in practice, but it would seem that the underlying physical principles are well enough understood to allow a satisfactory description of the radiation environment to which the green parts of the plant are exposed, provided that the relevant plant properties are available in sufficient detail.

The response of the assimilating components to irradiance can be quanti-tatively described in a number of ways. The choice for a particular response type is in general based on the data at hand, rather than on well-established theoretical considerations that prove the superiority of a particular type. In any quantitative description, the initial light use efficiency and the

maximum rate of gross CO_2 assimilation are the main parameters. Recently, Goudriaan et al. (1984) have treated the former in some detail.

In the framework of a whole crop model especially the dynamics of these characteristics over the entire growing period are of interest, as influenced by environmental conditions and crop properties. In Figure 1 some data are compiled collected from literature, on the effect of nitrogen concentration in leaves on their assimilatory activity. These data would suggest that a reasonably constant relation exists between both characteristics. However, how much of the residual variability is due to plant characteristics, growing conditions, or other factors is impossible to deduce from such data. A further complication arises from the fact that this relation holds for individual leaves, but in a field crop leaves of widely differing properties may be present. This requires some form of spatial integration. As long as all relations involved are linear, simple averageing may provide a satisfactory solution i.e. the average nitrogen content of the total leaf mass present, may be representative for its assimilatory capacity. However, it turns out that particularly in the post-anthesis phase, the distribution of nitrogen concentrations in the leaves can be very heterogeneous, thus creating a situation where most of the radiation is intercepted by leaves with relatively favourable characteristics and application of average nitrogen content will grossly underestimate the crop assimilatory performance. In the whole-crop model approach this provides an example where the need for simplification leads to a nuisance for the crop modeller.

An interesting but confusing observation is the fact that under controlled conditions considerable differences in assimilatory capacity among cultivars have been established (cf. Dantuma, 1973), but that effects of such differences in the field situation are either completely absent or cannot be shown to be of any importance for crop yield. The reason for those seemingly conflicting observations are unclear, but more sophisticated experimentation, especially the possibility to measure assimilation of individual leaves and of a whole canopy concurrently, may shed light on this problem.

2.2 Respiration

There is little argument about the fact that a substantial part of the carbohydrates fixed in the assimilatory process is subsequently respired.
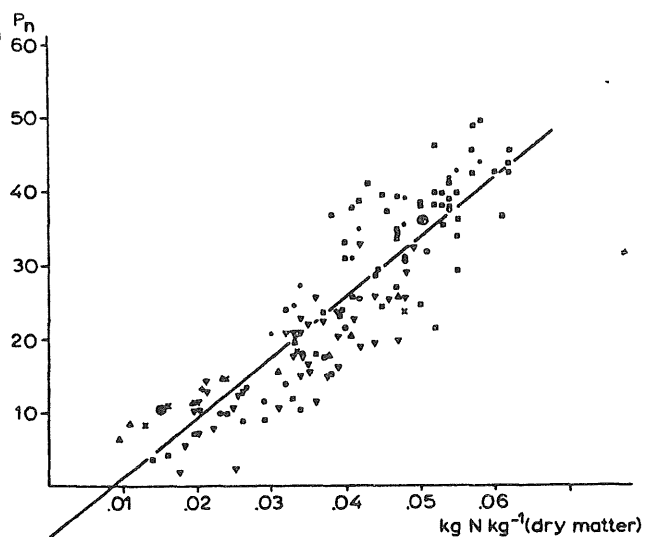
Figure 1. The relations between nitrogen concentration in the leaf tissue and the rate of net CO_2 assimilation.
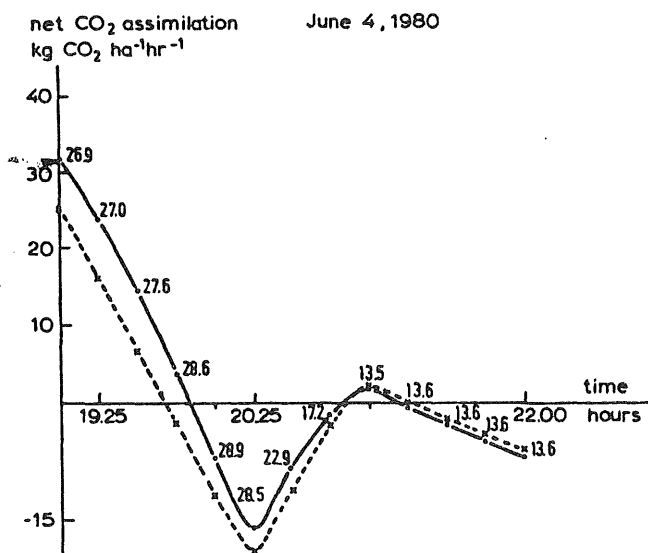

Figure 2. Measured (crosses) and simulated (dots) net CO_2 assimilation of a wheat crop in an enclosure. Numbers refer to air temperatures in the enclosure.

Generally, whole plant physiologists will add to this, to provide energy for biological functioning, although in view of recent discussions it might be well to add: or to dispose of surplus carbohydrates, although it is difficult to visualize where in the field situation such conditions could occur (viz. Goudriaan et al., 1984). In the schematized set-up of the whole crop model, the magnitude of respiration is derived as the sum of the energy required for the maintenance of existing tissue, defined as a function of dry matter present and its chemical composition, and the energy lost in the conversion of primary photosynthetic products into structural plant material, which is again dependent on the composition of the material being formed. The latter is assumed to include also the costs involved in the transport of assimilates from the active sites to the growing organs. The actual coefficients used in the description are derived from detailed biochemical treatment of the processes involved (Penning de Vries, 1975; 1974). However, experience shows, that it is often difficult to predict the respiration rate accurately under different and fluctuating conditions (Figure 2).

2.3 Assimilate partitioning

The assimilates fixed in the photosynthetic process are partitioned to various sinks in the growing plant. The partitioning pattern is clearly a genetically controlled mechanism, as may be deduced from the multitude of plant life forms that a look out of the window provides. The annual wheat plant that is the subject of the present presentation is characterized by a relatively short life cycle. Its strategy for survival is based on relatively rapid growth, accomplished by investing initially a large proportion of its assimilates in the formation of an active assimilatory apparatus. Later on, assimilates are used for the formation of the head-bearing stem and finally for the production of a large number of seeds necessary for propagation.

The actual proportion of the assimilates partitioned to any particular organ at a certain moment can be considered as an expression of the sink strength of that organ. The sink strength is probably related to the amount of meristematic tissue capable of growth. However, in the whole-crop model approach, processes at the cellular level cannot be incorporated, because of the wide differences in relaxation times (De Wit, 1970), so that partitioning is described by functions related to the phenological development of the crop. An example of the type of dates used to derive such a function is given

in Figure 3, illustrating the large variability found in published data. Part of this variability could be explained by differences in growing conditions, such as supply with water and nutrients. The partitioning of carbohydrates between shoot and root may then be governed by the so-called 'functional balance' principle, i.e. if those growth factors whose supply is governed by the magnitude of the below-ground parts are in short supply, more of the assimilates will be diverted to those organs, and vice-versa. This hypothesis was illustrated in a charming way by the work of Brouwer in the sixties (Brouwer, 1963). A recent review of these concepts (Lambers, 1983; Schulze, 1983) would indicate that the principles are valid, but that the controlling mechanism is still only vaguely understood.

Nevertheless, this question of partitioning of assimilates is of prime importance in the yield-determining processes of wheat, because plant breeders claim that - at least part of - the yield increase witnessed over time is due to a more favourable distribution of the assimilates over the different plant parts. For the reduced stature cultivars that certainly seems to be the case, because allocation to the spike is favoured at the expense of stem growth. For the development of whole-crop models it would be advantageous if that process could be described in terms of measurable quantities, such as cell numbers or amount of meristematic tissue.

On the whole, it must be admitted that the processes underlying the partitioning of assimilates to the various plant parts are poorly understood and that the approaches used in whole-crop models are at best descriptive, rather than explanatory. Hence, the need for a proper description to predict grain yields, which is the main emphasis of all our efforts, results in a nuisance for the modeller, who must assume some arbitrary control mechanism, that in practice often defeats the purpose.

2.4 Dry matter production

After partitioning of the assimilates to the sinks distinguished in the model: leaf blades, stems & sheaths, roots, grains and a store of non-structural carbohydrates, they are converted into structural plant material. For each of the vegetative organs this is achieved by multiplying with a conversion efficiency.

The efficiency of conversion is calculated from the composition of the material being formed. In the schematized description, only carbohydrates and
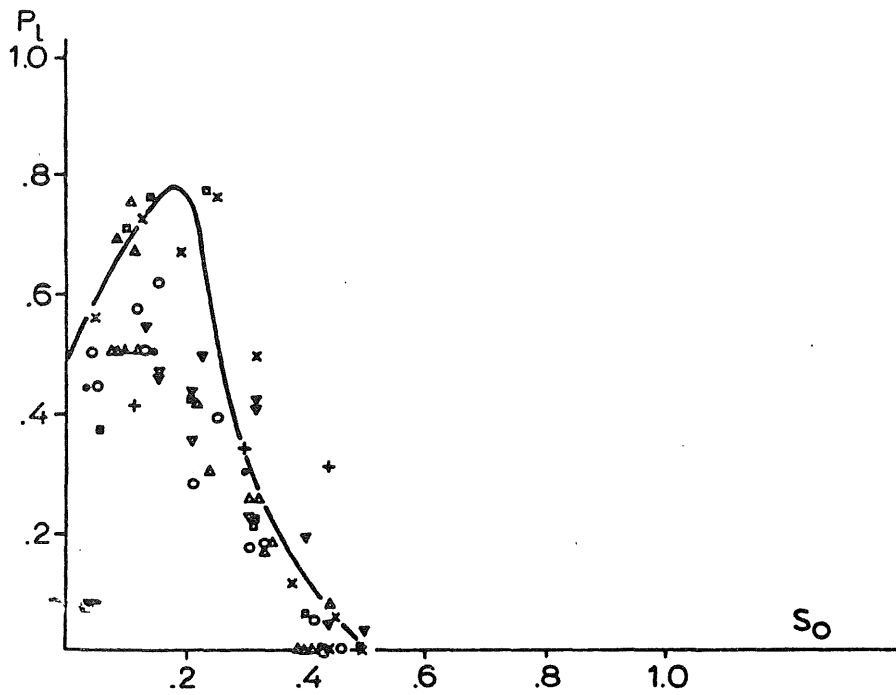
Figure 3. The relation between development stage of the wheat crop (0 = emergence; 0.5 = flowering; 1 = maturity) and the fraction assimilates allocated to the leaf blades.

proteins are distinguished, and it is assumed that the composition of the material growing any particular day is equal to the average composition of the material present, for each of the organs.

Under conditions of shortage of nitrogen and/or water, the growth of the leaf blades is hampered and the assimilates that cannot be utilized by the blades are distributed among the other sinks in proportion to their relative sink strength, as expressed by the actual values of the partitioning factors.

For the grains a different formulation is applied: first the potential growth rate is calculated from the grain number and the potential rate of dry matter accumulation per individual grain, which is defined as a function of temperature:

$$G_p = N_G \cdot C_c \tag{1}$$

where,

G_p is potential growth rate of the grains, kg $ha^{-1}d^{-1}$

N_G is number of grains

C_c is capacity for dry matter accumulation of an individual grain (= f(T))

If this growth rate can be realized from the current assimilate supply, growth proceeds at the potential rate. If assimilate supply falls short of the requirement, it can be supplemented by part of the reserve store of non-structural carbohydrates that can be mobilized, so that potential growth rates can be maintained for a considerable period of time, even though current assimilation may fluctuate substantially. The growth rate drops below the potential value only, if the combined supply from current assimilation and mobilized reserves cannot support these rates. Growth is then determined by assimilate availability.

2.5 Organ formation

In many studies in the last decades, heavy emphasis has been placed on the fact that grain yield is closely correlated to the number of grains (Spiertz and van Keulen, 1975; Fischer, 1978). These results have had an impact on

actual farming practice, for instance in Germany where farmers have resorted
to very high seeding densities in order to achieve high grain numbers.
However, the number of grains per unit area is the outcome of a long series
of processes that include the formation of the various organs of the plant.
There is first of all the tillering capacity, that determines how many shoots
will be present in the subsequent crop growth stage. In practice, only a
limited number of these tillers result in spikes, while a substantial propor-
tion never reaches the reproductive stage. In the next stage, the number of
spikelets per spike is determined, and again there seems to be a substantial
surplus when compared to the actual grain number that is achieved. Subse-
quently, the number of competent florets per spikelet is determined and
finally grain set determines how many of those florets result in actual
kernels.

In individual experiments, often a very good correlation is found between
grain number and the weight of the spike at some moment in the plant's life
cycle (Fischer, 1983; Darwinkel, 1978). It is , however, questionable whether
that is a direct causal relationship, because the weight of the spike at a
given moment is the result of the integrated effect of assimilate supply
during the period of spike growth, the partitioning of the assimilates to
that particular organ and the length of the period available for growth of
the organ. The picture that arises from these considerations is that the
wheat crop tries to maintain optimum flexibility, by initiating at any point
in its phenological development, a surplus of organs, that in a subsequent
stage can be adjusted, according to the growing conditions prevailing at that
time.

Obviously, the crop must have some sort of information system on which to
rely for the determination of the organ numbers in the course of development.
In the state-variable approach, tangible quantities are considered to be
governing crop behaviour, such as the leaf area index, the weight of the root
system, or the nitrogen content of the leaves. However, in order to sense the
possibilities for further development, the crop has to retain information on
the current activities, like the rate of CO_2 assimilation and the current
growth rate of various organs. In considering this information, a distinction
can be made between the message that must be transferred and the means by
which this transfer is effectuated (the hardware). The latter could be
envisaged as hormonal systems in the crop such as the levels of cytokinines,
giberellic acid or abscisic acid. However, in whole-crop models, the message

is much more important than the means by which it is transmitted (de Wit and
Penning de Vries, 1983). In the present model, this message is therefore
related to the current crop activity level as represented by the daily CO_2
assimilation level.

The rate of organ formation at any point in time is described by an
equation of the type:

$$R_o = (R_{mx} - R_a) / T_a \qquad (2)$$

where,

R_o is the rate of organ formation in number of organs $ha^{-1} d^{-1}$

R_{mx} is the maximum number of an organ that can be maintained per
ha

R_a is the actual number of an organ present per ha

T_a is the time constant for organ formation in d

The maximum number of organs that can be maintained at any point in time
is a function of the availability of carbohydrates for growth of the organ,
modified by the development stage:

$$R_{mx} = C_f / U_x \qquad (3)$$

where,

C_f is carbohydrate supply to the growing organs in kg $ha^{-1} d^{-1}$

U_x is the minimum carbohydrate requirement for the formation of
a viable organ in kg $organ^{-1} d^{-1}$

The minimum carbohydrate requirement for the formation of a viable organ
is defined in dependence of the development rate, to account for the fact,
that in practice it appears that an organ needs a certain minimum size to be
viable. Hence, when the development rate is high, and the period for the
formation of a certain organ is short, the daily carbohydrate requirement
must be high to produce that minimum size of the organ. Hence:

$$U_x = U_{x.,o} \times d_r \qquad\qquad (4)$$

where,

$U_{x,o}$ is the basic carbohydrate requirement for formation of an organ in kg organ^{-1}

d_r is the development rate of the crop in d^{-1}

In this way, formation of plant organs is dependent on the supply of carbohydrates at particular points in the development of the crop. Integration of those values over the time period available for the formation of a certain organ, leads to the notion that the wheat crop is aiming at the formation of a number of organs that is commensurate with its carbohydrate supply.

The formation of leaf area follows directly from the increase in dry weight of the leaf blades by assuming a constant specific leaf weight of the growing material. The check in leaf blade growth under sub-optimum growing conditions results thus concurrently in a reduced leaf area index.

Leaves may die from either water shortage, nitrogen shortage or from senescence. The first one is related to the transpiration deficit, the second one to the nitrogen concentration in the leaf blades in comparison to the maximum concentration, while the third one is effectuated by assuming a fixed life span of the leaves under optimum growing conditions. If suboptimum growing conditions have resulted in leaf death before their life span is completed, senescence is not effective.

2.6 Nitrogen economy of the crop

One of the objectives of a whole-crop model is the development of management systems that ensure farmers an optimum return from their endeavors. In the framework of actual farming practice, one of the most important management tools available is the supply with nitrogen fertilizer. Two major problems are involved in predicting the effect of fertilizer application on crop performance:
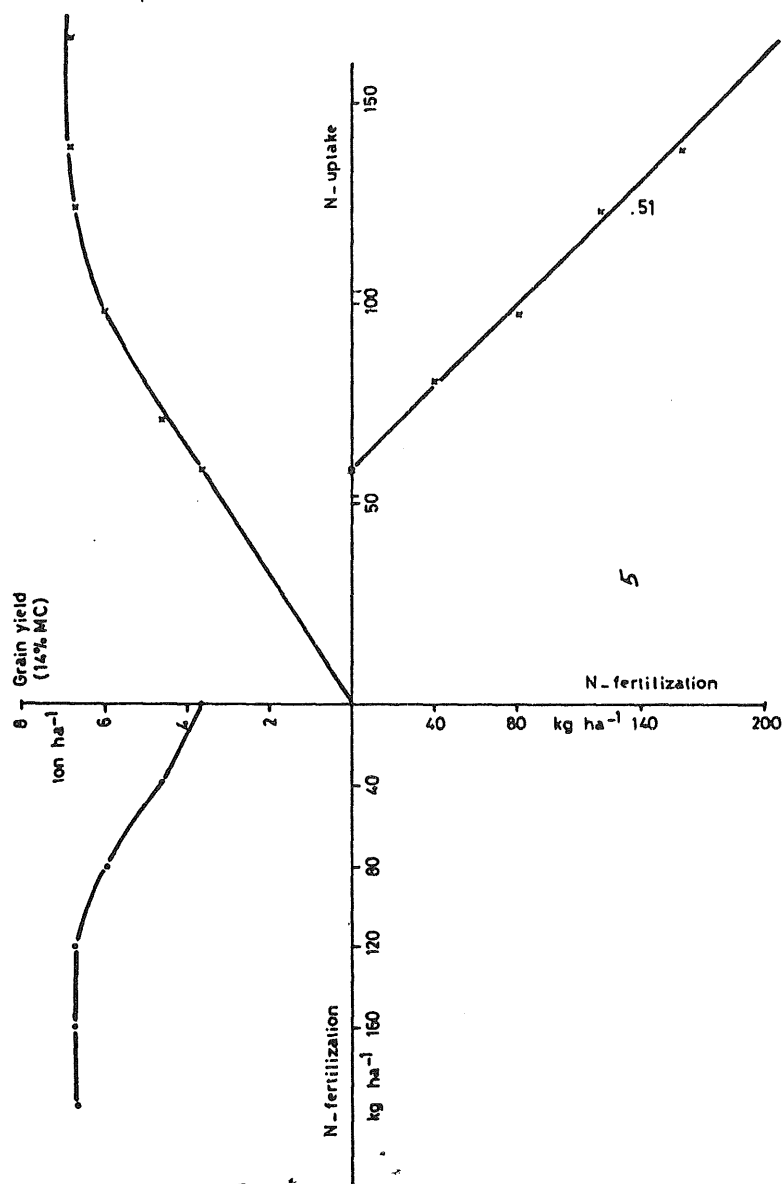
Figure 4. The relation between grain yield and nitrogen uptake (upper right), that between nitrogen application and nitrogen uptake (lower right) and that between nitrogen application and grain yield (upper left) for a winter wheat crop in the Netherlands.

1) the element is added to the soil system and is subject there to various processes that may render it (temporarily) unavailable to the crop. An illustration of this effect is given in Figure 4, referring to an experiment with winter wheat in the Netherlands. Fertilizer application does not manifest itself by higher levels of mineral nitrogen in the soil profile, at least not in a form that is detectable by traditional analysis techniques. To predict uptake by the canopy, a reasonable estimate of availability in the soil is however necessary.

2) if available nitrogen in the soil is known, uptake by the vegetation must be estimated.

In the framework of a whole-crop model the demand for nitrogen is a major determinant. A convenient way to describe that demand is the definition of an optimum nitrogen concentration that the canopy tries to achieve, and to express the demand as the difference between that value and the actual content in the tissue:

$$D_N = W_c \times (c_o - c_a) \tag{5}$$

where,

D_N is nitrogen demand in kg ha^{-1}

W_c is weight of the vegetation in kg ha^{-1}

c_o is optimum nitrogen concentration in the tissue

c_a is actual nitrogen concentration in th the tissue

Such a formulation requires definition of c_o. Examination of experimental evidence suggests at least two factors that have to be taken into account. First, the optimum nitrogen concentration is not constant, as even under optimum nitrogen supply the concentration in the tissue decreases with age, presumably because in the course of time more protein-poor supporting components are produced. Secondly, the optimum nitrogen concentration is not identical for the different plant organs: at any point in time the concentration in, for instance, leaf blades is higher than in stem or roots. To account for these effects, D_N, is calculated as the sum of the nitrogen demands of the various plant organs, distinguished in the model, and c_o is defined for each of the organs as a function of the phenological development stage of the crop.

Another aspect to be considered here is that of crop behaviour under sub-optimum supply of nitrogen. If insufficient nitrogen is available to meet the demand of the growing vegetation, an allocation problem arises: where is the limited amount that is taken up utilized. One way of looking at this is again via the functional balance principle, which suggests that in a situation of limited nutrient availability, the organ responsible for its supply is favoured, both because uptake could be enhanced in that way and because that organ is closest to the source. However, there is no evidence that points in that direction: there is no large difference in distribution of nitrogen between various organs under different levels of supply and nitrogen that is supplied to a nitrogen-deficient crop is not monopolized by the root system (van Dobben, 1963). In the model therefore, the available nitrogen is partitioned in proportion to the values of D_N for each of the various vegetative plant organs.

The nitrogen economy of the grains is treated in a different manner: all the nitrogen incorporated in the grains is assumed to originate from the vegetative tissue; it arrives thus in the grain in reduced form. The demand for nitrogen in the grains is determined by the grain number and a temperature-dependent capacity of the individual grain for nitrogen accumulation:

$$D_{NG} = N_G \cdot C_N \qquad (6)$$

where,

D_{NG} is the demand for nitrogen of the grains

N_G is the grain number

C_N is the capacity for nitrogen accumulation of an individual grain ($= f(T)$)

The availability of nitrogen for the grains is determined on one hand by the amount of nitrogen in the vegetative material, and on the other hand by its mobility.

Not all the nitrogen in the vegetative organs can be translocated, because part is incorporated in structures from which it cannot be re-mobilized. Thus the nitrogen potentially available for transport to the grain is that contained in leaves, stems and roots minus the immobilizable residual portion. Only part of that nitrogen is transformed in components that can be transported, i.e. that proportion of the proteins that is degraded each day.

The relative rate of protein turnover is a function of air temperature. There is competition for these nitrogenous components between the vegetative organs and the growing grain. It is assumed now, that the competitive ability of the vegetative organs is inversely related to their average nitrogen content, i.e. if the nitrogen concentration declines, a greater fraction of the mobile nitrogen will be exported to the grains. This formulation leads to a situation where the rate of nitrogen accumulation in the grains can remain constant over a considerable range of nitrogen concentrations in the vegetative material, as is often observed.

2.7 The soil system

To describe the relevant processes in the soil, mainly those related to the water balance and the nitrogen balance, the soil system is divided into a number of homogeneous compartments, not necessarily of equal thickness. Greater detail can be achieved by specifying more compartments of smaller size.

In each compartment five state variables are tracked: its moisture content, its total content of mineral nitrogen (comprising NO_3^-, NH_4^+ and any other inorganic components), its stable organic matter content, its content of fresh organic matter and its microbial population.

The moisture balance of each compartment is described by: (For a more detailed description of the soil moisture balance, reference is made to van Keulen, 1975).

$$dW_i = I_i - D_i - E_i - T_i \qquad (7)$$

where,

dW_i is the rate of change in moisture content, $mm\ d^{-1}$

I_i is the rate of influx of moisture over the upper boundary, $mm\ d^{-1}$

D_i is the rate of outflow of moisture over the lower boundary, $mm\ d^{-1}$

E_i is the rate of water loss by soil surface evaporation, $mm\ d^{-1}$

T_i is the rate of water loss by crop transpiration, $mm\ d^{-1}$.

Influx and outflow of moisture only take place during rain or irrigation, it being assumed that in that event the compartments are filled up till field capacity from the top one downwards, until all incoming moisture is dissipated, or until the surplus has drained below the potential rooting zone. Flow between compartments as a result of developing potential gradients is thus disregarded.

To obtain the rate of water loss by soil surface evaporation, a descriptive procedure is used, representing the redistribution of moisture following withdrawal from the top compartment. Total daily soil surface evaporation E_t, an important component of total field water use, especially under (semi-)arid conditions, is calculated by a Penman-type equation, taking into account the reducing effects of shading by the vegetation and the formation of a mulch layer. For each compartment then holds:

$$E_i = f_i \cdot E_t$$

where,

f_i is proportionality factor, defined as a function of soil moisture content and depth below the surface: $\sum_{i=1}^{n} f_i = 1.$

The rate of water loss by crop transpiration is a function of the evaporative demand of the atmosphere, determining potential transpiration, and the combined effect of moisture distribution and root distribution in the soil profile. Root distribution refers to vertical extension only, as no root density effects are taken into account.

For each soil compartment:

$$T_i = T_t \times R_{ei}/R_{et} \times f_w \qquad (8)$$

where,

T_t is potential transpiration of the vegetation, mm d^{-1}

R_{ei} is effective root length in compartment, mm

R_{et} is total effective root length in soil profile, mm $\left(= \sum_{i=1}^{n} R_{ei} \right)$

f_w is reduction factor for soil water uptake, function of moisture content in compartment.

The value of R_{ei} is co-determined by the vertical extension of the root system in a compartment and its actual moisture content. This formulation allows for partial compensatory uptake from wetter soil layers if part of the root system is located in dry soil.

Actual crop transpiration is then obtained by:

$$T_a = \sum_{i=1}^{n} T_i \qquad (9)$$

For the description of the nitrogen balance, four nitrogen pools are distinguished (for more detail see Seligman and van Keulen, 1981). In the mineral pool no distinction is made between various forms of inorganic nitrogen, it being assumed that they are all equally available for plant uptake.

The nitrogen in the stable organic material, that has at least once undergone microbial conversion, decreases by decomposition of the material and increases by addition of stable components originating from decomposing fresh organic material:

$$dN_{si} = A_{si} - n_s \cdot D_{si} \qquad (10)$$

where,

dN_{si} is rate of change of nitrogen content in stable organic material, kg N d^{-1}

A_{si} is rate of accretion of N in stable organic matter, kg N d^{-1}

n_s is nitrogen concentration in stable organic material

D_{si} is rate of decomposition of stable organic material in kg d^{-1}

The rate of decomposition is defined as a specific rate, maintained under optimum conditions, and is further affected by soil moisture and temperature conditions.

The fresh organic material, consisting of crop residues and roots of last year's crop is characterized by its composition in terms of proteins/sugars, cellulose/hemicellulose and lignin. This subdivision is made on the basis of the resistance to microbial decomposition of each of the components, which are decomposed in the order of increasing resistance. The specific rate is different for the various components, but the influence of moisture and

temperature is taken into account analogous to that for the stable organic
material, while the C/N ratio of the material is also taken into account.

$$dN_{fi} = - n_f \cdot D_{fi} \tag{11}$$

where,

dN_{fi} is rate of change of nitrogen content in fresh organic
material, kg N ha^{-1}

n_f is nitrogen concentration in the component currently
decomposed

D_{fi} is rate of decomposition of the fresh organic material, kg d^{-1}.

Part (or all) of the nitrogen that is mineralized during decomposition of the
organic material is immobilized for the formation of microbial tissue. The
rate of change in microbial biomass, dN_{mi}, is calculated as:

$$dN_{mi} = (N_{mxi} - N_{mai})/TC \tag{12}$$

where,

N_{mxi} is maximum size of the microbial population, determined
by either carbon or nitrogen availability, kg N ha^{-1}

N_{mai} is actual size of the microbial population, kg N ha^{-1}

TC is time constant for adaptation of microbial population, d.

Finally, the store of mineral nitrogen is balanced by:

$$dN_i = dN_{si} + dN_{fi} - dN_{mi} + I_{ni} - D_{ni} - U_{ni} \tag{13}$$

where,

I_{ni} is rate of influx of mineral nitrogen over upper boundary,
kg N ha^{-1} d^{-1}

D_{ni} is rate of outflow of mineral nitrogen over lower boundary,
kg N ha^{-1} d^{-1}

U_{ni} is rate of uptake of nitrogen by the vegetation, kg N ha^{-1} d^{-1}

Both I_{ni} and D_{ni} are calculated from the flow of water over the respective
boundaries and the concentrations of mineral N in the compartments. The
outflow of nitrogen is defined as:

$$D_{ni} = (N_i + I_{ni} \cdot dT)/(W_i + I_i \cdot dT) \times D_i \qquad (14)$$

with dT the time step of integration. Thus, to calculate the concentration in the outgoing water, the mineral nitrogen present in a compartment plus that entering by mass flow is mixed completely with the moisture present in the compartment plus that flowing in.

To calculate the uptake of N by the vegetation two terms are distinguished: nitrogen is transported by the transpiration stream into the vegetation, as long as a demand for the element exists. If the concentration in the tissue is equal to or exceeds the maximum value, nitrogen is actively excluded.

When the total demand is not met by mass flow, the remainder may be supplied by diffusion to the roots (van Keulen et al., 1975), if sufficient mineral nitrogen is available in the wet rooted soil. Uptake by diffusion from the various compartments is governed by the relative amount of mineral N present in each compartment.

Hence;

$$U_{ni} = N_i/W_i \cdot T_i + F_{di} \qquad (15)$$

$$F_{di} = (D_N - \sum_{i=1}^{n'} N_i/W_i \cdot T_i) \cdot N_i/(\sum_{i=1}^{n'} N_i) \qquad (16)$$

where,

F_{di} is rate of uptake of nitrogen by diffusion, kg ha^{-1} d^{-1}

n' is compartment number containing the root tip.

3. Performance of the model

The model was tested in first instance with data collected in an extensive research program on actual and potential production in semi-arid regions carried out in the northern Negev desert of Israel (van Keulen et al., 1982).

In figure 5a measured and simulated growth curves are presented for a wheat crop well supplied with nitrogen in the '79/'80 growing season. This was a very favourable season with a total rainfall of 365 mm - against 250 mm as the long-term average - reasonably favourably distributed. Total dry matter production of the crop reached thus 15000 kg ha^{-1}, compared to 14000 kg ha^{-1} in the simulation. The grain yield of 3.4 t ha^{-1} (from hand harvest
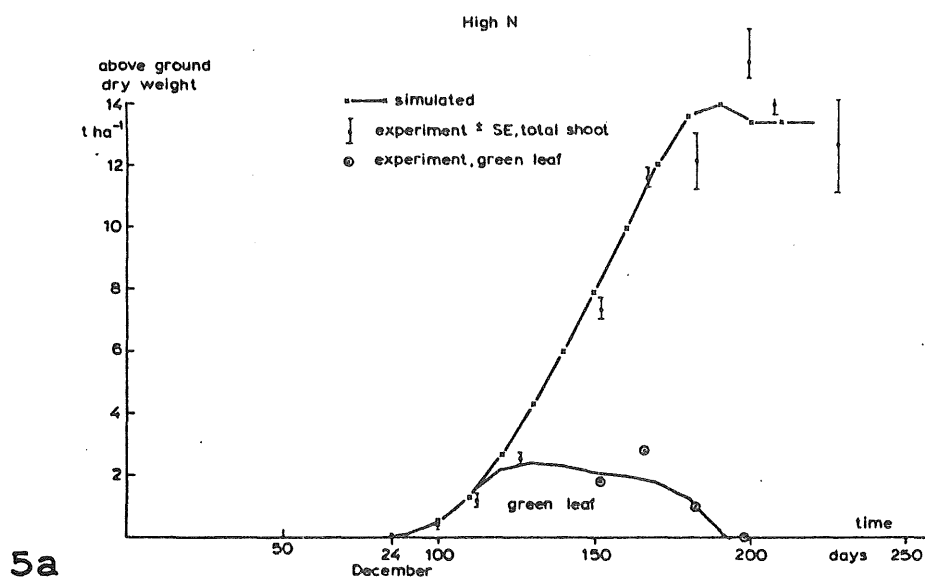
5a
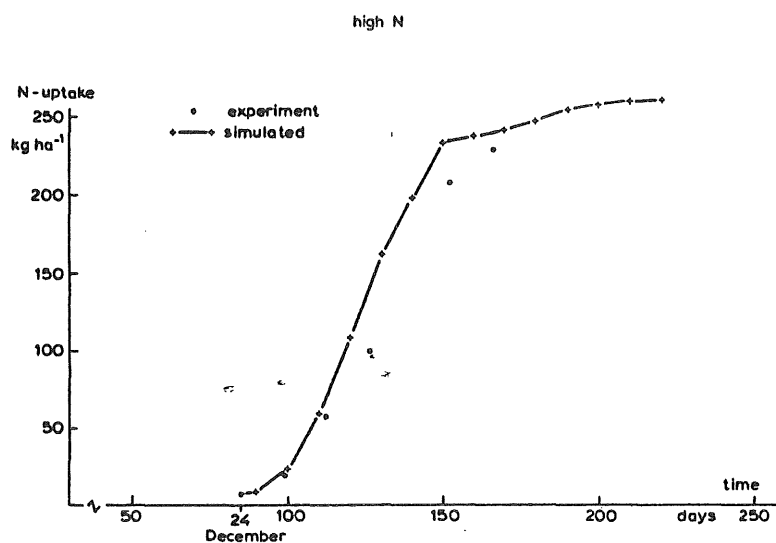
5b

Figure 5. Measured and simulated cumulative dry matter production (5a) and course of N uptake (5b) of a wheat crop in Israel under high N application.
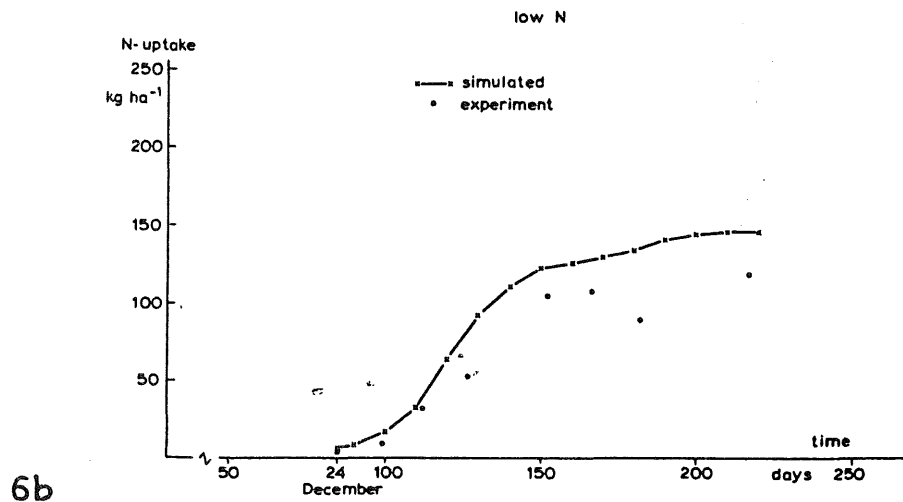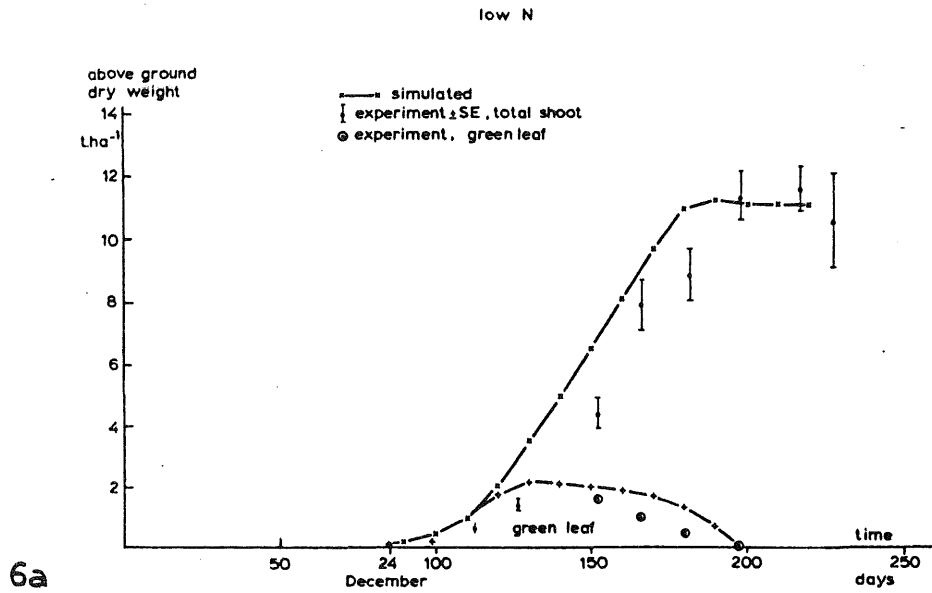
low N

6a

low N

6b

Figure 6. Measured and simulated cumulative dry matter production (6a) and course of N uptake (6b) for a wheat crop in Israel under low N application.

of 10 m^2), is rather low due to a very sudden drought spell in early april - day 185 till 190 - when a dry and hot wind from the desert (the so-called chamsin) struck the area. The phenomena associated with this weather, such as accelerated leaf death and a check in photosynthetic production, are satisfactorily described by the model, which led to a simulated grain yield of 3.3 t ha^{-1}.

In Figure 5b, where measured and simulated nitrogen uptake by the vegetation are compared, the most striking phenomenon is the substantial loss of nitrogen towards the end of the growing season. Part of this loss might be the result of leaf fall during the drought period, but that certainly does not account for all of the loss, because the fallen leaves were carefully collected at sampling. Such losses of nitrogen from the above ground parts of annual crops have been reported in the literature (van Keulen and van Heemst, 1982), but a really satisfactory explanation is still lacking. It seems highly unlikely that remobilization and transport to the root system is responsible in annual crops, that rely on seed production for propagation and survival.

In Figure 6 the results are presented for a crop growing under nonfertilized conditions. Nitrogen availability in this situation was still fairly high because of residual nitrogen in the soil, originating from the preceding season that was rather dry and resulted in incomplete uptake of the available nitrogen. It appears that the simulated nitrogen uptake is overestimated, especially between day 120 and 150, which results also in overestimation of the growth rate during that period. The overall effect of lower N availability is, however, well represented by the model description even though the simulated grain yield of 3.2 t ha^{-1} is lower than the 3.7 t ha^{-1} actually observed.

A comparison with the optimum N treatment highlights a problem, associated with the use of nitrogenous fertilizers under these semi-arid conditions. Liberal N-supply during the early stages of growth results in luxuriant vegetative production with its associated water loss by transpiration. A consequence is that early cessation of the rain, or high evaporative demand during the grain filling phase results in early water stress for the luxuriant crop and hence in reduced grain yields. Application of fertilizers under these conditions should therefore be carried out judiciously, taking into account the delicate balance between under-utilization of favourable growth conditions and the penalty associated with unfavourable conditions.

4. <u>Conclusions</u>

The whole-crop model presented in this contribution was developed with the particular aim of studying the interactive effects of water and nitrogen shortage on wheat production in an erratic and unpredictable environment. This starting-point has governed the choice for model development and model formulation. The emphasis on these two growth factors has undoubtedly led to simplification in the representation of some important processes that could be of importance in situations where environmental conditions are closer to their optimum or can be better controlled.

Nevertheless, development of this model has shown that our understanding of the basic processes that govern crop production both under optimum and sub-optimum conditions is still fragmentary at points. That seems, however, no reason to end these attempts to 'put things together', because the instrument is suitable for testing pertinent questions, it generates research objectives, and it may help the breeder in formulating clearer goals.

It may be concluded therefore, that unless a more suitable and powerful analysis method is developed, crop modelling and simulation remains an adequate tool in plant and crop physiological research.

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