A simulation model of plant growth
at different levels of nitrogen availability

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Preface

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Louise Spek and Marcel van Oijen
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11. SUMMARY
In this report we present a simulation model of the nitrogen and carbon metabolism of a maize plant in the vegetative state. A short description of a preliminary version of this model has been published earlier (van Oijen, et al., 1986).

Our prime interest in building the model was not the maize metabolism per se, but rather the elucidation of mechanisms underlying the growth and interdependence of different organs (or organ systems) of higher plants. We focus on the diurnal rhythms of root and leaf chemical composition and the transport of compounds between them.

In the study of this level of organisation of biological systems, mathematical treatment is rather underdeveloped. There is a gap between crop simulation modelling and growth analysis on the one hand, and mathematical analysis and modelling of biochemical/biophysical systems on the other. The work that has been done in the intermediate field of plant physiological models, was directed for the most part at mimicking the over-all plant behaviour, without incorporating underlying mechanisms. This has had repercussions on the adequacy of crop simulation models (Lang and Thorpe, 1983). A simulation model can be seen as a complex of submodels, each of which is a simplified or "summarized" version of a model of a subsystem, as studied for its own sake. The two perhaps main common weaknesses of crop simulation models, i.e. simulation of photosynthate partitioning and leaf area increase, may stem from the scarcity of lower level models of these processes, that could be summarized and built into the larger model. Of course there is still no consensus regarding the way integration of activity between different plant parts is maintained. Unclarified are e.g. the relative importance of plant water relations and nutritional status (carbon compounds, macro- and micro nutrients) in favouring root or shoot growth; the role of hormones (causal, catalytic or side-effect); the transport of chemical compounds between organs (mainly determined by source or sink strength, or transport system capacity) etc. The model we present here can be seen as a condensation of our views regarding questions like these. The model structure, that will later be described in detail, reflects the emphasis we lay on nutritional hypotheses.
Because of the lack of consensus in whole plant physiology, the model could be classified as largely speculative. But the envisaged use of the model does not lie in precise prediction of plant behaviour (as would be needed for management purposes), but in research guidance. Building and utilization of the model should be steps in a research programme, in which experimental and modelling work coincide. The role of the modelling work then lies in suggesting relevant experiments, testing hypotheses, explaining observed phenomena and finally, allowing model experiments regarding the effects of differences in environments and/or plant characteristics.

The above mentioned uses of the model will be expressed in the last two chapters of this report. But we first give a short overview of more or less comparable modelling activities, and subsequently a description of the model.

In this general introduction, we will describe a range of possible methods of modelling the concurrent growth of different plant organs, in order of increased incorporation of mechanisms. Where deemed appropriate, examples from the literature will be mentioned, especially where nitrogen supply or metabolism is involved. Many of the mentioned models are also discussed in one or more of the following review articles: Penning de Vries (1981, 1983), Apel et al. (1985). As said earlier, most work in inter-organ relations modelling, has been aimed at the reproduction of phenomena, irrespective of underlying mechanisms. Extreme examples of this approach are allometric equations for the dynamics of organ dimension ratios as given by, amongst others, von Bertalanffy (1969). These equations let organ ratios be determined by fixed power functions of the total dimensions of organisms. These functions have to be empirically determined. Slightly less empirical in nature are models in which not the ratios of organ dimensions themselves, but the ratios of organ growth rates are empirically determined functions of time or of temperature sum.

Nitrogen metabolism has no place in such models, though a direct effect of external nitrogen availability on overall growth rate could be incorporated (as in Patten, 1972).

The next step towards mechanismic modelling is taken, when the
dynamics of shoot-root ratios are made dependent on system variables instead of time, but when differences in chemical composition between plant parts are still not incorporated. This kind of modelling requires the explicit incorporation of both shoot activity (photosynthesis) and root activity (water or nutrient uptake) dependent variables, in order to achieve a functional equilibrium between shoot and root.

Such models might, for example, make the distribution of growth rates, over root and shoot, dependent on the plant relative water content, dry matter percentage, carbon-nitrogen ratio (discussed extensively in Mäkelä, 1986) or nitrogen content on a dry weight basis (Hirose, 1986). The distribution of growth rates, over root and shoot, dependent on plant relative water content and dry matter percentage, necessitate the separate calculation of both water uptake and transpiration in the model. The distribution of growth rates, over root and shoot, dependent on the carbon-nitrogen ratio, or nitrogen content on dry weight basis, which are more of interest here, necessitate the calculation of nitrogen uptake in models of this or more complex type. In the case shoot nitrogen loss cannot be neglected, it has to be modeled too. Apel et al. (1985) give examples of the modelling of ammonia exchange between leaves and atmosphere.

Nitrogen uptake rate has been modeled as positively correlated with source strength (nitrogen concentration in the root environment (Seligman et al., 1975; Jones et al., 1980; Novoa, 1979)), with sink strength (lack of nitrogen accumulation in the plant (Seligman et al., 1975; Reuss and Innis, 1978)), and with uptake capacity (root weight (Cooper and Thornley, 1976; Mäkelä, 1986; Hirose, 1986a; Seligman et al., 1975)). The uptake rate thus calculated can be modified by transpiration rate (Jones et al., 1980), temperature and/or soil water potential (Reuss and Innis, 1978). For further examples and more extensive discussion of nitrogen uptake modelling, see Apel et al. (1985).

Since the plant in these models is still treated as chemically homogenous, the effect of plant nitrogen content on growth rate is usually restricted to modifying total plant potential growth rate (that is, possible growth rate, given the atmospheric conditions).
An effect of plant nitrogen concentration on developmental rate is a part of the models of Reuss and Innis (1978) and of Angus and Moncur (1985).

Next we can distinguish models in which organ growth rates are no longer made directly dependent on whole plant variables, but solely on the level of local variables.

These models tend to make a distinction between structural nitrogen and carbon compounds on the one hand and nonstructural, or "free", compounds on the other. The growth rate of different organs is then often taken to be positively correlated with the product of the local free nitrogen and free carbon concentrations (Cooper and Thornley, 1976; Jones et al., 1980). The biomass of the different organs is generally supposed to have a constant carbon-nitrogen ratio.

Respiration associated with nutrient uptake, can be separately calculated (Johnson, 1983) or simply be expressed through a lower root growth efficiency.

The models of this type are, as indicated above, compartmentalized in that they distinguish levels of variables in different organs. This makes a quantification of rates of transport of materials between distinct organs necessary.

Models of transport of nitrogen compounds towards growing seeds or fruits, are quite often incorporated into larger simulation models (Seligman et al., 1975; Sinclair and de Wit, 1975; more examples of redistribution modelling given in Penning de Vries, 1983). Transport rates are then usually made dependent on strength of both source (nitrogen concentration in the vegetative shoot parts) and sink (difference between an empirically determined "optimal" and the actual nitrogen concentration in the reproductive organs). Similar ways of modelling have been applied to the transport of nitrogen compounds from the root system to the shoot (Cooper and Thornley, 1976; Reuss and Innis, 1978). All these (sub)models implicitly presuppose the existence of a still unknown signalling mechanism through which vascular loading rates within the source tissue are influenced by the concentration at the sink.

The compartmentalization of these models allows two extra types of mechanism for tuning the activities of root and shoot to each
other: 1) local feedback inhibition (decrease of nitrogen uptake by increasing root nitrogen content and of photosynthesis by leaf carbohydrate accumulation); 2) distant stimulation (increase of nitrogen uptake by increasing levels of energy providing carbohydrates; increase of photosynthesis by increasing levels of, enzyme system enlarging, leaf nitrogen compounds). So because of the higher model resolution, lower level regulatory mechanisms can be introduced. This kind of low level modelling is not rare (as mentioned above). With regard to nitrogen metabolism, the model of Novoa (1979; Novoa and Loomis, 1981) can be mentioned. Novoa's model distinguishes three cell types (nutrient uptaking root cells, and leaf cells that either do or do not photosynthesize). The metabolism of each cell type is treated in great detail. The model comprises different cell organelles/compartments, containing an array of inorganic and organic nitrogen compounds, capable of interconversion and membrane transport according to established laws of enzyme kinetics. The integration of the three celltype activities is, on the contrary treated very superficially by the introduction of oversimplified transport rules. Whole plant behaviour is therefore not simulated realistically. Apel et al. (1985) consider this failure to be due to as yet insufficient knowledge of low level regulatory mechanisms (the incorporation of which is indeed not only a possibility in low level models, but also a necessity). Still, improvement may be accomplished by summarising the cellular submodels and modelling transport more mechanistically.

In spite of their sceptics regarding low level nitrogen metabolism modelling, Apel et al. (1985) do indicate ways in which N-status of leaves could determine the value of parameters in several detailed leaf photosynthesis models.

Finally there are models in which the transport system itself is explicitly represented as one or more model components.

Several mathematical models of carbohydrate transport in the phloem have been published so far, but rarely as integrated parts of larger crop or plant simulation models (exception: Meyer et al., 1979). Such phloem models were generally developed for similar reasons as our plant model presented in this report,
namely for quantifying hypotheses, thereby rendering them more easily testable.

The above mentioned models cannot be used completely or partly in explaining the plant physiological phenomena we are interested in. We may divide the models in two separate groups:

1 Models that do not distinguish enough different biochemical compounds and/or pathways and do not incorporate enough mechanisms of transport between organs to embody hypotheses that may explain over-all plant behaviour.

These models incorporate empirically determined quantifications of those relationships we want to explain. They are generally used in simulating seasonal crop growth with irradiance and water supply as the main driving variables.

2 Models that are too detailed at the biochemical process level or regarding phloem transport, to allow effective integration in a plant simulation model.

These models are built for explaining behaviour and/or evaluating hypotheses concerning lower levels of organisation than the whole plant. The simulated time period generally does not exceed one day.

We conclude that the structure of our model must be between the two groups, with respect to the number of distinguished organs, division of biomass in different chemical compounds, detail of modelling transport within the plant as well as with respect to model time step and length of simulated period.

How this conclusion is effectuated, is described in the following chapters.
2 MODEL STRUCTURE

2.1 Introduction

Although the model has a general character, maize plants were chosen to simulate growth in dependence on nitrogen and carbon metabolism. The choice of young maize plants and the regimes for the model plant environment are derived (partly) from experiments performed by Spek (1981, 1984a, 1984b). This was done for two reasons:

1 Possibility of extracting model parameter values from experimental data.
2 Reduction of model complexity regarding environmental variables, in to allow extra emphasis in the model structure on physiological mechanisms.

The model plants are growing on an aerated culture solution, initially well supplied with nutrients, but the nitrate concentration in the medium can be changed. The photoperiod is 16h/day with a light intensity of 60W/m². Effects of relative humidity or temperature are assumed to be negligible. These variables therefore do not occur in the model.

2.2 Description of relational diagrams

The relational diagram of the model is shown in Fig 1. The model plants are divided in three parts:
- Growing shoot parts: meristematic and elongating tissue
  In the computer program given as SY (=Shoot Young)
- Mature shoot parts: full grown tissue.
  In the computer program given as SO (=Shoot Old).
- Roots, divided in two parts.
  In the computer program given as R1 and R2.
Nitrate is taken up from the medium, indicated by the rectangle in the lower left corner.
The rectangles represent model quantities, the horizontal arrows represent chemical conversions and the vertical arrows represent transport processes.
The two processes by which matter is imported in the plant are NO3 uptake by the roots and photosynthesis by the mature shoot parts. The NO3 taken up by the roots, is partly transported to the mature shoot parts through the xylem and partly assimilated to amino acids in the roots. The remainder is accumulated in the roots. In the mature shoot parts, NO3 is also assimilated to amino acids; the remainder is accumulated. (The growing shoot parts cannot receive NO3 in the model). Amino acids are transported through the phloem from the mature to the growing shoot parts and to the roots. Through the xylem, amino acids are transported from the roots to the mature shoot parts. Structural nitrogen (structural N) is formed from the amino acids in all three plant parts. Structural N can be degraded to amino acids.

Soluble carbohydrates (soluble C), assimilated in the mature shoot parts are transported through the phloem to the growing shoot parts and to the roots. In all three plant parts, structural carbon (structural C) is formed from soluble C. Structural C can not be degraded in the model.

Loss of soluble C in respiration takes place in all three plant parts (respiration).
The relations between quantities and processes are described in section 2.2.3.

Fig 2 indicates the most important relations between a number of variables and extension growth.

Extension growth in maize roots is diffusely dispersed over the entire root system, contrary to the more localized growth in the shoot, and therefore difficult to simulate. In the model, shoot extension growth is made proportional to the size of growing shoot parts only, whereas root extension growth is treated as proportional to the whole of the root system. The relative growth rate (RGR) of both growing shoot parts and roots depends, according to a saturation curve, on the level of structural N. So root RGR depends only on this level of structural N, but total shoot RGR depends also on the ratio of growing shoot tissue to mature shoot tissue. This ratio varies according to the measure in which extension growth is balanced by the process of ageing (the shifting of material from the
Fig: Relational diagram of the model, showing all model quantities and processes, except those involved in extension growth. Horizontal arrows: chemical conversions, vertical arrows: transport. Abbreviations: grw. shoot = growing shoot parts, mat. shoot = mature shoot parts, struct C (N) = structural carbon (nitrogen), resp. = respiration, phot. = photosynthesis.
Fig. 1. Relational diagram of some of the quantities and processes involved in extension growth. fwt= fresh weight, sol. C= soluble carbohydrates, str. N= structural nitrogen, synth.=synthesis, other abbreviations as Fig. 1.
growing to the mature tissue). The effect of the level of soluble C is exerted by 1) its influence on amino acid synthesis, 2) on the buildup of structural N and 3) on the rate of transport processes across membranes.

2.3 Description of model assumptions

2.3.1 Introduction

The most important lines of the computer program are described in this section. This includes the uptake and transport processes and the assimilation and dissimilation processes (see section 2.2.2; see chapter 7 for a listing of the model program.) For each process, attention will be given to the following items:

- Description of the hypothetical background of the program line(s), with literature references.
- The line as given in the computer program (indicated with <>), with the units of the different variables and constants placed under the line.
- If necessary, the lines defining the separate variables and constants in the main line (<>).
- The graphical reproduction of the supposed relationship(s).

Model lines are presented in which abbreviations are used in the following way:

The X, in the descriptions, stands for SO (Shoot Old), SY (Shoot Young), R1 and R2 (Root part 1 and Root part 2, respectively) (see section 2.2.2), or a combination of these plant parts. To describe processes in SO and SY, the terms mature and growing shoot parts, respectively will be used.

An alphabetical list with the explanation of the abbreviations, used in the model, is given in chapter 9.

The computer language used is ACSL (Advanced Continuous Simulation Language). A short explanation of the meaning of the operators used is given in chapter 8.
2.3.2 Growth in fresh weight of roots and shoot

In these lines a potential rate of growth in fresh weight is calculated by multiplication of a potential relative growth rate (0.01 and 0.16 g/g/h, for roots and growing shoot parts, respectively) with the fresh weight existing (XFWT). The degree in which the plant realizes this potential growth rate, the actual growth rate (XFWTG), was made dependent on:

1) The concentration of structural nitrogen.
   The dependence is expressed in the value for XFGNR (see Figs 3 and 5).
   A correlation between the external nitrogen concentration and relative growth rate (RGR), was found in birch and grey alder (Ingestad and Lund, 1979; Ingestad, 1980, 1981 and 1982). Below a certain N concentration, there will be no more growth (Novoa and Loomis, 1981). The maximum and minimum values for nitrogen concentration found in tissues of C₄ plants (Penning de Vries, 1982) and with radish (Schulze et al., 1985) varied with plant age and in different plant parts (Venekamp et al., 1985, with maize). Wilson (1975) found a correlation between leaf organic N concentration and leaf RGR and net assimilation rate.
   Figs 3 and 5 show, that below 0.0005 gN/g fresh weight for roots and 0.002 gN/g for growing shoot parts, growth stops in the model. These values are based on our experimental data with maize (Spek, 1984a, 1984b). A dependence on plant age was not introduced.

2) The concentration of soluble carbohydrates.
   The dependence is expressed in the value for XFGCR (see Figs 4 and 6). A correlation between total nonstructural carbohydrates and RGR was found by Gent (1984) for tomato plants. Figs 4 and 6 show, that under a certain estimated low concentration of soluble carbohydrates (0.0017 gC/g), XFGCR will decline linearly to zero.

The structural nitrogen and soluble carbohydrate concentration at the start of the simulation correspond with about half of the chosen potential RGR. This gives the possibility of a variable RGR between low and high values dependending on the C and N conditions of the tissues. The factors XFGNR (1) and XFGCR (2) are called realisation
factors. With higher values for XFGNR, depending on structural N or for XFGCR, depending on soluble C, a higher growth rate can be reached. These factors are multiplied because of a supposed interaction between structural N and soluble C in growth realisation.
Growth in fresh weight of roots:

\\langle RnFWTg = .01 \times RnFWT \times RnFGNR \times RnFGCR \\
g/h = g/g/h \times g \times (-) \times (-)

.01 g/g/h = potential relative growth rate

\\langle RnFWT = \text{INTEG} (RnFWTG, RnFWTI)
\\langle RnFGNR = \text{BOUND} \ (0.,1., (RnCOSN - .0005) / RnCOSN)
\\langle RnFGCR = \text{BOUND} \ (.8,1.2, .8 + 240. \times RnCOC)

Fresh weight and concentrations at time zero:

\begin{align*}
RnFWTI &= 8.035 \ g \ (\text{Weight of half root system}) \\
RnCOSN &= 0.0017922 \ gN/g \\
RnCOC &= 0.0008401 \ gC/g \\
RnCOSC &= 0.0140012 \ gC/g
\end{align*}

Remarks concerning the program lines:

n stands for 1 or 2

** = sign for multiplication

![Graph 3](#)

![Graph 4](#)
Growth in fresh weight of shoot:

\[ \text{SFWTG} = 0.16 \times \text{SYFWT} \times \text{SFGNR} \times \text{SFGCR} \]

\[ \text{g/h} = \text{g/g/h} \times \text{g} \times (-) \times (-) \]

0.16 g/g/h = potential relative growth rate

\[ \text{SYFWT} = \text{INTEG} (\text{SFWTG} - \text{SYFWTS}, \text{SYFWTI}) \]

SYFWTS = see page

\[ \text{SFGNR} = \text{BOUND} (0, 1, (\text{SYCOSN} - 0.002) / (\text{SYCOSN} - 0.0014)) \]

\[ \text{SFGCR} = \text{BOUND} (0.8, 1.2, 0.8 + 240 \times \text{SYCOC}) \]

Fresh weight and concentrations at time zero:

\[ \text{SYFWTI} = 4.67 \text{ g} \]

\[ \text{SYCOSN} = 0.0026039 \text{ gN/g} \]

\[ \text{SYCOC} = 0.0008565 \text{ gC/g} \]

\[ \text{SYCOSC} = 0.0111884 \text{ gC/g} \]
2.3.3 Ageing (shifting of material)

The maturation of newly formed cells is a more or less continuous process. In the model, a constant fraction of the fresh weight of shoot young is shifted to shoot old, per unit of time. This relative maturation rate is taken to be 0.072 g/g/h. In reality this fraction may be variable, depending on plant species, the developmental stage of the plant and environmental conditions.

The model line defining the shifting of fresh weight does not include the shifting of the chemical compounds: amino acids, structural N, soluble C and structural C in the young shoot parts. For the shifting of these compounds, separate lines exist.

The amount of shifting carbon compounds depends on the concentrations of soluble C and structural C in the young shoot parts. The shifting amount of nitrogen was made dependent on the average of amino acid and structural N concentrations in the growing and the mature shoot parts. This has been done to obtain a shift in the C/N ratio during maturation of the cells.

Changes in ratio between total C and N in maturating cells might be partly due to an increasing portion that the vacuole includes from the whole cell volume. Schulze et al. (1985) found, that NH3-N was highest in the young developing leaves of radish and that it decreased with expansion growth.
Ageing (shifting of material)

<> SYFWTS = .072 * SYFWT
    g/h = g/g/h * g

.072g/g/h = Fraction of fresh weight, shifted in 1 hour.
SYFWT : see page 18

Shifting chemical compounds:
<> SYAAS = .5 * SYFWTS * (SYCOAA + SOCOAA)
<> SYSNS = .5 * SYFWTS * (SOCOSN + SYCOSN)
    gN/h = (-) * g/h * (gN/g + gN/g)

<> SYCS = SYFWTS * SYCOC
<> SYSCS = SYFWTS * SYCOSC
    gC/h = g/h * gc/g

Concentration at time zero:
SYCOAA = .0002441 gN/g
SYCOSN = see page 13
SYCOC = " 13
SYCOSC = " 13
2.3.4 Photosynthesis

Through the process of photosynthesis, carbohydrates become available in the model plants. The line for this process is based on a description of de Wit et al. (1978) for the light response curve of CO2 assimilation. Photosynthesis was made dependent on the concentration of structural N (see PHOTM), and on the concentration of soluble C (see PHOCFB).

Explanation of the terms:

PHOTM: Potential maximal photosynthesis. In the calculation of PHOTM, 770 is the ratio of the chosen value for maximum photosynthesis (2 g C/m2/h, de Wit et al., 1978) and the concentration of structural N at the start of the simulation (0.0026 gN/g at t=0). The photosynthetic apparatus is built up of nitrogen for a considerable part. (RuBPC-ase and PEP-carboxylase form about 30-40% of the soluble protein [Schmitt and Edwards, 1981]). A relationship between nitrogen content and rate of assimilation at light saturation has been found by several authors (NaTr, 1975; Mooney, 1981, Hunt et al., 1985a, 1985b, 1985c; van Keulen and Seligman, 1987).

0.0136: light use efficiency

Leaf area (LA), is calculated by multiplication of the specific leaf area (SLA, on a fresh weight basis) and the total fresh weight of the mature leaves. SLA is a constant in the model, although it is known that SLA can change with nitrogen content of the tissues (Hunt et al., 1985).

PHOCFB: A negative feedback mechanism dependent on the stored soluble C in the mature shoot parts was added, to prevent too high soluble C levels. The presence of a mechanism by which accumulated soluble C may result in a depression of the rate of photosynthesis was shown by Hartt (1963), Neales and Incall (1968) and NaTr (1974). Above an estimated content (0.002 gC/g), there is a linear reduction of photosynthesis, until photosynthesis stops completely (at 0.004 gC/g).
Photosynthesis

\[
\text{SOPHOT} = \text{PHOTM} \times \left(1 - \exp\left(-\frac{0.0136 \times \text{LIGHT}}{\text{PHOTM}}\right)\right) \times \text{LA} \times 0.55 \times \text{PHOCFB}
\]

\[
gC/h = gC/m2/h \times (-) \times m2 \times (-)
\]

\[
\text{PHOTM} = 770 \times \text{SOCOSN}
\]

\[
gC/m2/h = gC/gN/m2/h \times gN/g
\]

\[
\text{LA} : \text{see page 37}
\]

\[
\text{PHOCFB} = \text{BOUND} (0, 1, 2, .500, \times (\text{SOCOC} - \text{SOCOCT}))
\]

\[
\text{SOCOCT} : \text{Soluble carbohydrates in shoot old, available for transport. See page 31.}
\]

Concentrations at time zero:

\[
\text{SOCOSN} = 0.0026039 \text{ gN/g}
\]

\[
\text{SOCOC} = 0.0016274 \text{ gC/g}
\]

\[
\text{SOCOC} - \text{SOCOCT} = 0.0016274 - 0.0010551 = 0.0005723 \text{ gC/g}
\]
Energy is needed for the metabolic processes of the plant and to maintain existing structures. Transport processes in the plant and physiological (and morphological) adaptation to changing environmental conditions also require energy. This energy is derived from respiration processes in the plant in which normally carbohydrates are the energy source (Challa, 1976). Part of the energy is derived directly from light energy in leaves. In the literature respiration processes are schematically divided in:

a) growth, b) maintenance, and c) ion uptake
(Penning de Vries et al., 1974; Penning de Vries, 1975; Veen, 1980; Lambers et al., 1983). To calculate the quantity of soluble C used in respiration we made the following subdivision:

1) Biochemical conversions:
   a) Formation of amino acids from NO$_3$ (XNAA).
   b) Formation of structural N from amino acids (XAASN).
   c) Formation of structural C compounds from soluble C (XCSC).

2) Transport processes:
   a) Uptake of NO$_3$ from the medium into the root (MnRnN).
   b) Transport of NO$_3$ and amino acids via the xylem from roots to the shoot (RnSON, RnSOAA).
   c) Transport of soluble carbohydrates from the mature shoot parts to the growing shoot parts and the roots through the phloem (SOXC).
   d) Loading of amino acids in the phloem (SORnAL) for transport from the mature shoot parts to the growing shoot parts and the roots.

3) Maintenance of ionic gradients.
   Ions can be accumulated against an ionic gradient in the vacuole. Energy is required for uptake against a concentration gradient, and that in turn maintains a concentration difference. In the mature shoot parts, part of the energy needed is derived directly from light energy. The value of the variable LEFT determines the delivery of energy (see next section).

The total energy costs consists of the costs for the three types of processes listed. The calculations for the costs of the energy
demanding processes are based on calculations of Penning de Vries et al. (1974). The alternative pathway for respiration (Lambers and Posthumus, 1980), was not taken into account for reasons of simplicity and because of scarcity of relevant data.
Use of soluble carbohydrates in respiration:

1) Biochemical conversions:

\[
\begin{align*}
\text{RnSPB} &= \text{RnNAA} \times 1.44 + \text{RnCSC} \times 0.12 + \text{RnAASN} \times 1.28 \\
\text{SORSPB} &= \text{LEFF} \times (\text{SONAA} \times 1.44 + \text{SOCSC} \times 0.12) + \text{SOAASN} \times 1.28 \\
\text{SYRSPB} &= \text{SYCSC} \times 0.12 + \text{SYAASN} \times 1.28 \\
\text{gC/h} &= - \frac{\text{gN/h} \times \text{gC/gN}}{\text{gC} \times \text{gN}} \times \text{gN/h} \times \text{gC/gN}
\end{align*}
\]

2) Transport processes:

\[
\begin{align*}
\text{RnSPT} &= \text{MnRnN} \times 0.99 + \text{RnSON} \times 0.04 + \text{RnSOAA} \times 0.067 \\
\text{SORSPT} &= (\text{R1SON} + \text{R2SON}) \times 0.04 + (\text{SOR1C} + \text{SOR2C} + \text{SOSYC}) \\
&\quad \times 0.053 + (\text{R1SOAA} + \text{R2SOAA} + \text{SOR1AL} + \text{SOR2AL} + \text{SORAL}) \times 0.067 \\
\text{gC/h} &= \frac{\text{gN/h} \times \text{gC/gN}}{\text{gC} \times \text{gN}} \times \text{gN/h} \times \text{gC/gN}
\end{align*}
\]

3) Maintenance of ionic gradients:

\[
\begin{align*}
\text{RnSPI} &= \text{BOUND}(0, 1, -1) \times 20000. \times \text{RnCOC} \times \text{RnDM} / 3750. \\
\text{SORSPI} &= \text{BOUND}(0, 1, -1) \times 20000. \times \text{SOCOC} \times \text{SODM} / 3750. \\
\text{SYRSPI} &= \text{BOUND}(0, 1, -1) \times 20000. \times \text{SYCOC} \times \text{SYDM} / 3750. \\
\text{gC/h} &= \frac{\text{g/gC}}{\text{gC/g}} \times \text{g} / \text{g/gC/h}
\end{align*}
\]

Total respiration: \( \text{RnRESP} = \text{RnSPB} + \text{RnSPT} + \text{RnSPI} \)
\( \text{SORRESP} = \text{SORSPB} + \text{SORSPT} + \text{SORSPI} \)
\( \text{SYRESP} = \text{SYRSPB} + \text{SYRSPT} + \text{SYRSPI} \)
2.3.6 **Light effect on respiration in the photosynthesizing shoot parts.**

In leaves, light energy can be used for a number of energy demanding processes (Penning de Vries, 1979; Hansen and Jensen, 1977; Kylin, 1960; Raven, 1976). In this model, only the mature shoot parts have this possibility, because these plant parts are fully exposed to the light. During the dark period the energy for assimilation and dissimilation processes is derived from respiration processes as in the growing shoot parts and in the roots.

\[
\text{LEFF} = 1 - \text{LIGHT} / 60
\]

\[
( - ) = (-)
\]
2.3.7 Nitrate (net) uptake.

A potential specific uptake rate for NO3 (RUPTM) is multiplied by the total root fresh weight (RnFWT), to obtain a potential uptake rate. The potential specific uptake rate (RUPTM) has been chosen about twice as high as the uptake rate found in our experiments. This gives the possibility to obtain a flexible actual uptake rate (MnRnN), which can take values, higher than the values found under standard conditions (see also 2.2.4). Uptake rate has been made conditional on:

1) The NO3 concentration in the medium (MnNLIM, Fig 10).
   Until very low NO3 concentrations in the medium, NO3 uptake will not be hampered in the model plants. A constant uptake rate until very low concentrations of NO3 the medium was found by Olsen (1950), with Brassica. Edwards and Barber (1976, with maize), found a maximum influx occurred above a concentration of 21μM.
   Values varied with plant age and were greatest with 18-24 days old plants. In the model, changes with age were not taken into account.
   We assumed that the depletion zone around the roots would be negligible in a well aerated nutrient solution.

2) The concentration of soluble carbohydrates in the roots (RnCLIM, Fig 11).
   NO3 uptake and ion uptake in general, is an active process (Bowling et al., 1966; Ivanko, 1971; Ivanko and Ingverson, 1971; Schulze et al., 1985; Ezeta and Jackson, 1975), which will need carbohydrates.
   A higher NO3 uptake in the light than in the dark was found by Schulze et al. (1985) with Lolium plants, while Veen (1981) found with maize a higher sugar concentration and NO3 uptake in the light.
   Because of the assumption of Michaelis-Menten characteristics in uptake processes (Doddema, 1987; Doddema et al., 1978, 1979a, 1979b; Novoa and Loomis, 1981; van de Dijk, 1981; van de Dijk et al., 1982; Clarkson, 1985; Schulze et al., 1985) a curvilinear dependence of NO3 uptake on soluble C concentration has been made.

3) The NO3 concentration in the roots (RnNFB, Fig 12).
   This is a feedback mechanism, that limits the NO3 concentration in
the tissues. No distinction has been made between NO3 accumulated in the vacuole or NO3 present in the cytoplasm. The importance of NO3 in the cell for NO3 uptake has been found by MacKown et al. (1983) and Steingräver (1986). Fig 12 shows that above a difference in the NO3 concentration of 0.0023 gN/g, between the roots and the medium net NO3 uptake becomes increasingly difficult in the model plants. At a concentration difference of 0.0048 gN/g, net uptake will be zero.

The minimum of these three factors is multiplied with the potential uptake rate, to obtain the actual uptake rate (MnRnN).

The actively absorbing region of roots is just a part of the total root (Clarkson, 1985). A constancy of this fraction during the simulated period was supposed.
Nitrate uptake

\[
\text{gN/h} = \text{gN/g/h} \times \text{g} \times (-)
\]

RUPTM = .0002 gN/g/h
\(\text{RnFWT} : \text{see page 17}\)
\(\text{MnNLIM} = \text{BOUND} \ (0., 1., \text{MnCON} / \text{MCONMI})\)
\(\text{RnCLIM} = \text{RnCOC} / (\text{RnCOC} + \text{RKMC})\)
\(\text{RnNFB} = \text{BOUND} \ (0., 1., 1.92 \times 10^{-400.} \times (\text{RnCON} - \text{MnCON})\)

MCONMI = .000001 gN/cm³ (g) (Minimum value for NO₃ concentration in medium)

Concentrations at time zero:

\[
\text{MnCON} : \text{variable}
\]

RKMC = .0005 gC/g
\(\text{(RnCON} - \text{MnCON}) = -0.0007733 \text{ gN/cm³ (g)}\)
2.3.8 Carbohydrates in shoot, available for transport.

From the shoot as source of carbohydrates, partitioning to other plant parts takes place. It is known, that the leaves can accumulate a part of the formed carbohydrates during the light period, while during the dark period carbohydrates derived from this pool are transported to other plant parts (Challa, 1976).

In the model, only the mature shoot parts are able to photosynthesize. The soluble C are transported to the growing shoot parts and to the roots. Fig 13 shows, which fraction of the soluble C will be available for export (SOCOCT), and which fraction will be stored (SOCOC-SOCOCT), in dependence on the concentration of soluble C in the mature shoot parts. The dependence is curvilinear, i.e. at low concentrations a relatively large proportion of the soluble C is available for transport. With increasing concentrations, the fraction of carbohydrates stored increases. In this way, the amount of transportable sugars (soluble C) will be buffered against too abrupt changes in export rate.
Carbohydrates in shoot, available for transport.

<> SOCOCT = SOCTM * SOCOC / (SOCTM + SOCOC)
gC/g = gC/g * (-)

SOCTM = .003 gC/g (Maximum concentration of soluble carbohydrates available for transport.)

Concentrations at time zero:
SOCOC = see page 22
SOCOSN = see page 22
SOCOC - SOCOC = see page 22

Fig 13
2.3.9 Transport of soluble carbohydrates through the phloem.

Recently, understanding of the process of phloem loading, transport and phloem unloading of carbohydrates has increased (Ho and Baker, 1982; Lang, 1983; Wolswinkel, 1985; Patrick, 1984) but so many details are involved that it cannot yet be incorporated in this model. The idea however that transport via the phloem is in essence a mass flow, as proposed by Münch (1930), still holds (Waldhauser and Komor, 1978). For maize roots, work of Giaquinta et al. (1983) shows, that translocated sucrose is unloaded from the phloem and transferred to the surrounding root cells via the symplasm (and that sucrose is hydrolysed by a vacuolar invertase prior to metabolism).

The transport of soluble C from the mature shoot parts to the growing shoot parts and to the roots is defined as function of the difference in concentration between soluble C in the source available for transport and the concentration of soluble C in the sinks (SOCOCT-XCOC) (Fig 14 and 15). There is no transport, if XCOC exceeds SOCOCT. The amount transported depends also on the volume of the source and sinks (SOFWT and XFWT, respectively). Multiplication with a transport constant (CSOXC) gives the total amount of soluble C transported per hour.

(For estimation of the constants see 2.2.4.)
Transport of soluble carbohydrates through the phloem:

\[ \text{SORnC} = \text{CSORC} \times \text{SOFWT} \times \text{RnSKF} \times \text{DIM} \times (\text{SOCOCT}, \text{RnCOC}) \]

\[ \text{gC/h} = \frac{1}{h} \times g \times (\text{-}) \times \frac{\text{gC}}{g} \]

CSORC = 3.1/h
RnSKF = RnFWT/(SYFWT+RFWT)
SOCOCT: see page 31

SOFWT: see page 37
RnFWT: see page 37

Concentration at time zero:
\[ (\text{SOCOCT} - \text{RnCOC}) = 0.0010551 - 0.0008401 = 0.000215 \text{ gC/g} \]

\[ \text{day-might rhythm} \]

\[ \text{Fig. 14} \]
Transport of carbohydrates from shoot old to shoot young:

\[ \text{SOSYC} = \text{CSOSYC} \times \text{SOFWT} \times \text{SYSKF} \times \text{DIM} \text{ (SOCOCT, SYCOC)} \]

\[ gC/h = \frac{1}{h} \times g \times (-) \times (gC/g) \]

CSOSYC = 2.5/h

\[ \text{SYSKF} = \frac{\text{SYFWT}}{(\text{SYFWT} + \text{RFWT})} \]

\[ \text{SFWT} = \text{SYFWT} + \text{SOFWT} \]

SYFWT: see page 18

SOFWT: see page 37

Concentrations at time zero:

\[ \text{SYCOC} = \text{see page 18} \]

\[ \text{SOCOCT} - \text{SYCOC} = 0.0010551 - 0.0463582 - 0.0453031 = -0.0453031 \text{ gC/g} \]
2.3.10 Transport of NO₃ through the xylem.

After entrance into the roots NO₃ can be assimilated, accumulated or transported to the shoot. These processes compete for the NO₃. A considerable amount of the NO₃ taken up can be transported in the xylem sap to the green parts of plants (van Die, 1963; Pate, 1973). Ivanko (1971) found for maize that about 40-50% of the total nitrogen transported in the xylem was NO₃. This is in agreement with our observations on maize (not published). The amount of transported NO₃ per unit of time (RnSON) has been defined as a function of:

1) Transpiration rate (TRANSP).

The transpiration stream acts only as a medium for transporting chemical compounds (Ivanko, 1974), while ions are actively excreted into the xylem (van Andel, 1953, with tomato). Bowling (1966), and Bowling, Macklon and Spanawick (1966), with Ricinus communis and Helianthus annuus. Brouwer (1956), found with Vicia faba a major part of the ions in the transpiration stream arrived there by means of a process, dependent on metabolism. The concentration in the xylem seems to depend on the velocity of the water transport and the rate of the transport of ions from the symplasm to the xylem vessels (Brouwer, 1965). Thus although there is a relationship between NO₃ transport and transpiration, this is not a direct one (Simpson et al., 1982).

In maize, the mature shoot parts are most freely exposed in the air. Meristems and partly the elongation zones are enclosed by older leaves. For reasons of simplification, in the model only mature shoot parts are able to transpire.

A maximum transpiration rate per unit leaf area (gH₂O/m²/h) multiplied by the total leaf area, gives a potential transpiration rate (g H₂O/h). Transpiration rate (TRANSP) has been made dependent on light conditions (Fig 16) (Novoa and Loomis, 1981; Schulze et al., 1985; Simpson et al., 1982: a higher transpiration rate is found in the light than in the dark). Goudriaan and van Keulen (1979), found for maize under +N and -N conditions a linear relationship between the rate of net CO₂ assimilation and the conductance for water vapour. From this we can conclude, that the transpiration rate under +N and -N conditions is about the same.
(From own experiments also.)

2) Nitrate concentration in the roots (RnCON) (Fig 17).
   With increasing NO₃ concentrations in the roots, more NO₃ will be exuded into the xylem (Schulze et al., 1985; Steingrüber, 1986).

3) The root fraction capable of transport (RnFWT/RFWT).
   Because a split root system was simulated, only that part of the root system, transporting NO₃ was taken into account. The specific water uptake (mol H₂O/g) was made equal for both parts of the root system under different NO₃ supply.
Transport of NO3 through the xylem

\[ \text{RnSON} = \text{TRANS} \times \text{AMAX1}(0., \text{RnCON - RCONMI}) \times \frac{\text{RnFWT}}{\text{RFWT}} \]

\[ \text{gN/h} = \text{gH2O/h} \times \text{gN/g} \times (-) \]

\[ \text{TRANS} = \text{LA} \times 160. \times \frac{(\text{LIGHT} + 20.)}{(\text{LIGHT} + 100.)} \]

\[ \text{gH2O/h} = \text{m2} \times \text{gH2O/m2/h} \times (-) \]

\[ \text{LA} = \text{SLA} \times \text{SOFWT} \]

\[ \text{m2} = \frac{\text{m2}}{\text{g}} \times \text{g} \]

\[ \text{SLA} = 0.002 \text{ m2/g} \]

\[ \text{SOFWT} = \text{INTEG(SYFWTS, SOFWTI)} \]

\[ \text{RCONMI} = 0.000195 \text{ gN/g} \quad \text{(minimum value)} \]

Fresh weight and concentration at time zero:

\[ \text{SOFWTI} = 42.03 \text{ g} \]

\[ \text{RnCON} = 0.00056 \text{ gN/g} \]

**TRANSPiration:**

- Michaelis-Menten function of LIGHT
- 50% realisation if LIGHT = 60 Wm2
- 20% realisation if LIGHT = 0 Wm2

\[ \text{---------} \text{ LIGHT + 20 / LIGHT + 100} \]

\[ \text{RnCON} < \text{RCONMI} \Rightarrow \text{TRACON} = 0 \]

\[ \text{RnCON} > \text{RCONMI} \Rightarrow \text{TRACON} = \text{RnCON} - \text{RCONMI} \]

---

![Graph 1](image1.png)

![Graph 2](image2.png)
2.3.11 Transport of amino acids through the xylem.

The xylem sap contains apart from NO₃, different organic nitrogen compounds, among which amino acids. (Bollard, 1960 (with maize) (van Die, 1963; Hofstra, 1964; Ivanko, 1971; Pate, 1973). About 30-55% of the nitrogen transported in maize is in organic form (Ivanko, 1971; Pate, 1973; own observations, not published). (The major forms of amino acids exported by the roots are: glutamine, asparagine and ureides (Oaks, 1965, 1966; Oaks and Hirel, 1985; Pate, 1973; Ivanko, 1971)). Amino acids in the xylem are a mixture of amino acids, formed in the roots, and amino acids which were transported from the shoot through the phloem to the roots (Pate, 1973; Simpson et al., 1982). (With the nitrogen in amino acids, carbon in the form of carbon skeletons is retranslocated through the plants) Keltjens et al. (1986), found that in the roots of maize plants more NO₃ was reduced than required for the roots demand and that a significant phloem flow of nitrogen from the shoot to the roots takes place. It was found for wheat (Cooper et al., 1986), that most of the nitrogen translocated from shoot to roots is re-exported from roots to shoot.

In the program the line for amino acid transport (RnSOAA) is similar to the line for nitrate transport. The determining factors are:

1) The transpiration rate.

2) The amino acid concentration in the roots (Fig 18).

One pool of amino acids in the tissues was simulated, although it is known, that several pools of individual amino acids exist in maize (Ivanko, 1971; Oaks, 1965).

3) The root fraction (RnFWT/RFWT).

The part of the root system from which the amino acids are exported, has to be taken into account.
Transport of amino acids through the xylem.

\[ R_nSOAA = TRANSP \times A_{MAX1} (0., R_nCOAA - RCOAMI) \times R_{nFWT} / R_{FWT} \]

\[ gN/h = gH_2O/h \times gN/g \]

\[ TRANSP = \text{see page 37} \]

\[ R_nCOAA = 0.000168 \, gN/g \quad \text{(concentration at time zero)} \]

\[ RCOAMI = 0.000033125 \, gN/g \quad \text{(minimum value)} \]

\[ RCOAA < RCOAMI \implies TRACOAA = 0 \]

\[ RCOAA > RCOAMI \implies TRACOAA = RCOAA - RCOAMI \]

\[ TRCOAA \]

\[ RnCOAA \]

\[ \text{Fig. 12} \]
2.3.12 Amino acids in shoot, available for transport.

Amino acids in leaves can originate from:
1) the new formation of amino acids, 2) protein turnover, and 3) transport from the roots.

In the mature leaf parts of the model plants, the amino acids are derived also from these sources.

A part of the amino acids will probably be used in protein formation, a part will be transported to the growing apices of the shoot and to the roots (Pate, 1966; Simpson et al., 1982).

In the model, a certain amount of the amino acids will be available for transport. Fig 19 illustrates the assumption, that the amount depends curvilinearly on the concentration of amino acids in the mature parts. (Half of the amino acids present will be transportable, when the concentration of amino acids is 0.00045gN/g.) The construction used is such that there will be an increasing availability of amino acids with an increasing amino acid concentration, while the fraction of amino acids available for transport decreases.
Amino acids in shoot, available for transport.

\[ SOCOAT = SOATM \times SOCOAA / (SOATM + SOCOAA) \]

\[ gN/g = gN/g \times ( - ) \]

\[ SOATM = .00045 \, gN/g \quad ( = SOCTM / .0066667 ) \]

(Maximum concentration of amino acids, available for transport.)

Concentration at time zero:

\[ SOCOAA = .0002441 \, gN/g \]
2.3.13 Loading of amino acids in the phloem for transport from shoot old to the roots and to shoot young.

Loading of amino acids was assumed to be dependent on:

1) The concentration of soluble C in the mature shoot parts.
   Loading of amino acids in the phloem is an active process and needs sugars for energy.

2) The total amount of amino acids available for transport (SOCOAT).
   This is calculated by multiplication of SOCOAT with the fresh weight of the mature shoot parts (SOFWT).

3) A transport constant (CALSOX).

4) The amino acid concentration of the phloem (XCOPA) (Figs 20 and 21)
   Within a certain estimated interval, the loading is linearly dependent on the amino acid concentration of the phloem (between 0.00005 gN/g and 0.0001 gN/g). Outside this interval, loading is zero (below 0.00005 gN/g) or is not affected by the concentration above 0.0001 gN/g).

5) The sink fraction (XSKF).
   The amino acids have to be partitioned between the root system and the growing root parts. When entering the root system, the solutes transported through the phloem are partitioned between the two root parts. The fresh weight of the growing shoot part additioned with the weight of the root parts, compose the total sink (weight) of the plant.

To determine the unloading, the fraction each plant part takes from the whole sink, is calculated.

The overall effects of these five factors is accounted for in a multiplicative way.
Loading of amino acids in phloem, for transport from shoot old to roots:

\[ \text{SORnAL BOUND}(0., 1., -1. +20000. \times \text{SOCOCET}) \times \text{CALSOR} \times \]

\[
\text{gN/h} = (-) \times 1/h * \\
\text{SOFWT} \times \text{SOCOAT} \times \text{RnSKF} \times \text{SOnALR} \\
g \times \text{gN/g} \times (-) \times (-)
\]

\[
\text{CALSOR} = .25/h \\
\text{SOCOAT} : \text{see page L41} \\
\text{RnSKF} = \text{RnFWT} / (\text{SYFWT} + \text{RFWT}) \\
\text{SOnALR} = \text{BOUND}(0., 1., \text{CALR} - \text{CMALR} \times \text{RnCOPA}) \\
\text{CALR} = 2. \\
\text{CMALR} = 200000. \text{g/gN} \\
\text{RnCOPA} = \text{RnPAA} / \text{SOFWT} \\
\text{RnPAA} = \text{INTEG} (\text{SORnAL} - \text{SORnAU}, \text{RnPAAI}) \\
\text{SORnAU} : \text{see page L46}
\]

Concentrations at time zero:

\[
\text{RnPAAI} = .001031 \text{ gN} \\
\text{RnCOPA} = .00001227 \text{ gN/g}
\]
Loading of amino acids in phloem, for transport from shoot old to shoot young:

\[ \text{SOSYAL} = \text{BOUND}(0.,1.,-1.+20000. \times \text{SOCOCT}) \times \text{CALSOY} \times \]
\[ gN/h = (-) \times 1/h \times \]
\[ \text{SOFWT} \times \text{SOCOAT} \times \text{SYSKF} \times \text{SOYALR} \]
\[ g \times gN/g \times (-) \times (-) \]

\text{CALSOY} = 2.4 /h
\text{SOFWT} : \text{see page 37}
\text{SOCOAT} : \text{see page 44}
\text{SYSKF} = \text{SOFWT} / (\text{SOFWT} + \text{RFWT})

\[ \text{SOYALR} = \text{BOUND}(0.,1., \text{CALR} - \text{CMALR} \times \text{SYCOPA}) \]
\text{CALR} = \text{see page 43}
\text{CMALR} = \text{see page 43}
\text{SYPAAI} = \text{INTEG} (\text{SOSYAL} - \text{SOSYAU}, \text{SYPAAI})
\text{SOSYAU} : \text{see page 46}

At time zero:
\[ \text{SYPAAI} = .0003 \text{ gN} \]
\[ \text{SYCOPA} = .000007138 \text{ gN/g} \]
2.3.14 Unloading of amino acids from the phloem.

Little is understood about the unloading of amino acids from the phloem. This part therefore is highly speculative. Unloading is assumed to be dependent on:

1) The ratio of amino acids to soluble carbohydrates in the phloem (XPAA / XPHC).

Amino acid transport has been made dependent on related to the sugar transport. The ratio between sugars and amino acids in the phloem therefore is used to calculate the rate of unloading of amino acids.

2) The rate of transport of soluble carbohydrates from the mature shoot parts to the sinks (SOXC).

When amino acid assimilation in the sinks decreases, as a consequence amino acid concentration increases and may become too high. By incorporation of the term (XPAA * 80.) in the model line, the unloading cannot exceed a certain rate. (See also transport of soluble carbohydrates, 2.3.9).
Unloading of amino acids from phloem, in roots:

\[
\text{SORnAU} = \text{AMIN} (\text{SORnC} \times \text{RnPAA} / \text{RnPHC}, \text{RnPAA} \times 80.)
\]

\[
gN/h = gC/h \times gN/gC, \quad gN \times 1/h
\]

\[
\text{RnPAA} : \text{see page 43}
\]

\[
\text{RnPHC} = 0.2 \times \text{SOFWT} \times \text{SOCOCT} \times \text{RnSKF}
\]

\[
0.2 : gC/gC
\]

\[
\text{SOFWT} : \text{see page 37}
\]

\[
\text{SORnAL} : \text{see page 43}
\]

\[
\text{RnPAAI} : \text{see page 43}
\]

\[
\text{SOCOCT} : \text{see page 31}
\]

\[
\text{RnSKF} = \text{RnFWT} / (\text{SYFWT} + \text{RFWT})
\]

Unloading of amino acids from phloem, in shoot young:

\[
\text{SOSYAU} = \text{AMIN} (\text{SOSYC} \times \text{SYPAA} / \text{SYPHC}, \text{SYPAA} \times 80.)
\]

\[
gN/h = gC/h \times gN/gC, \quad gN \times 1/h
\]

\[
\text{SYPHC} = 0.2 \times \text{SOFWT} \times \text{SOCOCT} \times \text{SYSKF}
\]

\[
gC = g \times gC/g \times (-)
\]

\[
0.2 : \text{see page 46}
\]

\[
\text{SOFWT} : \text{see page 37}
\]

\[
\text{SOCOCT} : \text{see page 31}
\]

\[
\text{SYPAA} : \text{see page 44}
\]

\[
\text{SYSKF} : \text{see page 44}
\]
2.3.15 **Synthesis of structural carbon compounds from soluble carbohydrates in roots, shoot old and shoot young.**

It is supposed that the formation of structural C compounds will predominantly take place in growing cells. With high soluble C levels, thicker cell walls will be formed in the young cells but also mature cell walls will thicken.

A potential formation rate of structural C compounds is calculated by multiplication of a potential specific rate of structural C formation (XCSCM) with the fresh weight (XFWT). An actual rate of formation (XCSC) is made dependent on:

1) The concentration of soluble C (XCLIM, Figs 11, 27, 33).
   Because of the enzymatic nature of the formation of structural C, the relationship with the concentration of soluble C was made curvilinear (according to Michaelis-Menten kinetics).

2) A feedback mechanism (Figs 22 and 23).
   Above a certain threshold concentration of structural C, further formation will be increasingly hampered until zero.
Synthesis of structural carbon compounds from soluble carbohydrates in roots:

\[
\text{RCSCM} = \text{RCSC} \times \text{RnFWT} \times \text{RnCLIM} \times \text{RnSCFB}
\]

\[
gC/h = \frac{gC}{g/h} \times g \times (-) \times (-)
\]

RCSCM = 0.0001632 gC/g/h
RnFWT: see page 17

\[
\text{RnSCFB} = \text{BOUND}(0., 1., 9., -500. \times \text{RnCOSC})
\]

RnCLIM = see page 29
RnCOSC = see page 17

Fig. 22
Synthesis of structural carbon compounds in shoot old and shoot young.

\[
\begin{align*}
< \text{SOCSC} &= \text{SOCSCM} \times \text{SOFWT} \times \text{SOCLIM} \times \text{SOSCFS} \\
< \text{SYCSC} &= \text{SYCSCM} \times \text{SYFWT} \times \text{SYCLIM} \times \text{SYSCFS} \\
gC/h &= gC/g/h \times g \times (-) \times (-) \\
\end{align*}
\]

SOCSCM = .00179 gC/g/h
SYCSCM = .00179 gC/g/h
SOCLIM: see page 53
SYCLIM: see page 58

\[
\begin{align*}
< \text{SOSCFS} &= \text{BOUND}(0.1,1.9 - 80. * \text{SOCSC}) \\
< \text{SYSCFS} &= \text{BOUND}(0.1,1.9 - 80. * \text{SYCSC}) \\
\end{align*}
\]

Concentrations at time zero:
SOCSC = .0223769 gC/g
SYCSC = see page 19
2.3.16 Synthesis of amino acids from nitrate in roots and shoot old.

Via the xylem, \( \text{NO}_3 \) is transported from the roots to the shoot, where part of the \( \text{NO}_3 \) reduction takes place (Pate, 1973; Beevers and Hageman, 1969). In maize, \( \text{NO}_3 \) reduction is found in shoot and roots (Ivanko and Maxianova, 1974; Oaks et al., 1980; Keltjens, 1981). In maize, 50% of all absorbed \( \text{NO}_3 \) was assimilated in the roots (Keltjens et al., 1986). Own experiments showed a high nitrate reductase activity in the roots of maize (Spek, 1981). In the light, \( \text{NO}_3 \) reduction in leaves is directly coupled with light reactions (Guerrero, 1981), and reduction is very rapid. In the dark, photosynthetic and non-photosynthetic cells can use carbohydrates (or other reduced compounds) for the reduction of \( \text{NO}_3 \) to \( \text{NH}_3 \) (Minotti, 1970). After a starvation period for nitrogen, rate of formation of amino acids is considerably increased (Ivanko, 1971, Ivanko and Ingverson, 1971).

It is assumed in the model, that only the mature shoot parts receive \( \text{NO}_3 \) through the transpiration stream (see section 2.3.10). Little or no \( \text{NO}_3 \) and Nitrate Reductase Activity (NRA) was found in the growing regions of the leaves, and \( \text{NO}_3 \) concentration increased from the division zone to the mature leaf parts (own observations on maize, not published). Amino acid synthesis in our model includes the whole process of assimilatory reduction of \( \text{NO}_3 \) and the subsequent formation of amino acids. Ammonia was not taken into account, because it is not transported and ammonia concentrations in cells are generally very low.

A potential rate of formation of amino acid is calculated by multiplication of a potential specific rate of formation of amino acids (XNAAM) and the fresh weight (XFWT). The actual rate of formation is dependent on:

1) The nitrate concentration of the tissue (XCON) (Figs 24, 26).

This is a curvilinear relationship, because \( \text{NO}_3 \) reduction (Beevers, 1976) and amino acid formation are enzymatic processes that can be described by Michaelis-Menten kinetics.

2) The concentration of soluble carbohydrates in the tissues (XCOC) (Figs 11, 27).
The carbon skeleton in amino acids originates from the soluble C. Soluble C are also needed for the generation of energy in the formation of amino acids and cell walls. A positive relationship between endogenous sugar level and the capacity to reduce $\text{NO}_3$ was found in the shoots (Aslam and Huffaker, 1984; Oaks, 1985) and the roots (Minotti, 1970; Abrol et al., 1983). A curvilinear relationship is used (Michaelis-Menten kinetics), because of the enzymatic nature of amino acid formation. In the model, the carbon skeletons for amino acid formation are derived directly from the soluble C pool (transamination or decarboxylation were not taken into account).

3) A feedback mechanism to inhibit or prevent the formation of amino acids (Figs 25, 28)

There is evidence for regulation of the biosynthesis of certain amino acids by amino acids. It has also been suggested that ammonium or product(s) of ammonium assimilation may alter the rate of nitrate reductase (Doddema, 1982; Radin, 1975). Experiments with maize root tips (Oaks, 1965), suggest that leucine normally supplied to the intact root tip by the transport system, could similarly inhibit the endogenous synthesis of leucine. A comparable mechanism regulates amino acid formation in the model. Fig 28 shows that formation is increasingly inhibited until zero, between concentrations of 0.001936 - 0.003872 gN/g.

4) Light intensity (Fig 29)

In leaves, $\text{NO}_3$ reduction and amino acid formation are dependent on light energy (Stulen and Bosgraaf, 1985; Schulze et al., 1985; Steingrüber, 1986). Canovas et al. (1986), found for tomato, that leaf glutamine synthetase activity (decreases with plant growth and) shows diurnal variation with a maximum in the light and a minimum in the dark. This suggests that regulation may be controlled by the energy charge. The $\text{NO}_3$ not reduced accumulates. The relationship between light energy and amino acid formation is assumed to be curvilinear.
Synthesis of amino acids in the roots:

\[ R_{nAA} = R_{nAAAM} \times R_{nFWT} \times AMIN1 \ (R_{nNLIM}, \ R_{nCLIM}, \ R_{nAAFB}) \]

\[ gN/h = gN/g/h \times g \times (-) \]

- \( R_{nAAAM} = 0.000072 \ gN/h \)
- \( R_{nFWT} \): see page 17
- \( R_{nCLIM} \): see page 19

\[ R_{nNLIM} = R_{nCON} \div (R_{nCON} + R_{KMN}) \]

\[ R_{nAAFB} = BOUND(0, 1, 2, - R_{nCOAA} / 0.000625) \]

\( R_{nCOAA} \): see page 34
Synthesis of amino acids in shoot old:

\[ \text{SONAA} = \text{SONAAM} \times \text{SOFWT} \times \text{AMIN1} \times (\text{SONLIM} \times \text{SOCLIM} \times \text{SOAAFB} \times \text{SOLLIM}) \]

\[ \text{gN/h} = \text{gN/g/h} \times \text{g} \times (-) \]

\[ \text{SONAAM} = 0.000058 \text{ gN/g/h} \]
\[ \text{SOFWT} : \text{see page 34} \]

\[ \text{SONLIM} = \text{SOCON} / (\text{SOCON} + \text{SOKMN}) \]
\[ \text{SOCLIM} = \text{SOCOCT} / (\text{SOCOCT} + \text{SOKMC}) \]
\[ \text{SOAAFB} = \text{BOUND}(0., 1., 2. \times \text{SOCOAA} / 0.001936) \]
\[ \text{SOLLIM} = \text{LIGHT} / (\text{LIGHT} + \text{SOKM}) \]

Concentrations at time zero:

\[ \text{SOCON} = 0.0008137 \text{ gN/g} \]
\[ \text{SOCOAA} = \text{see page 41} \]
2.2.17 Soluble carbohydrates for skeletons in amino acid formation, in roots and shoot old.

In the line for the formation of amino acid only the nitrogen is taken into account. The carbon required for the skeletons of the amino acids has to be quantified. The quantity of carbon used for the formation of amino acids is calculated from the rate of formation of amino acids and the fraction of carbon in amino acids.

\( \Delta RnCAA = RnNAA \times 3.2 \)
\( \Delta SOCAA = SONAA \times 3.2 \)
\[ gC/h = gN/h \times gC/gN \]
2.3.18 Synthesis of structural nitrogen compounds from amino acids in roots, shoot old, and shoot young.

The structural N compounds consist of enzymes and membrane proteins (see Introduction, 2.3.1). In maize leaves, about 70% of the total nitrogen was found in proteins (Venekamp et al., 1985). The rate of formation is variable, depending on the nitrogen status of the plants (Ivanko, 1971; maize).

A potential rate of formation of structural N compounds is calculated by multiplication of a potential specific rate of formation (XASNM) and the fresh weight of the tissues (XFWT).

The actual rate of formation is described as a function of:
1) The concentration of amino acids in the tissue (Figs 30-32).
   As for other formation processes, a curvilinear relationship between the rate of formation and a substrate concentration (we chose the amino acids) was supposed.
2) The concentration of soluble carbohydrates in the tissues (Fig 11, 27, 33).
   Protein synthesis is an energy requiring process, and thus needs carbohydrates. This dependence is also curvilinear, according to Michaelis-Menten kinetics.

The minimum of these two factors is multiplied with the potential rate of formation to obtain the actual rate (XAASN).
Synthesis of structural N compounds in the roots:

\[ \diamond \text{RnAASN} = \text{RASNM} \times \text{RnFWT} \times \text{AMIN1 (RnALIM, RnCLIM)} \]
\[ gN/h = gN/g/h \times g \times (-) \]

\[ \text{RASNM} = 0.0000704 \, gN/g/h \]
\[ \text{RnFWT} : \text{see page 17} \]

\[ \diamond \text{RnALIM} = \text{RnCOAA} / (\text{RnCOAA} + \text{RKMAA}) \]

\[ \text{RnCLIM} = \text{see page 29} \]
\[ \text{RKMAA} = 0.00017 \, gN*/g \]
\[ \text{RnCOAA} : \text{see page 32} \]

\[ \text{Fig 30} \]
Synthesis of structural N compounds in shoot old:

<> SOAASN = SOASNM * SOFWT * AMIN1 (SOALIM, SOCLIM)

\[ gN/h = \frac{gN}{g/h} \times g \times (-) \]

SOASNM = .0000832 gN/g/h
SOFWT : see page 31
<> SOALIM = SOC0AA / (SOC0AA + SOKMAA)

SOCLIM : see page 5.3
SOKMAA = .00024 gN/g
SOC0AA = see page 41
Synthesis structural N compounds in shoot young:

\[ \diamond \quad \text{SYAASN} = \text{SYASNM} \times \text{SYFWT} \times \text{AMIN1 (SYALIM, SYCLIM)} \]
\[ gN/h = gN/g/h \times g \times (-) \]

\[ \text{SYASNM} = 0.0009168 \, gN/g/h \]
\[ \text{SYFWT} : \text{see page 10} \]

\[ \diamond \quad \text{SYALIM} = \text{SYCOAA} / (\text{SYCOAA} + \text{SYKMAA}) \]

\[ \diamond \quad \text{SYCLIM} = \text{SYCOC} / (\text{SYCOC} + \text{SYKMC}) \]

\[ \text{SYKMC} = 0.0005 \, gC/g \]
\[ \text{SYKMAA} = 0.00024 \, gN/g \]
\[ \text{SYCOAA} = \text{see page 10} \]
\[ \text{SYCOC} = \text{see page 10} \]

Fig. 32

Fig. 33
2.3.19 Degradation of structural nitrogen compounds to amino acids in roots, shoot old and shoot young.

Organic compounds are continuously formed and degraded in cells (turnover). In vigorously growing cells, net import of nitrogenous compounds is needed. In mature cells, export is balanced by import, especially from the roots. In senescing tissues, export exceeds import. A reduced nitrogen supply will accelerate senescence and death of mature cells, because transport is preferably directed to the younger tissues.

It is assumed, that in all three plant parts distinguished, nitrogen degradation takes place (in growing and mature shoot parts and in the roots). Circulation of amino acids between mature shoot parts and roots takes place. There is no transport of nitrogenous compounds from growing to mature shoot parts or to the roots. Thus, growing shoot parts are dependent for their nitrogen supply on the mature shoot parts. The process of degradation is described as a constant degradation rate (XKSNA) (Fig 34) times the quantity of structural N compounds in the plant parts.

In reality degradation may be dependent on age and physiological (and morphological) condition of the tissues.
Degradation of structural N compounds.

\[ \begin{align*}
\text{RnSNA} &= \text{RnSN} \times \text{RCSNA} \\
\text{SOSNA} &= \text{SOSN} \times \text{SOCSNA} \\
\text{SYSNA} &= \text{SYSN} \times \text{SYCSNA}
\end{align*} \]

\[ \text{gN}/\text{h} = \text{gN} \times 1/\text{h} \]

\[ \begin{align*}
\text{RCSNA} &= 0.004 /\text{h} \\
\text{SOCSNA} &= 0.008 /\text{h} \\
\text{SYCSNA} &= 0.008 /\text{h}
\end{align*} \]

Initial values at time zero:

\[ \begin{align*}
\text{RnSNI} &= 0.0288 \text{ gN} \\
\text{SOSNI} &= 0.10944 \text{ gN} \\
\text{SYSNI} &= 0.01216 \text{ gN}
\end{align*} \]
2.4 Determination of initial values and parameter estimation

Introduction
The literature, own experiments and calibration have been the source for initialization and parameter setting in our model. In this paragraph we will give a short overview of these sources for different model variables and processes.

Initial values and variables
The initial values of fresh and dry weight of roots and shoot were taken from own experiments. In these experiments the concentrations of nitrate, total nitrogen, water soluble carbohydrates and total carbon were also measured. These data were used, together with data of Penning de Vries (1974) regarding the chemical composition of young maize plants, to calculate the initial values of the model variables NO$_3$, AA, SN, SC and C.

Process parameters: general principles
Most processes are described by Michaelis-Menten functions of substrate concentrations. These functions are characterized by rate maxima and Km-values. In general we set the Km-values equal to actually measured concentrations under normal conditions. Consequently the rate maxima were set to twice the actually measured process rates. At these settings the process rates are very sensitive to deviations of substrate concentrations from initially normal levels. In this way effective operation of negative feedback is assured in the model. We suppose that stability in real plants is also partly due to actual concentrations lying in the "sensitive region". Where processes can be influenced by several factors, we generally applied the law of the factor most in minimum.

In the remainder of this paragraph, we will give some additional information about the parameter setting of processes where the application of the "general principles of parameter setting" was not as straightforward as suggested in the foregoing lines.
Growth and ageing parameters

The root potential relative growth rate has been set to 0.01 g/g/h, i.e. twice the actual root relative growth rate as determined in our own experiments (Spek, 1981, 1984a, 1984b). We assume that normally the structural nitrogen and soluble carbohydrate contents of the root only allow 50% of the potential rate to be actually reached.

In the same experiments, a value of ca. 0.008 g/g/h was found for the actual RGR of the whole shoot. As for the root we doubled this value giving a potential RGR of 0.016 g/g/h. This high level of total shoot RGR is due to the fast division and elongation of cells in the growing shoot region. This region takes up only 10% of total shoot biomass. Therefore the model value for young shoot potential RGR is 10 * 0.016 = 0.16 g/g/h. The ageing constant (0.072 g/g/h "shifted" from growing to non-growing shoot parts) follows immediately from the shoot RGR, if we assume that the fraction growing shoot tissue remains constant at 10%. In that case the constant relative ageing rate must be equal to 0.9 * the actual RGR = 0.9 * 0.08 = 0.072 g/g/h. This value corresponds rather nicely with the average duration of cell elongation of 12h, found by Jones Brown and Hesketh (1980).

Photosynthesis parameters

The value of 0.0136 gC/J*s/h for the photosynthetic efficiency at light compensation, was taken from de Wit et al. (1978) after expressing their value of 0.5 kgCO2/J*s/h in our units. The value of the photosynthetic maximum in our model (0.55*770*SOCOSN) equals, at the initial SOCOSN, the value of 1.14 gC/h/m2 found by Goudriaan and van Keulen (1979) for nitrogen receiving maize plants. (Non-nitrogen fed maize plants had a maximum of 0.46 gC/h/m2.

Transpiration

A Michaelis-Menten function of light intensity was fitted to our own experimental data regarding average transpiration rates, measured during the light and the dark periods.

Transport parameters

The structure of our transport equations has been elucidated elsewhere (see 2.3). The parameters found in these equations were estimated on
the basis of experimenting with the model itself, for optimally nitrogen-fed situations. The thus determined parameters were not modified after the simulation of nutritionally suboptimal situations.

Protein turn-over
Our values of 10% (roots) and 20% (shoot) for the daily degradation of structural nitrogen were based on model calibration departing from the value of 10% given by Penning de Vries (1975).

Respiration
All parameters regarding the respiration costs of different processes were derived from the work of Penning de Vries et al. (1974, 1975) with the exception of ion uptake respiration rate, where data of Veen (1980) were used.
3. MODEL RESULTS

3.1 Introduction

The results of three model experiments are given and discussed. At the start of the simulated period, young maize plants grown on a culture solution with ample supply of nutrients and well aerated, were given the following treatments:

A = A continued supply with ample amounts of NO3: +NO3 plants
B = Half the root system deprived of NO3: +/-NO3 plants
C = The whole root system deprived of NO3: -NO3 plants

The simulated period lasted 10 days.

Three plant parts were distinguished: mature shoot parts, growing shoot parts and roots (divided in two parts). (see: 2.2.2).

The components distinguished in the different plant parts are NO3 (not in the growing shoot parts), amino acids (AA), structural nitrogen (SN=proteins), soluble carbohydrates (C) and structural carbon (SC=cellwall carbohydrates). AA are formed from NO3; SN is formed from AA; SN can be degraded into AA; SC is formed from C and can not be degraded. Time courses of the concentrations of these components in the plant parts are given and expressed on basis of fresh weight. Time courses over ten days (with every hour output of data) of the following variables in the three model experiments (A, B, and C) will be presented:

- concentrations of the chemical compounds distinguished in the different plant parts
- dry matter production
- photosynthesis
- root-shoot ratio (on dry matter basis)
- carbon/nitrogen ratio
- cycling of nitrogen and carbon compounds in the plants
- assimilation of carbon and nitrogen compounds and dissimilation of proteins
- respiration.

After the description of the model experiments, a sensitivity analysis
with respect to some model parameters is presented. Influence of the changed parameters on growth, will be discussed briefly.
3.2 Changes in fresh and dry weight

Model graphs (Fig 35)

Fresh and dry weight are expressed in grams. Diurnal fluctuations in fresh weight increase were only found in the growing shoot parts of the A (+N03) and B (+/-N03) plants. In dry weight increase, diurnal fluctuations were found in all parts of the A and B plants. In these plants, a net increase was found in the light; in the shoot a decrease in the dark; in the roots of the A plants a small increase after the start of the dark period.

In the mature shoot parts of the C (-N03) plants, fresh weight increase was severely reduced and dry weight increase stopped. Both fresh and dry weight of the growing parts of these C plants showed a decrease after the second simulated day.

A continuing increase in fresh and dry weight was found in the roots in all three situations.

The consequences of these dynamics in fresh and dry weight increase for the dry matter percentage (DMP), were calculated in the model for the mature and growing shoot parts, the total shoot and the roots (Table I). Table II shows the dry matter percentage for shoot and roots of experimental maize plants, subjected to treatments that were comparable with the model plants A and C (Spek, 1981, 1984a, 1984b). Those simulated values, that have corresponding values in the real experiment (+N03 and -N03) will be emphasized here. In the B situation, the DMP values for the shoot and the -N03 roots were between those for the A and C plants; in the +N03 roots of the B plants, DMP was higher than in the other three root types. In the real A plants, DMP decreased slightly during the simulated period of ten days, in contrast with the real situation, where an increase was found in shoot and roots. The increase in the real plants was not caused by an increase in soluble C (see 3.3.4), but was probably due to an increase in cellwall material (see 3.3.5). In the simulated A plants, no soluble C accumulated (in agreement with experimental results), but there was no fractional increase in cellwall material. This is associated with a too slow decrease in the fraction of growing tissue (= SY/(SY + SO)).
With decreasing NO3 supply (A->B->C), the model plants showed a slight increase in DMP in shoot and roots. In the experimental plants, an increase in DMP (+NO3->-NO3) was only found in the shoot (Table I and II). In these plants, the increase in dry weight in the shoot was reduced, but not in the roots. Shoot soluble C could no longer be used in the formation of organic N compounds. (see 3.3.4 and 3.3.5). Shoot and roots of the model plants reacted the same: some decrease in the +NO3 plants and a more or less stable DMP in the C plants. The general conclusion with regard to the model is, that DMP was relatively constant, both over treatments and time. See Discussion for further explanation. In the remainder of this paragraph, therefore, only dry weight increase will be discussed with the consequences for the shoot-root ratio.

- Mature shoot parts

After ten days, the dry weight of the B and C plants was 77.2% and 34.5%, respectively, of that of the A plants. The Relative Growth Rate (RGR) (table III) in the C plants was reduced severely already after five days, compared with the A plants. Reduction in the B plants was less severe.

- Growing shoot parts

After ten days, the dry weight of the B plants was 82.8% of that of the A plants. The dry weight of the C plants was only 1.1% of that of the A plants. In the sequence A->B->C, RGR decreased (table III). In the B plants it increased during the simulated period; but less than in the A plants and decreased to negative values in the C plants.

- Total shoot (growing + mature shoot parts) (Fig 35a)

The results for the total shoot are weighted averages of the values for the mature and growing shoot parts. The dry weight of the B and C plants after ten days was 81.9% and 32.7%, respectively, of that of the A plants. RGR in the shoot increased in time in the A
plants; decreased and increased then again in the B plants; and decreased continuously in the C plants (table III).

- Roots (Fig 35b)

After ten days, dry weight of the -NO₃ and +NO₃ roots of the B plants was 0.34% and 31.3%, respectively, higher than half the weight of the roots of the A plants. Half of the root system of the C plants was 5.7% higher than half of the root system of the A plants.

Table III shows the RGR for the three treatments. The highest values in RGR were reached in the +NO₃ roots of the B plants in the second half of the simulated period, followed by the A roots, the -NO₃ roots of the B plants and then the C roots. In the middle of the simulated period, RGR in the B and C roots reached a maximum (highest for the +NO₃ roots of the B plants).

Differential changes in shoot and root growth rates under the different NO₃ treatments, caused the changes in shoot to root ratio as shown in table V. Especially shoot growth was sensitive to changes in nitrogen availability as may be deduced from the earlier and stronger reaction of shoot RGR, compared to the A plants, to restricted N supply. An increase in shoot-root ratio was observed in the A plants (17%) and a decrease in the B (19.6%) and C (62.8%) plants.

Model explanation

Variations in the increase in fresh weight of the growing shoot parts of the A and B plants, are due to fluctuations in concentration of soluble C and the concentration of structural N compounds, on which the increase in fresh weight depends in the model (see: 2.2.3). A decrease in fresh weight of growing shoot tissue occurs, when the continuous maturation of this tissue cannot be compensated by new growing tissue formation due to concentrations of soluble C and/or structural N compounds. The relative maturation rate of the growing shoot parts is assumed to be constant, so fluctuations in fresh weight of the mature shoot parts, are a direct consequence of such fluctuations in the growing shoot parts.
Diurnal fluctuations in dry weight are mainly due to fluctuations in the concentration of soluble C. In the A plants and in the mature and growing shoot parts of the B plants, the decrease in dry weight during the dark period is due to a net loss of carbohydrates in respiration. A net increase in soluble C takes place during the light period in all treatments (Fig 36a, 36b, 36c).

Shoot growth is more sensitive to reduced N concentrations of N than root growth, which causes differential changes in RGR in these plant parts. Consequently, the shoot-root ratio changes. The decrease in shoot-root ratio in the B plants is caused by a decrease in shoot growth and an increase in the growth of the +NO3 roots, while the growth of the -NO3 roots continues, with some decrease during the second half of the simulated period. The -NO3 roots of the B plants, maintain a higher RGR than the C plants, due to a continued transport of C and N from the shoot through the phloem. Total shoot weight of the B plants increases, while shoot growth of the C plants is stopped.

Reality

Relative growth rates (RGR) and dry matter percentages (DMP), based on experiments with maize (Spek, 1981, 1984a and 1984b), are shown in Table II and IV, respectively. After NO3 withdrawal from the nutrient solution (-NO3), RGR of the shoot decreased compared to the +NO3 plants. For the roots of both treatments, RGR was about the same. In the shoot of the -NO3 plant, DMP increased relative to that of the +NO3 shoot, while in the roots, DMP increase was about the same for the -NO3 and +NO3 plants.

The changes in growth rate and DMP, caused a change in shoot-root ratio as shown in table VI. The shoot-root ratio of the -NO3 plants decreased during the most part of the experimental time, but increased at the end. Shoot-root ratio was relatively lower in the -NO3 plants than in the +NO3 plants, where it increased in time. Decreases in shoot-root ratio after NO3 omission were found by Brouwer et al. (1962) with Lolium and other cereals and by Radin et al. (1978), with cotton.

When half of the root system was deprived of NO3, the +NO3 part of the root system showed compensatory growth for the decreased RGR of the
-NO3 part (Lambers et al., 1982; de Jager, 1985; own observations, not published). Robinson and Rorison (1983), found in a split-root system, that growth of the fast growing species of Holcus lanatus and Lolium perenne decreased after localized N supply, while the slow growing Deschampsia flexuosa showed no reduction in dry weight production. Shoot-root ratio decreased in H. lanatus and L. perenne and did not change in D. flexuosa. The causes of the decrease in shoot-root ratio were both increased growth of the roots and reduced shoot growth.

Diurnal changes in dry matter increase were found in beans (Brouwer, 1963). The decrease in the dark is attributed to loss of carbohydrates in respiration. Dialy cycles in dry weight increment in shoot and roots of Zea mays, are also found by Pearson et al., cited by Pearson (19).

Discussion

In shoot and roots of the real +NO3 plants (Table II), dry matter percentage (DMP) increases in time. Probably this is due to an increase in the formation of supporting tissue, which exists predominantly of structural C compounds. The higher increase in DMP, over time in the shoots of the real -NO3 plants compared with the real +NO3 plants (Table II), is probably due to a continued formation of soluble C and structural C compounds in the -NO3 plants, while shoot growth is reduced, after withdrawal of NO3 from the nutrient solution (Table IV). Root growth of the -NO3 plants is not reduced during a part of the experimental time, compared with the +NO3 plants (Table IV). This is probably an important reason, why DMP of the roots of the -NO3 plants differ less from the control plants, than DMP of the shoot. The formed dry matter in the roots is compensated by growth.

DMP in the simulated -NO3 (C) plants (Table I), is rather stable in time. The relative increase compared with the model A plants, is due to a continued formation of soluble C and structural C compounds, while shoot growth reduces and ceases, after withdrawal of NO3 from the nutrient solution (Table III). DMP in the A plants probably reduces, due to a more increased RGR of the roots, compared with the
shoot (Table III), which causes a decrease in S/R ratio, with less photosynthetic leaf area per unit of plant weight. Thus, less carbohydrates are available for the total plant.

In the shoots of the simulated B plants, changes in DMP, RGR, S/R ratio and increase in dry weight, were between those of the A and C plants (Table I, III, V, Fig 35a, respectively). This is due to a reduced NO3 supply at the start of the simulation period. Growth of the shoot continues, although at a lower level. As in real plants (de Jager, 1985, with maize), RGR of the +NO3 root part of the split-root system increases, compared with the control A plants. RGR of the -NO3 root part is intermediate between A and C plants. Although very reduced, N compounds are transported to the -NO3 roots via the shoot of these B plants and assimilated. Therefore, DMP in these roots is somewhat lower than in the roots of the -NO3 (C) plants. Due to the higher concentrations of soluble C and structural C compounds, DMP in the -NO3 roots of the B plants is even higher than in the roots of the A plants. The high DMP in the +NO3 roots of the B plants compared with the C plants, is caused by a higher increase in the formation of chemical compounds, than an increase in growth rate. Due to the increase in growth of the +NO3 root part of the B plants, total dry weight in these plants increases more than in the A and C plants (Fig 35b).

In the simulated A plants (+NO3), dry weight of the total shoot increases only somewhat less (ca. 9%), within nine days, than the real plants (Fig 35a; Spek, 1981). In the simulated C plants (-NO3), the decrease in dry weight was too high (67% decrease), compared with the real -NO3 plants. The reduction in weight of the growing shoot parts of the C plants, appears to be too fast in the simulated plants. A reducing amount of tissue is maturating. This causes the high decrease in growth of the total shoot. As in experiments with real plants, root growth after withdrawal of NO3, is much less effected than shoot growth (Fig 35b; Brouwer, 1961, 1962a and 1962b; Spek, 1981). Dry weight of the roots of the A and C plants after nine days was higher by 24.7% and 8%, respectively, than in the real plants.

The results of the B plants can not be exactly compared with experimental data. In the experiments of de Jager (1985), one fourth of the root system received NO3 in the split-root systems. A relative
increased (compensatory) growth rate, of the +NO3 roots was found in these plants. For wheat this was found by Lambers et al. (1982). In our model B plants, at the start of the simulation, half of the root system, received NO3. Still, from the results of de Jager, a less reduced shoot growth of the simulated B plants, compared with the C plants can be expected, due to (increased) uptake of NO3 by the +NO3 root part of the +/-NO3 (B) plants. In the model, the -NO3 part reacted as a whole system deprived of NO3 (C plants).

Both the simulated A plants and the real +NO3 plants, show an increase in shoot-root ratio in time (Table V). This was also found by Foth (1962) for maize. The reduction in shoot-root ratio in time in the simulated C plants, is due to the strongly reduced shoot growth. The somewhat decreased shoot-root ratio in the B plants, is due to a reduced RGR of the +NO3 roots, while the RGR of the -NO3 roots is only somewhat reduced.
## Table I

Dry matter percentage (DMP)

<table>
<thead>
<tr>
<th>plants:</th>
<th>mature shoot parts</th>
<th>growing shoot parts</th>
<th>total shoot</th>
<th>roots - part + part</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>mature shoot parts</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>8.4</td>
<td>8.4</td>
<td>8.4</td>
<td></td>
</tr>
<tr>
<td>after 1 day</td>
<td>8.2</td>
<td>8.1</td>
<td>8.1</td>
<td></td>
</tr>
<tr>
<td>&quot; 5 days</td>
<td>8.1</td>
<td>8.4</td>
<td>8.5</td>
<td></td>
</tr>
<tr>
<td>&quot; 9 &quot;</td>
<td>8.0</td>
<td>8.2</td>
<td>8.2</td>
<td></td>
</tr>
<tr>
<td>&quot; 10 &quot;</td>
<td>8.0</td>
<td>8.1</td>
<td>8.2</td>
<td></td>
</tr>
<tr>
<td>growing shoot parts</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>5.1</td>
<td>5.1</td>
<td>5.1</td>
<td></td>
</tr>
<tr>
<td>after 1 day</td>
<td>4.8</td>
<td>4.7</td>
<td>4.7</td>
<td></td>
</tr>
<tr>
<td>&quot; 5 days</td>
<td>4.6</td>
<td>5.5</td>
<td>5.8</td>
<td></td>
</tr>
<tr>
<td>&quot; 9 &quot;</td>
<td>4.6</td>
<td>5.3</td>
<td>6.0</td>
<td></td>
</tr>
<tr>
<td>&quot; 10 &quot;</td>
<td>4.6</td>
<td>5.1</td>
<td>6.1</td>
<td></td>
</tr>
<tr>
<td>total shoot</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>8.1</td>
<td>8.1</td>
<td>8.1</td>
<td></td>
</tr>
<tr>
<td>after 1 day</td>
<td>7.9</td>
<td>7.8</td>
<td>7.8</td>
<td></td>
</tr>
<tr>
<td>&quot; 5 days</td>
<td>7.7</td>
<td>8.2</td>
<td>8.4</td>
<td></td>
</tr>
<tr>
<td>&quot; 9 &quot;</td>
<td>7.7</td>
<td>8.0</td>
<td>8.2</td>
<td></td>
</tr>
<tr>
<td>&quot; 10 &quot;</td>
<td>7.7</td>
<td>7.9</td>
<td>8.2</td>
<td></td>
</tr>
<tr>
<td>roots - part + part</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>5.4</td>
<td>5.4</td>
<td>5.4</td>
<td></td>
</tr>
<tr>
<td>after 1 day</td>
<td>5.1</td>
<td>5.0</td>
<td>5.2</td>
<td></td>
</tr>
<tr>
<td>&quot; 5 days</td>
<td>4.9</td>
<td>4.9</td>
<td>6.0</td>
<td></td>
</tr>
<tr>
<td>&quot; 9 &quot;</td>
<td>4.8</td>
<td>5.0</td>
<td>5.6</td>
<td>5.2</td>
</tr>
<tr>
<td>&quot; 10 &quot;</td>
<td>4.8</td>
<td>5.0</td>
<td>5.6</td>
<td>5.2</td>
</tr>
</tbody>
</table>

(total shoot = mature shoot parts + growing shoot parts)
Table II

Dry matter percentage (DMP)

<table>
<thead>
<tr>
<th>plants:</th>
<th>+NO3</th>
<th>-NO3</th>
</tr>
</thead>
<tbody>
<tr>
<td>shoot</td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>8.2</td>
<td>8.2</td>
</tr>
<tr>
<td>after 4 days</td>
<td>9.4</td>
<td>9.8</td>
</tr>
<tr>
<td>after 9 &quot;</td>
<td>10.2</td>
<td>14.4</td>
</tr>
<tr>
<td>roots</td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>5.5</td>
<td>5.5</td>
</tr>
<tr>
<td>after 4 days</td>
<td>5.7</td>
<td>6.2</td>
</tr>
<tr>
<td>after 9 &quot;</td>
<td>7.1</td>
<td>7.2</td>
</tr>
</tbody>
</table>

Table III

RGR, on basis of dry weight
(Mean value over one day, g/g/d)

<table>
<thead>
<tr>
<th>plants:</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mature shoot parts</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>day 1</td>
<td>.175</td>
<td>.171</td>
<td>.167</td>
</tr>
<tr>
<td>&quot; 5</td>
<td>.184</td>
<td>.162</td>
<td>.062</td>
</tr>
<tr>
<td>&quot; 9</td>
<td>.185</td>
<td>.153</td>
<td>.0056</td>
</tr>
<tr>
<td>&quot; 10</td>
<td>.185</td>
<td>.156</td>
<td>- .000017</td>
</tr>
<tr>
<td>growing shoot parts</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>day 1</td>
<td>.049</td>
<td>.069</td>
<td>.098</td>
</tr>
<tr>
<td>&quot; 5</td>
<td>.189</td>
<td>.123</td>
<td>- .261</td>
</tr>
<tr>
<td>&quot; 9</td>
<td>.190</td>
<td>.173</td>
<td>- .057</td>
</tr>
<tr>
<td>&quot; 10</td>
<td>.189</td>
<td>.164</td>
<td>- .671</td>
</tr>
<tr>
<td>total shoot</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>day 1</td>
<td>.167</td>
<td>.165</td>
<td>.163</td>
</tr>
<tr>
<td>&quot; 5</td>
<td>.184</td>
<td>.160</td>
<td>.053</td>
</tr>
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<td>&quot; 9</td>
<td>.185</td>
<td>.154</td>
<td>.0027</td>
</tr>
<tr>
<td>&quot; 10</td>
<td>.185</td>
<td>.169</td>
<td>- .0035</td>
</tr>
<tr>
<td>roots</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>day 1</td>
<td>.133</td>
<td>.104</td>
<td>.142</td>
</tr>
<tr>
<td>&quot; 5</td>
<td>.153</td>
<td>.173</td>
<td>.209</td>
</tr>
<tr>
<td>&quot; 9</td>
<td>.160</td>
<td>.151</td>
<td>.188</td>
</tr>
<tr>
<td>&quot; 10</td>
<td>.161</td>
<td>.143</td>
<td>.178</td>
</tr>
</tbody>
</table>

(total shoot = mature shoot parts + growing shoot parts)
Table IV

RGR, on basis of dry weight

<table>
<thead>
<tr>
<th>plants:</th>
<th>+NO3</th>
<th>-NO3</th>
</tr>
</thead>
<tbody>
<tr>
<td>shoot</td>
<td></td>
<td></td>
</tr>
<tr>
<td>day 1</td>
<td>.206</td>
<td>.223</td>
</tr>
<tr>
<td>&quot; 5</td>
<td>.188</td>
<td>.126</td>
</tr>
<tr>
<td>&quot; 9</td>
<td>.144</td>
<td>.112</td>
</tr>
<tr>
<td>roots</td>
<td></td>
<td></td>
</tr>
<tr>
<td>day 1</td>
<td>.111</td>
<td>.251</td>
</tr>
<tr>
<td>&quot; 5</td>
<td>.141</td>
<td>.147</td>
</tr>
<tr>
<td>&quot; 9</td>
<td>.139</td>
<td>.131</td>
</tr>
</tbody>
</table>

(source: Spek, 1981, 1984a and 1984b)
Table V

<table>
<thead>
<tr>
<th>plants:</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>at the start</td>
<td>4.4</td>
<td>4.4</td>
<td>4.4</td>
</tr>
<tr>
<td>after 1 day</td>
<td>4.5</td>
<td>4.6</td>
<td>4.6</td>
</tr>
<tr>
<td>&quot; 5 days</td>
<td>4.9</td>
<td>4.2</td>
<td>3.5</td>
</tr>
<tr>
<td>&quot; 9 &quot;</td>
<td>5.2</td>
<td>3.6</td>
<td>1.9</td>
</tr>
<tr>
<td>&quot; 10 &quot;</td>
<td>5.3</td>
<td>3.5</td>
<td>1.6</td>
</tr>
</tbody>
</table>

Table VI

<table>
<thead>
<tr>
<th>plants:</th>
<th>+NO3</th>
<th>-NO3</th>
</tr>
</thead>
<tbody>
<tr>
<td>at the start</td>
<td>4.2</td>
<td>4.2</td>
</tr>
<tr>
<td>after 4 days</td>
<td>5.3</td>
<td>3.9</td>
</tr>
<tr>
<td>after 9 days</td>
<td>6.6</td>
<td>4.8</td>
</tr>
</tbody>
</table>

(source: Spek, 1981, 1984a and 1984b)
### Table V

**Simulation**

<table>
<thead>
<tr>
<th>plants:</th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>at the start</td>
<td>4.4</td>
<td>4.4</td>
<td>4.4</td>
</tr>
<tr>
<td>after 1 day</td>
<td>4.5</td>
<td>4.6</td>
<td>4.6</td>
</tr>
<tr>
<td>&quot; 5 days</td>
<td>4.9</td>
<td>4.2</td>
<td>3.5</td>
</tr>
<tr>
<td>&quot; 9 &quot;</td>
<td>5.2</td>
<td>3.6</td>
<td>1.9</td>
</tr>
<tr>
<td>&quot; 10 &quot;</td>
<td>5.3</td>
<td>3.5</td>
<td>1.6</td>
</tr>
</tbody>
</table>

**Shoot-root ratio, on basis of dry weight**

(source: Spek, 1981, 1984a and 1984b)

### Table VI

**Experiment**

<table>
<thead>
<tr>
<th>plants:</th>
<th>+NO3</th>
<th>-NO3</th>
</tr>
</thead>
<tbody>
<tr>
<td>at the start</td>
<td>4.2</td>
<td>4.2</td>
</tr>
<tr>
<td>after 4 days</td>
<td>5.3</td>
<td>3.9</td>
</tr>
<tr>
<td>after 9 days</td>
<td>6.6</td>
<td>4.8</td>
</tr>
</tbody>
</table>

Shoot-root ratio, on basis of dry weight

(source: Spek, 1981, 1984a and 1984b)
### 3.3 Carbon-Nitrogen ratio

**Model graphs (Fig 54a, 54b, 54c)**

Daily fluctuations in C/N ratio were found in the +NO3 [A] and +/-NO3 [B] plants in all plant parts and in the mature shoot parts of the -NO3 [C] plants. With decreasing NO3 gift, (A->B->C plants) the C/N ratio increased, except in the +NO3 roots of the B plants, having a C/N ratio about the same as those of the A plants. Table VII gives model results regarding the C/N ratio, for several days after the start of the simulation. These data correspond in time with the experimental data received for maize (Table VIII).

- **Mature shoot parts (Fig 54a)**

  In the A, B and C plants, the C/N ratio started to increase at the beginning of the light period, and to decrease at the beginning of the dark period. Daily maximum and minimum values of the B plants increased until day five and subsequently decreased again. After ten days, daily maximum and minimum values in the B plants were only 9.9% and 8.9%, respectively, higher than in the A plants. In the C plants, daily maximum and minimum values increased continuously during the simulated period and were 133% and 147% higher, than in the A plants at day ten. The maximum and minimum C/N ratios after ten days were for A: 9.6 and 8.9; for B: 10.5 and 9.7; and for C: 22.4 and 21.9, respectively.

- **Growing shoot parts (Fig 54b)**

  In the A and B plants, the daily pattern was somewhat more complicated than in the mature shoot parts. There was only a marginal daily fluctuation in the C plants. In the A plants, there was a slight increase in C/N ratio after the start of the dark period. Subsequently a decrease during the dark period and the first part of the subsequent light period, before increasing again. In the B plants, also a daily maximum was found in the dark period.
and a minimum in the light period. These plants showed an increase in daily maximum and minimum values until day five and subsequently a decrease. After ten days, daily maximum and minimum values in the B plants were higher by 9.1% and 19.6%, respectively, than in the A plants. In the C plants, these values were 50.4% and 71.5% higher, than in the A plants.

The extremes of the C/N ratio at day ten were: 7.8 and 6.7 for the A plants; 8.5 and 8.0 for the B plants; and 11.7 and 11.5 for the C plants.

- Roots (Fig 54c)

In the roots of the A plants and the +N03 roots of the B plants, a decrease in C/N ratio occurred during the simulated period. The decrease during a part of the light and dark period was not compensated by the increase during the remainder of the period. During the remainder of the period, the daily maximum in the roots of the A plants, was 88.8% of that at the first day; in the +N03 roots of the B plants the daily maximum was 86.5% of that at the first day. In the -N03 roots of the B plants and in the C roots, only marginal fluctuations were found. The C/N ratio increased during the simulated period. At day ten, the C/N ratio in the -N03 roots of the B plants and in the C roots was 185% and 140%, respectively, higher than the maximum value at the first day.

The maximum and minimum C/N ratios found at day ten were for A: 8.0 and 7.2, for the +N03 roots of the B plants: 7.7 and 6.9, for the -N03 roots of the B plants: 16.6 and 16.2 and for the C plants: 22.0 and 20.9.
<table>
<thead>
<tr>
<th>plants:</th>
<th>A= (+N03)</th>
<th>B= (-/+N03)</th>
<th>C= (-N03)</th>
</tr>
</thead>
<tbody>
<tr>
<td>mature shoot parts</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>9.2</td>
<td>9.2</td>
<td>9.2</td>
</tr>
<tr>
<td>after 1 day</td>
<td>8.8</td>
<td>9.2</td>
<td>9.7</td>
</tr>
<tr>
<td>&quot; 4 days</td>
<td>8.9</td>
<td>10.8</td>
<td>16.1</td>
</tr>
<tr>
<td>&quot; 5 &quot;</td>
<td>9.0</td>
<td>10.8</td>
<td>17.4</td>
</tr>
<tr>
<td>&quot; 9 &quot;</td>
<td>9.2</td>
<td>10.0</td>
<td>21.6</td>
</tr>
<tr>
<td>&quot; 10 &quot;</td>
<td>9.2</td>
<td>9.9</td>
<td>22.6</td>
</tr>
<tr>
<td>growing shoot parts</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>7.6</td>
<td>7.6</td>
<td>7.6</td>
</tr>
<tr>
<td>after 1 day</td>
<td>6.8</td>
<td>7.0</td>
<td>7.4</td>
</tr>
<tr>
<td>&quot; 4 days</td>
<td>6.5</td>
<td>8.8</td>
<td>10.5</td>
</tr>
<tr>
<td>&quot; 5 &quot;</td>
<td>6.5</td>
<td>8.9</td>
<td>10.6</td>
</tr>
<tr>
<td>&quot; 9 &quot;</td>
<td>6.7</td>
<td>8.2</td>
<td>11.5</td>
</tr>
<tr>
<td>&quot; 10 &quot;</td>
<td>6.7</td>
<td>7.9</td>
<td>11.8</td>
</tr>
<tr>
<td>roots</td>
<td>-N03</td>
<td>+N03</td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>8.5</td>
<td>8.5</td>
<td>8.5</td>
</tr>
<tr>
<td>after 1 day</td>
<td>8.9</td>
<td>10.4</td>
<td>8.9</td>
</tr>
<tr>
<td>&quot; 4 days</td>
<td>8.3</td>
<td>13.3</td>
<td>8.1</td>
</tr>
<tr>
<td>&quot; 5 &quot;</td>
<td>8.2</td>
<td>14.1</td>
<td>8.0</td>
</tr>
<tr>
<td>&quot; 9 &quot;</td>
<td>8.0</td>
<td>16.1</td>
<td>7.6</td>
</tr>
<tr>
<td>&quot; 10 &quot;</td>
<td>7.9</td>
<td>16.3</td>
<td>7.5</td>
</tr>
</tbody>
</table>

Model explanation

The relative increase in C/N ratio in the B and C plants compared with the A plants, is due to a continued formation of soluble C in photosynthesis after N03 was withheld from the nutrient solution. These carbohydrates are partly used in growth (cell formation), leading to dilution of nitrogen. The C/N ratio in the A plants is rather stable in time. There is only some decrease in C/N ratio in the roots. Uptake of N03, photosynthesis and assimilation of
chemical compounds are rather in balance, as well as the partitioning of C and N compounds between the different plant parts. This balance is disturbed after NO3 is withheld from the nutrient solution (B and C plants). This causes the increase in C/N ratio. In the B plants, there is a restoration of the balance between C and N compounds towards the control (A plants) during the simulated period, in the shoot parts. This is due to the increased NO3 uptake rate and growth rate of the +NO3 root part of the B plants. The C/N ratio in this root part and in the roots of the A plants is about the same, but decreases a little in both treatments. This is due to a higher increase in N than in C. The lower increase in C/N ratio in the B plants than in the C plants, is due to a continued uptake and assimilation of NO3 in the B plants, during the simulated period. Circulation of amino acids through the plants causes a less increased C/N ratio in the -NO3 roots of the B plants compared with the C plants.

The diurnal fluctuations in C/N ratio, are predominantly due to fluctuations in the concentration of soluble C.

Reality

Table VIII experiment
C/N ratio in maize plants with NO3 or without NO3

<table>
<thead>
<tr>
<th>plants:</th>
<th>+NO3</th>
<th>-NO3</th>
</tr>
</thead>
<tbody>
<tr>
<td>shoot</td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>8.5</td>
<td>8.5</td>
</tr>
<tr>
<td>after 4 days</td>
<td>9.3</td>
<td>20.0</td>
</tr>
<tr>
<td>&quot; 9 &quot;</td>
<td>10.6</td>
<td>41.5</td>
</tr>
<tr>
<td>roots</td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>8.3</td>
<td>8.3</td>
</tr>
<tr>
<td>after 4 days</td>
<td>8.3</td>
<td>20.0</td>
</tr>
<tr>
<td>&quot; 9 &quot;</td>
<td>9.9</td>
<td>32.8</td>
</tr>
</tbody>
</table>

(Source: Spek, 1984a, 1984b)
An increase in C/N ratio under nitrogen shortage is a common feature in crop plants (Novoa and Loomis, 1981). In experiments with maize (own observations, not published), the following C/N ratios were observed (Table VIII).

Discussion

As in real plants, the C/N ratio increases in the model plants under N shortage. This is caused in the model plants as well as in the real plants by a reduction in N concentration, due to growth (dilution of N) and to an increase in the concentration of C (soluble C and structural C), due to a continued photosynthesis. The C/N ratios, as given in Table VII and VIII, are more stable for the model plants, than for the real plants. Formation of supporting tissues in the real plants could be a factor for the increase in the C/N ratio in time.

The C/N ratio after nine days in the shoots of the model C plants is only 50% of that in the real -NO3 plants (Table VII and VIII). For the roots this was 36.6%. The higher increase in C/N ratio in time in the real -NO3 plants compared with the model C plants, can partly be caused by a higher decrease in concentration of N in the real plants than in the model C plants.

The B plants take an intermediate position between A and C plants. There is a continued and even increased NO3 uptake rate in the +NO3 roots of these plants and amino acids transported to the shoot and assimilated in the shoot are transported to the -NO3 root part. This is also found in real plants (de Jager, 1985). One can imagine, that daily fluctuations in soluble C concentration in real plants can eventually generate daily fluctuations in C/N ratio.
3.4 Soluble carbohydrate concentration

Model graphs (Fig 36)

The concentration of soluble C is expressed as gC/g (on basis of fresh weight). Daily fluctuations in soluble C concentration were found in plants under all treatments (+N03 [A], +/-N03 [B] and -N03 [C]) and in all plant parts. Soluble C concentration increased during the entire light period, except in the C plants, where a plateau in the curve was reached. It decreased again after the start of the dark period until the next light period. With decreasing N03 supply (B and C treatment, respectively) soluble C concentration in the plants tissues increased. In the C plants, rather stable daily maximum and minimum values were reached five days after the start of the simulated period. In the +/-N03 plants, daily maximum and minimum values increased until day six and decreased subsequently. A part of the soluble C was not stored in the mature shoot parts and could be transported to other plant parts. The concentration of these sugars, showed a diurnal rhythm too, though slightly less pronounced than in the total amount of soluble carbohydrates.

- Mature shoot parts (Fig 36a)

In the B and C plants, the daily maximum and minimum reached higher values than in the A plants. At day ten, the maximum value in the A plants was 33.2% lower than in the B plants, and 59.8% lower than in the C plants. For the minimum value this was 97% and 99.7%, respectively, that day.

- Growing shoot parts (Fig 36b)

In the B and C plants, the daily maximum and minimum reached higher values than in the A plants. At day ten, the daily maximum in the A plants was 80.9% of that in the B plants and 60.9% of that in the C plants. For the daily minimum, this was 3.1% and 0.5%, respectively, that day.
The daily maximum concentrations in the -NO₃ and +NO₃ roots of the B plants and in roots of the C plants, reached higher daily maximum and minimum values than in the roots of the A plants. At day ten, the daily maximum in the roots of the A plants was 77.7% of that in the -NO₃ roots of the B plants, 81.1% of that in the +NO₃ roots of the B plants and 62.7% of that in the roots of the C plants. The daily minimum in the A plants, was 2.3% of that in the -NO₃ roots of the B plants, 3.5% of that in the +NO₃ roots of the B plants and 6% of that in the roots of the C plants.

The difference in maximum value between A and C in all plant parts, was somewhat lower at day ten than at day six. This was predominantly due to an increase in soluble C concentration in the A plant parts (for mature shoot parts, growing shoot parts and roots this was 5.8%, 5.2% and 3.8%, respectively).

Model explanation

Daily fluctuations in the mature shoot parts are caused by a net production of soluble C during the light period. During the dark period, the photosynthates, in these plant parts, are used for energy demanding processes and for translocation to the growing shoot parts and to the roots. Daily fluctuations in soluble C concentration in growing shoot parts and roots are due to fluctuations in translocation of soluble C from the mature shoot parts and the use of soluble C in energy demanding processes. With nitrogen shortage (B and C plants), accumulation of soluble C is caused by a reduction in the use of soluble C in assimilation and transport processes, while photosynthesis is relatively less reduced. The reduction shoot growth and the increase in soluble C accumulation have, however, reduce the formation of soluble C through reduction of photosynthesis.

In the C plants, a new equilibrium in soluble C formation and use of soluble C is reached about five days after the start of the simulated period. In the B plants, daily maximum and minimum values decrease after five days, due to increasing activity of energy demanding
processes. This increase has been made possible by increasing NO$_3$ uptake rates, caused by both higher root sugar concentration and a temporary higher growth rate of the +NO$_3$ root part.

Reality

Daily fluctuations in starch and sugar concentration were found by Challa (1976) in cucumber plants, grown under short and low light conditions. At the end of the dark period, rather low values were found. With longer light periods, no fluctuations were found in sugar concentrations. In general, higher values for these carbohydrates were present in the light than in the dark. In the shoots, starch concentrations reached highest values, whereas in the roots the sugar concentrations were generally higher. During the light period, starch is formed in the shoot. In the dark, sugars are formed from starch, for use in shoot and roots. Hofstra (1966), found an increase in sugar concentration in tomato roots during the day. Pronounced daily changes in carbohydrate pools (starch, sucrose and hexose sugars) were observed in all plant parts (leaves, petioles, stems and roots) of soybean, during the photosynthetic period (an increase in the light and a decrease in the dark), by Kerr et al. (1985), Hendrix and Huber (1986), by cotton plants. In these plants, they found daily fluctuations in sucrose concentration. It is well known, that under poor N conditions, the soluble carbohydrate concentration rises in the plants (Alberda, 1965, for grasses; Louwerse, 1967, for tomato; Ivanko, 1971, for maize; Deinum, 1971, for Lolium; Ivanko, 1971, with maize; Radin et al., 1978, with cotton; Lambers et al., 1980, with Plantago; Talouizte et al., 1984, for wheat seedlings). Before effecting the photosynthesis, the chlorophyll concentration has to be reduced considerably (Brouwer, personal communication, Hunt, 1985a, 1985b, 1985c). Growth rate is reduced, before the chlorophyll concentration is reduced.

Table IX, shows results from an experiment with maize plants.
Table IX

<table>
<thead>
<tr>
<th></th>
<th>experiment</th>
<th>soluble sugars in maize mg/100mg(dry weight)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>+N03</td>
<td>-N03</td>
</tr>
<tr>
<td>shoot</td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>2.75</td>
<td>2.75</td>
</tr>
<tr>
<td>after 7 days</td>
<td>1.95</td>
<td>11.52</td>
</tr>
<tr>
<td>roots</td>
<td></td>
<td></td>
</tr>
<tr>
<td>at the start</td>
<td>1.75</td>
<td>1.75</td>
</tr>
<tr>
<td>after 7 days</td>
<td>1.95</td>
<td>9.66</td>
</tr>
</tbody>
</table>

(source: Spek, 1981)

In a split-root experiment with maize (de Jager, 1982), it was found, that the ethanol soluble sugar concentration in the roots and shoots of the +N03 plants was lower than in the -N03 plants (about 50% for the shoots and 30% for the roots, after 12 days). The soluble sugar concentration in the -N03 and +N03 roots of the +/-N03 plants and their shoot followed the sugar concentration of the +N03 plants.

Discussion

The occurrence of daily fluctuations in soluble C concentration in shoots as well as in roots is in agreement with literature data. The simulation results agree best with the experimental results of Kerr et al. (1985), i.e. an increase in the light and a decrease in the dark in all plant parts. Challa (1976) found, however, that in cucumber shoots especially the starch concentration fluctuated. Fluctuations in the roots were less pronounced. Because of the alternating storage and release of sugars into and out of the starch pool in the cucumber plants, the sugar concentration in these plants is more stable than in the model plants. The very low concentrations of soluble C in our model at the end of the dark period may not be found under experimental conditions (Challa, 1976; Lambers and Posthumus, 1980). An accumulation of soluble C in the C plants (low nitrogen conditions)
is in agreement with empirical results.

Table X soluble carbohydrate concentrations

<table>
<thead>
<tr>
<th></th>
<th>simulation</th>
<th>experiment</th>
</tr>
</thead>
<tbody>
<tr>
<td>after 7 days</td>
<td>A&lt;B</td>
<td>A&lt;C</td>
</tr>
<tr>
<td>%</td>
<td>%</td>
<td>%</td>
</tr>
<tr>
<td>mature</td>
<td></td>
<td></td>
</tr>
<tr>
<td>shoot parts</td>
<td>55.2</td>
<td>81.6</td>
</tr>
<tr>
<td>growing</td>
<td></td>
<td></td>
</tr>
<tr>
<td>shoot parts</td>
<td>52.5</td>
<td>72.9</td>
</tr>
<tr>
<td>roots -N03</td>
<td>46.5</td>
<td>65.9</td>
</tr>
<tr>
<td></td>
<td>43.8</td>
<td></td>
</tr>
</tbody>
</table>

(source: Spek, 1981)

Table X, shows that the differences in soluble C concentration between the model A and C plants and the experimental +N03 and -N03 plants are of the same magnitude. Both in experiment and model, differences are greater in the shoot than in the roots. In the experimental plants more than in the model plants, soluble sugar concentration in the +/-N03 plants followed the concentration of the +N03 plants (de Jager, 1982), which is lower than in the -N03 plants. However, in the B plants, soluble C concentration decreased towards that in the A plants during the second half of the simulated period.
3.5 Concentration of structural carbon compounds

Model graph (Fig 37)

Structural carbon compounds in the model represent cellwall carbohydrates (cellulose) (see: 2.2.2). The concentration of structural C compounds is expressed as gC/g (fresh weight). Daily fluctuations were only found in the growing shoot parts of the +NO3 [A] and the +/-NO3 [B] plants. With decreasing NO3 supply (B plants and the -NO3 plants [C]), higher concentrations of structural C compounds were reached.

- Mature shoot parts (Fig 37a)

The concentration of structural C compounds fluctuated only marginally in the A plants. After ten days, the concentration of structural C compounds in the B and C plants was 2.4% and 6.1%, respectively, higher than in the A plants.

- Growing shoot parts (Fig 37b)

A diurnal rhythm was found in the A and B plants. In the A plants, a daily maximum was found in the dark period and a daily minimum just after the start of the light period. In the B plants, the daily minimum was shifted during the simulated period from the beginning of the light period to the second half of this period, whereas the daily maximum shifted to the end of the dark period. After ten days, the daily maximum value in the B plants was 24.6% higher than in the A plants. At that time, the concentration of structural C compounds in the C plants was 77.3% higher than the daily maximum in the A plants. The decrease in difference between daily maximum in A and B plants is due to an increase of 4.7% in concentration in the A plants and a decrease of 8.1% in the B plants.
- Roots (Fig 37c)

In the A plants, the concentration of structural C compounds at the start of the dark period of day ten, was only 86.8% of that of the starting value, with only marginal daily fluctuations. In the +N03 and -N03 roots of the B plants and in the C plants, concentration of structural C compounds at the end of day ten were 32.6%, 11.6% and 37.7%, respectively, higher than in the A roots.

Model explanation

- Mature shoot parts (Fig 37a)

(In the A plants, marginal fluctuations in the concentration of structural C compounds are caused by daily fluctuations in the rate of structural C formation, while fresh weight growth is not fluctuating. Degradation of structural C compounds is not incorporated in the B and C plants, fresh weight growth is more reduced than formation of structural C. This causes an increase in the concentration of structural C compounds.

- Growing shoot parts (Fig 37b)

Daily fluctuations in structural C compounds are caused by fluctuations in overall formation of structural C compounds in the A and B plants, due to daily fluctuations in the translocation of soluble C to the growing shoot parts. In the B plants, the increase in daily maximum and minimum value until the fifth day, and the subsequent decrease are due to an increase and a decrease in the formation rate of structural C compounds, caused by changes in soluble C concentration. In the C plants, concentration of structural C compounds increase because fresh weight is more reduced than the formation of structural C compounds, in these growing shoot parts.

- Roots (Fig 37c)
In the A plants, the decrease in concentration structural C compounds during the simulated period is the result of a relative increase in fresh weight. In the +NO3 roots of the B plants, the concentration of structural C compounds decreases hardly, due to an increased formation of these compounds. (Fresh weight also is increased.) In the roots of the C plants and in the -NO3 roots of the B plants, formation of structural C compounds has increased, while growth is hardly reduced. This causes an increase in the concentration of structural C compounds.

Reality

For sugar cane it was found, that with increasing nitrogen application, fiber content is almost the reverse of that on moisture content (Dilwijn van, 1952). When sugar concentration in plant tissues increases, probably cellulose formation might be increased. From experimental data with maize, it appeared that under nitrogen starvation the cell wall fraction, on basis of fresh weight, increased. A part of the increase can probably ascribed to a decrease in cell volume, while the total amount of cells is not and probably decreased. This gives more cell wall material to cell volume.

Discussion

The model results and the experimental results show both an increase in cell wall material under nitrogen shortage. It would be interesting to study the rate of formation (and degradation) of structural C compounds and the consequent distribution pattern (not in the sense of transport but in the sense of place) in the different plant parts and under the different N treatments. This compared with assimilation and dissimilation processes of amino acids, structural N, soluble C and structural C compounds, may give more insight in the causes of the observed phenomena in experimental plants.
3.6 Nitrate concentration

Model graphs (Fig 38)

Daily fluctuations in NO3 concentration, expressed as gN/g (on basis of fresh weight), were found in the +NO3 situations (+NO3 plants [A] and +/-NO3 plants [B]). Daily minimum and maximum values in the A plants were rather constant during the simulated period but fluctuated in the B plants. In the -NO3 roots of the B plants and in the -NO3 plants [C], NO3 concentration decreased rapidly within one or two days.

- Mature shoot parts (Fig 38a)

In the A and B plants, the NO3 concentration increased during the dark period and decreased during the light period. In the B plants, daily maximum and minimum values decreased until day five and subsequently increased. After ten days, the minimum and maximum values in the B plants were 84.5% and 85.8%, respectively, of that in the A plants.

In the C plants, the NO3 concentration had decreased to 38% of the corresponding value in the A plants at the start of the dark period of the second day, and to 4% at the start of the dark period of the fourth day.

- Roots (Fig 38b)

In the roots of the +NO3 plants (A and B plants), a somewhat more complicated daily fluctuation was found than in the shoots. In the roots of the A plants, the NO3 concentration first increased and subsequently decreased during the dark period. The decrease continued for some time after the onset of the light period, and then increased again until some time into the dark period. The fluctuations in the +NO3 roots of the B plants lagged somewhat behind the fluctuations in the roots of the A plants, maximum and
minimum fluctuations were higher in the B roots from the first day on. The daily minimum and maximum values in the +N03 roots of the B plants increased until day seven and subsequently decreased till the end of the simulated period. After ten days, the maximum value in the roots of the B plants was 32.1% higher than that in the roots of the A plants.

In the -N03 roots of the B plants and in the roots of the C plants, the N03 concentration decreased continuously to 3% of the corresponding value in the A plants at the start of the dark period of the second day.

In the A plants, the average N03 concentration in the shoots was about twice as high as in the roots. The N03 concentration in the mature shoot parts was higher in the A plants than in the B plants, but the opposite was the case for the (N03 receiving) roots.

Model explanation

N03 concentration in the various plant parts is highly dependent on N03 uptake by the roots. The uptake shows a diurnal pattern due to daily fluctuations in the concentration of soluble C as a consequence of photosynthesis.

- Mature shoot parts (Fig 38a)

N03 concentration increases during the dark period (although transport to the shoot is reduced) due to the reduced rate of assimilation of N03 to amino acids. The reverse occurs during the light period. In the B plants, N03 concentration still increases for some time after the onset of the light period. This is due to a later reduction of N03 translocation to the shoot of these plants, after the onset of the light period. The decrease in maximum and minimum N03 concentration in the B plants until day five is due to a reduced translocation of N03 from the roots to the shoot. Increased root growth in the B plants and increased N03 uptake rate from day five on and an increased transport, cause an increase in the N03 concentration in the shoot.

- Roots (fig 38b)
The sharp increase in NO₃ concentration in the roots of the A plants and +NO₃ roots of the B plants after the start of the dark period is caused by a strong reduction in NO₃ transport to the shoot following decreased transpiration rates, at continued NO₃ uptake. The decrease in concentration in the A plants in the dark period is caused by a reduced NO₃ uptake rate, due to lack of soluble C. In the B plants, where the soluble C concentration is higher (Fig 35), a relatively higher uptake rate can be maintained resulting in a continuing increase in NO₃ concentration until 1-2 h before the end of the dark period. At the start of the light period, transpiration rate increases instantaneously, while NO₃ uptake increases at a slower pace following the supply of soluble C. Uptake and transport are therefore out of balance for some time. This causes a temporary decrease in NO₃ concentration in the roots. NO₃ accumulates again when more NO₃ is taken up than transported.

Thus the higher NO₃ concentration in the +NO₃ roots of the B plants compared with the A plants is due to a relatively higher uptake rate in the B roots. The amount of NO₃ taken up per plants, however, is higher for the A plants than for the B plants, because in case of the A plants, a larger amount of roots receive and take up NO₃.

Reality

In the leaves, daily fluctuations in NO₃ concentration were found by Hansen (1980), van de Dijk (1981) and Steingrøver (1986). In the roots of Lolium, no distinct diurnal rhythm could be distinguished (Hansen, 1980). Daily fluctuations are the result of variations in the balance between nitrate uptake, translocation and nitrate reduction (Hansen, 1980; Steingrøver, 1986). When plant parts are deprived of NO₃, its concentration in roots and shoot decreases rapidly, by assimilation of NO₃ and growth. In the roots, 5% and in the shoots 16% remained after 48 hours. In the shoots, NO₃ concentration was reduced to 4% within four days (Spek, 1981). It was also observed, that the NO₃ concentration on a dry weight basis, was about identical in shoot and roots of plants receiving NO₃. On a fresh weight basis, however, the NO₃ concentration is higher in the shoots than in the roots.
In a split-root system, it was found (de Jager, 1982), that the NO3 concentration in the +NO3 roots of maize plants, reached identical values as in the +NO3 control plants, while it was lower in the -NO3 root part as in the roots of the -NO3 plants. The NO3 concentration in the shoots of the +/-NO3 plants in the real plants was only somewhat higher than in the +NO3 control plants (de Jager, 1982).

Discussion

In the model plants, NO3 is only present in the mature shoot parts. This is based on experimental results, in which no NO3 was found in the youngest leaf parts of maize (own observations). From work of Veen and Kleinendorst (1985) with Lolium perenne and of Bloem and (19 ), it is known, that NO3 in the vacuole can be replaced by organic molecules (amino acids and organic acids) for osmotic regulation.

Daily variations in NO3 concentration in the shoot are in agreement with experimental data (Hansen, 1980; Steingrüber, 1986). NO3 concentration increased during the dark period and decreased during the light period, as in our model. These effects are due to variations in NO3 uptake, NO3 reduction and translocation, even if the concentration of soluble C in the model plants is not limiting. In Lolium roots, a more or less constant NO3 concentration during the light period was observed by Hansen (1980), whereas in the model, NO3 concentration changed in the light. As in real maize plants (Spek, 1981, 1984), the NO3 concentration in the shoot parts declined to low values within four days, and in the roots within two days (3-5% of the control). In the split-root system, the NO3 concentration in the +NO3 root part was high, as in the real situation (de Jager, 1982). In that situation, however, the NO3 concentration after six days was the same as in the control plants; in the model plants it remained higher. The concentration in the -NO3 root part follows that in the roots of the -NO3 plants in the model and in the experiment.
3.7 Amino acid concentration

Model graphs (Fig 39)

The amino acid concentration is expressed as gN/g (on fresh weight basis). When plants received NO3 (+NO3 plants [A] and +/-NO3 plants [B]), daily fluctuations in amino acid concentration were found. In -NO3 plants [C] daily fluctuations disappeared.

- Mature shoot parts (Fig 39a)

In the A and B plants, the concentration decreased after the onset of the dark period. In the A plants, it increased again later during that period. In the light period, the amino acid concentration increased both in the A and B plants (in the A plants after a small decrease at the start of the light period). The maximum amino acid concentration stabilized within one day at lower levels (48%) than the value calculated at the start. After ten days, the daily maximum in the B plants was only 91.3% of that in the A plants.

In the C plants, the amino acid concentration was continuously as low as the minimum in the A and B plants.

- Growing shoot parts (Fig 39b)

In the A and B plants, a daily minimum value was found in the dark period and a daily maximum in the light period. In the A plants a sharp increase started in the second half of the dark period which continued in the light. Subsequently, the concentration decreased sharply, followed by a more gradual decrease, continuing till the second half of the dark period. The daily maximum decreased 23.1% in the course of the simulated period. In the B plants, the amino acid concentration increased for a few hours after the onset of the light period and subsequently decreased till the end of the dark period. The maximum value in the B plants was only 34% of that of the A plants after nine days. (Day nine is used as a reference here instead of day ten, because no distinct maximum was found on that
day.) In the C plants, the amino acid concentration showed during about four days some initial fluctuation. At day ten, the concentration of amino acids in these plants was 65% of the minimum value of the A plants (at day nine this was 59%). Minimum value of the A plants at day ten (59% at day nine).

- Roots (Fig 39c)

In the roots of the A plants, and in the +N03 roots of the B plants, a minimum value was found in the light and a maximum value in the dark. In these roots, an increase in amino acid concentration was found after the onset of the dark period. In the roots of the A plants, amino acid concentration started to decrease in the middle of the dark period, and continued to decrease during part of the light period. Subsequently, the amino acid concentration increased again during the remainder of the light period, although at a slower pace than after the start of the dark period. From day five till day ten, the amino acid concentration in the +N03 roots of the B plants decreased sharply after the start of the light period and then increased again, as in the A plants, less sharply than after the start of the dark period. In the B plants, daily maximum and minimum increased during the simulated period. At day ten, the daily maximum in the +N03 roots of the B plants was 17.3% higher than in the roots of the A plants.

In the -N03 roots of the B plants, the amino acid concentration decreased parallel to that in roots of the C plants during about 1.5 days after the start of the simulated period. From then on, daily fluctuations disappeared in the roots of the C plants. In the -N03 roots of the B plants, the concentration decreased in the dark and increased until a rather stable level was reached in the light period. After ten days, the daily maximum in the -N03 roots of the B plants was only 31.7% of that in the roots of the A plants. The amino acid concentration in the roots of the C plants then was only 13% of the corresponding maximum value in the roots of the A plants.

Model explanation
- Mature shoot parts (Fig 39a)

Daily fluctuations in amino acid concentration in the mature shoot parts are mainly the result of differences in the rate of amino acid formation between the light and the dark period. (Amino acid formation only takes place in the light in these plant parts.) The increase in the dark period is due to transport of amino acids from the roots.

In the B plants, the amino acid concentration decreases during the entire dark period because amino acid export to other plant parts is not compensated by import of amino acids from the +NO3 root part.

Daily maximum values are highest for the A plants, because more NO3 is transported to the shoot parts of these plants.

In the C plants, the amino acid concentration shows a daily pattern till the NO3 concentration in the tissues reaches very low values (nearly zero). The amino acid concentration in these C plants is maintained by a continuous turnover of structural N.

- Growing shoot parts (Fig 39b)

The only source of amino acids in the growing shoot parts is amino acids transported from the mature shoot parts. The increase in amino acid concentration in the A plants in the dark is due to a reduced formation rate of structural N from amino acids, while reduction in fresh weight growth during this period reduced the dilution of amino acids. (Formation of proteins is limited by the soluble C concentration.) On the other hand, the subsequent decrease in amino acid concentration in the light is the result of increase in formation of structural N and growth. After three days, fresh weight of the meristems (growing shoot parts) of the B plants does not decrease any more during the second half of the dark period.

From then on the amino acid concentration decreased during the entire dark period.

The strong reduction in amino acid concentration in the growing shoot parts of the C plants reflects the amino acid concentration in the mature shoot parts of these plants.
The amino acid concentration in the NO3 receiving roots (roots of the A plants and the +NO3 roots of the B plants) parallels the NO3 concentration. Transpiration rate has an influence on both concentrations. As with NO3, amino acid transport is lower during the dark period due to a lower transpiration rate.

The -NO3 roots of the B plants receive amino acids from the mature shoot parts through the phloem. After the start of the light period amino acids increases in these roots due to a higher import from the mature shoot parts. Amino acid concentration decreases after the start of the dark period due to reduced translocation. Between these times, an equilibrium situation is reached between translocation of amino acids to the roots and formation of structural N.

The relatively sharp decrease in amino acid concentration in the roots of the C plants during 1.5 d after the start of the simulated period, is due to protein formation and dilution by growth. Later, the decrease is due to dilution by growth. Assimilation and dissimilation of structural N continues. Due to formation of amino acids in structural N degradation, a pool of amino acids exists. Through phloem and xylem, these amino acids can cycle in the plant.

The diurnal rhythm of amino acid concentration in the roots of tomato plants was studied by Hofstra (1964), in a greenhouse. The maximum amino acid concentration in the roots was rising throughout the experiment, with a decline at noon or 4 h later. No data were given for the shoot.

More experimental data are needed for validation of model behaviour with respect to amino acids.
3.8 Concentration of structural nitrogen compounds

Model graphs  (Fig 40)

Concentration of structural N compounds is expressed as gN/g. Daily fluctuations were found in the growing shoot parts under +N\textsubscript{03} situations (+N\textsubscript{03} plants [A] and +N\textsubscript{03} roots of the +/-N\textsubscript{03} plants [B]). In the -N\textsubscript{03} situations (-N\textsubscript{03} roots of the +/-N\textsubscript{03} plants [B] and in the -N\textsubscript{03} plants [C]), structural N decreased during the simulated period, and the daily fluctuation disappeared.

- Mature shoot parts  (Fig 40a)

There was only a marginal daily fluctuation in the A and B plants. In the B plants, the concentration of structural N compounds decreased in the first half of the simulated period and increased again in the second half. After ten days, the concentration of structural N compounds in the B plants was 97.7% of that in the A plants.

In the C plants, the concentration of structural N compounds after ten days was 57.6% of that in the A plants.

- Growing shoot parts  (Fig 40b)

In the A and B plants, the concentration of structural N compounds increased at the onset of the light period, and after reaching a maximum at about the middle, decreased again, to reach a minimum at the end of the dark period. The extremes, however, were less pronounced in the B plants. The daily maximum in the B plants decreased until day four and then increased again in the following days. After nine days, the daily maximum in the B plants was only 93.7% of that in the A plants, while the daily minimum value was 4.7% higher than in the A plants. The corresponding value for the C plants was 74.9% of that of the A plants.
- Roots (Fig 40c)

Only a marginal fluctuation was found in the roots of the A and B plants. The difference in the concentration of structural N compounds between roots of the A and B plants and roots of the A and C plants increased during the simulated period. At the end of the simulated period, the concentration in the +NO3 roots of the B plants was 16.9% higher than in the roots of the A plants and the concentration in the -NO3 roots of the B plants and in the roots of the C plants was only 60% and 53.7%, respectively, of that in the A plants.

Model explanation

- Mature shoot parts (Fig 40a)

After a reduction in NO3 supply (B plants) or a complete cessation (C plants), concentration of structural N compounds decreases. In the C plants, there is a continuous decrease as growth continues without increment in the total amount of structural N. In the B plants, the decrease is less pronounced, because of a continuing, although reduced increment in total structural N. The increase in the concentration of structural N compounds is due to a higher uptake activity of the +NO3 root part.

- Growing shoot parts (Fig 40b)

The increase in the concentration of structural N compounds in A and B plants during the light period is caused by an increase in rate of formation of structural N compounds, due to an increase in soluble C and amino acid concentration. The reduction in the concentration of structural N compounds is due to a decrease in formation rate of structural N compounds as a consequence of a reduced amino acid concentration. This is because the degradation rate of structural N compounds depends on the total amount of structural N, which changes much less than the concentration of structural N. Changes in structural N degradation
rate are negligible. The reduction in the concentration of structural N compounds in the C plants is caused by a reduction in the formation rate, due to a reduction in the concentration of amino acids. (Due to lack of NO3, the new formation of amino acids stops.)

- Roots (Fig 40c)

The high concentration of structural N compounds in the +NO3 roots of the B plants is caused by the increase in the rate of formation of structural N, due to an increase in the rate of formation of amino acids, following a stimulated NO3 uptake rate. The slight increase in the roots of the A plants is caused by a relatively lower growth in fresh weight compared to the rate of formation of structural N compounds. The concentration of structural N compounds in the roots of the C plants decreases, due to both a reduced rate of formation of structural N and a continued fresh weight growth. The -NO3 roots of the B plants receive amino acids from the shoot through the phloem and are thus able to form new structural N. The structural N concentration therefore decreases much less in these roots than in the roots of the C plants.

Reality

Structural N (=proteins) in the model will be compared with organic N (proteins + amino acids) in experimental results. The amino acids in organic nitrogen form only a minor part of the total organic N. Maize plants deprived of NO3, show a rapid decrease in organic N concentration (Spek, 1984). In six days, N concentration was decreased by 72.3% in the shoots and 66.7% in the roots, on a dry weight basis. No distinctions had been made between mature and growing shoot parts. N concentration changes with age of the plants (Simpson, 1986) and varies between plant parts (Venekamp et al., 1985, with maize).

Discussion
As in real plants, a reduction in concentration of structural N compounds found under N shortage in the model plants (C plants and the mature shoot parts and the -N03 root parts of the B plants. In a split-root system it was found (de Jager, 1984) with maize, that the N concentration in NO3 free and NO3 fed roots followed the N concentration of the +NO3 and -NO3 control plants. The shoots of the +/-NO3 plants in these experiments had a somewhat lower N concentration than the +NO3 controls. The -NO3 controls decreased in N concentration. The model results are similar to these empirical results, except that the concentration of structural N compounds in the +NO3 roots of the B plants is somewhat higher than in the A roots. With wheat also, higher N concentrations were found in the NO3 fed roots than in the NO3 free roots (Lambers et al., 1982). As in real plants (Lambers et al., 1982; de Jager, 1982), N concentration in the shoot of the A and B plants was about the same.

The reduction in the concentration of structural N compounds in the C plants is less fast than in the real plants (Spek, 1984a, 1984b). In the model plants, the concentration of structural N compounds in shoot and roots after ten days, was higher, 30% and 20%, respectively, than in reality.
3.9 Respiration rate

Model graphs (Fig 41)

Respiration rate is expressed as gC/g/h (on basis of fresh weight). Respiration costs in the model are composed of C costs for 1) biochemical processes, 2) transport processes and 3) maintenance of ionic gradients. (See section: 2.2.3.5)

In all cases in which plants received NO\textsubscript{3} (+NO\textsubscript{3} plants [A] and +/-NO\textsubscript{3} plants [B]), daily fluctuations were found. Daily fluctuations were highest in the A plants. When the supply of NO\textsubscript{3} was stopped (-NO\textsubscript{3} plants [C]), respiration rate diminished and fluctuations disappeared.

- Mature shoot parts (Fig 41a)

In the A and B plants, respiration rate decreased after the start of the dark period and increased after the start of the light period. Maximum and minimum values were found at the start and the end of the dark period, respectively. Hardly any difference in daily maximum was found between the A and B plants after day seven of the simulated period; at day ten, respiration rate was 3% higher in the A plants. The corresponding value in the C plants was only 50.7% of that in the A plants. The daily minimum value in the A plants was only 8.9% of that in the B plants and only 11% of the corresponding value in the C plants, at day ten. Thus the B and C plants did not reach the low daily minimum of the A plants.

- Growing shoot parts (Fig 41b)

In the A and B plants, respiration rate increased after the start of the light period, reaching a peak after a few hours and decreases from there on, till the end of the dark period. In the A plants, lower minimum and higher maximum values were reached than in the B plants. At the end of the simulated period (except for the extremes) the values for the A and B plants were very similar during a part of the day. The decreasing difference in respiration rate between A
and B plants was caused by a decrease in daily minimum and maximum value in the A plants and an increase in the B plants. The daily maximum at the end of day nine, was for the B and C plants 79.1% and 37.8%, respectively, of that for the A plants. The daily minimum value for the A plants at day ten was 6.4% of that of the B plants and 8.2% of that of the C plants.

- Roots (Fig 41c)

An increase was found during the light and a decrease during the dark period in A and B plants. In the +N03 roots of the B plants, the increase continued for some hours in the dark period. As a consequence, the daily maximum was found in the dark period in these B roots. Daily maximum and minimum values increased until day seven in the +N03 roots of the B plants. In the roots, as in shoots, the respiration rate was more stable in the B treatment. The minimum value in the roots of the A plants was lower than that in the +N03 and -N03 roots of the B plants and in the roots of the C plants; at day ten 93.5%, 62.1% and 66.5%, respectively. The maximum value in the -N03 roots of the B plants and in the roots of the C plants was only 18.6% and 14.2%, respectively, of that in the A plants. Daily maximum and minimum in the +N03 roots of the B plants were both higher than in the A roots. The maximum value in the +N03 roots of the B plants was 7.6% higher than in the A plants. The model results for respiration rates are composed of respiration costs for different energy demanding processes, among which N03 uptake (see: 2.2.3.5). The model results for N03 uptake will be compared with experimental results and are therefore mentioned here. Respiration costs for N03 uptake at the end of day ten were 18.8%, 17.0% and 0.0% of total plants respiration costs, for the A, B and C plants, respectively. Expressed as percentages of root respiration costs, these values are 52.7%, 44.4% and 0.0%, respectively.

Model explanation

Respiration in the mature shoot parts and roots consists of respiration for a) maintenance of ionic gradients, b) transport
processes and c) biochemical (assimilation) processes. In the growing shoot parts, respiration does not include energy for transport processes.

- Mature shoot parts (Fig 41a)

The shape of the curves is largely determined by the respiration rate of the biochemical processes, under the different N regimes. The higher respiration rate in the dark period in the B plants is caused by their relatively high soluble C concentration. There is no increase in respiration in the C plants during the light period, as due to reduced growth, less energy is needed for biochemical- and transport processes. The respiration processes in these plants are never limited by availability of soluble C. The lack of daily fluctuations in respiration rate is due to the rather constant amino acid and structural N concentrations.

- Growing shoot parts (Fig 41b)

The energy costs for biochemical processes mostly determine the daily fluctuations in respiration rate. The peaks at the start of the light period in the A and B plants are caused by peaks in structural N synthesis, due to an increase in import of amino acids and soluble C. The minima at the end of the dark periods are caused by low rates of structural C formation. In the B plants respiration during the dark period decreases less than in the A plants as a consequence of higher soluble C concentrations in the C plants, so that respiration processes continue at a high level in the B plants. The C plants show a continuous decrease in respiration due to a reduced rate of energy demanding processes as N03 uptake and N assimilation. Respiration is highly correlated with soluble C availability.

- Roots (Fig 41c)

In the +N03 roots, the highest respiration requirements are linked to the transport processes, in which ion uptake has the major share.
For the -NO3 roots, the highest respiration requirements are associated with biochemical processes. As for the shoots, the daily pattern is directly related to the biochemical and transport processes. The low respiration rates during the dark periods in the A plants are caused by shortage of soluble C as energy source and in assimilation processes as C skeleton.

Reality

The model calculates energy costs for transport and assimilation processes. We compare these data with measurements on CO2 delivery from and O2 consumption of plant parts. CO2 delivery and O2 uptake are both a measure for respiration rate. (CO2 as a product of substrate respired for energy delivery and O2 as terminal electron acceptor in the cytochrome pathway.)

Diurnal fluctuations in respiration rate in shoots and roots are shown by Challa (1976) in cucumber plants, grown under low-light conditions, Hansen (1980) in Lolium plants, and Veen (1980) in maize. Respiration rates were higher during the light than during the dark period. Hansen (1980) and Massimino et al. (1980) in maize found higher respiration rates at higher light intensities. CO2 production by maize roots showed diurnal fluctuations (increase in the light and decrease in the dark), when NO3 was present in the medium (own observations). Respiration rates were closely coupled with NO3 supply (Hansen, 1980). Veen (1980) found for maize plants, growing under standard conditions, that about 50% of the total root respiration (O2 uptake) was associated with ion uptake. NO3 depletion caused reduction in respiration rate. Oxygen uptake decreased by about 40% after a short period of depletion (a diluted nutrient solution). Van de Werf et al. (in press), also found high respiration costs for ion uptake (60%).

Daily fluctuations in O2 uptake and CO2 delivery correspond with fluctuations in sugar concentration (Challa, 1976; Veen, 1980), which suggests a connection. NO3 uptake and assimilation are highly energy demanding processes. When these processes are changed in activity, respiration rate changes either.
Discussion

Although daily fluctuations in respiration rate are reported in the literature, they are generally much less extreme than our simulation results. Challa (1976) found in his short day plants (8 h light) relatively low values at the end of the dark period. When NO3 is supplied (A plants), the low respiration rates found in our model plants are the result of very low soluble C concentrations. Lambers and Posthumus (1980), however, showed that in maize roots at the end of the dark period, even at low light intensity during the light period, (10W/m2) hardly any reduction occurred in the respiration rate of a respiration pathway, which delivers hardly any useful energy (alternative respiration pathway). Because of the overflow function of the alternative pathway for the respiration of sugars, its high activity this suggests that there was no sugar shortage in the roots. Reduction in respiration rate after withdrawal of NO3 from the medium is in agreement with experimental data (Hansen, 1980; own experiments). In this situation, soluble C concentrations in the model plants increase, also in agreement with experimental data (Louwerse, 1967; Spek, 1984;). The enhanced NO3 uptake by experimental plants, again supplied with NO3 (Veen, 1980; Ivanko, 1971), is ascribed to mobilization of the accumulated sugars in uptake and (NO3-) assimilation processes (Louwerse, 1967). In the model, respiration costs for NO3 uptake are in agreement with results of Veen (1980) (A plants).
3.10 Nitrate uptake

Model graph (Fig 42)

Nitrate uptake by the roots, expressed as gN/g/h (on basis of fresh weight), was higher during the light than during the dark period. The uptake rate in the +N03 roots of the B plants decreased much less (e.g. 33.4% at day nine) during the dark period than that in the roots of the A plants (97.2% decrease at day nine). Daily maximum and minimum values in the +N03 roots of the B plants increased slightly until day six and subsequently decreased. At day ten, the daily maximum value was 5.6% higher in the +N03 roots of the B plants, than in the roots of the A plants.

In the -N03 roots of the B plants and in the roots of the roots of the C plants, uptake rate decreased within the first light period to 5% of that of the roots of the A plants.

Model explanation

The fluctuations in N03 uptake are the consequence of fluctuations in the concentration of soluble C in the roots (as energy source for N03 uptake) and not by a high N03 concentration in the roots (as a feedback mechanism) or by a limiting N03 concentration in the medium. The +N03 roots of the B plants have a higher uptake rate than the roots of the +N03 plants, due to their higher soluble C concentration. Changes in daily maximum and minimum values in these roots are due to changes in soluble C concentration during the simulated period. These changes are caused by the adjustment in growth of the B plants after the altered situation in N03 supply, at the start of the simulation.

Reality

Pearson et. al, (1981), concluded, that the lower rate of influx of N03 in the roots of maize plants, in the dark, was not associated with
a constancy in nitrate efflux during the day. Reduction and translocation also were lower during the dark period. Veen (1977, 1980, 1981) found for maize a higher NO3 uptake rate in the light than in the dark period. This was ascribed to a lower rate of NO3 reduction in the dark. Schulze et al., (1985) observed in radish the same phenomenon. A corresponding phenomenon was ascribed to a higher supply of carbohydrates to the roots in the light, by Abrol et al. (1983).

Louwerse (1967), working with decapitated tomato plants, observed a correlation between carbohydrate concentration and ion uptake. Hansen (1980) explained the diurnal rhythm in NO3 uptake in Lolium as a result of changes in NRA (Nitrate Reductase Activity) in the shoot (influenced by light) and changes in carbohydrate transport to the roots.

Discussion

Veen (1977) with maize and Hansen (1980) with Lolium, did not find such large fluctuations in NO3 uptake as shown in the model. The fluctuations in the model are the consequence of fluctuations in soluble C concentrations, which reached very low values in the dark period. A correlation between the soluble sugar concentration in root tissues and NO3 absorption was found by Champigny and Talouizte (1986) in wheat seedlings. In the model a direct influence of NRA on NO3 uptake (Hansen, 1980) was not assumed. It could be, however, that in our model the influence of soluble C concentration is overestimated. An alternative explanation for the large fluctuations in the model results, is the absence of NO3 compartmentalization in the model which would give the possibility of a feedback on the uptake of only part of the root NO3. Ezeta and Jackson (1975), found with detopped corn seedlings, that storage NO3 was effectively isolated from both the translocation pathway and the reduction pathway.

Experiments are needed to improve the functional relations in the model. (Continuous measurements of NO3 influx and net NO3 uptake [according to the method of Deane-Drummond, 1986], especially after changes in NO3 supply, until the plant has been adapted to the new
situation).
3.11 Phloem transport

3.11.1 Transport of soluble carbohydrates

Model graphs (Fig 44)

Transport of carbohydrates from the mature shoot parts to the growing shoot parts and to the roots is expressed as gC/g/h. Day/night fluctuations in transport rate both to the growing shoot parts and to both root parts were formed.

- Transport to the growing shoot parts (Fig 44a)

In the +N03 situations (+N03 plants [A] and +/-N03 plants [B]), the rate of transport increased during the light and decreased during the dark period. It never reached stationary levels. In the A plants there was a sharp transition immediately after the start of the light and the dark period. (Sugar concentrations reached very low values in shoot and roots in the dark period in these plants.) Daily minimum transport rates were higher in the +/-N03 plants, increased until day seven and decreased subsequently. Daily average rates in transport to growing shoot parts were higher in the B plants, than in the A and C plants. The reduction in transport rate during the dark period of day nine was 98.4% in the A plants and 50.8% in the B plants.

In the -N03 plants the daily fluctuations in transport rate decreased during the simulated period. During the first five days, the daily averages of carbohydrate transport to the growing shoot parts were higher in these C plants than in the A plants. Transport in the C plants at day ten was 39.8% lower than the maximum value in the A plants at the end of the light period.

- Transport to the roots (Fig 44b)
The rate of transport was higher during the light period than during the dark period. Sharp transitions were found at the start of the light period and the dark period. During the light period, there was no net change in transport to the roots of the A plants. In the last complete light period, the decrease in transport to the +N03 roots of the B plants was 5.8%, to the -N03 roots 18.8% and to the C roots 22.9%, in the last complete light period.

In the +N03 plants the daily maximum was always higher and the daily minimum always lower than in the -N03 plants. Daily maximum and minimum values of transport to the +N03 roots of the B plants were always higher than those to the roots of the A plants. The daily maximum rate of transport to the -N03 roots of the B plants was always lower and the daily minimum was often lower than that to the roots of the A plants.

One hour after the start of the light period at day nine, the rate of transport in the C plants was 61% lower than that in the A plants. The rate of transport to the -N03 and +N03 roots of the B plants was 48% lower and 14.3% higher, respectively, than to the roots of the A plants.

Model explanation

The fluctuations in rate of carbohydrate transport to the growing shoot parts and to the roots are due to variations in photosynthetic activity. The instantaneous rates depend on the difference in soluble C concentration between the source tissue (mature shoot parts) and the sink tissues (growing shoot parts and roots). The initially (C plants) or permanently (B plants) higher rates of transport to growing shoot parts in C and B plants, are caused by accumulation of soluble C in the source tissues as a result of the relatively low carbon utilization rate in non-nitrogen fed roots. The higher rate of transport to the +N03 roots of the +/-N03 plants than to the -N03 roots of these plants is due to a higher use of soluble C in the +N03 roots, and hence a lower soluble C concentration.
Diurnal fluctuations in sugar translocation rate were found by Sharkey and Pate (1976) in Lupinus albus. Farrar and Farrar (1985) found daily fluctuations in sugar transport through the phloem of barley plants. (Phloem sap was collected from distal tips of fruits). Challa (1976) found in cucumber plants, growing under low light conditions, daily fluctuations in starch and sugar concentration in leaves, stems and roots. In the dark period, the reserves (starch) were used up. From this a diurnal fluctuation in sugar transport rate in these plants can be concluded, when taken into account that sugars released from the starch pool in the shoot are probably transported through the phloem to stem and roots. Farrar and Farrar (1986), found for barley that in the dark, starch mobilization started immediately and that of sucrose increases. Translocation rate in the dark was then 77% of that in the light. Gordon (1986), found diurnal patterns of photosynthate allocation and partitioning among sinks. Hendrix and Huber (1986), found a diurnal variation of carbon export rate from mature cotton leaves.

Discussion

The daily fluctuations found in the model are large in comparison with the fluctuations found by Sharkey and Pate (1976) and Challa (1976). In the B and C plants, sugar transport to the roots increased after the start of the light period and subsequently decreased in the course of the light period until the end of the dark period, similar to the experimental results of Sharkey and Pate (1976). In the other situations, transport rates to roots of the A plants and to the growing shoot parts of all plants, transport rates only decreased in the dark. The large fluctuations in transport rate in our model are the result of large fluctuations in the soluble C concentration in the mature shoot parts. In Challa's (1976) experiments, the starch concentration showed a large diurnal variation, whereas the concentration of soluble sugars was far more stable. A more detailed simulation of the phloem transport is also needed. Therefore, a
better understanding of phloem transport is needed.
3.11.2 Phloem loading of amino acids

Model graphs (Figs 45a, 46a)

Loading of amino acids into the phloem for transport from the mature to the growing shoot parts and to the roots is expressed in gN/g/h (on basis of fresh weight of the mature shoot parts plus the growing shoot parts or, of the fresh weight of the mature shoot parts plus that of the roots). A diurnal fluctuation in loading rate was shown when NO3 was supplied to the plants (+NO3 plants [A] and +/-NO3 plants [B]). In the -NO3 plants [C] fluctuations in the loading rate disappeared during the simulated period.

- Loading for transport to the growing shoot parts (Fig 45a).

Immediately after the start of the light period, the rate of loading increased sharply in the A and B plants. Subsequently, it decreased until the end of the light period in both the A and B plants. During the dark period, the loading rate decreased in the A and B plants. In the B plants, there was a decrease in the rate of loading throughout the whole dark period, while in the A plants a constant loading rate was shown from the second to the third or fourth hour, followed by a sharp decrease to very low values at the end of the dark period. We can summarize these results as follows: going from A to B to C plants, daily fluctuations as well as average values decreased. Daily maximum values decreased fastest in C plants: they fell to 49% of the level in the A plants at day 3, and 14% at day 5. B plants were intermediate: 48% of the level of the A plants at day five, 75% at day nine.

- Loading for transport to the roots. (Figs 46a)

The general picture of amino acid loading for transport to roots was similar to that for the growing shoot parts: smaller fluctuations and lower values, in the order A to B to C. In the roots receiving
N03 (A plants and +N03 roots of the B plants), the rate of loading increased during the light period and decreased during the dark period. In the A plants very low values were reached in the dark period. At the end of the third light period, the loading rate for the +N03 roots of the B plants was 17.2% lower than for the roots of the A plants. At day ten, the daily maximum for the +N03 roots of the B plants was 5.9% higher than for the roots of the A plants.

In the -N03 roots of the B plants, rate of loading decreased in the course of the light period after an increase immediately after the start of the light period. The daily maximum during the last complete light period was 33.1% lower for these roots than for the roots of the A plants.

During the entire dark period the rate of loading decreased in the roots of the A and B plants. The rate of loading for translocation to the roots of the B plants did not decrease as much as that for the A roots during the dark period. There was a fast increase and decrease immediately after the start of the light and the dark period, respectively, which occurred especially in the +N03 plants. The rate of loading for the roots of the C plants decreased substantially in the course of the simulated period and was at the end 67.7% lower than the daily maximum in the A plants.

Model explanation

Loading of the phloem was made dependent in the model on: 1) the concentration of soluble C in the source (mature shoot parts), 2) the total amount of amino acids, available for transport, 3) the amino acid concentration in the phloem, 4) the sink size and 5) a transport constant (2.3.13).

- Loading for transport to the growing shoot parts. (Fig 45a)

In the A plants, the sharp increase in the rate of loading of amino acids after the start of the light period is due to an increase in soluble C concentration, which then no longer limits the rate of loading. In the B plants, the increase in rate of loading after the
start of the light period is due to an increase in amino acid concentration in the mature shoot parts. In these plants, the soluble C concentration is not limiting for the rate of loading. The decrease in the course of the light period in the A and B plants is caused by a decrease in the ability of the phloem to take up amino acids, due to an increase in the amino acid concentration in the phloem. Availability of soluble C or amino acids is not limiting. The decrease in loading rate in the dark period in the B plants is the consequence of a reduced amino acid concentration throughout; in the A plants the decrease is due to a reduced amino acid concentration during five hours from the start of the dark period and then predominantly by a reduced soluble C concentration (which causes the sharp decrease in loading rate in the second half of the dark period). The lower rate of phloem loading in the B plants compared to that in the A plants is due to a higher amino acid concentration in the phloem sap and a lower fresh weight, which results in a lower sink strength. During the simulated period the daily maximum and minimum amino acid concentration in the B plants decreased until day six, due to a reduced NO3 uptake by the roots, and increased thereafter, due to an increased NO3 uptake rate. A higher rate of NO3 uptake allows formation of more amino acids if availability of soluble C is not limiting. In the -NO3 plants, the rate of loading is limited by the amino acid concentration in the mature shoot tissues rather than by the soluble C concentration.

- Loading for transport to the roots. (Fig 46a)

The sharp increase in the rate of loading in the A plants immediately after the start of the light period is the result of an increase in the concentration of soluble C (which then no longer limits loading of amino acids). Continued increase in the rate of loading is the result of the increase in amino acid concentration in the mature shoot parts. In the +NO3 roots of the B plants, the increase in rate of loading in the light period is due to the increase in amino acid concentration in the mature shoot parts. (The concentration of soluble C is not limiting). During 2-4 h before the end of the light period, a reduction in the rate of
loading was caused by a reduction in amino acid concentration in the phloem. From day five onwards, an increased loading rate during the light period was due to a greater sink size (fresh weight roots) compared to the A plants, caused by an increased relative growth rate of the roots of these B plants. Directly after the start of the dark period, the rate of loading decreased in the A and B plants, due to the reduction in amino acid concentration in the mature shoot parts. In the A plants, the very low rates of loading (for instance 3 hrs before the end of the dark period) were the consequence of a reduction in soluble C concentration. The fast increase in the rate of loading after the start of the light period (in the -N03 roots of the B plants), was the result of an increase in amino acid concentration in the mature shoot parts. The subsequent decrease during the dark period is the consequence of an increase in amino acid concentration in the phloem. The concentration of soluble C is not limiting here. Lower rates of loading in the B plants compared with the A plants were due to an increased amino acid concentration in the phloem. During the dark period, the decrease in rate of loading was the result of a reduction in the amino acid concentration in the mature shoot parts.

In the roots of the -N03 plants, the rate of loading was limited by the amino acid concentration in the mature shoot parts. This concentration continuously decreased during the simulated period, causing a further reduction in rate of loading.

To summarize: The rate of loading was predominantly determined by the amino acid concentration in the source tissues and the phloem sap. In the A plants, the availability of soluble C was limiting the rate of loading at the end of the dark period and the start of the light period.

Reality and Discussion are treated after discussing unloading phenomena.
3.11.3 Phloem unloading of amino acids

Model graphs (Figs 45b, 46b)

Unloading of amino acids from the phloem in the growing shoot parts and into the roots was expressed as g N/g/h (on basis of fresh weight of mature shoot parts plus growing shoot parts or fresh weight of growing shoot parts plus that of roots) Diurnal fluctuations continuously showed up in the +N03 situations (+N03 plants [A] and the +/-N03 plants [B]). In the -N03 plants [C], diurnal fluctuations diminished during the simulated period.

- Unloading in the growing shoot parts. (Fig 45b)

The pattern for the rate of unloading was similar to that for the rate of loading in the A and B plants. At day five, the daily maximum rate of unloading in the B plants was 58.2% and at day nine 73.7% of the maximum value of the A plants. In the course of the simulated period the rate of unloading decreased continuously in the C plants and reached 20.4% of the daily maximum value of the A plants at day five and 1.4% at day nine.

- Unloading in the roots (Fig 46b).

In the A plants, the rate of unloading increased during the whole light period, with a sharp increase in the first hour. During the dark period, the rate of unloading decreased with a slight increase in the second hour. Unloading in the +N03 roots of the B plants showed a similar pattern as in those of the A plants. On the third day, the daily maximum value was 14.1% lower than in the A plants and at day ten 7.5% higher. In the -N03 roots of the B plants, a peak occurred early in the light period, followed by a decrease during the second hour of this period. From then on a more gradual decrease took place until the end of the light period. During the dark period, the rate of unloading decreased further after a fast
decrease in the first hour. In these roots, the value three hours after the start of the light period was 49% of the daily maximum of the A plants at day five and 60.8% the last light period. In the roots of the C plants, daily fluctuations in the rate of unloading diminished in the course of the simulated period. At day ten, the daily maximum value was 32% of the maximum value in the roots of the A plants that day.

Model explanation

- Unloading in the growing shoot parts. (Fig 45b)

The increase in rate of unloading of amino acids in the A plants directly after the start of the light period is the result of an increase in soluble C transport from the mature to the growing shoot parts and an increase in the amino acid/soluble C ratio in the phloem. In the B plants, the increase in the light period is predominantly due to an increase in the rate of soluble C transport. The decrease during the light period in the A and B plants is caused by a decrease in the amino acid/soluble C ratio in the phloem. During the dark period, the rate of unloading decreases due to a decrease in the rate of soluble C transport, although the amino acid/soluble C ratio increases. The very low rates of unloading in the A plants at the end of the dark period are due to very low rates of soluble C transport and a decreased amino acid/soluble C ratio at the end of this period. In the -NO3 plants, unloading rate continuously decreased after day four, due to a decrease in the rate of soluble C transport.

- Unloading in the roots (Fig 46b)

The increase in the rate of unloading in the roots of the A plants and in the +NO3 roots of the B plants in the first hour of the light period is caused by an increase in the rate of soluble C transport. The subsequent increase is predominantly due to an increase in amino acid/soluble C ratio in the phloem. (The ratio increases after an
initial decrease at the transition of dark to light.) The decrease (in the A and B plants) during the dark period is due to a decrease in the rate of soluble C transport. Due to an increase in the amino acid/soluble C ratio in the phloem of the A plants, the rate of unloading increases during the second hour of the dark period. Comparing the roots of the A and B plants quantitatively, the following can be concluded: The +NO3 roots of the B plants show a higher rate of soluble C transport than the roots of the A plants (Fig 46b), but due to a lower amino acid/soluble C ratio in the phloem, the rate of unloading in the roots of the B plants during the light period is lower than in those of the A plants, until day six. The decrease in shoot/root ratio in the B plants (caused by the decreased RGR of the shoot), is related to the higher unloading in the +NO3 plants roots, compared with the A plants, after day five. The increase in the rate of unloading after the start of the light period in the -NO3 roots of the B plants, is caused by an increase in the rate of soluble C transport. The sharp decrease following that is due to the sharp decrease in amino acid/soluble C ratio directly after the start of the light period. The subsequent gradual decrease in the rate of unloading is the consequence of a gradual decrease in the rate of soluble C transport and in the amino acid/soluble C ratio in the phloem. The decrease in the rate of unloading during the dark period is due to a decrease in rate of soluble C transport. The high daily maximum rate of unloading in these roots, one hour after the start of the light period, compared to that in the roots of the A plants is caused by the relatively high amino acid/soluble C ratio in these roots. The daily fluctuations in the rate of unloading in the -NO3 roots of the B plants, is due to fluctuations in soluble C transport.

Fluctuations in the rate of unloading in all situations are predominantly due to variations in rates of soluble C transport. A lower amino acid/soluble C ratio in the phloem causes a lower rate of unloading in the B plants than in the A plants during a large part of each day. Unloading in the B plants is higher than in the A plants at the end of the dark period and at the start of the light period. This is caused by better maintenance of soluble C transport due to
higher soluble C concentrations in the source tissues of the B plants. The higher soluble C concentrations are the result of a less reduction in photosynthesis than in the use of soluble C in uptake, transport and assimilation processes (except in the +NO3 roots of these B plants). s 1 Reality: Loading and unloading of the phloem

Phloem transport is probably driven by a pressure flow mechanism, as proposed by Münch (1930). The physiological mechanisms of phloem loading, phloem unloading and transport of assimilates via the phloem are subject of intensive study (Pate et al., 1979; Smith et al., 1980; Layzell et al., 1981; Lang, 1983; Giaquinta, 1983; Wolsinkel, 1983, 1985; Patrick, 1984).

Quantitative information about transport of soluble C and nitrogenous compounds from the shoot to a whole or a divided root system are available (Lambers et al., 1982; Simpson et al., 1982; de Jager, 1985; Stulen, 1986). Part of the nitrogen transported to the roots is exported again to the shoots. It also appears, that roots fed with NO3 are able to import more carbohydrates and therefore more amino acids (N-compounds) in the roots (Lambers et al., 1982). Diurnal changes in C and N concentration in the phloem sap are found by Sharkey and Pate (1976). After the start of the light period, transport rate increased and decreased again during the rest of this period and the following dark period.

Discussion: Loading and unloading of the phloem

The mechanism for phloem transport in the model has been based on the pressure flow hypothesis of Münch (1930). In the simulated situations, transport rate of amino acids (and sugars) is higher to the more active sink regions in the +NO3 situations, with higher rates of assimilation in these tissues. The total amount of amino acids transported per hour to the +NO3 roots of the B plants, however, is somewhat lower than to the roots of the A plants. Transport can be higher to the roots of the A plants because of a higher amino acid concentration in the phloem sap.

An increase in transport rate in the light, and a decrease in the dark were also found in experiments of Sharkey and Pate (1976). Transport
to the growing shoot parts in A and B plants and to the roots of the B plants, decreased in the light period after an initial increase, until the end of the dark period, as in the experiments of Sharkey and Pate (1976).

Net transport of sugars and amino acids to the -NO3 roots of the B plants seems to be too high in the model compared with data found by Lambers et al. (1982). The -NO3 roots of the B plants show no decrease in growth in dry weight (and no substantial decrease in growth in fresh weight). This means that the sink strength in the -NO3 roots (of the B plants) remains too high, or in other words, reduced import of nitrogen via the phloem is balanced by reduced export of nitrogen to the shoots via the xylem. In summary: in the model, nitrogen cycling (shoot - root - shoot) rates are reduced in B and, especially in the C plants, but net assimilation of the cycling nitrogen compounds remains virtually the same as in A plants (and is even raised in B and C plants, compared with the A plants, when expressed as amount utilized per amount imported via the phloem).

To improve the model and for a better understanding of transport processes, observations on concentrations of several components in the phloem sap and calculations about the rate of transport might be useful.
3.12 Transpiration

Model graph (Fig 47)

The transpiration rate, expressed as gH2O/m2/h, was exactly the same for all treatments (+N03 plants [A], +/-N03 plants [B] and -N03 plants [C]) and showed a distinct day/night rhythm.

Model explanation

When the light period starts, there is an immediate increase in leaf conductance and energy input in the model, causing a sharp increase in transpiration rate. The reverse occurs when the dark period begins. Transpiration rate was not made dependent on the influence of nitrogen concentration on leaf conductance, but it was taken to be linearly correlated with leaf surface only. Transpiring leaf surface is calculated from mature leaf fresh weight by multiplication with a constant specific leaf area (SLA). Total transpiration therefore varies among treatments, in dependence of shoot fresh weight. Parameters (SLA, transpiration rate per m2 leaf surface in dark and light) were derived from own experiments (unpublished).

Reality

Differences in transpiration rate between light and dark well known (Veen, 1977; Hansen, 1980; Radin and Boyer, 1982; Simpson et al., 1982; Schulze et al., 1985). Transpiration was found to be higher in the light than in the dark period. The pattern in the daily fluctuations could be of a different shape. Hansen (1980) found, with Lolium multiflorum, a higher and constant transpiration rate during the light period compared with the dark period, while Simpson et al. (1982) found, with wheat plants, growing in a controlled environment, after a sharp increase at the start of the light period a decrease in the course of the light period.
Transpiration, water relations relations within the plant and growth, are closely coupled phenomena, as is well known. A low nitrogen level in the plant decreased the hydraulic conductivity of sunflower plants (Radin and Boyer, 1982). Water deficit in expanding leaf blades then increased in these plants and the turgor dependent growth decreased. The water deficit in these sunflower plants was generated by transpiration. Expansion was restricted mostly by daytime (highest rate of transpiration). According to Radin (1983), this is in dicotyledonous plants the reason for reduced leaf growth. In cereals (maize), leaf expansion was more closely dependent on the assimilation rate. Expansion zones in cereals are protected for water loss by a preceding leaf.

In contrast to findings of Radin (1982), in own experiments with maize plants it was found, that under nitrogen shortage, leaf expansion growth decreased in the light. Probably this was caused by a reduced water potential.

Discussion

A distinct day/night rhythm in transpiration rate is in accordance with literature data. Changes in leaf conductance during the day, dependence on nitrogen concentration and age, were not taken into account in the model. Hansen (1980) found a drop in the transpiration rate with nitrogen starvation. Yoshida and Coronel (1976), give data showing a decreased conductance of the stomata. Radin (1982), made a distinction between dicotyledons and cereals in their response in growth on nitrogen deficiency. For dicotyledons, the hydraulic conductance plays an important role in growth response in their nitrogen deficient plants. In cereals, changes in assimilation rate are of higher importance for growth reduction. In own experimental maize plants, nitrogen starvation caused an increase in soluble C concentration, cell volume decreased and leaf elongation growth in the light was reduced till the rate of leaf elongation in the dark. These phenomena resemble the results of Radin (1983) with dicotyledons. Therefore, in our plants, the influence of nitrogen deficiency on hydraulic conductivity may be of higher importance than in the cereal
plants of Radin (1983).
In the model plants, reduction in fresh weight growth of the shoots of the -NO3 plants is due to a reduced concentration of structural N compounds. The concentration of soluble C is increased, in spite of a reduction in the rate of photosynthesis.
3.13 Transport of NO₃ through the xylem

Model graph (Fig 48)

The rate of transport of NO₃, from the roots to the mature shoot parts, is expressed in gN/g/h (on basis of fresh weight). As a consequence of the assumptions made in the model, only the roots receiving NO₃ can take up and transport NO₃. The rate of transport showed complex diurnal fluctuations, with highest values in the light period and lowest values in the dark period. Immediately after the start of the light period, transport rates from the roots of the +NO₃ plants [A] and the +NO₃ roots of the +/-NO₃ plants [B]) showed a fast increase followed by a decrease and then an increase again. (Changes in these roots of the A and B plants are not of the same magnitude.) Immediately after the start of the dark period, transport rate decreased rapidly, followed by an increase which continued in the B plants but was followed in the A plants by a decrease until the end of the dark period.

In the +NO₃ roots of the B plants, daily maximum and minimum values increased until day six and decreased thereafter in the course of the simulated period. At the end of the light period of day nine, the transport rate in the roots of the B plants was 3.1% higher than in the roots of the A plants.

In the -NO₃ plants [C] and in the -NO₃ roots of the B plants, NO₃ export fell to 5% of the level in the A plants within the first day.

Model explanation

Transport rate is generally highest during the light period because of the higher transpiration rate and the higher NO₃ concentration in the roots. These higher NO₃ concentrations are due to an increased NO₃ uptake rate in the light, caused by an increased concentration of soluble C in the light. The sharp increase and decrease after the start of light and the dark period, respectively, are caused by the
sudden changes in transpiration rate at the transition of light and dark. The decrease in transport in the light and the increase in the dark, are the result of changes in the rates of nitrate reduction (increase in the light and decrease in the dark) caused by changes in soluble C supply from the shoots. These changes in soluble C supply lead to reduced/increased availability of NO3 for transport. A secondary effect of soluble C supply to the roots, stimulation of nitrate uptake, dominates thereafter. The +NO3 roots of the B plants do not always show a decrease of transport in the dark period. In these roots, after four days, transport rate increases almost during the whole dark period due to a higher rate of NO3 uptake in comparison with the A plants, as the result of a higher concentration of soluble C. The -NO3 root parts of the B plants do not supply NO3 since it has been supposed, that no NO3 is translocated from the shoot to the roots. For rice it was found recently, that some NO3 can be present in the phloem (Hagashi and Chino, 1986).

For Reality and Discussion see Section 3.14.
3.14 Transport of amino acids through the xylem

Model graph (Fig 49)

The rate of transport of amino acids from the roots to mature shoot parts through the xylem is expressed in gN/g/h (on basis of fresh weight). The daily pattern in transport rate resembles that for NO3 transport. An important difference, however, is the possibility of transport of amino acids from the -NO3 roots of the B plants to the shoot. The amount of amino acids translocated from these roots is low and shows a diurnal rhythm (a higher rate of transport in the light than in the dark period). At the end of the light period of day ten, the rates of transport from the -NO3 and the +NO3 roots of the B plants are only 9.3% and 89.6%, respectively, of that of the roots of the A plants.

In the roots of the C plants, the rate of transport of amino acids to the shoot is after one day only 38% of that from the roots of the A plants and falls during day four to 5% of the value for the A plants.

Model explanation

The daily pattern produced by the model can be explained in a similar way as for NO3 transport in the +NO3 situations. The rate of transport is a function of the rate of transport of water and the amino acid concentration in the roots. Hence when transpiration rate increases, more amino acids are transported. The amino acid pool in the -NO3 roots of the B plants is sustained by import of amino acids from the phloem and by degradation of structural N compounds. Therefore, export of amino acids to the shoot can also take place from these roots. The amount of amino acids transported is low, however, because of the very low amino acid concentration in these roots. During the light period that concentration is only slightly above the minimum level, below which transport ceases.
Reality: Nitrate and amino acid transport

Pearson et al. (1981), found for maize a reduced translocation of [15N]-nitrate from the roots to the shoot. They found a linear relationship between [15N] influx and [15N] translocation. Simpson et al. (1982) found, in wheat, a higher rate of transport of nitrogenous compounds (NO₃ and organic nitrogen) in the light than in the dark, as a result of variations in the rate of transpiration. The concentration of nitrogenous compounds in the xylem sap was identical during light and dark period. The authors supposed that more NO₃ would have been transported when available. The increased rate of water flow stimulated NO₃ uptake and loading into the xylem.

A daily pattern in rate of NO₃ transport although not identical to that reported by Simpson et al. (1982), was also found by Schulze et al. (1985) in radish. Variations in NO₃ concentration of the xylem during the day were probably the result of variations in rate of uptake by the roots, transpiration rate, and rate of NO₃ reduction in the roots. In these experiments, the NO₃ concentration in the external medium was high.

Amino acids are translocated from the shoot to the roots through the phloem (Pate et al., 1979; Layzell et al., 1981; Simpson, 1986; Stulen, 1986), also to the NO₃ free roots. The amount of amino acids transported to the NO₃ free roots is however very small (Lambers et al., 1982a). Hansen (1980) found diurnal variations in NO₃ concentrations in the root xylem in Lolium; concentrations in the light being higher than in the dark.

Discussion: Transport of nitrate and amino acids through the xylem

The amount of NO₃ and amino acids transported through the xylem depends on the transpiration rate. This is the result of the assumption of a linear relationship in the model between the rate of transport of NO₃ and amino acids and the transpiration rate. Such a linear relationship, however, does apparently not exist in reality (Clarkson, 1974; Simpson et al., 1982). A more adequate formulation for the rate of transport of NO₃ and amino acids has to be found. To
improve the model more information on the relationships between N\textsubscript{03} concentration in the root tissues, N\textsubscript{03} concentration in the xylem sap and transpiration rate is needed.
3.15 Formation of structural carbon compounds

Model graphs (Fig 50a, 50b and 50c)

The rate of formation of structural C compounds from soluble C is expressed in gC/g/h. Diurnal fluctuations in this rate were found for the various plant parts of the +N03 plants [A] and the +/-N03 plants [B]. An increase was found in the light period and a decrease in the dark period. In the -N03 plants [C] fluctuations diminished or disappeared completely.

- Mature and growing shoot parts (Figs 50a, 50b)

In the +N03 situations (+N03 plants and +/-N03 plants), the rate of formation of structural C compounds decreases during the dark period and increases after the start of the light period. In the growing shoot parts the increase continues throughout the light period, but in the mature shoot parts of the A plants the rate of formation decreases again in the course of the light period. Fluctuations were most pronounced in the A plants. In the mature shoot parts, the daily maximum value in the B plants was 64.8% of that in the A plants, and the daily minimum in the A plants was only 9.6% of that in the B plants at day ten. In the C plants, the rate of formation of structural C compounds decreases during the simulated period and reaches 50% of that in the A plants on the third day. In the growing shoot parts, daily maximum values are practically identical in the A and B plants, while the daily minimum value in the A plants was at day ten only 4.6% of that in the B plants. Hence the rates in the B plants are more stable and, on average, higher. In the -N03 plants [C], the rate of formation after fluctuating for two-three days decreases nearly continuously in the course of the simulated period. In the growing shoot parts, the rate of formation in the C plants at day ten was only 35.6% of that of the daily maximum in the A plants at the end of the light period.
The rate of formation of structural C compounds increases with a decrease in $\text{NO}_3$ supply (A, B and C situation, respectively). The highest rates are found therefore in the C plants (though a marked decrease is apparent after day eight), followed by the B and the A plants. In the A and B plants daily fluctuations continue throughout the simulated period. The rate of formation increases in the light and decreases in the dark. At day ten, the maximum and minimum values are 5.5% and 94.5% lower, respectively, in the roots of the A plants than in the $+\text{NO}_3$ roots of the B plants. For the $-\text{NO}_3$ roots of the B plants this was 6.6% and 95.7%, respectively. At the end of the light period of day ten, the rate of formation in the C plants was 11.1% lower than in the A plants.

Model explanation

Daily fluctuations in the rate of formation of structural C compounds and the amplitude of these fluctuations are predominantly governed by the daily fluctuations in soluble C concentration. The rate of formation is progressively inhibited when the concentration of structural C compounds increases above a threshold value. This feedback mechanism has an influence throughout the simulated period in the shoot.

- Mature and growing shoot parts (Figs 50a and 50b).

In both the growing and mature shoot parts, there is an inhibition in the rate of formation of structural C compounds, due to the high concentration of structural C compounds (feedback mechanism). These are highest in the mature shoot parts. The concentration of structural C compounds is higher in the C plants than in the B plants and lower in the A plants. This causes an increasing inhibition in the rate of formation of structural C compounds from A to B and C plants. Diurnal fluctuations in the rate of formation in the B plants are caused by the fluctuating concentrations of soluble C. The increase in daily maximum and minimum value in the mature
shoot parts after day six is due to a decreased inhibition by the feedback mechanism.

- Roots (Fig 50c)

The rate of formation of structural C compounds in the roots of the B and C plants is higher than in the roots of the A plants, due to higher soluble C concentrations. In the C plants, the negative feedback mechanism becomes operative only after day eight. Because of the smaller reduction in growth in the roots compared to the shoots under nitrogen shortage, the concentration of structural C compounds in the roots will increase slower than in the shoots. The inhibition in formation of structural C compounds is therefore less in the roots than in the shoots.

Reality

Cell wall formation predominantly occurs in the extension zones of the plants. Cellulose (structural carbon in the model) is the principal constituent of cell wall and vascular tissue. During the development of the cell, the morphology and composition of the cell wall changes. These changes are governed by of the protoplast. It is also well known that under influence of environmental conditions cell walls may vary in thickness and probably also in composition. Fluctuations in rate of leaf elongation during the day, are well-documented. Under nitrogen shortage, the elongation rate is reduced (Birkby, K, cited by Monteith and Elston, 1983; own observations).

Discussion

The large fluctuations in the rate of formation of structural C compounds are found in the A plants do not seem entirely realistic, although fluctuations can be expected. A higher rate of formation means the formation of thicker cell walls, which occurs in the roots of the B and C plants. In the mature shoot parts of these plants,
thinner cell walls are formed than in the A plants. Influence of the nitrogen status of the plants on the structure, thickness and/or composition of the cell walls of the roots and the shoots can be expected. With high nitrogen supply more carbohydrates are used in processes in which nitrogen is taken up and assimilated, less carbohydrates remain for cell thickening. Frequent measurements of structural C concentration and composition of the cell walls are needed for comparison with the model results.
3.16 Formation of amino acids from N\textsubscript{03}

Model graphs (Fig 51)

Formation of amino acids from NO\textsubscript{3} is expressed as gN/g/h (on basis of fresh weight). A diurnal rhythm is found in all +NO\textsubscript{3} situations (+NO\textsubscript{3} plants [A] and the mature shoot parts and the +NO\textsubscript{3} roots of the +/-NO\textsubscript{3} plants [B]).

- Mature shoot parts (Fig 51a)

In these plant parts amino acids are formed from NO\textsubscript{3} only during the light period. The rate of formation increases and decreases sharply after transition from light to dark and inversely. During the light period the rate of formation is essentially constant. The decrease during the light period was only 4.1% in the A plants and 51% in the B plants at day nine. The daily maximum rate of formation in the +/-NO\textsubscript{3} plants first decreases in the course of the simulation, and is 22.7% lower than in the A plants at day four. Subsequently it increases again to reach a value, 8.4% lower than that in the A plants, at the end of the light period at day ten. In the -NO\textsubscript{3} plants amino acid formation from NO\textsubscript{3} ceased within five days.

- Roots (Fig 51b)

In the roots of the A plants the rate of formation increases sharply during the first hour of the light period and continues to increase throughout this period. After the start of the dark period, there is first an increase during three hours after which a sharp decrease follows during the remainder of this period. (A daily maximum was found in the dark period.) In the +NO\textsubscript{3} roots of the B plants the rate of formation increases throughout the dark period and decreases after the start of the light period for about five hours to reach a more or less constant level. The daily maximum value in the roots of the A plants is 12.6% lower than that in the roots of the B
plants at day ten.
In the -NO3 roots of the B plants and in the roots of the C plants amino acid formation decreases to 50% of that of the roots the A plants within one day, and reaches the 5% level at the second day.

Model explanation (Fig 51)

- Mature shoot parts. (Fig 51a)

The diurnal rhythm in rate of amino acid formation from NO3 in these plant parts is predominantly due to its dependence on light intensity. It is assumed in the model that in the dark, no formation can take place. Due to the distinct sharp diurnal fluctuations in soluble C concentration in the A plants, the rate of formation is limited by sugar availability only during the first two hours after the start of the light period. After that, the rate of formation is governed by the NO3 concentration. In the +/-NO3 plants, the NO3 concentration governs amino acid formation throughout the light period, from four days after the start of the simulated period. Availability of soluble C is not limiting. Due to a decrease in NO3 concentration during the light period, the rate of formation decreases slightly in the A and B plants during that time. The fluctuations in daily maximum value in the +/-NO3 plants are due to parallel fluctuations in NO3 concentration. The lower rate of formation in the B plants compared with the A plants is due to a lower NO3 concentration. Thus, the NO3 concentration plays an important role in the rate of amino acid formation in the shoots. When NO3 is withheld from the nutrient solution at the start of the simulated period (C plants and -NO3 roots of the B plants, amino acid formation declines to zero.

- Roots. (Fig 51b)

The sharp increase in rate of formation during first hour of the light period, in the roots of the A plants, is caused by a sharp increase in soluble C concentration. During the remainder of that
period, NO3 concentration governs the rate of amino acid formation. The increase after the start of the dark period is the result of increase in NO3 concentration, caused by reduced NO3 transport to the shoot. The subsequent decrease in rate of formation to very low values at the end of the dark period, is due to a decrease in soluble C concentration. In the +NO3 roots of the B plants, availability of soluble C never limits the rate of formation of amino acids. Fluctuations are always due to fluctuations in NO3 concentration. A higher rate of formation in the +NO3 roots of the B plants, compared with roots of the A plants, is due to a higher NO3 concentration in these plant parts. It is obvious that the decrease of the in rate of formation in the -NO3 roots of the B plants and in the roots of the C plants (-NO3 plants) is due to the lower NO3 availability. Hence, the relative high soluble C concentration in the +NO3 roots of the B plants causes the rate of amino acid formation to be always governed by the NO3 concentration. In the A plants on the other hand the large fluctuations in soluble C concentration lead to a situation where during part of the day the rate of amino acid formation is governed by availability of soluble C.

Reality

It is well documented that light (intensity) influences the rate NO3 reduction in leaves (Beevers et al., 1965; Abrol et al., 1983). Pearson et al. (1981), found for maize roots a lower reduction of NO3 during the dark period. Diurnal patterns in reduction rate in leaves were described in some detail by Stulen and Bosgraaf (1985) for tomatoes and by Steingröver (1986) for spinach. Nitrate reduction increased in the light and decreased in the dark. According to Stanford (1984, cited by Schulze et al. 1985), the rate of formation of amino acid is higher in the light than in the dark. In the roots, NADH could be important in controlling the rate of NO3 reduction (Stulen, 1986). The general opinion is that availability of carbohydrates is not rate-limiting for NO3 reduction under normal conditions. Hansen (1980) found oscillations in NRA (Nitrate
Reductase Activity) in tops and supposed a connection with NO3 uptake.

Discussion

The diurnal fluctuations in rate of amino acid formation from NO3 in the shoots are in agreement with literature data (Hansen, 1980; Stulen and Bosgraaf, 1985; Schulze et al. 1985). Higher rates of formation were reported during the light period than during the dark period.

For roots less data are available. The absence however of a direct dependence of NRA in the roots on light intensity, (Abrol at al., 1983), suggests less fluctuating rates of NO3 reduction and amino acid formation in the roots. The large fluctuations in rate of formation found in our model reflects therefore probably too large fluctuations in soluble C concentration in the roots. Under standard conditions, soluble C is probably not ratelimiting, or only at the end of the dark period. Data on daily fluctuations in NO3 reduction rates in shoots and roots under different conditions are needed to improve the model descriptions or provide data for model validation.
3.17 Formation of structural nitrogen compounds from amino acids.

Model graphs (Fig 52)

The rate of formation of structural N compounds is expressed in gN/g/h (on basis of fresh weight). Diurnal fluctuations are found in A (+N03) and B (+/-N03) plants in all plant parts (growing and mature shoot parts and roots). In the -N03 [C] plants, a daily fluctuation disappeared during the simulated period.

- Mature shoot parts (Fig 52a)

In the A and B plants, the rate of formation increases during the light period and decreases during the dark period. In the A plants, there is a sharp increase in the first hour of the light period and a fast decrease at the end of the dark period. During the first five light periods the rate of formation is clearly highest in the A plants. The difference in daily maximum value between A and B plants decreased in the course of the simulation. At day ten, the daily maximum value in the A plants is 6% higher, the daily minimum 81% lower than that in the B plants. After four days, diurnal fluctuations in the C plants have nearly disappeared. The formation rate in the C plants diminished during the simulated period and was at day ten 67.7% of the maximum value of the A plants.

- Growing shoot parts (Fig 52b)

In the A and B plants, the rate of formation of structural N compounds increases for some time (3-4 h) after the start of the light period. Subsequently the rate of formation decreases in the A plants. In the B plants, a period of constant formation rate is found before it decreases. In the dark, the rate of formation decreases both in the A and B plants interrupted by a period of a constant rate of formation (which does not coincide in the A and B plants). Differences in daily maximum values between the A and B
plants decreases in the course of the simulated period. The difference in rate of formation between the maximum and the minimum value for the B plants was 42.2% at day nine.

In the C plants, the rate of formation at the end of the light period of day ten was only 38.1% of that in the A plants.

- Roots (Fig 52c)

Diurnal fluctuations in the roots varied more among the different treatments, than in the shoot parts. The rate of formation is higher in the +N03 roots of the B plants than in the roots of the A plants. In the A plants, the rate of formation shows a fast increase immediately after the start of the light period then a short decrease (by which a peak is formed) and then an increase again. In the B plants, an initial decrease after the start of the light period is followed by a slow increase. The rate of formation in the roots of the B plants increases throughout the dark period, while in the A plants it decreases sharply after an initial increase. The minimum difference between A and B plants occurs at the end of the light period when the rate of formation in the B plants is 8.4% higher than in the A plants, at day ten. At the end of the dark period, the daily maximum values are reached in the B plants, whereas in the A plants the daily minimum is reached. The daily maximum in the A plants was also found in the dark period.

In the -N03 roots of the B plants, the rate of formation increases sharply after the start of the light period, soon reaches a maximum, and then decreases until the end of the dark period. The increase became less steep during the simulated period. The rate of formation at the end of the light period at day ten was 48.8% lower than in the A plants at that time.

In the C plants, daily fluctuations decreased in the course of the simulated period. At the end of the light period of day ten, the rate of formation was 27.6% of that in the roots of the A plants.

Model explanation

- Mature and growing shoot parts (Fig 52a and 52b)
Following the start of the light period, the soluble C concentration is no longer the rate-limiting factor in the formation of structural N compounds in the A plants. From that moment until a few hours before the end of the dark period, the amino acid concentration governs the rate of formation. During the last 2-4 h of the dark period, soluble C supply is limiting. In the B and C plants, the rate of formation is always limited by the concentration of amino acids, i.e. fluctuations in that concentration determine the fluctuations in rate of formation of structural N compounds. Soluble C supply is never limiting because of the relatively high soluble C concentration in comparison with the A plants. The continuous low rate of formation in the C plants, is due to the low amino acid concentration.

- Formation in the roots. (Fig 52c)

Following the start of the light period, the soluble C concentration increases sharply in the roots of the A plants, and the rate of formation of structural N compounds is governed by the amino acid concentration until about the middle of the following dark period. The very low rates of formation if structural N compounds in the second half of the dark period are the result of the very low soluble C concentrations. In the roots of the B and C plants, formation of structural N compounds and its daily fluctuations are always governed by the amino acid concentration.

Reality

Relationships between amino acid concentration and rate of formation of structural N compounds is not well known from literature. It is well documented, that under carbohydrate shortage (low light intensities), structural N formation can decrease and growth limited (Challa 1976).

Discussion

Daily variations in rate of structural N formation have not been
reported. Variations may occur as a consequence of diurnal fluctuations in carbohydrate supply. In the model the decrease in structural N compounds in the C plants is too slow in comparison with experiments on maize (Spek, 1984a and 1984b). There is need for a better understanding of relationships between amino acid concentration, concentration of structural N compounds and formation of structural N compounds under different conditions. Measurements during several days could provide data for a better description of formation of structural N compounds.
3.18 Degradation of structural nitrogen compounds

The rate of degradation is expressed as gN/g/h (on basis of fresh weight per plant part). Daily fluctuations in rate of degradation are found in the growing shoot parts of the +NO3 plants [A] and the +/-NO3 plants [B]. Hardly any fluctuations are found in the other plant parts. In the -NO3 plants, no fluctuations at all are found.

Model graphs

- Mature shoot parts (Fig 53a)

Hardly any fluctuations are found. The rates of degradation were generally highest in the A plants, but they differed only 6.1% with those the B plants before the dark period of day five and 2.6% before the dark period of day ten (A>B).

In the C plants, the rate of degradation decreased continuously in the course of the simulated period and was 58% of that in the A plants before the start of the dark period of day ten.

- Growing shoot parts (Fig 53b)

In the A and B plants diurnal fluctuations were found. The rate of degradation of structural N compounds increased after the start of the light period for about 7-9 hours and then decreased until the end of the dark period. The rate of degradation in the B plants at the end of the light period of day ten was 2.5% lower than that in the A plants. In the -NO3 plants, the rate of degradation decreased in the course of the whole simulated period and was 19.4% lower than that in the A plants at the end of the light period of day ten. The maximum value for the B plants was 6.2% lower than for the A plants at day ten.
SOR1C = CSORC * SOFWT * R1SKF * DIM(SOCOCT, R1COC)
SOR1AL = BOUND(0., 1., -1.+20000.*SOCOCT) * CALSOR * SOFWT * SOCOAT * ...
R1SKF * SO1ALR
SOR1AU = AMIN1(SOR1C * R1PAA / R1PHC, R1PAA * 80.)
SOR2C = CSORC * SOFWT * R2SKF * DIM(SOCOCT, R2COC)
SOR2AL = BOUND(0., 1., -1.+20000.*SOCOCT) * CALSOR * SOFWT * SOCOAT * ...
R2SKF * SO2ALR
SOR2AU = AMIN1(SOR2C * R2PAA / R2PHC, R2PAA * 80.)
SOSYC = CSOSYC * SOFWT * SYSKF * DIM(SOCOCT, SYCOC)
SOSYAL = BOUND(0., 1., -1.+20000.*SOCOCT) * CALSOY * SOFWT * SOCOAT * ...
SYSKF * SOYALR
SOSYAU = AMIN1(SOSYC * SYPAA / SYPHC, SYPAA * 80.)

R1NAA = RNAAM * R1FWT * AMIN1(R1NLIM, R1CLIM, R1AAFB)
R2NAA = RNAAM * R2FWT * AMIN1(R2NLIM, R2CLIM, R2AAFB)
SONAA = SONAAAM * SOFWT * AMIN1(SONLIM, SOCLIM, SOLIM, SOAAFB)

R1AASN = RASNM * R1FWT * AMIN1(R1CLIM, R1ALIM)
R2AASN = RASNM * R2FWT * AMIN1(R2CLIM, R2ALIM)
SOAASN = SOASNM * SOFWT * AMIN1(SOCLIM, SOALIM)
SYAASN = SYASNM * SYFWT * AMIN1(SYCLIM, SYALIM)

R1SNAA = R1SN * RCSNA
R2SNAA = R2SN * RCSNA
SOSNAA = SOSN * SOCSNA
SYSNAA = SYSN * SYCSNA

R1CAA = R1NAA * 3.2
R2CAA = R2NAA * 3.2
SOCAA = SONAA * 3.2

R1CSC = RCSCM * R1FWT * R1CLIM * R1SCFB
R2CSC = RCSCM * R2FWT * R2CLIM * R2SCFB
SOCSC = SOCSCM * SOFWT * SOCLIM * SOSCFB
SYCSC = SYSCSM * SYFWT * SYCLIM * SYSCFB
LEFF = \text{-LIGHT/60.}
R1RSPI = BOUND(0.,1.,1.+20000.*R1COC)*R1DM/3750.
R2RSPI = BOUND(0.,1.,1.+20000.*R2COC)*R2DM/3750.
SORSPI = BOUND(0.,1.,1.+20000.*SOCOC)*SODM/3750.
SYRSPI = BOUND(0.,1.,1.+20000.*SYCOC)*SYDM/3750.

R1RSPT = M1R1N*.99 + R1SOAA*.067 + R1SON*.04
R2RSPT = M2R2N*.99 + R2SOAA*.067 + R2SON*.04
SORSPT = (R1SON + R2SON) *.04 + (SOR1C + SOR2C + SOSYC) *.053 + ...
(R1SOAA + R2SOAA + SOR1AL + SOR2AL + SOSYAL) *.067
SYRSPT = 0.

R1RSPB = R1NAA*1.44 + R1CSC*.12 + R1AASN*1.28
R2RSPB = R2NAA*1.44 + R2CSC*.12 + R2AASN*1.28
SORSPT = LEFF*(SONAA*1.44 + SOCSC*.12) + SOAASN*1.28
SYRSPB = SYCSC*.12 + SYAASN*1.28

R1RESP = R1RSPB + R1RSPT + R1RSPI
R2RESP = R2RSPB + R2RSPT + R2RSPI
SORESP = SORSPT + SORSPT + SORSPI
SYRESP = SYRSPB + SYRSP + SYRSP

CHR1N = M1R1N - R1SON - R1NAA
CHR2N = M2R2N - R2SON - R2NAA
CHSON = R1SON + R2SON - SONAA

CHR1AA = - R1SOAA + SOR1AU + R1NAA - R1AASN + R1SNAA
CHR2AA = - R2SOAA + SOR2AU + R2NAA - R2AASN + R2SNAA
CHSOAA = R1SOAA + R2SOAA - SOR1AL - SOR2AL - SOSYL + SONAA - SOAASN + SOSNAA + SYAAS
CHSYAA = + SOSYAU - SYAASN + SYSNAA - SYAAS

CHR1C = SOR1C - R1CAA - R1CSC - R1RESP
CHR2C = SOR2C - R2CAA - R2CSC - R2RESP
CHSOC = SOPHT - SOR1C - SOR2C - SOSYC - SOCAA - SOCSC - SORESP + SYCS
CHSYC = + SOSYC - SYCSC - SYRESP - SYCS
R1FWT = INTEG(R1FWTG, R1FWTI)
R2FWT = INTEG(R2FWTG, R2FWTI)
SYFWT = INTEG(SFWTG - SYFWTS, SYFWTI)

SOFWT = INTEG(SYWFT, SOFWTI)
M1N = INTEG(-M1R1N, M1NI)
M2N = INTEG(-M2R2N, M2NI)
R1N = INTEG(CHR1N, R1NI)
R2N = INTEG(CHR2N, R2NI)
SON = INTEG(CHSON, SONI)

R1AA = LIMINT(CHR1AA, R1AAI, 0, 1000000.)
R2AA = LIMINT(CHR2AA, R2AAI, 0, 1000000.)
SOAA = LIMINT(CHSOAA, SOAAI, 0, 1000000.)
SYAA = LIMINT(CHSYAA, SYAAI, 0, 1000000.)

SYPAA = INTEG(SOSYAL - SOSYAU, SYPAI)

R1PAA = INTEG(SOR1AL - SOR1AU, R1PAI)
R2PAA = INTEG(SOR2AL - SOR2AU, R2PAI)

R1SN = INTEG(R1AASN - R1SNAA, R1SNI)
R2SN = INTEG(R2AASN - R2SNAA, R2SNI)
SOSN = INTEG(SOAASN - SOSNAA + SYSNS, SOSNI)
SYSN = INTEG(SYAASN - SYSNAA - SYSNS, SYSNI)

R1C = INTEG(CHR1C, R1CI)
R2C = INTEG(CHR2C, R2CI)
SOC = INTEG(CHSOC, SOCI)
SYC = INTEG(CHSYC, SYCI)

R1SC = INTEG(R1CSC, R1SCI)
R2SC = INTEG(R2CSC, R2SCI)

SOSC = INTEG(SOCSC + SYSCS, SOSC)
SYSC = INTEG(SYSCSC - SYSCS, SYSCI)

END $ "OF DERIVATIVE"
In this region, the values are calculated at the end of each simulated hour.

\[ R_{1\text{DMP}} = \frac{R_{1\text{DM}}}{R_{1\text{FWT}}} \]
\[ S_{0\text{DMP}} = \frac{S_{\text{ODM}}}{S_{\text{OFWT}}} \]
\[ R_{2\text{DMP}} = \frac{R_{2\text{DM}}}{R_{2\text{FWT}}} \]
\[ S_{\text{YDMP}} = \frac{S_{\text{YDM}}}{S_{\text{YFWT}}} \]

\[ R_{1\text{CNR}} = \frac{(R_{1\text{SC}} + R_{1\text{C}} + R_{1\text{AA}} \times 3.2 + R_{1\text{SN}} \times 3.38)}{(R_{1N} + R_{1\text{AA}} + R_{1\text{SN}})} \]
\[ R_{2\text{CNR}} = \frac{(R_{2\text{SC}} + R_{2\text{C}} + R_{2\text{AA}} \times 3.2 + R_{2\text{SN}} \times 3.38)}{(R_{2N} + R_{2\text{AA}} + R_{2\text{SN}})} \]
\[ S_{\text{OCNR}} = \frac{(S_{\text{OSC}} + S_{\text{OC}} + S_{\text{OAA}} \times 3.2 + S_{\text{OSN}} \times 3.38)}{(S_{\text{ON}} + S_{\text{OAA}} + S_{\text{OSN}})} \]
\[ S_{\text{YCNR}} = \frac{(S_{\text{YSC}} + S_{\text{YC}} + S_{\text{YAA}} \times 3.2 + S_{\text{YSN}} \times 3.38)}{(S_{\text{YAA}} + S_{\text{YSN}})} \]

\[ R_{\text{FSWTR}} = \frac{R_{\text{FWT}}}{S_{\text{FWT}}} \]
\[ R_{\text{SDMR}} = \frac{R_{\text{DM}}}{S_{\text{DM}}} \]

TERMT(T .GE. FINTIM): To control, if it is time to transfer to the TERMINAL section.

END $ "OF DYNAMIC"

TERMINAL
CALL LOG
END $ "OF TERMINAL"

END $ "OF PROGRAM"

SET TITLE = "NMODEL"

Specified values in prepar list for tables and graphs:

PREPAR T , ...
        R1DM, R2DM, SODM, SYDM

SET FTSPLT = .T.

START
Specified values for graphs:

SET NXPPL=240, NGXPPL=40
PLOT "XLO"=0., "XHI"=240., R1DM, "LO"=0., "HI"=3.
PLOT "XLO"=0., "XHI"=240., R2DM, "LO"=0., "HI"=3.
PLOT "XLO"=0., "XHI"=240., SODM, "LO"=0., "HI"=30.
PLOT "XLO"=0., "XHI"=240., SYDM, "LO"=0., "HI"=3.

Frequency of time intervals for output data:

PRINT "NCIPRN"=1, "ALL"
STOP
8. MEANING OF USED ACSL OPERATORS

ACSL = Advanced Continuous Simulation Language

AMAX1:

\[ y = \text{AMAX1} (x_1, x_2, A, \ldots, x_n) \]

Y will be given the value of the maximum \( x_i \).

BOUND:

\[ y = \text{BOUND} (ll, ul, x) \]

\[ y = \begin{cases} 
ll, & x < ll \\
=, & ll \leq x \leq ul \\
ul, & x > ul 
\end{cases} \]

DIM:

\[ y = x_1 - x_2 \text{ if } x_1 > x_2 \]
\[ y = 0.0 \text{ otherwise} \]

INTEG (integration):

state = \text{INTEG} (deriv, ic)
\[ y = \text{LIMINT} (yd, ic, ll, ul) \]

state = a simple variable or subscripted array name with
a single integer CONSTANT subscript.
deriv = an arithmetic expression of arbitrary complexity.
ic = a simple non-subscripted variable, a real constant
or a general expression enclosed in parenthesis.
yd = an expression for the derivative
ic = \( y(0) \) may be omitted if zero

ll = lower limit on y
ul = upper limit on y
### 9. Alphabetical List of Abbreviations in Program

Remarks: 1) abbreviations in text:
- \( n = 1 \) or \( n = 2 \) (refers to separate root halves)
- \( K_m \) value = Michaelis-Menten constant
- \( gC \) = grams Carbon
- \( gN \) = grams Nitrogen

2) The abbreviations that indicate "constants" refer to constants on the basis of fresh weight.

3) The abbreviations that indicate "amounts", "areas", "volumes" or "weights" refer to values per individual plant.

---

**CALR** = Constant, used in calculating Amino acid Loading, Realisation

**CALSOR** = Constant, value for Amino acid Loading, for transport from Shoot Old to Roots

**CALSOY** = Constant value for Amino acid Loading, for transport from Shoot Old to Shoot Young

**CHRnAA** = rate of Change, by transport and chemical conversions, in Roots\((n)\) in amount of Amino Acids

**CHRnC** = rate of Change, by transport and chemical conversions, in Roots\((n)\) in amount of soluble Carbohydrates

**CHRnN** = rate of Change, by uptake, transport and chemical conversions, in Roots\((n)\) in amount of Nitrate

**CHSOAA** = rate of Change, by transport and chemical conversions, in Shoot Old in amount of Amino Acids

**CHSOC** = rate of Change, by photosynthesis, transport and chemical conversions, in Shoot Old in amount of soluble Carbohydrates
CHSON = rate of CHange, by transport and chemical conversions, 
in Shoot Old in amount of Nitrate .................... gN/h
CHSYAA = rate of CHange, by transport and chemical conversions 
in Shoot Young in amount of Amino Acids ............ gN/h
CHSYC = rate of CHange, by transport and chemical conversions, 
in Shoot Young in amount of soluble Carbohydrates .... gC/h
CMALR = Constant, Multiplying factor for Amino acid 
Loading, Realisation ................................... g/gN
CSORC = Constant value for transport from Shoot Old to 
Roots of soluble Carbohydrates .................... 1/h
CSOSYC = Constant value for transport from Shoot Old to 
Shoot Young of soluble Carbohydrates ............. 1/h

- L -

LA = Leaf Area .............................................. m²
LEFF = Light intensity EFFECT .............................. (-)
LIGHT = LIGHT intensity .................................... W/m²

- M -

MCONMI = Medium, Concentration of Nitrate, Minimum value ...... gN/g
MnCON = Medium(n), Concentration of Nitrate ............... gN/g
MnN = Medium(n), amount of Nitrate ....................... gN
MnNI = Medium(n), amount of Nitrate, Initial value ....... gN
MnNLIM = Medium(n), concentration of Nitrate, Limitation .... (-) 
(concerning uptake)
MnVOL = Medium(n), Volume ............................. cm³ = g
MnRnN = Medium(n) to Roots(n), Nitrate transport ........ gN/h

- P -

PHOCFB = PHotosynthesis, concentration of soluble 
Carbohydrates, Feedback ............................. (-)
PHOTM = PHOTosynthesis, Maximum value .................... gC/m2/h

- R -

RAAI = Roots, amount of Amino Acids, Initial value ............ gN
RASNM = Roots, Amino acids to Structural Nitrogen,
        Maximum value ...................................... gN/g/h
RCI = Roots, amount of soluble Carbohydrates,
      Initial value ........................................ gC
RCOAMI = Roots, Concentration of Amino acids, Minimum value ... gN/g
RCNMI = Roots, Concentration of Nitrate, Minimum value ....... gN/g
RCSCM = Roots, soluble Carbohydrates to Structural Carbon,
        Maximum value ...................................... gC/g/h
RCSNA = Roots, Constant value, Structural Nitrogen to
        Amino acids ........................................ 1/h
RFWT = Roots, total Fresh Weight (R1FWT + R2FWT) ............... g
RDM = Roots, total Dry Matter (R1DM + R2DM) ............... g
RFWTI = Roots, total Fresh Weight, Initial value ............ g
        (R1FWTI + R2FWTI)
RKMAA = Roots, Km-value for Amino Acids in realisations ...... gN/g
RKMC = Roots, Km-value for soluble Carbohydrates in
        realisations ........................................... gC/g
RKMN = Roots, Km-value for Nitrate in realisations .......... gN/g
RNAAM = Roots, Nitrate to Amino Acids, Maximum value ...... gN/g/h
RNI = Roots, amount of Nitrate, Initial value ................ gN
RPAAI = Roots, amount in Phloem of Amino Acids,
        Initial value ........................................ gN
RSCI = Roots, amount of Structural Carbon, Initial value ..... gC
RSDMR = Roots / Shoot, Dry Matter Ratio ..................... ( - )
RSFWTR = Roots / Shoot, Fresh Weight Ratio ................... ( - )
RSNI = Roots, amount of Structural Nitrogen, Initial value .... gN
RUPTM = Roots, UPTake rate, Maximum value .................... gN/g/h
RnAA = Roots(n), amount of Amino Acids ......................... gN
RnAAFB = Roots(n), Amino Acids, Feedback ...................... ( - )
RnAAI = Roots(n), amount of Amino Acids, Initial value ....... gN
RnAASN = Roots(n), Amino Acids to Structural Nitrogen ........ gN/h
RnAAWT = Roots(n), Amino Acids, Weight ....................... g
<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>RnALIM</td>
<td>Roots(n), content of Amino acids, LIMitation (in various processes)</td>
</tr>
<tr>
<td>RnC</td>
<td>Roots(n), amount of soluble Carbohydrates</td>
</tr>
<tr>
<td>RnCAA</td>
<td>Roots(n), soluble Carbohydrates, incorporation in Amino Acids</td>
</tr>
<tr>
<td>RnCC</td>
<td>Roots(n), weight of soluble Carbohydrates plus structural Carbon</td>
</tr>
<tr>
<td>RnCCS</td>
<td>Roots(n), RnCC plus weight of Structural nitrogen</td>
</tr>
<tr>
<td>RnCCSA</td>
<td>Roots(n), RnCCS weight of plus Amino acids</td>
</tr>
<tr>
<td>RnCCSX</td>
<td>Roots(n), RnCCS plus weight of nitrate</td>
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<tr>
<td>RnCI</td>
<td>Roots(n), amount of soluble Carbohydrates, Initial value</td>
</tr>
<tr>
<td>RnCLIM</td>
<td>Roots(n), concentration of soluble Carbohydrates, LIMitation (in various processes)</td>
</tr>
<tr>
<td>RnCNR</td>
<td>Roots(n), total Carbon / total Nitrogen, Ratio</td>
</tr>
<tr>
<td>RnCOAA</td>
<td>Roots(n), Concentration of Amino Acids</td>
</tr>
<tr>
<td>RnCOC</td>
<td>Roots(n), Concentration of soluble Carbohydrates</td>
</tr>
<tr>
<td>RnCON</td>
<td>Roots(n), Concentration of Nitrate</td>
</tr>
<tr>
<td>RnCOPA</td>
<td>Roots(n), Concentration of Phloem-Amino acids</td>
</tr>
<tr>
<td>RnCOSC</td>
<td>Roots(n), Concentration of Structural Carbon</td>
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<tr>
<td>RnCOSN</td>
<td>Roots(n), Concentration of Structural Nitrogen</td>
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<tr>
<td>RnCSC</td>
<td>Roots(n), amount of soluble Carbohydrates for Structural Carbon formation</td>
</tr>
<tr>
<td>RnCWT</td>
<td>Roots(n), soluble Carbohydrates, Weight</td>
</tr>
<tr>
<td>RnDM</td>
<td>Roots(n), Dry Matter</td>
</tr>
<tr>
<td>RnDMP</td>
<td>Roots(n), Dry Matter Percentage</td>
</tr>
<tr>
<td>RnFGCR</td>
<td>Roots(n), Fresh weight Growth in dependence on soluble Carbohydrates, Realisation</td>
</tr>
<tr>
<td>RnFCNR</td>
<td>Roots(n), Fresh weight Growth in dependence on structural Nitrogen, Realisation</td>
</tr>
<tr>
<td>RnFR</td>
<td>Roots(n), FRaction, for calculating:</td>
</tr>
<tr>
<td></td>
<td>a) initial weight of separated root parts with initial amounts of chemical substances.</td>
</tr>
<tr>
<td></td>
<td>b) medium volume with initial nitrate concentration</td>
</tr>
<tr>
<td>RnFWT</td>
<td>Roots(n), Fresh Weight</td>
</tr>
<tr>
<td>RnFWTG</td>
<td>Roots(n), Fresh Weight, Growth</td>
</tr>
<tr>
<td>Symbol</td>
<td>Description</td>
</tr>
<tr>
<td>--------</td>
<td>-------------</td>
</tr>
<tr>
<td>RnN</td>
<td>Roots(n), amount of Nitrate</td>
</tr>
<tr>
<td>RnNAA</td>
<td>Roots(n), Nitrate to Amino Acids</td>
</tr>
<tr>
<td>RnNFB</td>
<td>Roots(n), content of Nitrate, FeedBack</td>
</tr>
<tr>
<td>RnNI</td>
<td>Roots(n), amount of Nitrate, Initial value</td>
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<tr>
<td>RnNIGHT</td>
<td>Roots(n), amount of Nitrate, WeighT</td>
</tr>
<tr>
<td>RnPAA</td>
<td>Roots(n), amount of Phloem Amino Acids</td>
</tr>
<tr>
<td>RnPAAI</td>
<td>Roots(n), amount of Phloem Amino Acids, Initial value</td>
</tr>
<tr>
<td>RnPHC</td>
<td>Roots(n), PHloem, amount of soluble Carbohydrates</td>
</tr>
<tr>
<td>RnRESP</td>
<td>Roots(n), RESpiration, soluble carbohydrates for respiration processes</td>
</tr>
<tr>
<td>RnRSPB</td>
<td>Roots(n), RESpiration, soluble carbohydrates for Biochemical conversions</td>
</tr>
<tr>
<td>RnRSPI</td>
<td>Roots(n), RESpiration, soluble carbohydrates for maintenance of Ionic gradients</td>
</tr>
<tr>
<td>RnRSPT</td>
<td>Roots(n), RESpiration, soluble carbohydrates for Transport processes</td>
</tr>
<tr>
<td>RnSC</td>
<td>Roots(n), amount of Structural Carbon</td>
</tr>
<tr>
<td>RnSCFB</td>
<td>Roots(n), concentration of Structural Carbon, FeedBack</td>
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<tr>
<td>RnSCI</td>
<td>Roots(n), amount of Structural Carbon, Initial value</td>
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<tr>
<td>RnSCWT</td>
<td>Roots(n), Structural Carbon, WeighT</td>
</tr>
<tr>
<td>RnSN</td>
<td>Roots(n), amount of Structural Nitrogen</td>
</tr>
<tr>
<td>RnSKF</td>
<td>Roots(n), Sink Fraction</td>
</tr>
<tr>
<td>RnSNI</td>
<td>Roots(n), amount of Structural Nitrogen, Initial value</td>
</tr>
<tr>
<td>RnSNWT</td>
<td>Roots(n), Structural Nitrogen, WeighT</td>
</tr>
<tr>
<td>RnSNA</td>
<td>Roots(n), Structural Nitrogen to Amino Acids</td>
</tr>
<tr>
<td>RnSOAA</td>
<td>Roots(n) to Shoot Old, Amino Acids transport</td>
</tr>
<tr>
<td>RnSON</td>
<td>Roots(n) to Shoot Old, Nitrate transport</td>
</tr>
</tbody>
</table>

#NEWPAGE

SDM = Shoot Dry Matter (shoot young + shoot old) ............. g
Shoot, Fresh weight Growth, in dependence on soluble Carbohydrates, Realisation .................. ( - )
Shoot, Fresh weight Growth, in dependence on structural Nitrogen, Realisation .................. ( - )
Shoot, Fresh Weight (shoot young + shoot old) ........ g
Shoot, Fresh Weight Growth ................................ g/h
Specific Leaf Area, here defined as leaf area per unit of shoot fresh weight ...................... m²/g

Shoot Old, amount of Amino Acids ......................... gN
Shoot Old, amount of Amino Acids, Initial value ........ gN
Shoot Old, concentration of Amino Acids, Feedback ... ( - )
Shoot Old, Amino Acids to Structural Nitrogen ........ gN/h
Shoot Old, Amino Acids, Weight .......................... g
Shoot Old, Amino Acids, Limitation (in various processes) ................................ ( - )
Shoot Old, Amino acids to Structural Nitrogen, Maximum value ........................................ gN/g/h
Shoot Old, content of Amino acids, available for Transport, Maximum value ...................... gN/g
Shoot Old, amount of soluble Carbohydrates, incorporation in Amino Acids ....................... gC/h
Shoot Old, weight of soluble Carbohydrates ........... gC
Shoot Old, weight of soluble Carbohydrates plus structural Carbon ................................... g
Shoot Old, SOCC plus weight of Structural nitrogen ...... g
Shoot Old, SOCCS plus weight of Amino acids .......... g
Shoot Old, SOCCSA plus weight of nitrate .............. g
Shoot Old, SOCCX (X = amino acids + nitrate)

Shoot Old, amount of soluble Carbohydrates, Initial value ........................................ gC
Shoot Old, concentration of soluble Carbohydrate, Limitation (in various processes) ........... ( - )
Shoot Old, total Carbon / total Nitrogen, Ratio gC/gN
Shoot Old, Concentration of Amino Acids .............. gN/g
<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>SOCOAT</td>
<td>Shoot Old, Concentration of Amino Acids, available for Transport</td>
<td>gN/g</td>
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<tr>
<td>SOCOC</td>
<td>Shoot Old, Concentration of soluble Carbohydrates</td>
<td>gC/g</td>
</tr>
<tr>
<td>SOCOCT</td>
<td>Shoot Old, Concentration of soluble Carbohydrates, available for Transport</td>
<td>gC/g</td>
</tr>
<tr>
<td>SOCON</td>
<td>Shoot Old, Concentration of Nitrate</td>
<td>gN/g</td>
</tr>
<tr>
<td>SOCOON</td>
<td>Shoot Old, Concentration of Organic Nitrogen</td>
<td>gN/g</td>
</tr>
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<td>TRANSP</td>
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10. **BIBLIOGRAPHY**


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simulated growth of the part of the root system, which did not receive NO3, behaved like the growth of a whole root system deprived of NO3, whereas in the experimental plants root growth was reduced. For the improvement of the model, the transport mechanisms, as simulated, have to be improved. Moreover, a better knowledge of the time courses in real plant processes, experiments about balances between soluble carbohydrates and structural carbon as protein formation and degradation, in dependence of N availability, are desirable.