

MODELING THE PRODUCTIVITY OF AGRICULTURAL CROPS IN RESPONSE TO WATER AND NITROGEN AVAILABILITY

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Abstract

Interception of photosynthetical active radiation, water and nitrogen uptake are the most important processes governing crop growth and production. Each of these processes is handled in a general way, and based on experimental evidence the main features are depicted. Light interception by a crop canopy determines the potential growth rate, provided the water and nitrogen uptake rates are optimal. Reasons for yield reductions in response to water and nitrogen shortage are clarified.

During the growing period, the availability of growth factors can vary widely. Dynamic simulation models are a valuable tool in studying the quantitative aspects of crop growth processes. The way in which potential growth processes are modeled is presented. As water and nitrogen shortages put restrictions on the potential growth, these effects are modeled by their impact on relevant physiological processes.

Finally, attention is paid to the practical use of simulation models with respect to agricultural crop productivity.

Key words

Crop production models, water, nitrogen availability.

1. INTRODUCTION

Intensive agricultural production is faced with high costs of land and machinery and expensive input factors such as fertilizer application, diseases, insect and weed control. Decisions on crop husbandry practice

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are to be made against the background that only high yields make farming profitable under these conditions. Each individual action has to be paid back through an increased yield or by the prevention of a yield loss. One must comprehend the way by which final yields are brought about to manage a crop properly. Since a number of interacting processes are involved, the incorporation of a relevant knowledge on these processes into a dynamic model is most suited to obtain an integrated picture of crop growth and production.

When growth factors are optimally available, final crop yield is determined by the available radiant energy from the sun during the growth period. Even under conditions of high input agriculture, water and nitrogen stress may temporarily occur during the growing season, leading to yield levels substantially below the aimed potential ones. Data on obtained yields show variations as wide as 50 to nearly 100 % of the potential maximum level. This indicates poor management with respect to growth factors and/or the use of less suitable land.

With crop growth models it is possible to calculate the maximum dry matter production under optimal conditions on a certain field (Buringh et al., 1975). This information is important in order to estimate how far the water requirements of the crop can be met by the water storage in the soil and by the rainfall during the growing season. With respect to the nitrogen requirement of the crop the application rate is derived from the difference between optimal nitrogen content in the expected dry matter produced and the supply of nitrogen by the soil.

Secondly, models that calculate crop growth in water and/or nitrogen shortage conditions can update the available amounts of water and nitrogen in the soil at any moment during the growing season. Therefore, only one initial measurement is needed at the beginning of the growth period. Of course, this is a most valuable aid in the proper management of a crop.

2. FINAL YIELD AND AVAILABILITY OF GROWTH FACTORS

2.1. LIGHT INTERCEPTION AND BIOMASS PRODUCTION

According to Gallagher and Biscoe (1978) the crop growth rate can be expressed as the product of the intercepted photosynthetically active radiation (PAR) and a conversion efficiency. For the latter, a value of 2.2 g DM produced per MJ absorbed (PAR) is measured for cereals (Gallagher & Biscoe, 1978).

At each moment, the interception of radiation is determined by the leaf area. Growth of the leaves increases the leaf area which, in turn, promotes the growth rate of the leaves (positive feedback). This leads to an exponential growth until the crop canopy is closed. As long as the

soil cover is complete, nearly all radiation is intercepted and the growth rate of the crop becomes proportional to the radiation intensity. At the end of the growing period the leaf area is reduced due to senescence of the leaves. As a consequence, less radiation is absorbed and the growth rate decreases.

In view of these considerations it must be clear that the variation in leaf area during the growing season determines dry matter production under optimal growth conditions.

Water and nitrogen availability can influence the seasonal course of the leaf area. Shortage of one or both of these growth factors delays the rapid, early growth of leaves and consequently leads to a reduced leaf area. Not only the juvenile growth period is influenced but also senescence of older leaves is enhanced. These two events bring along a reduction of green leaf area duration, which is recognized as an important determinant of the yield.

2.2. YIELD AND WATER USE

As water becomes the main limiting factor for crop growth, crop productivity is most conveniently calculated from water use. The water use efficiency, defined as the amount of water transpired per kg dry matter produced, is a frequently used concept. For C₃ plants, its value ranges from 300 to 400 kg water/kg DM produced, whereas for C₄ plants this value is in the order of 150 to 200 kg water/kg DM.

Although the water use efficiency concept can also be used to approach final yield under optimal growth conditions, this concept is mostly invoked as a first approach of yield when dealing with dry matter production limited by soil water availability. The amount of water available to the crop is roughly estimated as the sum of the initial water storage in the soil profile and the expected precipitation during the growing season.

The realizable production is then calculated as the amount of available water divided by the water use efficiency. This approach is restricted to situations with a distinct water shortage and a predictable amount of rain.

2.3. YIELD AND NITROGEN AVAILABILITY

A clear understanding of the relations between nitrogen availability, nitrogen uptake by the crop and the economical yield which can be obtained, is given by experiments conducted with different nitrogen application rates in which yield and nitrogen uptake are determined. The most important characteristics of the processes involved can be depicted in a graph with three quadrants (De Wit, 1953; van Keulen & Van

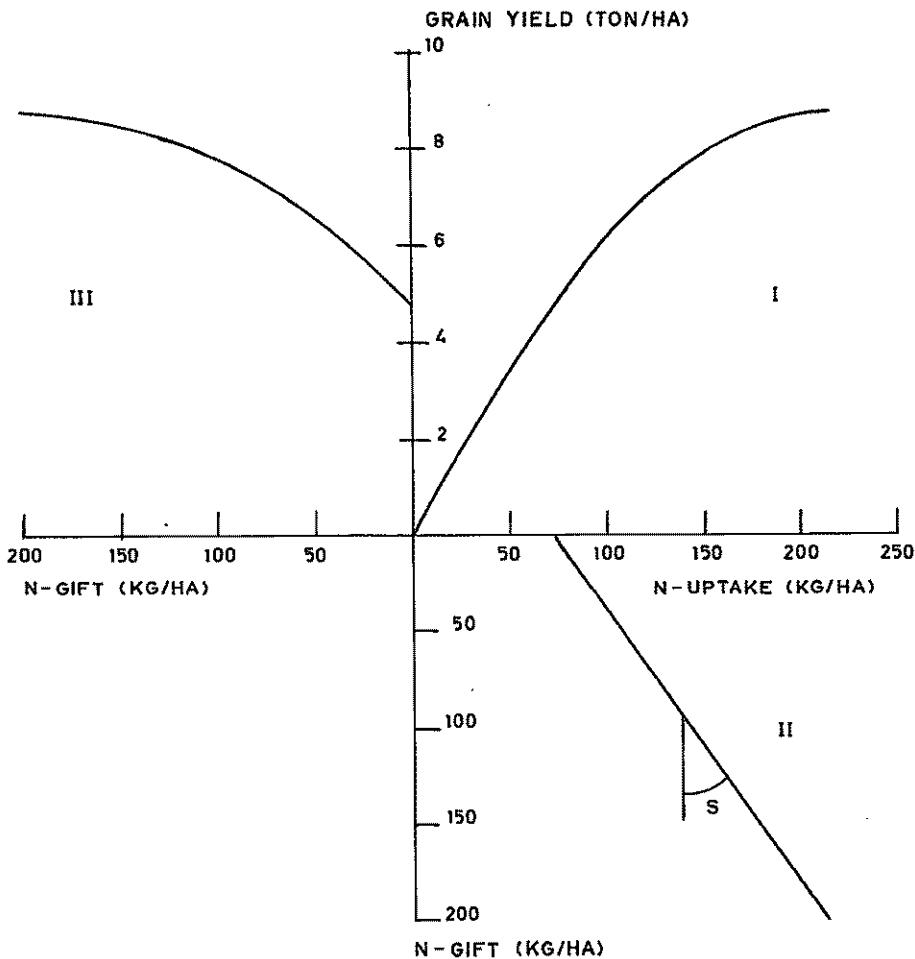


Fig. 1.

Three quadrant representation of experimental results of the effect of nitrogen application rates for cereals (The value s in quadrant II represents the recovery fraction of the fertilizer application).

Heemst, 1982). Following relations are hereby discussed (figure 1) : (i) yield versus N uptake (quadrant I); (ii) N application rate versus N uptake (quadrant II), and (iii) N application rate versus yield (quadrant III).

2.3.1. Yield versus N uptake

At high N uptake the dry matter production is no longer increasing with increasing nitrogen uptake, and an upper limit is reached. In circumstances of potential growth, dry matter is limited by the intercepted radiation. Whenever another factor, apart from light intensity, is

limiting, the production level becomes proportional to this factor. The response curve of yield to N absorbed goes through the origin. With cereals, grain production increases linearly at low values of N uptake. In this trajectory, N concentration in the plant is fixed at a minimum level. The N content of the plant tissue cannot be diluted any further, since the threshold value for growth is reached. For small cereal crops one finds a yield of about 70 kg grain for each kg N absorbed by the above-ground biomass (Van Keulen, 1977). Assuming a harvest index of 0.5 this corresponds to a N concentration of 1 % in the kernel and 0.4 % in the straw. This initial efficiency is crop specific and almost independent of growth circumstances (Van Keulen & Van Heemst, 1982). As the N uptake increases the N concentration in the kernel rises gradually. From the point of view of grain quality a minimum protein content is required, whereas high N contents are not valorized.

2.3.2. N application versus N uptake

When analyzing this quadrant, two important features are to be mentioned. The intercept of this curve with the horizontal axis represents the N absorbed from the unfertilized soil, while the slope of the straight line indicates the recovery fraction of N applied. Variation of the values of these two parameters are due to differences in soil characteristics such as organic matter content and soil structure, and to the soil water balance. The N uptake from the unfertilized soil is highly influenced by the amount and quality of the organic matter and the intensity of transformation processes, resulting in the release of mineral N. These processes are highly related to microbial activity in the soil as a result of (i) the amount and number of species of the soil microbial population, and (ii) the influence of the physical environment on their growth rate. The yearly net mineralization is highly variable from one place to another. The fraction of N applied absorbed by the crop within the year of application is also highly variable, mainly due to the type of nitrogen used (ammonium or nitrate N) and the way of application as well as the moisture content of the soil. Within a considerable range of N applications, the relation seems to be linear. Only at high application rates this linearity disappears because the capacity of the crop for any further N uptake seems to be insufficient.

The complement of the recovery fraction (that part of the N applied which is not taken up) does not necessarily mean a loss of N. This N may be fixed partly in the microbial biomass and can be released in another year, resulting in a higher N efficiency. However, soils with a yearly high N dressing, show a characteristic recovery of the N applied. There is only a slight influence of the crop rotation.

2.3.3. Yield response to N application

In this graph grain yield is directly related to nitrogen dressing. The curves obtained from different experiments hardly show a fixed pattern. By making the division into the quadrants I and II, one can reduce the variability between N application rate and yield found in different experiments.

2.3.4. Consistency of the relations

The given relations are only valid for situations where the nitrogen availability is more or less constant during the growing period. Under these conditions the N harvest index ranges from 0.74 to 0.82 (Spiertz, 1978; Campbell & Paul, 1978). The efficiency of nitrogen utilization by cereals, defined as the grain yield (kg) per unit (kg) nitrogen uptake, is well in relation with the N harvest index and the N concentration in the kernels. The latter is influenced by temperature and N availability, and amounts to almost 2 % for cereals grown under normal conditions. The consistency of the parameter values suggests a rather conservative system with respect to physiological, biological, chemical and soil physical processes which describe the competition for nitrogen between plant and soil microbial biomass. Considerable deviations from these relations can occur when the N availability differs strongly during the growing period. For instance, a poor N availability during tillering and stem elongation reduces the formation of shoots, causing a sparse crop.

Low water availability reduces N uptake, although relatively large amounts of mineral N can be present in the soil. This can occur even without any water stress symptoms. The available N can be situated in the upper dry soil layer, while water is withdrawn from deeper soil layers (Rehatta et al., 1979). Water stress during the grain filling period can stop crop growth. Due to accelerated senescence the crop dies while there is still a large amount of N in the leaves and the stems. This results in a low N use efficiency. Another kind of restrictions for which the given relations are not valid, are related to the N tolerance of the crop. This is strongly related to the lodging sensitivity of the crop. The N tolerance has increased by using modern semidwarf varieties and by the application of chemicals to reduce stem elongation. So, one can increase the nitrogen dressing which is necessary to realize high grain yields. Nevertheless, if the crop does lodge, the harvest index and grain yield can severely be reduced.

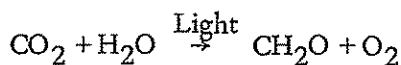
3. DYNAMIC MODELING OF GROWTH AND PRODUCTION

3.1. MODELING POTENTIAL GROWTH AND PRODUCTION

Under field conditions the climatological parameters are a given input

in relation to the growth of a crop. Water and nitrogen supply are manageable. In intensive cultivation systems it is possible to keep these two factors at an optimal level. Under these circumstances crop growth rate will be potential, provided the crop is kept free of diseases and weeds.

The process of photosynthesis is the first step in the production of dry matter :



The dynamic aspects of this process are first dealt with on the leaf level. The photosynthesis rate is limited by the radiant energy at low radiation levels, while at high radiation levels the process becomes substrate-(CO₂)-limited. A typical representation of the relation between radiation and the gross photosynthesis rate for a single leaf is shown in figure 2. The maximum efficiency at low radiation intensities is an important characteristic. For C₃ plants its value is about 8 10⁻⁹ kg CO₂ J⁻¹. At high radiation intensities (light saturation) the relation approaches a maximum value (asymptotically). The limiting factor is the rate at which CO₂ flows from the air to the photosynthesizing enzymes. For young leaves of C₃ plants the gross photosynthesis rate at light saturation is about 25 to 40 kg CO₂ ha⁻¹ h⁻¹.

Within a crop, leaves of distinct leaf layers show a typical range of orientation with respect to the direction of the sun rays.

Geometrical leaf orientation models enable us to differentiate the leaf surface into classes of equal irradiation intensity. The gross photosynthesis rate of a crop can be calculated as the sum of the individual gross photosynthesis rates of the distinct irradiation intensity classes. This procedure allows us to calculate the gross photosynthesis rate of a crop for each day of the year on condition that the irradiation intensity is known. Calculations are to be done for clear and overcast sky. For the same irradiation intensity on a horizontal surface, the distribution and interception of radiation in a crop canopy is different for direct (clear sky) and diffuse light (overcast sky). Figure 3 shows calculated values

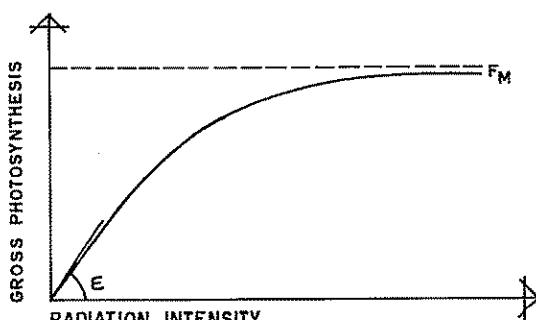


Fig. 2.
Gross photosynthesis rate as a function of radiation intensity for a single leaf (F_M is the maximum photosynthesis rate at light saturation; ϵ represents the initial light use efficiency).

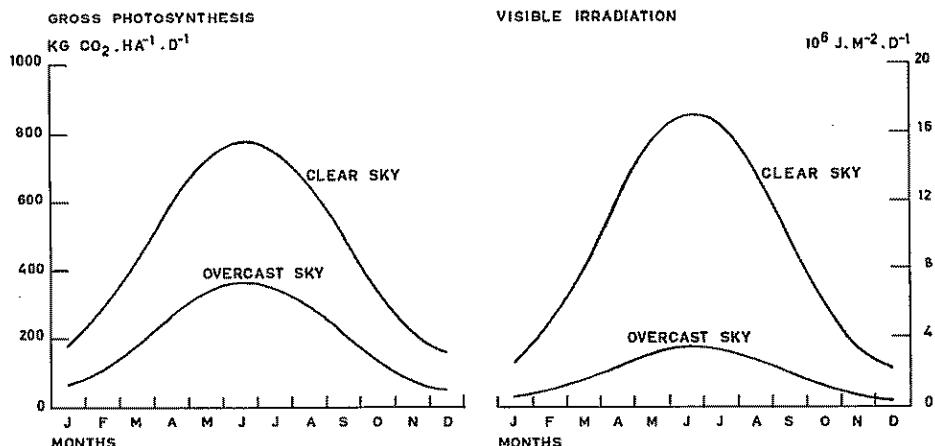


Fig. 3.

Yearly course of calculated gross photosynthesis and visible irradiation at a northern latitude of 50°, for a clear and overcast sky (procedure of Goudriaan & Van Laar, 1978). A closed canopy is considered with a leaf area of 5. The maximum photosynthesis rate of the individual leaves is taken at $30 \text{ kg CO}_2 \cdot \text{ha}^{-1} \cdot \text{h}^{-1}$; the initial light use efficiency used is $8 \cdot 10^{-9} \text{ kg CO}_2 \cdot \text{J}^{-1}$.

of the gross photosynthesis for a northern latitude of 50 degrees, for clear and overcast sky. The maximum leaf photosynthesis rate (at light saturation) is kept equal to $30 \text{ kg CO}_2 \text{ ha}^{-1} \text{ h}^{-1}$. A closed canopy is considered with a leaf area index equal to 5 (m^2 leaf area per m^2 soil surface, LAI).

If the soil cover is incomplete ($\text{LAI} < 5$) the incoming solar radiation is intercepted partially. A good estimate of the fraction of intercepted radiation is given by the following expression :

$$1 - e^{-k \text{LAI}}$$

A value of 0.6 can be assumed for the extinction coefficient k . The gross photosynthesis rate for conditions of incomplete soil cover can be calculated using the same fraction.

In many cases a day is partially clouded. Therefore, the fraction of time that the sky is overcast (f_{ov}) has to be calculated. This can be done in the following manner. The value of f_{ov} is set to zero if the measured irradiation (S) for the day considered equals the theoretically calculated irradiation for a clear sky (S_c). If the measured irradiation equals the theoretically calculated value for overcast sky (S_o , with $S_o = 0.2 S_c$), the value of f_{ov} is set to 1. For intermediate values of S , f_{ov} is interpolated linearly :

$$f_{\text{ov}} = 1 - \frac{S - S_o}{S_c - S_o}$$

The gross photosynthesis rates on clear (Pc) and overcast (Po) skies are used to calculate the gross photosynthesis rate (Pg) of an arbitrary day, in combination with the value of f_{ov} :

$$Pg = (1 - f_{ov}) \text{Pc} + f_{ov} \text{Po}$$

Gross carbohydrate production rate is calculated by multiplying Pg by 30/44. A net amount of carbohydrates (Pn), equal to the difference between gross carbohydrate production and maintenance respiration (R), is used for the growth of the different plant organs. Maintenance respiration can be calculated from the amount of biomass (W) already produced (Penning de Vries, 1975) : $R = 0.015 W$. Finally, the amount of carbohydrates is expressed as : $Pn = \frac{30}{44} Pg - R$.

In plants, synthesis of different biochemical components starts from the glucose molecule. A growth efficiency factor, giving the weight of dry matter produced per unit weight of glucose, is introduced to convert net carbohydrate production into dry matter accumulation. As an average a value of 0.7 is acceptable (Penning de Vries, 1975).

The potential growth rate can thus be written as (De Wit et al., 1978) :

$$\frac{dW}{dt} = 0.7 \left(Pg \frac{30}{44} - 0.015 W \right)$$

In a crop growth model this equation is integrated over the growing period. With respect to the partitioning of dry matter over different plant organs, a calculated development stage can be used.

3.2. MODELING GROWTH AND PRODUCTION AS INFLUENCED BY WATER SHORTAGE

Assimilation of CO₂ and loss of water (transpiration) takes place through stomatal openings. This explains the relation found between dry matter production and water use by the crop. Total water use includes transpiration and evaporation of water directly from the soil surface (= evapotranspiration). Under conditions of incomplete soil cover this latter process can play an important role. Dry matter production can therefore be best related to the water use by the crop and not to the evapotranspiration. In many simulation models the growth rate is reduced proportionally to the relative transpiration, being the ratio of actual to potential transpiration. Based on the energy balance method, potential transpiration (T_{pot}) can be calculated (Penman, 1948).

Actual transpiration (T_{act}) depends on the soil water uptake rate by the plant root system (U). In models the soil profile is divided into a number of compartments. Water uptake rate in each compartment (U_i) depends on (i) the available amount of water, and (ii) the density and

activity of the roots. When the soil dries out the water availability diminishes and a reduction factor (RF) can be introduced to account for this effect. There are many ways to divide T_{pot} over the different compartments. Assuming that the fraction TF_i of T_{pot} to be extracted from each compartment is known, the water uptake from each compartment (index i) can be written as : $U_i = (TF_i \cdot T_{pot}) RF_i$. The total water uptake rate is then :

$$U = \sum_{i=1}^{i=n} U_i$$

with n the number of compartments in the root zone.

To account for the effect of the difference between actual (supply) and potential transpiration (demand) on the growth rate of the crop, the factor T_{act}/T_{pot} can be used. In this case, the growth rate can be expressed as :

$$\frac{dW}{dt} = 0.7 \left(\frac{T_{act}}{T_{pot}} Pg \frac{30}{44} - 0.015 W \right)$$

3.3. MODELING GROWTH AND PRODUCTION AS INFLUENCED BY NITROGEN SHORTAGE

Crop growth models which attempt to simulate growth under N stress include variables which express the N content of the plant organs. Shortage of N influences the physiological processes which are involved in growth. In such models some values of physiological parameters are

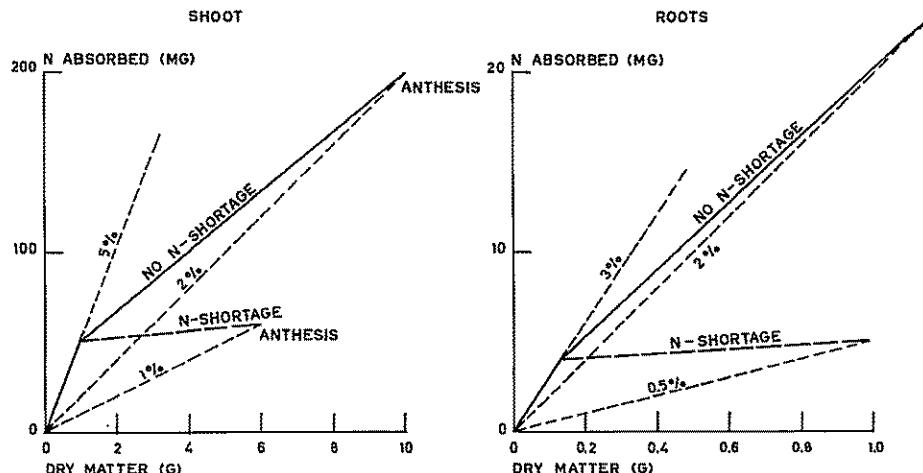


Fig. 4.

Uptake of nitrogen and dry matter increase of wheat plants grown under optimal and limited N-supply. The relations are shown for shoots and roots (after Van Dobben, 1961).

altered as the actual N concentration deviates from the optimal one.

Both dry matter and N content increase during the growth of the crop in a distinct pattern. For wheat, this is clearly demonstrated by an experiment of Van Dobben (1961). In figure 4 it is shown that the N percentage of the plant decreases with plant development even under optimal N supply. The formation of more structural material and the thickening of cell walls are responsible for this phenomenon. The sudden change in slope corresponds with the start of stem elongation. From this growth stage on the plant starts to dilute its overall N content of the above-ground parts, until it reaches approximately 1 % at anthesis. The course of N uptake with the dry matter increase in the roots is also depicted in figure 4. There is a great similarity between the phenomena observed in shoot and roots. The change in slope appears at the same growth stage, although it is less pronounced. The relations change considerably when plants are subject to suboptimal N supplies. In the experiment of Van Dobben (1961) the N supply was drastically lowered after the onset of stem elongation. The N content of the shoot drops severely. Even so, one can notice a remarkable decrease of the above-ground dry matter production at anthesis. Roots show a proportional decrease in N content but dry matter is hardly affected.

Turning to the point of modeling the N behaviour in plants, one has to consider : (1) a distinct relationship between crop growth rate and N uptake, or (2) a feedback of the N status to the growth rate.

Too little knowledge about the N uptake process is available to use the first approach. For the time being the second approach is applied satisfactorily. Moreover, such approach is consistent with the functional balance principle as proposed by Brouwer (1963). To relate N uptake to N status the following procedure is adopted. For each plant organ, a maximum, a minimum and a residual N concentration is defined as a function of development stage. The nitrogen demand of any plant organ is taken to be proportional to the difference between actual and maximum N concentration. Total N demand refers to the sum of the demands of the plant organs considered. The N supply is calculated as a function of the concentration of mineral N in the soil, the soil water content and the rooting depth and density. If the demand is always met by the supply then a potential growth situation exists. If not, the restricted N uptake is partitioned over the plant organs in a way which is proportional to their individual demand. In this way the N content of each organ is calculated as a function of time. The feedback of N status to actual growth rate consists of a reduction of the maximum, gross photosynthesis rate at light saturation of the individual leaves. This affects the daily gross photosynthesis rate of the leaf canopy.

4. ACHIEVEMENTS AND FUTURE GOALS IN THE MODELING OF AGRICULTURAL PRODUCTIVITY

From the agricultural point of view, modeling has clearly defined the yield which can be realized in a certain environment. Potential production figures were already calculated 20 years ago, purely based on plant physiological and environmental principles (De Wit, 1953).

During the last two decades, these figures acted as a target for the attainable yields by farmers. Intensive agricultural research, stimulated by the challenge to realize these calculated potential yields, resulted in improved crop husbandry practices and higher yielding cultivars. The gap between practical and theoretical possible yields has now narrowed considerably, as a result of these research activities.

More recently, the calculation of yields under (rather severe) growth limiting conditions has been attempted (Penning de Vries & Van Laar, 1982). These situations apply very often to developing countries, where high inputs are economically impossible and yields are restricted by these constraints.

Modeling shows to be helpful in defining the yield level when one or another growth factor is limiting; it is certainly a valuable tool in the planning of a gradual productivity development in these areas (Penning de Vries & Djiteye, 1982).

As in future models will improve and weak points will disappear, it may be expected that they will become an important tool in the management and decision making in crop growth on individual fields. As far as N fertilizer application is concerned, there is certainly a clear objective with respect to models which include water and nitrogen effects on growth.

Currently the advise for nitrogen application is based on the amount of inorganic nitrogen found in the soil profile after the winter and on the expected amount of nitrogen that will mineralize from the organic material in the soil during the growing season. When crop growth and nitrogen availability in the soil are simulated simultaneously a more dynamic picture of the nitrogen requirement for the crop arises and decisions concerning the second and eventually third nitrogen application (in the case of winter wheat) can be based on the actual situation, rather than on a mean situation. This leads either to a saving of nitrogen, to an increased economical yield or to a combination of both.

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Modelleren van de produktiviteit van landbouwgewassen op basis van water- en stikstof-beschikbaarheid

Samenvatting

De interceptie van fotosynthetisch actieve straling, water- en stikstofopname zijn de belangrijkste processen welke de groei en opbrengst van gewassen bepalen. Ieder van deze drie processen wordt vooreerst algemeen behandeld. Op basis van experimentele evidentie worden de voornaamste kenmerken ervan toegelicht. De potentiële groeisnelheid van gewassen wordt bepaald door de lichtonderschepping, op voorwaarde dat de vocht- en nutriënten-voorziening niet beperkend zijn. Opbrengstdervingen ten gevolge van water- en stikstoftekort worden besproken.

De diverse groefactoren kunnen sterk variëren in de loop van het groeiseizoen. Dynamische simulatiemodellen zijn daarom uitermate geschikt om kwantitatieve groeiaspecten van gewassen te bestuderen. De manier waarop potentiële groei van gewassen gesimuleerd kan worden is uitvoerig toegelicht. Water- en stikstoftekorten worden in modellen in rekening gebracht door hun invloed op een aantal fysiologische processen. Tenslotte wordt het praktisch gebruik van deze modellen met het oog op gewasproductie toegelicht.

Modélisation de la productivité des cultures en fonction de la disponibilité en eau et en azote

Résumé

La croissance et le rendement des cultures sont déterminés principalement par les processus d'interception de radiation active pour la photosynthèse, et par l'absorption de l'eau et des minéraux. Chacun de ces processus est d'abord discuté, puis à la suite d'évidences expérimentales, leurs caractéristiques principales sont éclaircies. La croissance des cultures est déterminée par l'absorption de radiation solaire, à condition que les besoins en eau et en éléments nutritifs sont satisfaits. La diminution de la croissance due au manque d'eau ou d'azote est traitée.

Les facteurs de croissance peuvent varier considérablement pendant la période de végétation. Des modèles dynamiques de simulation sont particulièrement adaptés à l'étude quantitative des aspects de la croissance. Il est expliqué comment la croissance potentielle peut être calculée. L'effet d'un manque d'eau ou d'azote est pris en considération pour certains processus physiologiques. Enfin, l'utilisation pratique des modèles de croissance est discutée.
