

Quantitative aspects of nitrogen nutrition in crops

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Abstract

The processes affecting the response of crops to nitrogen fertilizers are reviewed, with special emphasis on quantitative relationships that enable the development of deterministic models. Total dry matter production is described in terms of length of the growing period and average growth rate, and the effect of nitrogen status of the vegetation on both is discussed. Attention is paid to nitrogen influence on stomatal response and crop water use. It is shown that the effect of differential nitrogen nutrition can in some cases be described in terms of light interception, but not always. It is concluded that the present insight in the relevant processes is insufficient to use deterministic models directly for application in fertilizer practices at the farm level, but that further development of such models is an important aid in structuring thinking about the system.

Introduction

Nitrogen is an indispensable element for optimum functioning of crops, as was recognized early in literature on agricultural research, where Roberts [42] states 'as to the application of nitrate of soda to wheat when it has a yellow or sickly appearance in the spring . . . it will in a few days alter the sickly hue to a luxuriant green'. Some dozens of years later, the point was made more convincingly at about the same time by Gilbert and Lawes in the UK and von Liebig [30] in Germany. Since then, thousands of experiments have been carried out in which the relation between application rate of nitrogen fertilizer and yield has been established. The results of such experiments are, however, so strongly influenced by the environmental conditions during execution, that they can hardly be used for predictive purposes, such as the formulation of fertilizer recommendations under field conditions. There is, however, an urgent need for better recommendations, especially in view of the contribution of excess nutrients to environmental pollution, such as the nitrate load of

drinking water and the concentration of nitrous oxides and ammonia in the atmosphere.

Increasingly, therefore, it is suggested to use simulation models in which the effects of nitrogen status of the crop on the processes underlying growth, yield and development are described quantitatively, in combination with the processes of the nitrogen balance in the soil, that determine the availability of nitrogen to the crop [15].

However, it often appears that not all relevant processes and causal relations are sufficiently understood to permit their incorporation in deterministic models. In this paper a review is presented of the relevant processes underlying crop response to nitrogen nutrition, using, as much as possible, the wheat crop as an example, to pinpoint the gaps in our knowledge, that are constraints in the development of such predictive models.

Nitrogen status and dry matter production

Dry matter production, either the total for a crop, or of particular plant parts, such as the

tubers or the grains can, schematically, be described as the product of the mean rate of dry matter accumulation and the length of the period of growth. Assessment of the effects of nitrogen nutrition on yield and production should thus consider both aspects.

Length of the growing period

The phenological development of a crop cultivar, i.e. the order and rate in which the vegetative and reproductive plant organs appear is governed by both genetic properties and environmental conditions, notably temperature and day-length [10]. For cultivars adapted to the day-length of the environment in which they are grown, the temperature of the stem apex is the main driving force, which can be approximated by either air or canopy temperature.

In the literature conflicting evidence with respect to the effect of nitrogen nutrition on phenological development is reported [20, 47], i.e. nitrogen deficiency can either hasten or delay development, or have no effect. Nitrogen deficiency in the crop may lead to partial stomatal closure as a reaction to impaired photosynthesis [12, 13]. That in turn will lead to a change in the energy balance of the crop and hence to increased canopy temperatures. In the field, differences of up to 4°C have been recorded between crops well supplied with nitrogen and crops under nitrogen stress [43]. Under certain environmental conditions, an indirect effect of nitrogen shortage on the rate of phenological development and hence on the length of the growing period can thus be expected, leading to shorter growing periods. Severe stress can stop phenological development of the crop completely, so that the relative importance of both processes in particular situations determines the overall effect, which may be one of the reasons for the variable results reported.

Rate of dry matter production

The rate of dry matter production by a crop is the result of the balance between carbon dioxide assimilation and respiration, modified by the distribution of the dry matter formed. Quantification of the effect of nitrogen supply on the rate

of dry matter production requires therefore description of the effects on these individual processes, which have been studied in far less detail than the overall effect on cumulative dry matter production.

Carbon dioxide assimilation

The relation between the light-saturated rate of CO₂ assimilation and nitrogen content of individual leaves has been studied for many species, as reviewed by van Keulen and Seligman [26]. In practically all cases a strong positive correlation between the two was established, sometimes linear over the full range of concentrations studied, sometimes showing a saturating behaviour at higher nitrogen concentrations. Statistical analysis of the pooled data suggested a linear relationship at least up to a nitrogen content of 0.06 kg kg⁻¹ on a dry weight basis. Net assimilation became zero at a nitrogen content of 0.0038 kg kg⁻¹, and the slope of the line was 2.01 · 10⁻³ kg CO₂ m⁻² s⁻¹ per unit (kg kg⁻¹) increase in nitrogen content.

As carbon dioxide assimilation is expressed per unit leaf surface, it has been suggested that the nitrogen content should also be expressed on an area basis rather than on a dry weight basis [9]. The analysis referred to earlier did, however, not show any improvement in the goodness of fit when nitrogen content was expressed on an area basis.

The statistical analysis of the relation between maximum carbon dioxide exchange rate and nitrogen content shows that about 80 percent of the variation is explained. However, the residual variability may not only be due to inaccuracies in the measurements or inherent variability in the plant material, but may at least partially be functional and related to the level of nitrogen nutrition in the period prior to the measurements. In a study on carbon exchange rate of flag leaves of field-grown wheat at different levels of nitrogen nutrition, Marshall [32] found also a linear relation with nitrogen content, with a slope similar to that derived from the pooled data, but the nitrogen level at zero assimilation was higher for the high N treatment than for the low N treatment. Groot and van Dijk [19], studying barley leaves in the grain filling phase, showed that also the nitrogen use efficiency,

expressed as carbon exchange rate per unit nitrogen (the slope of the regression line) differed for leaves exposed to different nitrogen supplies. Both observations point in the direction of differences in the distribution of nitrogen between an active form, contributing to CO₂ assimilation and a non-active form, referred to as structural or storage protein [22]. Under abundant nitrogen supply a larger proportion of total leaf N would then be in the form of storage proteins [31].

Hence, for most situations a linear relation between nitrogen content and carbon exchange rate at light saturation exists, although the actual parameters describing that relation may vary appreciably, depending on pre-treatment. This phenomenon may also explain the reported curvilinearity in the relation between maximum carbon exchange rate and nitrogen content if leaves with a different history with respect to nitrogen nutrition are combined in the analysis [49].

The initial light use efficiency at the light compensation point seems not to be affected significantly by the nitrogen content of the leaves [19, 49]. However, as this parameter is difficult to determine accurately, it may well be that small differences in measured assimilation rate between canopies with different leaf nitrogen concentrations are due to differences in the initial slope.

Assimilate utilization

The assimilates fixed in the assimilation process are partly used in respiratory processes to provide energy for biological functioning and partly for growth of structural plant tissue. Respiration can schematically be distinguished in a maintenance component and a growth component.

Maintenance respiration of the various plant parts is a function of their weight, their chemical composition and ambient temperature. The major processes involved are the resynthesis of degraded proteins, maintenance of concentration differences across membranes and metabolic activity [38]. Different proteins in plant tissue may have very different life times, but an average rate of turnover in active leaf, stem and root tissue of 0.1 d⁻¹ may be assumed. Hence, tissue with higher nitrogen contents requires more energy for maintenance [28, 35, 49]. However, exact quantitative information is rather scarce.

At low nitrogen contents, protein turnover is apparently very low [21], probably because most of the residual nitrogen is in the form of storage proteins, and in that situation the energy requirements for protein turnover are very small compared to those for maintaining concentration gradients and metabolic activity.

The assimilates not used in maintenance respiration are available for increase in dry weight of the various plant organs. The partitioning pattern changes in the course of the plant's life cycle as a result of variations in sink strength of the various organs, which is probably related to the number of growing cells [48]. Under optimum growing conditions this pattern can be described as a function of phenological development only [26]. Under sub-optimum growing conditions, generally the partitioning pattern changes. Whether this is an active process or the result of a differential effect of stress on different organs is difficult to deduce from the available evidence. The often observed shift to lower shoot/root ratios under water stress led Brouwer [4, 5] to suggest that the effect of water stress is stronger on the conversion of primary photosynthates than on assimilation, so that the level of carbohydrate reserves in the plant increases, resulting in greater availability to the root system and stimulated root growth. He referred to this as the 'functional balance'. Although the concept has been questioned [29] an alternative explanation seems to be lacking so far.

Nitrogen deficiency also often leads to lower shoot/root ratios [6, 8, 9], which may be the result of the same functional balance. In addition, the partitioning between leaf blades and other above-ground organs is affected, resulting in a lower leaf weight ratio [7, 33, 36]. Practically all these results refer, however, to integrated results over a longer growing period, and the instantaneous effect of sub-optimum nitrogen concentrations in the tissue on assimilate partitioning is poorly documented. The degree of nitrogen stress is both difficult to quantify and hard to relate to assimilate partitioning using existing experimental data. Hence, more attention for these aspects is warranted.

The primary assimilates allocated to the various growing organs consist of a mixture of simple carbohydrates and nitrogenous compounds.

These products are converted into structural plant material and the energy required for transport and conversion, as well as the 'waste' products have to be taken into account [38]. In a schematized way growth respiration can be expressed in the carbohydrate requirement for biosynthesis, i.e. the amount of carbohydrate required to form one unit biomass of a specific composition. This requirement can be derived from a theoretical analysis of the pathways of biosynthesis [39], but it can relatively easily be determined from the composition, in terms of carbon and ash, of the material being formed [51]. In Table 1 the carbohydrate requirements for a number of plant components, as derived by Penning de Vries et al. [40] are given. The main uncertainty in quantifying growth respiration arises from the question which proportion of the energy costs of nitrate reduction have to be taken into account, and which proportion can be covered directly from sun energy in the leaves.

Hence, nitrogen affects substrate utilization by increasing the respiratory costs with increasing nitrogen content and changing the allocation, such that the shoot/root ratio and the leaf weight ratio increase.

Table 1. Carbohydrate requirements (g CH₂O/g dry weight) for biosynthesis of organic plant components (Source: [40])

Component	Carbohydrate requirement
Carbohydrates	1.275
Proteins	1.887* (2.784**)
Fats	3.189
Lignins	2.231
Organic acids	0.954

* synthesis from amides, no nitrate reduction costs

** nitrate reduction costs included

Organ formation

The direct effects of nitrogen status of the vegetation on organ formation are often difficult to disentangle from the indirect effects through the supply of assimilates [26]. Greenwood [16], Greenwood and Titmanis [17] and Wilson [53] in a series of experiments on wheat, *Lolium rigidum* and *Lolium perenne* found that the relative rate of leaf area expansion of the youngest expanding leaf was linearly related to total leaf nitrogen content (Fig. 1). A problem in quantitatively describing these effects is that optimum

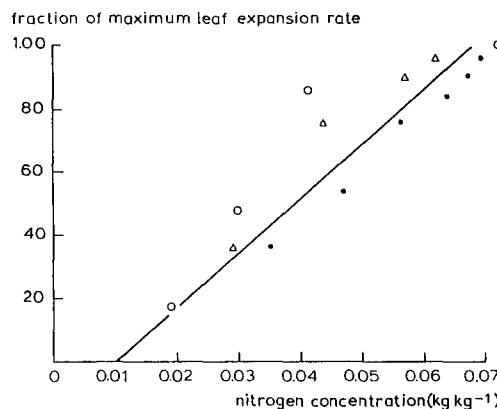


Fig. 1. The relation between the nitrogen content in the leaf and the relative rate of leaf area expansion; dots: *Lolium rigidum*; open circles: *Lolium perenne*; triangles: *Triticum aestivum* (Source: [16, 17]).

leaf nitrogen content declines with leaf age, hence a direct relation with absolute nitrogen content cannot easily be established. In the winter wheat experiments reported by Groot [18], leaf area index around anthesis varied between 1.7 and 5.5. Figure 2 shows that the relation between LAI and total nitrogen uptake by the crop at that moment is linear, suggesting a constant leaf area production per unit nitrogen uptake. This seems an interesting concept, which might be useful in describing the effects of nitrogen availability on leaf area dynamics. However, more detailed analysis is necessary to confirm these findings, also for other crops. Moreover, there are some conspicuous outliers (Bouwing 83/84), which need further explanation.

Tiller formation in gramineous crops, which is comparable to leaf formation, also appears to be directly influenced by the nitrogen content of the crop [1, 58]. To what extent the same holds for branching and formation of side shoots in other crops is difficult to judge from available experimental evidence. Again, these effects are confounded through indirect effects of assimilate availability.

Nitrogen nutrition and water use

Many studies have indicated that water use efficiency, i.e. the amount of dry matter produced per unit input of water, increases with higher

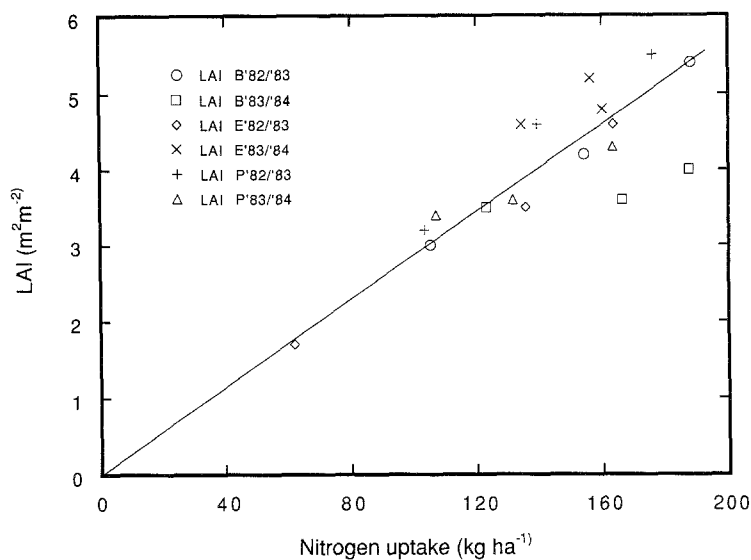


Fig. 2. The relation between total crop nitrogen uptake at anthesis and leaf area index (LAI) at that moment; B is Bouwing; E is Eest; P is PAGV (Source [18]).

nitrogen availability to the crop [2, 25, 52]. Interpretation of these results is hampered when no distinction is made between transpiration by plants and evaporation from the soil surface. Crops growing under nitrogen-deficient conditions generally have a much smaller leaf area than those optimally supplied with nitrogen, hence canopy closure occurs much later, if at all. Consequently, bare soil is exposed for a much longer period of time, which leads to a larger proportion of total water loss from the soil surface, resulting in reduced water use efficiency. This may be one of the reasons that in experiments on water use, where soil surface evaporation was prevented, nitrogen nutrition hardly affected water use efficiency [50, 54].

To examine the effects of nitrogen nutrition on plant water use, a better measure is the transpiration efficiency, the amount of carbon dioxide fixed per unit water transpired. Experiments where assimilation and transpiration were measured simultaneously on leaves of different nitrogen contents have not provided conclusive evidence. Transpiration efficiency was not affected in maize [13, 56] and *Panicum maximum* [3], but increased in *Festuca arundinacea* and *Panicum milioides*, in the latter species almost two-fold over a range in leaf nitrogen contents from 0.01 to 0.05 kg kg⁻¹ [3].

Shimshi [44, 45] has shown that transpiration

from nitrogen-deficient plants was lower when well-supplied with water, but that the situation reversed at soil water contents near wilting point, hence in water-stressed plants. That could be the result of the higher proportion of cell wall constituents in nitrogen-deficient plants, which reduces stomatal flexibility: the opening is restricted under favourable soil moisture conditions and full closure is prevented under water stress. Greater stomatal opening at higher leaf nitrogen contents has also been reported for rice [23, 57], wheat [46], sunflower and maize [13]. The relation between leaf conductance for water vapour, including boundary layer conductance, and leaf nitrogen content as derived from Yoshida and Coronel [57] is given in Fig. 3. The relation between stomatal conductance and leaf nitrogen content would also be linear and to the left of the calculated regression line, as boundary layer conductance under the measuring conditions would be practically constant. This linear relation suggests stomatal control through the CO₂ concentration in the sub-stomatal cavity, in such a way that the CO₂ concentration remains either constant or has a fixed ratio to the external concentration. Any impairment in assimilation will then lead to proportional stomatal closure and lower transpiration. Under what conditions this phenomenon is also operational in field conditions is not clear.

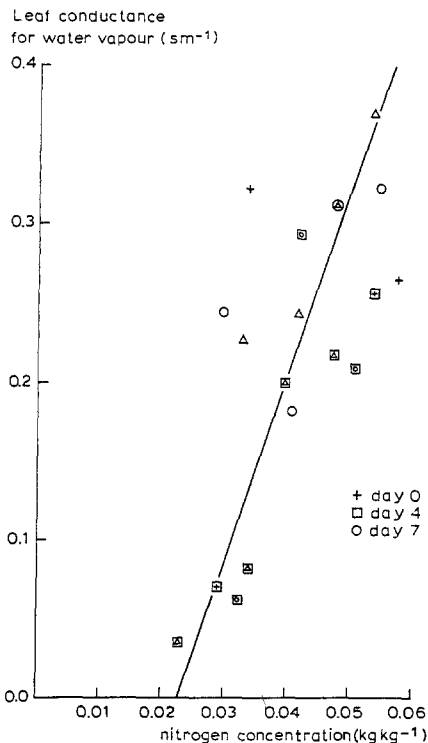


Fig. 3. The relation between the nitrogen concentration in the leaf blade and total leaf conductance for water vapour exchange for individual rice leaves (Source: [57]).

Hence, the quantitative effect of nitrogen status of the crop on water use and water use efficiency is difficult to predict and careful consideration in each situation is therefore necessary.

Crop response to fertilizer application

Countless nitrogen fertilizer experiments have been carried out, often with emphasis on determining response curves with the aim of establishing the optimum application rate, often expressed in economic terms, i.e. the quantity where the costs of the last unit of nitrogen applied is equal to the price of the additional yield obtained. In the last years the emphasis has shifted, as attention for environmental issues increased and restriction of losses of nitrogen to the environment has become a major consideration. Therefore, more attention is being paid to the physical aspects of the fate of applied fertilizer. The use of response curves provides only

limited information on those aspects, and moreover they show a large variability as illustrated in Fig. 4 for three sites from the winter wheat data set of Groot [18]. An alternative method of analysis [27, 55] that permits a distinction to be made between the response of crop uptake to increased nitrogen application and the response of the crop to increased uptake, is therefore more useful. The method is illustrated in Fig. 5, using the same data as in Fig. 4, with addition of the results of chemical analysis of the material harvested. These results show that the relation between nitrogen uptake and yield is invariable for the three sites that showed large differences in response curves. At low nitrogen availability grain yield is proportional to total nitrogen uptake, indicating constant limiting nitrogen con-

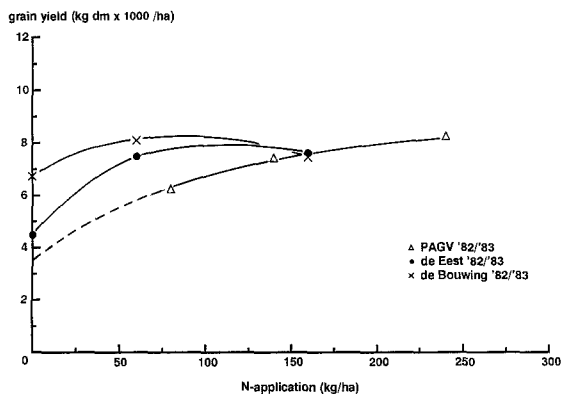


Fig. 4. The relation between nitrogen application and grain yield for winter wheat at three sites in The Netherlands (Source: [18]).

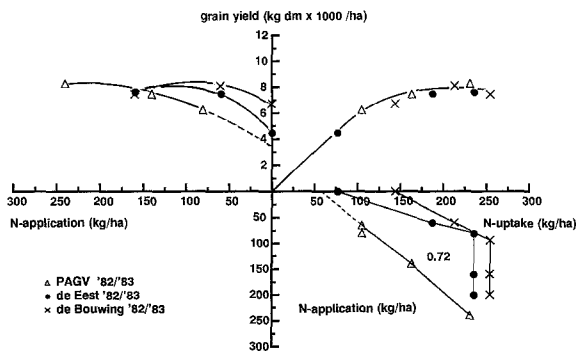


Fig. 5. The relation between total nitrogen uptake and grain yield (right upper quadrant), that between nitrogen application and nitrogen uptake (right lower quadrant) and that between nitrogen application and grain yield (left upper quadrant) for winter wheat at three sites in The Netherlands (Source: [18]).

centrations in both grain and straw. With increasing nitrogen uptake the concentration in the tissue at harvest increases, leading to deviation of the line from the linear and finally a plateau level is reached where some growth factor other than nitrogen availability is yield-determining.

The variability in the response curve thus arises from differences in the relation between nitrogen application and nitrogen uptake (lower right hand side of Fig. 5). Both, the uptake at zero fertilizer application (supply from natural sources) and the recovery fraction (ratio of additional uptake and application) vary substantially. In general this relation appears linear within the relevant range of application rates [24, 27] which suggests that the processes that determine availability of the element to the crop, including those that cause losses, are first-order processes, i.e. that their rates are proportional to the concentration of the element in the soil solution. This also holds for the PAGV data (Fig. 5), but cannot be judged for the two other sites, as at

the highest application rates the crops were probably 'saturated' with nitrogen throughout their life cycle, resulting in active exclusion of nitrogen, as was also observed in nitrogen fertilizer experiments on permanent pasture [41].

The recovery fraction appears 0.72 for the PAGV site, for the other two sites the value exceeds 1 for the lowest application rate. It is not clear what the reason is for this 'aberrant' behaviour.

Leaf area development in winter wheat appears closely related to nitrogen uptake (Fig. 2). Analyses of field crop behaviour in W.Europe suggest that cumulative dry matter production is often proportional to accumulated intercepted radiation [34], which is directly related to the intercepting green surface. In Fig. 6 the relation between cumulative intercepted photosynthetically active radiation (PAR) and cumulative dry matter production is given for the winter wheat crop at PAGV in the '83/'84 growing season. Intercepted photosynthetically active radiation

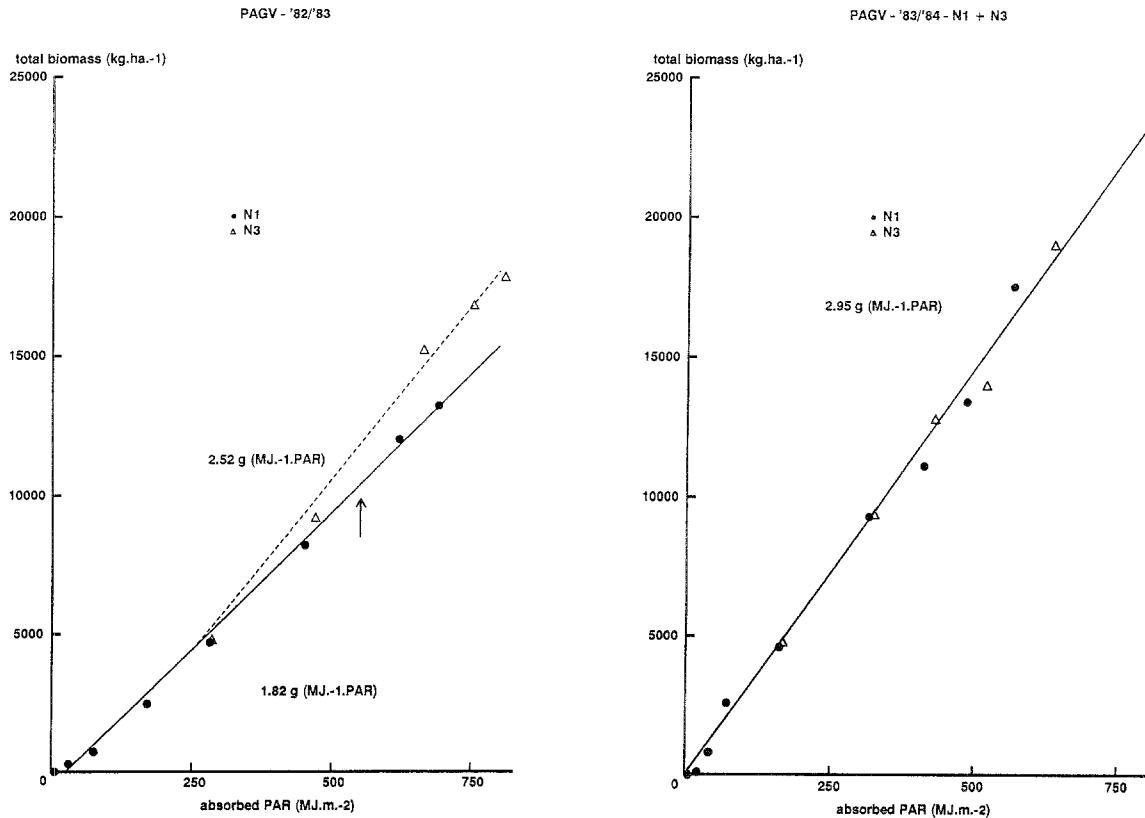


Fig. 6. The relation between cumulative absorbed photosynthetically active radiation and cumulative dry matter production for winter wheat at PAGV, The Netherlands in '82/'83 (left) and '83/'84 (right).

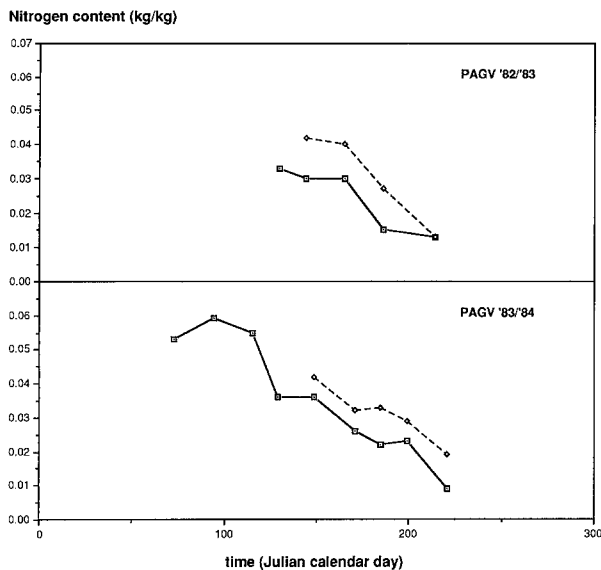


Fig. 7. Time course of nitrogen content in the green leaves of winter wheat at PAGV, The Netherlands, in '82/'83 (upper part) and '83/'84 (lower part); solid lines low N; broken lines diamonds high N (Source: [18]).

was calculated by interpolation in measured leaf area index, assuming an extinction coefficient of 0.6 for global radiation and assuming a proportion of 50% PAR. The results show that the difference in total dry matter production between the low and high nitrogen treatments can be fully explained by the differential radiation interception as a result of differences in leaf area development. The difference in nitrogen concentration in the green leaf mass (Fig. 7) apparently does not influence the radiation use efficiency, i.e. the amount of dry matter produced per unit PAR intercepted, which has a constant value of 2.95 g/MJ. This value is very similar to that reported for wheat and barley crops in the UK [11]. The situation is different for the '82/'83 season, where the high N treatment exhibits a clearly higher radiation use efficiency, although the differences in nitrogen content in the green leaves are not more pronounced than in the '83/'84 season. The latter results agree with those presented for winter wheat crops in the UK [14, 11].

Discussion and conclusions

The basic processes underlying crop response to nitrogen nutrition are not all fully understood

quantitatively, as discussed in the first part of this paper. The relation between radiation absorption and dry matter production (Fig. 6) is the integrated result of these processes, and differences in this relation under the influence of differential nitrogen nutrition would have to be explained in terms of these processes. It has been shown that light saturated assimilation rate is linearly related to nitrogen content in the leaves, but the ratio of 'active protein' to 'storage protein' may vary considerably, thus leading to variations in both the nitrogen content at the CO₂ compensation point and the nitrogen use efficiency. Moreover, as initial light use efficiency at the light compensation point seems to be far less affected by nitrogen content, the overall effect of leaf nitrogen content on canopy assimilation rate also depends on the prevailing radiation climate. Taking all of these factors into account, the effect appears to be difficult to predict in general terms.

Even if gross assimilation is higher at higher leaf nitrogen contents, part of that gain will be offset again by higher respiratory losses, as both maintenance and growth respiration are higher for tissues with higher nitrogen contents. Again, generally applicable quantitative relations are difficult to derive, as for instance for maintenance requirements also the ratio of active to storage protein plays a role. Moreover, temperature is important as maintenance respiration is much more sensitive to temperature than is gross assimilation, so that net assimilation is higher at lower temperatures.

Differences in nitrogen content may also lead to differences in distribution of assimilates among various plant parts. This will have consequences for the calculated radiation use efficiency, especially if a larger proportion is invested in the root system as a reaction to nitrogen deficiency, because generally only above-ground dry matter is considered in the analysis. Differences in the distribution between leaves and stem will only have a minor effect on that conversion efficiency, although it may affect total dry matter production by influencing the intercepting surface.

It must thus be concluded that it is not yet possible to quantitatively predict the effects of nitrogen nutrition on radiation use efficiency.

A large amount of work has been done on effects of nitrogen on crop performance and on the effects of nitrogen on individual processes. However, a systematic analysis also reveals that still major gaps in knowledge and insight exist, which makes it difficult to use the existing knowledge at the practical level, for instance in formulating fertilizer recommendations that result for the farmer in the required yield of the required quality and at the same time minimizes effects on the environment. Systems analysis and simulation in which the available knowledge is combined into a consistent framework, as illustrated with a number of examples in this volume, is a research tool that may help in making the gaps in knowledge explicit [26], and design experiments specifically geared to filling these gaps. At the moment it still seems rather premature to claim that the existing models could be of direct practical application for fertilizer practices at the farm level (cf. Otter-Nacke and Kuhlmann, this volume), but they certainly help in structuring the thinking of scientists and thus pointing to the most important processes and parameters.

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