QUANTITATIVE ASPECTS OF NITROGEN NUTRITION IN PLANTS
AND ITS MODELLING*

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1. Introduction

Green plants produce organic components from carbon dioxide and water under the influence of the sun's energy. The pioneering work, concurrently carried out by Liebig in Germany and Lawes & Gilbert in the U.K. more than a century ago, conclusively showed that plants have to take up inorganic nutrients from the soil to produce these organic components. Since that discovery it has been established that dozens of elements are necessary for unimpaired and optimum functioning of the biochemical machinery of the plant. Most of these are necessary in such small amounts however, that the supply from the seed, or from natural sources more than suffices. The situation is often different for the so-called macro-elements nitrogen, phosphorus and potassium that are needed in such large quantities, especially where crop management practices aim at very high yields, that the supply from natural sources falls far short of the demand. That has been shown thousand-fold and is being shown almost daily by the results of fertilizer experiments, indicating that addition of these elements from a fertilizer bag leads to higher yields up to a certain level. Unfortunately, interpretation of these fertilizer experiments seldom exceeds the descriptive level, thus only resulting in the conclusion that under the conditions of the experiment, the optimum nutrient application rate, either in physical terms or in economic terms would have been "x" kg ha^{-1}. The lack of explanatory conclusions prevents the use of such results for predictive purposes, i.e. for the formulation of fertilizer recommendations for the farmer in the practical situation. This lack of predictive power is especially serious for nitrogen in the present situation, where for the farmer the price of the fertilizer is hardly a motive for restricted use, but where for society the cost involved in air and water pollution due to excessive application of both organic and inorganic manures may become prohibitive.

A more promising approach would seem to describe the effects of nitrogen or its deficiency in terms of the processes that determine crop growth and yield, and predict on that basis the nutrient requirements for a certain target yield. An attempt in that direction, mainly oriented towards growth of a wheat crop is described in this contribution. This attempt leads to the conclusion that despite more than 100 years of research in the field of plant nutrition, many of the required relations appear to be either totally absent, or at best ambiguous. Nevertheless, some results are presented of a model in which these relations have been incorporated in a coherent framework.

2. Quantitative aspects of nitrogen status

Dry matter production, either the total for a certain crop, or that accumulated in a specific plant part such as the tubers or the grains, is the product of the length of the production period and the rate of dry matter accumulation during that period. The integrated effect of nitrogen on crop performance must thus be described by accounting for its effect on both components.

2.1 Effect on length of the growing period

The phenological development of the plant, i.e. the rate and order of appearance of vegetative and reproductive plant organs, is partly governed by genetic plant properties, and partly by environmental factors, notably day length and temperature. For at least a number of cultivars of spring wheat the effects of day length are relatively insignificant and moreover for most environments cultivars are available that suit the particular photoperiodic characteristics of that environment.

The driving force for development then becomes temperature and the relevant variable is presumably canopy temperature. This temperature results from the balance of radiation absorption by the vegetation and energy dissipation through transpiration. Any factor affecting the rate of transpiration will change the energy balance of the vegetation and hence its temperature.

It has been observed that nitrogen stress may cause stomatal closure at higher plant water potentials (Radin & Ackerson, 1981), or a reduction in water supply by increased root resistance (Radin & Boyer, 1984) and a consequent reduction in transpiration (Shimshi, 1970a; 1970b; Shimshi & Kafkafi, 1978). In the field, differences of up to 4 °C in canopy temperatures have been measured between fields optimally supplied with N and fields under nitrogen stress (Seligman et al., 1983). An indirect effect of nitrogen shortage on phenological development can thus be expected. Such effects have indeed been reported where a field-grown crop of wheat, growing under N deficient conditions, reached maturity up to 5 days earlier than crops growing with adequate nitrogen (Seligman et al., 1983). This delay would have needed somewhat less than 1 °C temperature difference during the main growing period between booting and early grain fill.

Severe stress can, of course, stop all development, although it is not clear at what point this can happen. This phenomenon may be at the basis of

the observation that relatively severe stress can delay phenological development (Angus & Moncur, 1977).

The effect of nitrogen status on the actual transpiration is discussed in more detail later in this paper.

2.2 Effect on carbon dioxide assimilation

The influence of nitrogen deficiency in the vegetation on dry matter accumulation, total production, and yield is well documented, but the effects on the basic processes of assimilation and respiration are far less clear. The level of CO_2 assimilation at different nitrogen levels in the leaves has been determined for many plant species, such as maize (Goudriaan & van Keulen, 1979; Ryle & Hesketh, 1969), sunflower (Goudriaan & van Keulen, 1979), cotton (Wong, 1979; Ryle & Hesketh, 1969), sugar beet (Nevins & Loomis, 1963), rice (Cook & Evans, 1983a; 1983b; Yoshida & Coronel, 1976; Takeda, 1961), grasses, both those with C_3 and C_4 photosynthetic pathways (Woledge & Pearse, 1986; Bolton & Brown, 1981; Lof, 1976; Wilson, 1975a; 1975b), wheat (Marshall, 1978; Osman et al., 1977; Dantuma, 1973; Osman & Milthorpe, 1971; Khan & Tsunoda, 1970a; 1970c), soya-bean (Boon-Long et al., 1982; Lugg & Sinclair, 1981; Boote et al., 1978), Eucalyptus spp. (Mooney et al., 1978) and tung (Loustalot et al., 1950). In all situations where nitrogen concentration of the leaves was determined concurrently, a strong correlation exists between the nitrogen concentration in the leaves and their photosynthetic performance.

Leaf nitrogen concentration can be expressed either on an area basis or on a dry weight basis, the specific leaf area being the conversion factor between the two. The literature cited above uses both methods. Where the specific leaf area is reported, the data can be expressed on a common basis. In Figure 1 some data for C_3 species are summarized from situations where it could reasonably be assumed that the applied photon flux density during the measurements was high enough to ensure light saturation. Nitrogen concentration in Figure 1 is expressed on a dry weight basis. The data suggest a linear relation between nitrogen concentration and net CO_2 assimilation rate, at least up to a nitrogen concentration of 0.06 kg kg^{-1}. The calculated regression line between nitrogen concentration and net assimilation rate at light saturation ($r^2 = 0.77$) shows a slope of 22.0 x 10^{-6} kg CO_2 m^{-2} s^{-1} for each unit increase in nitrogen concentration. Some of the residual variability could be due to different ages or development stages of

the experimental material. The intercept with the x-axis, reflecting the point where net assimilation becomes zero is at a nitrogen concentration of 0.0038 kg kg^{-1}.

Regressing net CO_2 assimilation on nitrogen concentration expressed on an area basis gives $r^2 = 0.76$. The regression line (Figure 2) has a slope of 0.71 x 10^{-7} kg CO_2 m^{-2} s^{-1} for each unit increase (10^{-3} kgm^{-2}) in nitrogen concentration and zero assimilation at a nitrogen concentration of 0.2 x 10^{-3} kgm^{-2}. The two slopes would be identical at a value of the specific leaf area of 31.25 m^{-2} kg^{-1}, a rather high value that would suggest that most experiments were conducted on young, thin leaves. The value of the specific leaf area where the intercepts of both relations would be identical is 19 m^2 kg^{-1}, i.e. much thicker than for the slope.

The general conclusion from the data presented here would thus be that the maximum rate of carbon dioxide assimilation is linearly related to nitrogen concentration over a wide range of concentrations. In individual experiments sometimes a "saturation"-type curve seems more appropriate, but that is difficult to derive from the lumped data. Thus, even for a relation studied so thoroughly no unequivocal conclusion is possible.

The effect of leaf nitrogen concentration on the initial light use efficiency, i.e. the slope of the CO_2 assimilation curve at low irradiance, is difficult to determine because of the small values involved and the variance in the data. No significant differences could be detected (Cook & Evans, 1983a; 1983b; Wilson, 1975a; 1975b), but it could well be that small differences in the slope are responsible for some of the measured differences in assimilation rate between canopies with different leaf nitrogen concentrations. For the time being, the influence of nitrogen concentration on gross CO_2 assimilation is thus fully accounted for by changing the value of the light saturated gross CO_2 assimilation rate of individual leaves, F_m, in dependence of the nitrogen concentration in the leaf blades, N:

$$F_m = 725 \ N - 2.75, \quad F_m \geqslant 0$$

2.3 Effect on dry matter production

2.3.1 Partitioning of assimilates to respiration and growth of various organs

The assimilates fixed by the photosynthetic process are used by the various sinks in the plants, including maintenance respiration. Sink strength, which is probably related to the number of growing cells in a particular organ, is an important determinant for assimilate distribution at any time.

Maintenance of the various living plant parts presumably has first priority. Maintenance respiration is dependent on the weight of an organ, its chemical composition, particularly its nitrogen concentration, (reflecting the rebuilding of continuously degrading proteins) and the ambient temperature (Penning de Vries, 1975). For each of the organs, i.e. roots, leaves, stems and grains, the carbohydrate requirement for maintenance respiration is calculated first. Although reasonable quantitative estimates of maintenance respiration have been proposed still a great deal of uncertainty exists with respect to accurate values and in some cases it appeared necessary to introduce 'fudge' factors to describe reality reasonably well (de Wit et al., 1978).

The effect of nitrogen concentration on maintenance respiration is accounted for by a multiplication factor that ranges between 1 and 2, which is about the range found in maintenance requirements per unit dry weight between protein-poor and protein-rich materials (Penning de Vries, 1975). At very low nitrogen concentrations, protein turnover is presumably low and has a small energy requirement compared to that needed for maintenance of the ionic balance within the cells and the transport of assimilation products. Also here quantitative information is rather scarce (Hanson & Hitz, 1983).

The assimilates remaining after subtraction of the maintenance requirements of the live organs of the crop, are available for the production of structural plant material. In a schematized setup, the currently produced assimilates are allocated to 5 compartments: leaf blades, stems, roots, grains and a reserve-pool of primary photosynthetic products. Under optimum growth conditions, the proportion of net assimilate allocated to each of the compartments is a function of the phenological state of the vegetation only, representing the variable sink strength of the various organs. Under sub-optimum growing conditions the partitioning changes. Whether this is an active process, or the result of a differential influence of stress on the growth of different organs is difficult to judge.

Brouwer (1965; 1963) suggested that insufficient moisture supply, resulting in loss of turgidity, affects the conversion of primary photosynthates into structural plant material ('growth') more strongly than CO_2 assimilation. As a result, the level of reserve carbohydrates in the plant increases, which makes more of them available for growth of the root system. As a consequence, water shortage changes the partitioning of assimilates between shoot and root. Brouwer referred to this phenomenon as the 'functional balance'.

Nitrogen shortage in the vegetation also favours growth of roots at the expense of above ground material, generally leading to lower shoot/root ratios at suboptimum nitrogen supply (Cook & Evans, 1983a; Campbell et al., 1977; Wilson & Haydock, 1971; Colman & Lazenby, 1970; Brouwer, 1965; Brouwer et al., 1962; McLean, 1957), which may be the result of the same functional balance. The partitioning between leaf blades and other above ground organs also changes under nitrogen-deficient conditions and generally results in a lower proportion of leaves (Campbell et al., 1983; van Os, 1967; McNeal et al., 1966; Boatwright & Haas, 1961). However, the instantaneous effect of suboptimum nitrogen concentrations in the tissue on partitioning of assimilates is difficult to quantify from existing experimental data. In our concept nitrogen stress at any particular point in time is defined as the difference between the maximum nitrogen concentration at a certain development stage and the actual nitrogen concentration, expressed as a fraction of the range between the maximum and the minimum nitrogen concentration. A criterion for the latter characteristic seems not self-evident.

Based on this reasoning these influences can schematically be described by assuming a growth check on the shoot compartments (leaf blades and stem) when nitrogen shortage occurs. The resulting "surplus" carbohydrates is partitioned between roots and the reserve pool. When stress is alleviated and reserve carbohydrates have accumulated, some can become available for subsequent leaf growth.

2.3.2 Conversion of assimilates into dry matter

The assimilates allocated to the various sinks are in the form of primary photosynthetic products, i.e. a mixture of carbohydrates and nitrogenous compounds. These primary products must be converted into structural plant material, and the energy required for this conversion must be taken into account. The magnitude of this growth respiration also depends on the chemical composition of the material being formed (Penning de Vries et al.,

1974; Penning de Vries, 1974). As a first approximation the composition can
be defined in terms of proteins and carbohydrates only, as these components
constitute the major part of the plant material. The proteins are assumed to
be formed from nitrates only, so that the costs of reduction have to be taken
into account.

The rate of increase in plant dry weight is thus obtained by dividing
the rate of assimilate supply by the specific assimilate requirement factor.
The latter is defined as 1.21 times the fraction of carbohydrates in the
currently formed material plus 2.27 times the fraction of proteins (Penning
de Vries, 1974). These values, based on detailed biochemical pathway analysis
are reasonably well-established, but the uncertainty in this case originates
mainly from the assumption that all proteins are formed from nitrate. This
description thus leads to higher conversion efficiencies for tissues with a
lower nitrogen concentration.

2.4 Influence on transpiration

The actual rate of transpiration of a canopy depends on the potential rate,
dicated by environmental conditions, and on the availability of water in the
rooted soil profile.

A process that needs attention in the present context is that of the
influence of the nitrogen status of the vegetation on its transpiration rate.
Many studies have indicated that water use efficiency, i.e. the amount of dry
matter produced per unit of water consumed, increases with increasing
nitrogen availability (van Keulen, 1975; Black, 1966; Viets, 1962). Interpre-
tation of these results is in most cases difficult, because no distinction is
made between transpiration by plants and evaporation from the soil surface.
Plants growing under nitrogen stress, are generally much smaller, as is their
leaf area, so that complete soil cover is reached much later than for plants
growing under optimum nutrient conditions, if at all. That leads to a much
larger proportion of non-productive water loss directly from the soil surface
and hence to a lower water use efficiency. In the early experiments on water
use, where direct evaporation from the soil surface was prevented, hardly any
influence of moderate nitrogen stress on water use efficiency was found
(Tanner & Sinclair, 1983; de Wit, 1958).

Recent experiments where assimilation and transpiration of plant species
were determined on individual leaves at different nitrogen concentrations,
have in general confirmed the latter hypothesis for maize (Goudriaan & van

Keulen, 1979; Wong et al., 1979) as illustrated in Figure 3 and <u>Panicum</u> <u>maximum</u> (Bolton & Brown, 1980), but far less so for tall fescue and <u>Panicum</u> <u>milioides</u> (Bolton & Brown, 1980). In the latter species the ratio of apparent photosynthesis to transpiration increased almost twofold over a range of N concentrations in the leaf from 0.01 to 0.05 kg kg^{-1}.

A comprehensive study on the interactions between nitrogen and water stress, mainly in cotton, has been conducted by Radin and associates (Radin, 1982; Radin & Boyer, 1982; Radin & Ackerson, 1981; Radin & Parker, 1979a; 1979b). They found that in nitrogen deficient plants, stomatal response to water stress becomes increasingly sensitive. In such plants, stomatal closure occurs at much higher plant water potentials than in plants adequately supplied with nitrogen, i.e. at values of - 1 MPa vs. - 1.8 MPa (Radin & Ackerson, 1981). Diurnal fluctuations in leaf water potentials, especially on bright days can easily lead to values as low as - 1 MPa in well-watered wheat plants and remain below that level for most of the day, (Hochman, 1982; Martin & Dougherty, 1975).

Shimshi (1970a; 1970b) has shown that transpiration in nitrogen-deficient plants is reduced at high levels of soil moisture, but that near wilting point the situation is reversed, possibly because of a much higher proportion of cell wall constituents in the N-deficient plants that reduces stomatal sensitivity. Consequently, stomatal opening is not only restricted under high soil moisture conditions, but full stomatal closure is prevented near wilting point. Evidence for greater stomatal opening with better N nutrition has also been found in rice (Ishihara et al., 1978; Yoshida & Coronel, 1976), wheat (Shimshi & Kafkafi, 1978), sunflower and maize (Goudriaan & van Keulen, 1979).

Radin & Boyer (1982) have shown that root conductivity is lower in N-deficient sunflower plants, so that lower turgor, higher plant water potentials and stomatal closure could follow. Lower transpiration rates due to nitrogen deficiency could therefore be effectuated by stomatal closure at higher leaf water potentials or by lower root conductivity. In the former case moisture stress would be secondary and possibly minor compared to nitrogen stress; in the latter case moisture stress induced by N-deficiency would be the more dominant.

Data on the relation between leaf resistance and leaf N concentration for rice have been published by Yoshida & Coronel (1976). Figure 4 is derived from their data and relates leaf conductance to N concentration in the leaf. In these data leaf conductance includes boundary layer conductance, so that stomatal conductance would necessarily be to the left of the eye-fitted regression line. The data in Figure 4 would suggest a linear relationship

between leaf conductance and N concentration in the leaf very similar to the
relation for maize in Figure 3. Such a relation would be indicative for
stomatal control through the CO_2 concentration in the substomatal cavity
(Goudriaan & van Laar, 1978). Any impairment of assimilation will lead then
to a proportional stomatal closure and decreased transpiration. It is,
however, not clear yet under what conditions this phenomenon can be expected
in the field.

The effect of nitrogen shortage on water use is therefore difficult to
predict and must be carefully reconsidered for each situation.

2.5 Nitrogen uptake

Uptake of nitrogen by the vegetation is dependent on its demand and on
availability of nitrogen in the soil. Nitrogen is needed in the plant for the
synthesis of new tissue, so that as the plant grows the demand for nitrogen
increases. With the accumulation of more structural carbohydrates, however,
the ratio of nitrogen to total biomass of each of the plant parts falls, even
when nitrogen is available in surplus (Vos, 1981; Seligman et al., 1976;
Dilz, 1964; van Burg, 1962; van Dobben, 1962; 1960). When nitrogen supply is
non-limiting, there is a negative linear relationship between the nitrogen
concentration in plant organs and the development stage of the crop.
Initially the total nitrogen concentration in the leaves is around 0.06 and
towards maturity it falls to around 0.02. Under similar conditions, the
nitrogen concentration in stem tissue falls from around 0.03 at the onset of
stem elongation to about 0.008 at maturity. Maximum nitrogen concentrations
in the root are more variable than in the shoot. Appropriate values under
conditions of surplus supply from the soil would be about 0.035 at seedling
emergence to 0.01 at maturity.

In our concept, the nitrogen demand of any plant part at any point in
time is defined as the difference between the maximum amount attained under
optimum N-supply and the actual amount in the tissue at that moment. The
total nitrogen demand of the canopy is then the sum of the nitrogen demands
of the component parts or organs, i.e. the leaves, the stem and the roots.
Grain nitrogen is assumed to be supplied by translocation from the vegetative
organs and so does not contribute directly to nitrogen demand.

Availability of nitrogen to the vegetation depends both on the amount
present in the soil and on the extent and density of the plant's root system
(van Keulen et al., 1975). In the wheat crop, root density is generally
relatively high, i.e. greater than 1 cm root length cm^{-3} soil (e.g. Gajri &
Prihar, 1985; Lupton et al., 1974), and so would make most of the mineral ni-

trogen in the rooted zone available for uptake within one day and almost all
within two days, provided that all or the greater part of that nitrogen is
present in the form of nitrates. As a consequence, the surplus demand of the
crop, exceeding mass flow supply can be met by diffusion, even when mass flow
is very low. Early in the season, before the root system of the crop is fully
expanded horizontally, some of the soil nitrogen, even within the rooted
depth may be unavailable. This is approximated by defining a maximum uptake
rate which is determined by the extent of the root system. Nitrogen uptake on
a daily basis is thus defined as the maximum of either the demand of the
crop, the amount available in the soil or the maximum uptake rate. This
formulation implies that uptake cannot exceed demand, so that if demand is
satisfied, further uptake of nitrogen is actively prevented, i.e. excess
nitrogen reaching the root surface by the transpiration stream is excluded.
This phenomenon occurs in experiments with plants grown in nutrient
solutions, where total uptake levels off beyond a certain concentration of
nitrogen in the solution even though transpiration continues (cf. Alberda,
1965). This also occurs in the field where uptake by the vegetation levels
off at high application rates (cf. Prins et al., 1981).

2.6 Distribution of nitrogen in the plant

The current uptake of nitrogen is distributed among the various vegeta-
tive plant organs, leaves, stems and roots, in proportion to their relative
demands. When supply cannot satisfy the total demand, roots do not have first
priority despite their closeness to the source (van Keulen, 1981; van
Dobben, 1963).

As the leaves age, some of their nitrogen can be transferred to other
tissues, where an unsatisfied demand for nitrogen exists. If senescence
occurs because of nitrogen shortage and leaves die, the nitrogen above an
immobilizable residual amount in the senescing organ is transferred to the
remaining live tissue. The unavailable level of nitrogen in the vegetative
organs is a function of the development stage of the vegetation, as younger
parts die with a higher residual N concentration (Seligman, unpubl. data;
Dilz, 1964). If leaves die for reasons other than N-deficiency some of the
translocatable N can be used to satisfy the N demand of other organs,
primarily the stem. In this way the stem serves as a temporary store for N
before translocation to the grain.

2.7 Translocation of nitrogen to the seed

Seeds receive most of their nitrogen in a reduced form, generally as amino acids that are translocated from the roots, leaves and stems (Donovan & Lee, 1978; Nair et al., 1978). From various studies it appears that the rate of nitrogen accumulation in the grains is fairly constant during the linear phase of grain growth (Vos, 1981; Donovan & Lee, 1978; Sofield et al., 1977). The rate of accumulation at any moment may be limited by the potential rate of accumulation in the grain (sink, Donovan & Lee, 1978; 1977) or by the supply rate from the vegetative parts (source).

The rate of nitrogen depletion from the vegetative parts of the plants is fairly constant as long as the nitrogen concentration in the tissue is above a threshold level of around 0.01 (Dalling et al., 1976). As the amount of nitrogen in the vegetative parts declines and the concentration approaches the residual level, the rate of depletion drops (Dalling et al., 1976). The rate of transfer from the vegetative tissue and the uptake rate by the seeds are dependent on temperature with a Q_{10} value of around 2 (Vos, 1981). Such a constant rate of depletion can be described as withdrawal from a turning-over pool of amino-acids that is maintained at a more or less constant level, when calculated on an integrated daily basis (Hanson & Hitz, 1983). As the amino-acids are transferred from the vegetative tissue to the grain, storage or relatively stable proteins, like RuBPC-ase are mobilized, triggered by a rise in the level of proteolases at the onset of grain growth. The level of proteolases stays relatively high during grain filling and drops only as the grain approaches maturity (Dalling et al., 1976).

This process of nitrogen depletion in the vegetative parts and translocation to the grain can be represented by first defining the maximum nitrogen accumulation rate in the grains as a function of grain number and temperature. The potential export rate from the vegetative tissue is equal to the total nitrogen content above a residual sequestered level, multiplied by the relative turnover rate. The latter is influenced by temperature, the moisture status of the vegetation and its non-structural carbohydrate level. The actual rate of export is derived from this value, taking into account the "nitrogen activity" of the vegetative tissue, expressed by its average nitrogen concentration. This conceptualization makes the notion of competition between vegetative tissue and seed explicit. Thus, if the vegetative tissue is "active" and has a high N concentration, its competitive ability is high and the nitrogen is easily retained. The opposite is true in the reverse case. All of these relations are difficult to quantity on the basis of existing insights in the nitrogen economy of plants. Very little

experimental work in this field appears to have been done, despite the relative importance of these processes for green area duration and hence grain yield on the one hand and grain nitrogen concentration, important for baking quality, on the other hand. The temperature effect is well-established and was discussed already in treating maintenance respiration (Vos, 1981; Penning de Vries, 1975).

The effect of water stress on nitrogen turnover is difficult to disentangle from senescence. Under water stressed conditions very often the nitrogen concentration of the leaf is higher (Halse et al., 1969; Fischer & Kohn, 1966c; Asana & Basu, 1963), maybe because rapid senescence reduces the period available for translocation. Yet, as the tissues senesce, protein breakdown is accelerated. It could therefore be assumed that when the transpiration deficit increases nitrogen turnover increases.

2.8 Effect on organ formation

2.8.1 Effect on leaf area formation

The nitrogen status of the vegetation influences the distribution of assimilates between the various organs of the plant (Subsection 2.3.1). Its effect on leaf area expansion can be represented through the reduction in assimilate flow to the leaves.

The effect of nitrogen status on leaf area expansion as illustrated in Figure 5, is derived from leaf expansion experiments on wheat, Lolium rigidum and L. perenne (Greenwood & Titmanis, 1966; 1967). The measurements were done on the youngest expanding leaf and the relationship to total leaf nitrogen is roughly constant over the duration of the experiments (up to 58 days). However, whole canopy nitrogen concentration declines with plant development. Because the nitrogen distribution within the live leaf mass is not defined, the reduction in leaf expansion must be defined as a function of the actual leaf nitrogen concentration, the maximum nitrogen concentration of the leaves at a given development stage, and the minimum concentration of nitrogen in severely depleted leaves.

Under conditions of prolonged nitrogen stress, part of the nitrogen in older tissue is mobilized and resynthesized for the formation of new organs. This nitrogen depletion causes death of the older tissue, the dying rate being related to the average nitrogen concentration in the leaf material. Stem tissue also dies under nitrogen shortage, particularly the leaf sheaths concurrent with the death of leaf tissue.

2.8.2 Effect on yield components

Formation of yield components, i.e. number of tillers, ears, spikelets, florets and grains is governed in the model by the assimilate supply necessary to create a viable organ. The effect of nitrogen status of the vegetation on organ formation is mediated largely through its effect on gross assimilation and hence on the assimilate supply to the various organs. However, tiller formation is affected directly by the nitrogen status of the vegetation, apart from assimilate availability (Yoshida & Hayakawa, 1970).

The problem here is that the effects of nitrogen status per se and the indirect effects on assimilate availability are difficult to disentangle and very little experimental work appears to have been done to separate the two effects. In cases where such attempts were made, the direct effect of N status appeared to be small (Pinthus & Millet, 1978).

3. Some quantitative consequences of nitrogen metabolism in crops

3.1 Yield-uptake and uptake-application relations

The processes and concepts outlined in the preceding chapter have been incorporated in a simulation model describing growth and yield of a spring wheat crop (van Keulen & Seligman, 1986). In this chapter some results obtained with that model will be discussed, especially with respect to the consequences of the nitrogen economy in the vegetation. The model has been validated and has shown to be able to describe the growth and yield of a spring wheat crop under semi-arid conditions with reasonable accuracy, for situations where either water or nitrogen may be the most constraining factors during (part) of the growing season.

The actual physical environment used in the simulation runs is not directly important, since the major concern is the sensitivity of the model to changes in crop characteristics related to the nitrogen economy. As detailed weather data were available for a site in the northern Negev desert of Israel, collected as part of a research project on actual and potential production in that region (van Keulen et al., 1981), some of these data were used to drive the model.

In the region irrigated wheat cultivation is practiced although not on a wide scale. However, effects of increased nutrient availability express themselves much more pronounced under conditions where other growth factors

are as close as possible to optimum. A set of simulation experiments was
therefore executed under the assumption of optimum moisture supply
throughout the growth cycle of the crop.

First, a fertilizer experiment was simulated, involving application of
fertilizer as a basic dressing either in ammoniacal form or in the form of
nitrate. The results presented in Figure 6 show that a unique relation exists
between grain yield and nitrogen uptake, irrespective of the type of
fertilizer applied. The response curve is of the well-known saturation type:
at low uptake rates a proportional relation exists between N uptake and grain
yield, at a slope of about 55 kg grain per kg N taken up. These results are
in agreement with experimentally determined response curves (van Keulen & van
Heemst, 1982), and reflect the fact that the N concentration in the grain can
be diluted to a minimum level of about 0.01 kg kg^{-1}, whereas translocation
from the vegetative tissue proceeds until a concentration of about 0.004 kg
kg^{-1} is reached. The remaining nitrogen in the vegetative plant parts is
sequestered in a non-remobilizable form (possibly in cell wall tissue). The
value of 55 kg kg^{-1} can be generalized from the equation

$$E = 1/(0.01 + s/g \pm 0.004),$$

with s and g the weight of straw and grain, respectively. It implies thus
that the efficiency of nitrogen utilization, expressed in kg grain produced
per kg N taken up, increases with increasing harvest index (van Keulen,
1986).

At increasing uptake rates, the concentration of nitrogen in the
harvested product increases and the yield-uptake curve deviates from the
linear. Finally a plateau level is reached, where increased uptake does not
lead to higher yield levels, because nitrogen is no longer the growth-
determining factor, but yield is determined by the combined effect of
radiation level and temperature. At that point, there is also a tendency for
decreased harvest indices, because abundant N supply in the vegetative stage
leads to luxurious vegetative growth and consequently to lower grain/straw
ratios.

The relation between nitrogen application and uptake is linear over the
full range of applications tested here, again in accordance with experimental
results (van Keulen & van Heemst, 1982; van Keulen, 1977). However, a marked
difference exists between the nitrate and the ammonium form of nitrogen. The
recovery fraction, i.e. the ratio between nitrogen uptake and nitrogen
application is 0.39 for the ammonium fertilizer and about 1.0 for the nitrate
form. The complete recovery of nitrate fertilizer is due to an assumed

absence of denitrification for the semi-arid conditions for which the model was developed. That assumption may not be justified under irrigated conditions. Moreover, leaching beyond the potential rooting zone does not occur, and so nitrate nitrogen is fully recovered in the vegetation. Ammonical nitrogen, on the other hand, is subject to volatilization under the prevailing conditions of relatively high temperatures and high pH in the soil. It should be realized of course that the fertilizer was assumed to be applied at the beginning of the growing season before the rains started, so that ample time was available for the volatilization process.

3.2   Influence of relative rate of nitrogen turnover in the vegetative tissue

The proteins in the vegetative tissue of plants are not stable, but continuously degrade and have to be resynthesized. Unfortunately, only limited information is available on the rate of turnover of proteins, and most of that refers to very young leaves, so that it is questionable whether those data may be applied to mature or senescing leaves. In mature normal-functioning leaves, where total protein content is more or less stable, the rate of protein turnover corresponds to breakdown and resynthesis of about 10% of the total protein each day (Penning de Vries, 1975; Huffaker & Peterson, 1974). It could well be that in senescing leaves that rate would be higher, either because the "activity" of the leaves decreases, or because the total protein content of the tissue is in a declining state.

Translocation of nitrogen from the vegetative tissue to the developing grains can only take place if the nitrogenous components are in a form that can be transported, i.e. degrated proteins.

To test the effect of increased turnover rates on crop performance, values of the relative turnover rate between $0.075 \ d^{-1}$ and $0.3 \ d^{-1}$ were tested in the model. The results presented in Figure 7 show that increasing turnover rates lead to both reduced grain yields and total dry matter yields, so that the harvest index remains more or less constant, except at the highest turnover rate where a slight drop in the harvest index occurs. These lower yields are the result of accelerated export of nitrogen from the vegetative tissue, including the leaf blades, leading to lower photosynthetic capacity and accelerated senescence.

The nitrogen harvest index, i.e. the ratio between total nitrogen in the grain at maturity and total nitrogen in the above ground material increases from 0.315-0.36 at the lowest turnover rate to 0.63-0.675 at the highest turnover rate, reflecting the more efficient translocation of nitrogen to the grains. The nitrogen concentration in the grains increases over the same

range from 0.009-0.011 kg kg^{-1} to 0.024-0.029 kg kg^{-1}. These results thus indicate a negative relation between grain yield and nitrogen concentration in the grain. These results are in accordance with experimental results where cultivars with high and low protein content in the grains are compared (Kramer, 1979; Mesdag, 1979).

An interesting question arising from these results is, whether genetic differences between high-protein and low-protein cultivars are the cause of lower yields, or are the results of differences in nitrogen turnover. In view of the interest in high N grains with an eye on baking quality an investigation of the genetic variability in nitrogen turnover rates would be of interest.

3.3 Influence of ontogenetic life time of the leaves

In the framework of effects of nitrogen economy on crop performance, a discussion on average life time of the leaves seems somewhat out of place. It appears, however, that a strong interaction exists between the life span of the leaves and the crop's nitrogen economy. The ontogenetic life span of the leaves plays a role only under conditions of high N supply, where leaf death is not influenced by translocation of N from the vegetative tissue to the grain.

In the model the life span of the leaves is related to temperature regime, i.e. leaves are assumed to function until they have accumulated a fixed number of day-degrees. The values defined in the model, expressed in days, refer to a situation with an average temperature of 15 °C, thus an average life span of 50 d assumes a temperature sum of 750 d°C.

The two seasons illustrated here differ in their reaction to increased leaf longevity: in 1976/1977 longer leaf activity increases both total dry matter production and grain yield, hardly affecting the harvest index. On the other hand in 1977/1978 increased leaf longevity hardly effects production, neither of grains, nor of total dry matter. The difference in reaction between the two seasons is not clear at first sight.

An interesting observation from the model results is, however, that in both seasons the nitrogen harvest index increases substantially with increasing life time of the leaves. In 1976/1977 from 0.50 at an average life span of 50 days to 0.60 at a life span of 70 days; for 1977/1978 the values are 0.53 and 0.63, respectively. The longer active life of the leaves permits prolonged translocation of nitrogen to the growing grains, hence a more "efficient" use of the element. This is also borne out by the nitrogen

concentration in the vegetative tissue at maturity, that is 0.014-0.015 kg kg^{-1} at a life span of 50 days and 0.011 at a life span of the leaves of 70 days.

Thus, longer leaf longevity creates a situation where, contrary to the effect of increased nitrogen turnover, increased grain yields are accompanied by higher nitrogen concentrations in the grain. Whether such variability is present in the gene pool is difficult to judge, but the effect should be similar when growth under relatively cool conditions is compared to growth under relatively warm conditions (Spiertz & Ellen, 1978).

4 Concluding remarks

In this contribution some aspects of the nitrogen economy of plants are discussed with a view on its consequences for growth and yield of a wheat crop. The conclusion must be that despite the enormous amount of work that has been done on the subject and the associated multitude of literature available still large gaps in our understanding of important basic processes exist.

It would seem that only application of systems analysis in which an attempt is made to "put things together" in a coherent framework, is a research tool that leads to the explicit expression of such lack of knowledge.

Moreover, such an analysis may help in formulating goals for plant breeders: the data in Figures 1 and 2 indicate that substantial variability exists in the relation gross assimilation-N concentration at the individual leaf level. That could be a trait to be pursued by plant breeders. Breeding for increased leaf longevity, that would lead to higher grain yields, associated with higher protein yields, could be another aim for plant breeders.

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CAPTIONS

Figure 1. The relation between nitrogen concentration in the leaf blade (on a dry weight basis) and the maximum rate of net CO_2 assimilation. •,o: Oryza sativa (Yoshida & Coronel, 1976); ▼: Triticum aestivum (Dantuma, 1973); ▽: Triticum aestivum (Marshall, 1978); ⊘: Panicum spp. (Brown & Wilson, 1983); + Hordeum murinum, ⊕ Phalaris minor (Lof, 1976); x Lolium perenne (Wilson, 1975); ▣ Oryza spp. (Cook & Evans, 1983a; 1983b); ▪ tung (Loustalot et al., 1950); ▲ Festuca arundinacea (Bolton & Brown, 1980).

Figure 2. The relation between nitrogen concentration in the leaf blade (on an area basis) and the maximum rate of net CO_2 assimilation. x Beta 'vulgaris (Nevins & Loomis, 1970); . Oryza spp. (Cook & Evans, 1983a; 1983b); ▲ Oryza sativa (Yoshida & Coronel, 1976); + Glycine max (Boon-Long et al., 1983).

Figure 3. The relation between the net rate of CO_2 assimilation (P_n) and the total conductance for water vapour exchange ($1/R_{H2O}$) of individual maize leaves, grown at optimum and sub-optimum N supply (Source: Goudriaan & van Keulen, 1979).
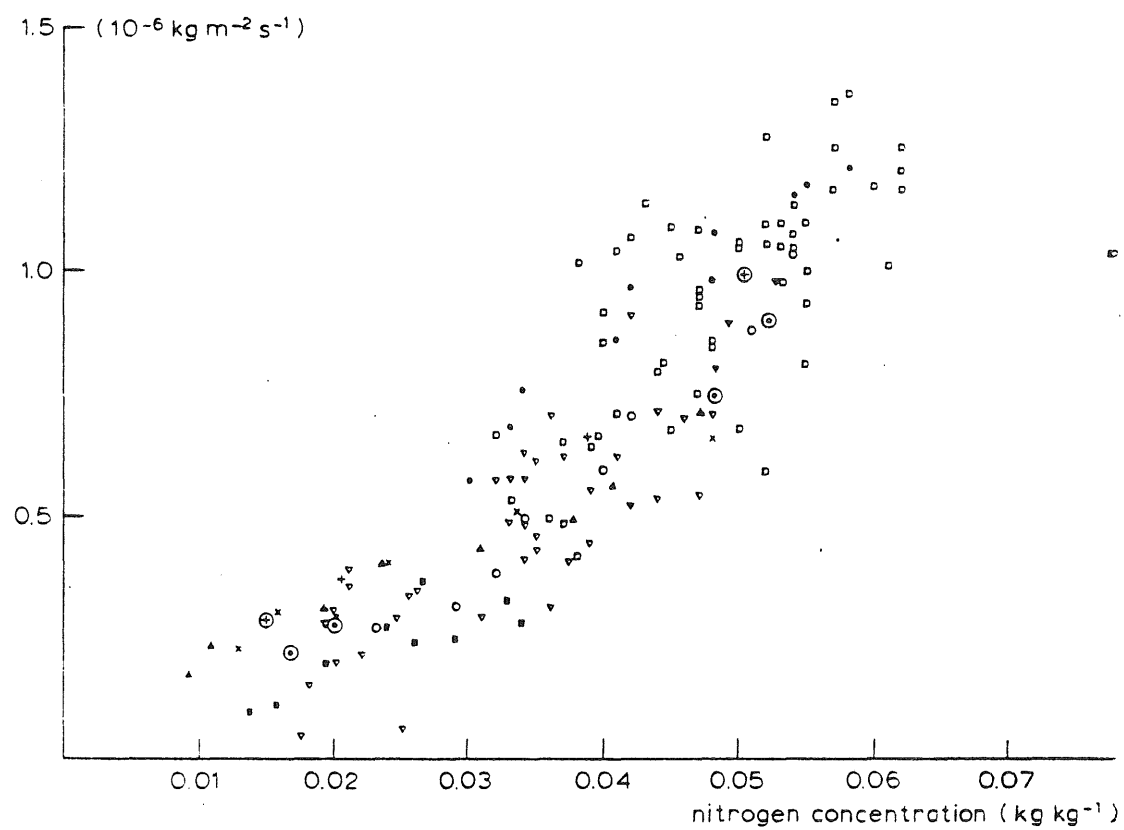
Figure 4. The relation between the nitrogen concentration in the leaf blade and total conductance for water vapour exchange for individual rice leaves (Source: Yoshida & Coronel, 1976).

Figure 5. The relation between the nitrogen concentration in the leaf and the relative rate of leaf area expansion.
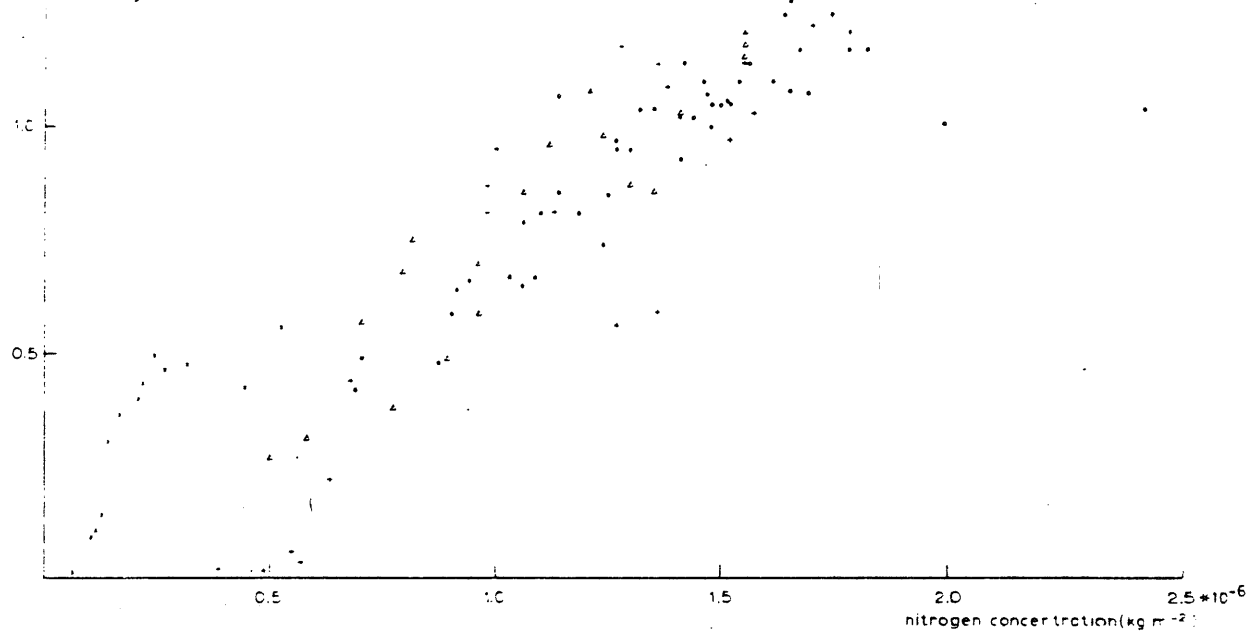
Figure 6. The simulated relation between total nitrogen uptake and grain yield, and that between nitrogen application and nitrogen uptake for a spring wheat crop grown in the northern Negev of Israel, for both ammonium and nitrate fertilizers.
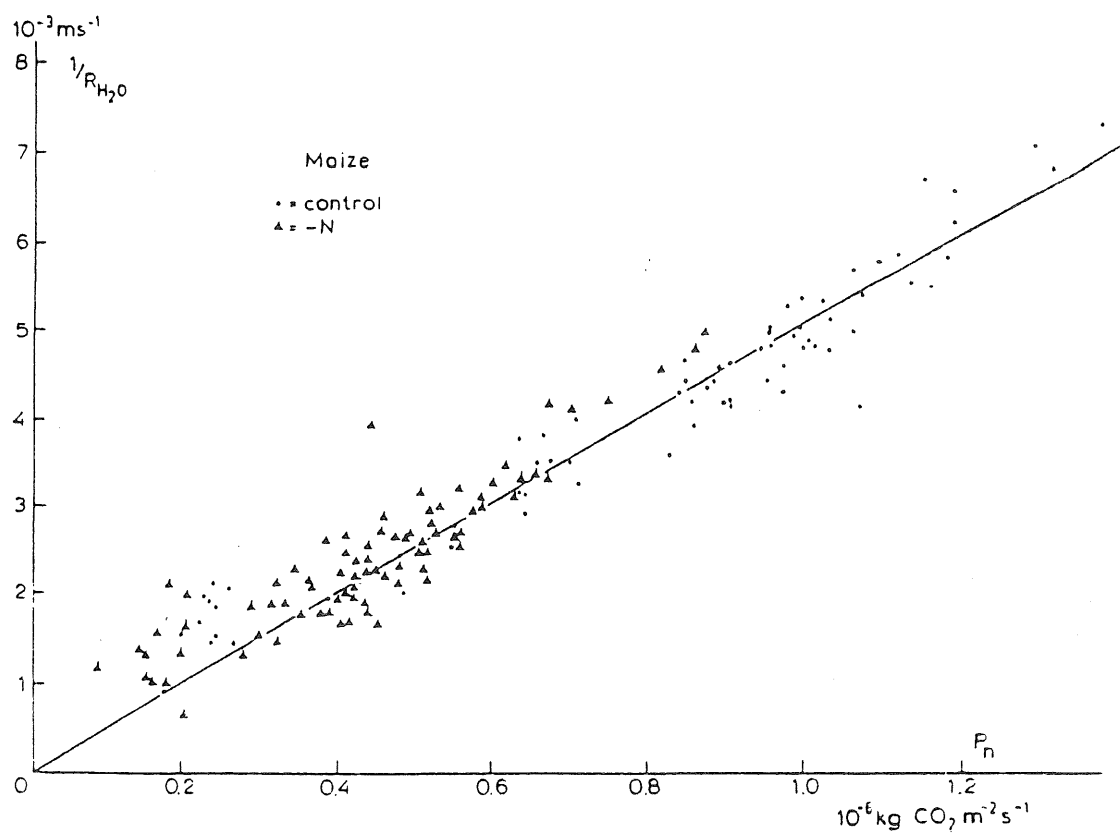
Figure 7. The simulated effect of the relative rate of nitrogen turnover in the vegetative tissue on grain yield and grain nitrogen concentration of a spring wheat crop grown in the northern Negev for two subsequent seasons.
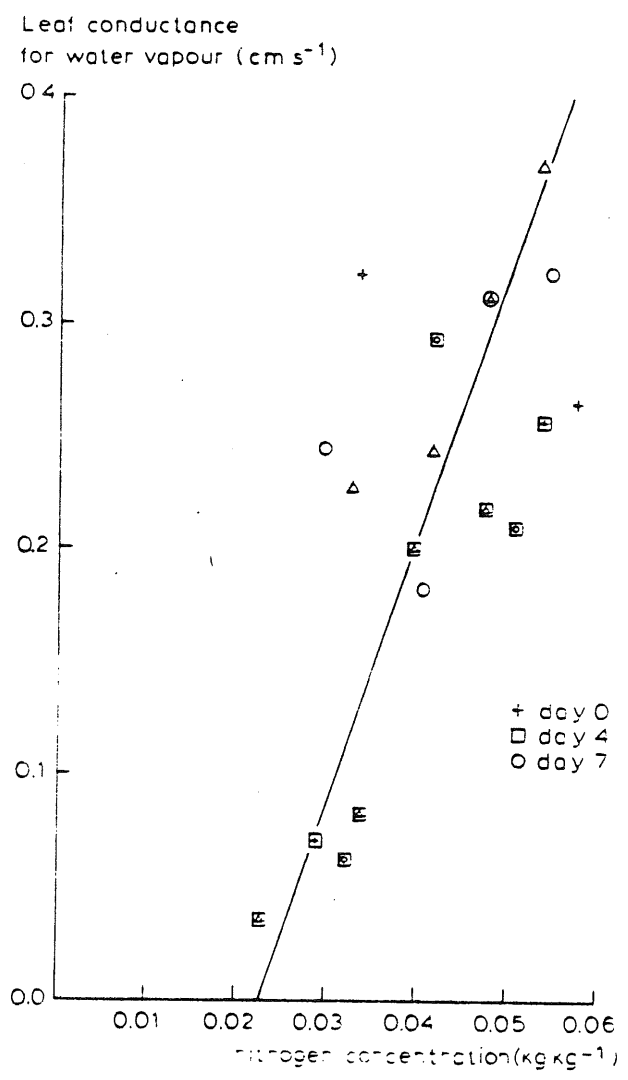
rate of net CO_2 assimilation $(10^{-6}\ kg\ m^{-2}\ s^{-1})$ versus nitrogen concentration $(kg\ kg^{-1})$

rate of net
CO₂ assimilation

(3 — (10⁻⁶ kg m⁻² s⁻))

1.0

0.5

0.5　　　　1.0　　　　1.5　　　　2.0　　　　2.5 *10⁻⁶

nitrogen concentration(kg m⁻²)

Leaf conductance
for water vapour (cm s^{-1})

+ day 0
☐ day 4
O day 7

nitrogen concentration(kg kg^{-1})

fraction of maximum leaf expansion rate

nitrogen concentration(kg kg^{-1})

6

grain yield
(kg hc⁻¹)

N concentration grain
(kg kg⁻¹)

x grain yield ——'75/'76
• N concentration ----'77/'78

0.075 0.10 0.15 0.20 0.30

grain yield
(kg hc⁻¹)

• '75/'76
x '76/'77
△ '77/'78
○ '78/'79

0.01 0.02 0.03
N concentration grain (kg kg⁻¹)