



N uptake and distribution in crops: an agronomical and ecophysiological perspective

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Abstract

The rate of N uptake of crops is highly variable during crop development and between years and sites. However, under ample soil N availability, crop N accumulation is highly related to crop growth rate and to biomass accumulation. Critical N concentration has been defined as the minimum N concentration which allows maximum growth rate. Critical N concentration declines during crop growth. The relationship between critical N concentration and biomass accumulation over the growth period of a crop is broadly similar within major C₃ and C₄ cultivated species. Therefore, the critical N concentration concept is widely used in agronomy as the basis of the diagnosis of crop N status, and allows discrimination between situations of sub-optimal and supra-optimal N supply. The relationship between N and biomass accumulation in crops, relies on the interregulation of multiple crop physiological processes. Among these processes, N uptake, crop C assimilation and thus growth rate, and C and N allocation between organs and between plants, play a particular role. Under sub-optimal N supply, N uptake of the crop depends on soil mineral N availability and distribution, and on root distribution. Under ample N supply, N uptake largely depends on growth rate via internal plant regulation. Carbon assimilation of the crop is related to crop N through the distribution of N between mature leaves with consequences for leaf and canopy photosynthesis. However, although less commonly emphasized, carbon assimilation of the crop also depends on crop N through leaf area development. Therefore, crop growth rate fundamentally relies on the balance of N allocation between growing and mature leaves. Nitrogen uptake and distribution also depends on C allocation between organs and N composition of

these organs. Within shoots, allocation of C to stems generally increases in relation to C allocation to the leaves over the crop growth period. Allocation of C and N between shoots and roots also changes to a large extent in relation to soil N and/or crop N. These alterations in C and N allocation between plant organs have implications, together with soil availability and carbon assimilation, on N uptake and distribution in crops. Therefore, N uptake and distribution in plants and crops involves many aspects of growth and development. Regulation of nitrogen assimilation needs to be considered in the context of these interregulatory processes.

Key words: Crop development, crop growth, nitrogen assimilation, nitrogen uptake, plant regulation, photosynthesis.

Introduction

Agriculture, previously dominated by productivity, now has multiple objectives. The environmental impact of crops and cropping systems, the quality of crop products, the low cost of production and hence increased N use efficiency, are among these objectives.

Understanding the processes that govern N fluxes, particularly N uptake and distribution in crops, is of major importance with respect to both environmental concerns and the quality of crop products. Nitrogen uptake and accumulation in crops represent two major components of the N cycle in the agrosystem. Nitrate ions not taken up by a crop, may potentially be leached to underground water. Modelling N uptake together with soil water transfers is, therefore, key in quantifying and preventing nitrate leaching. Although outside the scope

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of this paper, understanding N uptake and assimilation is also necessary in any attempt to improve the N use efficiency of crops through the adaptation of N fertilization strategies. Nitrogen use efficiency of crops can also potentially be improved through manipulating the N use efficiency of the individual plants. A key question which then arises is which plant process should and could be improved. Given that individual plants within crops are exposed to complex environmental conditions, due to competition for light above ground and for nitrogen and water below ground, it is necessary to evaluate the consequences of manipulating a particular process at the plant level on the overall N use efficiency of the crop.

Past agronomical research into N uptake, and its relation to yield, has mostly been considered empirical. The evaluation of crop N requirements and the analysis of yield components in relation to N supply were mostly directed toward the general objective of satisfying crop N demand (Greenwood *et al.*, 1986). A more functional approach linking plant productivity with N supply was developed in plant ecology, however, this approach was mostly directed toward a search for adaptive strategies of species under contrasting natural environments (Lambers and Poorter, 1992). Research conducted in the last 15 years has allowed the development of a functional approach for crops based on the ecophysiology of N uptake, N distribution and growth (Lemaire, 2001). The first objective of this paper is to review and provide a framework for an agronomical and ecophysiological basis for such a functional approach. The second objective is to illustrate that the processes involved in crop N uptake and utilization are highly interrelated and can, therefore, only be fully understood through a dynamic and integrated approach.

An agronomical approach of crop growth: the concept of critical N concentration

Nitrogen uptake of field crops is highly variable within a single year, between years, between sites, and between crops, even when the N supplies from both the soil and additional fertilizer inputs are plentiful. In situations with a generous N supply, the variability in the dynamics of N accumulation in crops, under different climatic conditions and for different species, can be greatly reduced when crop N content (amount of crop N per unit ground area) is related to crop biomass rather than time (Greenwood *et al.*, 1986; Lemaire and Salette, 1984). This suggests that with an adequate soil N supply, crop N uptake is to a large extent determined by crop growth rate. However, the increase in crop N content with crop mass is not linear, additional N uptake per unit of additional biomass declines as a crop gets bigger. This non-linear relationship between crop N content and crop

biomass appears to be a general phenomenon for vegetative crops as it has been reported for many species (Greenwood and Barnes, 1978; Greenwood, 1982; Penning de Vries, 1982; Lemaire and Salette, 1984; Charles-Edwards *et al.*, 1986; Greenwood *et al.*, 1990; Angus and Moncur, 1985). In several instances, crop N content has been related to crop biomass through the allometric relationship $N_{\text{content}} = aW^b$, where W represents crop biomass per unit ground area (Lemaire and Salette, 1984; Greenwood *et al.*, 1990). It unequivocally follows that $N\% = a'W^{1-b}$, where N concentration ($N\%$) is the percentage of plant mass which is N, and where a and a' differ by a factor dependent on the units adopted for N_{content} and for W . Critical N concentration ($N\%_{\text{critical}}$) is defined as the minimum crop N concentration required to achieve maximum crop growth rate (Greenwood *et al.*, 1986, 1991), and is analogous to the critical N content (minimum N content necessary to achieve maximum crop growth rate). The introduction of this concept has allowed rationalization of the analysis of field data. A statistical approach allowing the determination of critical N concentration of field-grown crops has been proposed (Justes *et al.*, 1994). Critical N concentration is not a goal in itself to follow during crop growth, but rather is a fundamental reference at any growth stage and in any environment, which allows the determination of whether crop N nutrition is supra-optimal (i.e. actual N content is in excess compared to the N content required for maximum growth rate), or sub-optimal with respect to crop growth rate (Fig. 1A). The discrepancy between actual $N\%$ and the corresponding critical $N\%$ at the same shoot biomass indicates the intensity of the N deficiency (or excess) experienced by a crop. Several authors have demonstrated that the reduction in crop growth rate is proportional to the ratio $N\%_{\text{actual}}/N\%_{\text{critical}}$ and have proposed the use of this ratio as a nitrogen nutrition index (Lemaire and Gastal, 1997). The usefulness of such an index is emphasized by the fact that the relationship between critical N concentration and crop mass does not vary substantially with major environmental factors, other than those affecting soil N supply (Lemaire and Salette, 1984; Lemaire and Denoix, 1987; Lemaire and Gastal, 1997).

Critical $N\%$ –biomass curves have been evaluated for several major crops. Comparing a range of cultivated species, Greenwood *et al.* concluded that the major factor which discriminates critical $N\%$ curves between species was their metabolic type, C_3 or C_4 (Greenwood *et al.*, 1990). The C_4 species were found to have a lower critical $N\%$ –biomass curve than C_3 species (Fig. 1B), presumably related to a lower content of photosynthetic proteins. Within the C_3 species, it was observed that legumes have critical $N\%$ –biomass curves almost identical to the critical curves of other C_3 species (lucerne in Lemaire *et al.*, 1985; french beans in Greenwood *et al.*, 1990; pea in

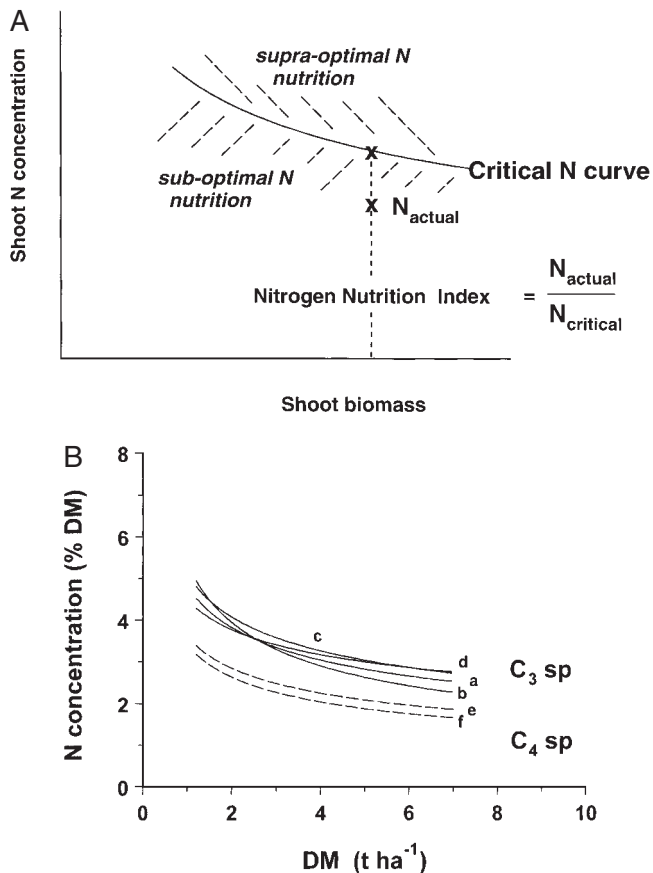


Fig. 1. (A) Critical N concentration curves: principles. (B) Relations available in the literature for different crops: a, perennial grasses ($N\%_c = 4.8W^{-0.33}$; Lemaire and Salette, 1984); b, wheat ($N\%_c = 5.35W^{-0.442}$; Justes *et al.*, 1994); c, pea ($N\%_c = 5.08W^{-0.32}$; Ney *et al.*, 1997); d, winter rape ($N\%_c = 4.48W^{-0.25}$; Colnenne *et al.*, 1998); e, maize, sorghum ($N\%_c = 4.1W^{-0.5}$; Greenwood *et al.*, 1990); f, maize ($N\%_c = 3.4W^{-0.37}$; Plénet and Lemaire, 1999).

Ney *et al.*, 1997). Since the early work (Greenwood *et al.*, 1990), critical N concentration has been evaluated in many cultivated species. The equations of the critical $N\%$ -biomass curves now currently available in the literature (Fig. 1B), confirm the earlier observation (Greenwood *et al.*, 1990) that the differences in curve parameters between various C₃ species are small in comparison to the difference between C₃ and C₄ species. Indeed as parameter determination relies on a statistical approach, it is still debatable whether the value of the parameters reported for the C₃ species differ significantly or not.

What can be learnt from this critical N concentration approach? Firstly, it suggests that the N uptake rate of field-grown crops is regulated not only by soil availability but also by the crop growth rate. This is an important point, because crop N uptake has often been considered in relation either to soil availability (N supply approach), or to crop growth (N demand approach), rarely to both simultaneously. Secondly, as N uptake per unit biomass

decreases as crop mass increases, it suggests that the dependence between N uptake and growth is probably complex. This will be examined using the basis of fundamental physiological and ecophysiological processes in the following paragraphs.

Crop N uptake in relation to soil N

Nitrogen acquisition of crop plants is usually dominantly by the uptake of NO_3^- and NH_4^+ , although soil organic nitrogen can be taken up by plants and may represent a significant proportion of total N absorption under particular ecological situations (acidic soils, low temperature environments). The mineral nitrogen content is generally greater in upper compared with lower soil layers, probably due to more favourable conditions for N mineralization in the upper part of the soil (higher content in organic matter; higher O_2 diffusion). This appears contrary to a dependence of crop N uptake on rooting depth. However, rooting depth determines the ability of a crop to intercept nitrate during periods of leaching and hence may be important from an environmental perspective. In this respect, not only the rooting depth of mature crops but also the rate at which roots of seedlings develop at depth will be important, particularly for crops which have an early phase of development during winter, the period where water drainage occurs most frequently. Rooting depth varies greatly between species and therefore each species requires individual evaluation. Several studies have indicated that soil N availability, although strongly altering shoot growth, does not significantly affect the dynamics of root growth at depth (Gabrielle *et al.*, 1998). The relatively small effect of N supply observed on rooting depth, in comparison to the large effect on shoot growth, probably relies on the decrease in root:shoot ratio observed with increasing N supply (Brouwer, 1962). Both root density and architecture also vary to a large extent between species (Fitter, 1991). In several species it has been observed that local NO_3^- application induces root proliferation due to an increased growth of laterals (Drew and Saker, 1975; Granato and Raper, 1989; Lambers *et al.*, 1982; Samuelson *et al.*, 1992; Robinson, 1994; Zhang and Forde, 2000). However, root growth responses to a localized N supply differ between species. In addition, a large range of root morphological plasticity in response to non-uniform distribution in soil N exists (Grime *et al.*, 1991; Robinson, 1994). As recently suggested, the impact of root proliferation on N uptake may be limited and more critical for plant-to-plant competition in N uptake, than for N uptake of a whole plant population such as a crop (Hodge *et al.*, 1999).

It has been reported in hydroponic studies that uptake of NO_3^- (or NH_4^+) depends on the NO_3^- (or NH_4^+)

concentration in the nutrient solution in a hyperbolic relationship often with multiphasic kinetics implying a complex regulation of uptake (Rao and Rains, 1976; Macduff *et al.*, 1989; Tischner, 2000; Glass *et al.*, 2002). Recently this has also been shown to apply to plants in the field throughout crop development (Devienne-Barret *et al.*, 2000). Interestingly, the latter study also showed that soil NO_3^- concentration regulates crop N uptake, not only under situations of low but also under situations of high soil NO_3^- concentration, when crop N is above its critical N concentration and where excess N accumulation in plants occurs. The regulation of whole plant and crop N uptake in heterogeneous soil remains poorly understood.

The amount of N taken up by the crop has a major impact on overall crop growth rate. The dependence of crop growth on crop N relies on several processes which will now be examined: leaf photosynthesis–N relationships, the distribution of N between leaves, leaf expansion and positioning and subsequent impacts on light interception (Novoa and Loomis, 1981; Sinclair and Shiraiwa, 1993).

Leaf N and leaf photosynthesis

The response of leaf photosynthesis to irradiance is largely dependent on the leaf N content. Photosynthetic proteins, including large amounts of Rubisco and, to a lesser extent, light harvesting complex proteins, represent a large proportion of total leaf N (Evans, 1983, 1989a; Field and Mooney, 1986). The physiological basis of the photosynthesis–leaf N relationship are reviewed in detail elsewhere (Lawlor, 2002). Numerous studies have reported that leaf photosynthesis at saturating light intensity (A_{max}) increases either linearly, or more generally asymptotically, with leaf N content (Evans, 1983, 1989a; Field and Mooney, 1986; see Grindlay, 1997, for a more comprehensive review). The A_{max} –leaf N relationship holds true whether leaf N content and A_{max} are expressed per unit leaf area or per unit leaf mass. The A_{max} –leaf N relationship shows a positive intercept on the N content axis, indicating that when leaf photosynthesis is theoretically zero leaves would still contain significant amounts of N, probably due to non-photosynthetic leaf N (Field and Mooney, 1986; Anten, 1995). The A_{max} –N relationship varies substantially in a wide range of plant species and plant types (Evans, 1989a). The variation is still significant within herbaceous species (Poorter and Evans, 1998), and at an intra-specific level (Nelson, 1988), but seems more limited within cultivated C_3 species (Evans, 1989a; van Keulen *et al.*, 1989), possibly as a result of selection pressure for yield.

By contrast to the large number of experimental reports on the A_{max} –N relationship, data concerning the

impact of leaf N content on light use efficiency are scarce. In part this may be due to no significant effect of leaf N content being observed on many occasions (Anten, 1995). However, a significant effect of leaf N content on light use efficiency has been reported in several studies (Hirose and Werger, 1987; Pons *et al.*, 1989; Muchow and Sinclair, 1994; Drouet, 1998; Gastal and Lemaire, 1997). The influence of leaf N on leaf light use efficiency has a very limited impact on instantaneous canopy photosynthesis especially under a high incident light intensity and when leaf area is low. However, its impact on canopy photosynthesis when integrated over a day or longer growth periods becomes more important, due to the increased duration of periods of low light intensity, and also under a crop of high leaf area index when a greater proportion of the leaves are shaded. The magnitude of the effect of leaf N content on light use efficiency of the leaf is likely to be species-dependent, possibly in relation to observed species differences in the partitioning of leaf N between Rubisco and light harvesting complex proteins (Evans, 1989a). The effect of leaf N content on light use efficiency may be more important in field studies than in studies under artificial lamps, as has been observed for tall fescue (F Gastal, unpublished data). This may also partly explain the limited attention devoted to the effect of N on light use efficiency, as many leaf photosynthesis studies have been conducted on plants grown under artificial light.

Nitrogen distribution between leaves of the canopy

A large body of data indicates that the nitrogen distribution between the leaves of a canopy is not uniform (Grindlay, 1997). Individual leaves in a canopy experience different light environments due to shading by upper leaves; they also differ in age. In addition, different leaves in the canopy may develop under different conditions of N supply because of fluctuations in soil N supply during crop growth whilst leaf production remains continuous. All these aspects will potentially lead to the observed non-uniform N distribution.

Leaves exhibit a structural and functional acclimation of the photosynthetic apparatus to the light intensity experienced during their growth (Reyss and Prioul, 1975; Prioul *et al.*, 1980a; Bjorkman, 1981). This occurs even when light intensity is modulated on only part of the shoot (Evans, 1989b). The light acclimation is largely reversible within a few days (Prioul *et al.*, 1980b).

As a result of this light acclimation process, when light intensity varies with leaf position or is manipulated artificially through stand density, the leaves of a canopy show an increase in N content per area basis (N_L) and

an increase in A_{\max} with increased light intensity received (on herbaceous species: Hirose and Werger, 1987; Pons *et al.*, 1993; Shiraiwa and Sinclair, 1993; Schieving *et al.*, 1992; Evans 1993*a, b*; Lemaire *et al.*, 1991; Anten *et al.*, 1995*a, b*; see Grindlay, 1997, for a thorough review and analysis). The effect of leaf age on N_L and A_{\max} appears to be more limited than the light acclimation effect, though it is recognized that both effects occur concurrently (Hikosaka *et al.*, 1994; Schieving *et al.*, 1992).

Species with relatively horizontal leaves show a steeper gradient in N_L , as a function of leaf area index, than species with more erect leaves (Anten *et al.*, 1995*a*). Several studies have reported that the gradient in N_L with leaf area index is exponential, in parallel with the light gradient, (Hirose and Werger, 1987; Pons *et al.*, 1989; Anten *et al.*, 1995*a*), however, other reports found a more linear relationship (Lemaire *et al.*, 1991; Evans, 1993*a, b*; Shiraiwa and Sinclair, 1993; Grindlay *et al.*, 1995; Dreccer *et al.*, 2000). This variation in the leaf area index– N_L relationship suggests that, despite the general and broad N_L response to light, species may differ in their acclimation responses. Other aspects such as leaf age or N remobilization capacity of the leaf may interfere with the light acclimation resulting in variations in the N distribution profile. A further complication arises with monocot species during vegetative development; they have large standing leaves across the canopy without any specific stem tissue. Leaves thus experience large changes in radiation from their base to their tip. With *Carex acutiformis* a gradient in N_L was observed along the lamina in relation to received light intensity, but this was less steep than on a dicot grown in the same experiment (Schieving *et al.*, 1992). This may result from a larger proportion of N invested in non-photosynthetic tissues of lamina bases to physically support upper lamina portions (Grindlay, 1997).

It has been reported in lucerne (Lemaire *et al.*, 1991, 1992) and in sunflower (Sadras *et al.*, 1993) that lamina N concentration decreases to a smaller extent than N_L , both during crop development and from the upper to the lower leaves in a canopy. The difference between leaf N_L and leaf $N\%$ profiles is related to variations in specific leaf area, which increases with canopy development and within a canopy from the upper to the lower laminae. In grasses, specific leaf area appeared to increase to a lesser extent from top to bottom of the canopy than in dicots (on sorghum: Charles-Edwards *et al.*, 1986; in *Lolium perenne* and *Festuca arundinaceae*: F Gastal, unpublished data), or even was found to decrease in *Carex acutiformis* (Pons *et al.*, 1993). As mentioned previously, grasses have a relatively large mass of structural tissue (midribs, sclerenchymae) in lower portions of laminae. This explains the limited increase or even the decrease in specific leaf area from top to bottom of the

canopy, and is also related to the more limited differences in N_L than $N\%$ profiles.

In general, N supply significantly alters the leaf area index– N_L profile in canopies (Fig. 2). However, several studies show that the effect of N supply on N_L at the top of the canopy is somewhat limited (Shiraiwa and Sinclair, 1993; Grindlay *et al.*, 1995; Dreccer *et al.*, 2000). The decline in N_L with increasing cumulative leaf area index from canopy top or in relation to transmitted light within the canopy, tends to be steeper under low N supply, though differences between slopes of the regressions are not always significant (Grindlay *et al.*, 1995; Anten *et al.*, 1995*b*; Dreccer *et al.*, 2000; Fig. 2). The leaf N content (N_L) at the bottom of the canopy is often as low under ample N supply as under limited supply (Fig. 2), because of the substantially larger leaf area index achieved in well fertilized canopies. Thus, overall, under increasing crop N supply, the amplitude of variation in N_L from top to bottom of the canopy is larger than under a low N supply. The limited number of field studies where the distribution of leaf N has been examined in relation to N supply, contrasts with the large number of studies on leaf allocation in relation to light and photosynthesis. There are indications that N supply may affect leaf area index– N_L profiles differently according to the developmental stage of the crops (Dreccer *et al.*, 2000); particularly during grain filling (Sadras *et al.*, 1993). Further work is needed to understand how N supply

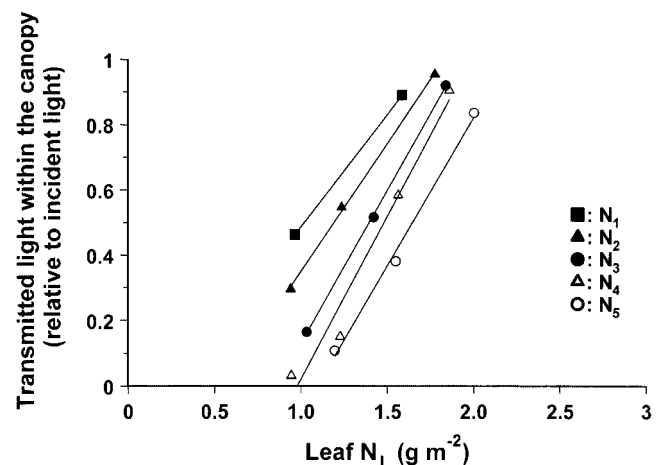


Fig. 2. Incidence of N supply on leaf N_L profile (N content per leaf area basis) from top to bottom of the canopy, plotted in relation to transmitted light within the canopy (F Gastal, unpublished data). Data were obtained on canopies of *Lolium perenne* in the field at the end of a spring growth period. The canopies received five N fertilization rates at the beginning of the spring (50, 75, 100, 125, and 150 kg N ha^{-1} referred to as N_1 , N_2 , N_3 , N_4 , and N_5 , respectively). The canopies were sampled by 10 cm deep layers from top to bottom of the canopy. Nitrogen content and leaf area were determined on leaves by canopy layer. (Transmitted PAR at depth z was calculated as $I_z/I_0 = \exp(-kLAI)$, where I_0 refers to incident PAR above the canopy, LAI refers to leaf area index and where k was taken from Bélanger *et al.*, 1992.)

affects leaf N distribution at different stages of crop growth and development.

Impact of leaf N distribution and photosynthesis–N relations on crop growth

From the top to the bottom of a canopy, individual leaves require progressively less N to maximize their carbon assimilation, due to light attenuation within the canopy and due to the lower amount of N needed to maximize leaf photosynthesis under lower light intensities. Hence it has been suggested that leaf N gradients observed in canopies represent a way to maximize carbon assimilation by the canopy (Mooney and Gulmon, 1979; Field, 1983; Hirose and Werger, 1987). In fact, it has been shown that the actual non-uniform N distribution between leaves in a canopy increases the daily canopy carbon assimilation by 20–40% (depending on species, daily radiation and model assumptions) compared with a theoretical uniform N distribution (Hirose and Werger, 1987; Sinclair and Shiraiwa, 1993; Anten, 1995; Chen *et al.*, 1993; Schieving *et al.*, 1992; Drouet, 1998; Warren and Adams, 2001). However, several studies conducted on various herbaceous species concluded that leaf N gradients experimentally observed in canopies are less steep than gradients that would maximize canopy photosynthesis (Hirose and Werger, 1987; Pons *et al.*, 1989; Evans 1993b; Anten *et al.*, 1995; Drouet, 1998). The adaptation of leaf N content to light intensity during leaf growth, and subsequent N mobilization related to changes in light environment of the leaf during canopy development, may apparently interfere with other physiological aspects or constraints (leaf age; N mobilization capacity of mature or senescing leaves).

Leaf N distribution within the canopy with its consequences for leaf and canopy photosynthesis, are major determinants of the radiation use efficiency (RUE) of a crop (Sinclair and Shiraiwa, 1993). Thus the relationships between N supply, leaf N distribution, and leaf and canopy photosynthesis discussed above, provide a fundamental basis to explain the almost systematic effect of crop N supply on RUE (Muchow and Davis, 1988; Sinclair and Horie, 1989; Bélanger *et al.*, 1992; Muchow and Sinclair, 1994; Bélanger and Richards, 1997). Most of these studies allow the relative effect of N on RUE and on light interception to be evaluated. The effect of N on light interception of the canopy is often substantial and additional to its effect on RUE (Muchow and Davies, 1988; Bélanger *et al.*, 1992; Muchow and Sinclair, 1994). Thus the effect of N on crop growth through its effect on leaf growth is generally as important as its effect on photosynthesis. However, the situation can arise where significant crop N shortage only occurs after canopy closure and thus after maximum light interception is

achieved. In these situations, as illustrated by a study with maize where favourable soil N mineralization and rapid leaf area expansion occurred early in crop development despite a limited N fertilization rate (Plénet, 1995), the effect of N on crop growth is predominantly through its effect on RUE.

Since the effect of N on crop growth is generally due to both an effect of N on leaf photosynthesis and on light interception via leaf growth, it follows that there is a trade-off between allocation of N to maintain N_L and thus photosynthesis of existing leaves, and allocation of N to develop additional leaf area, as pointed out previously (Sinclair and Horie, 1989). Although the first aspect has been covered extensively, the balance between allocation of N to maintain leaf photosynthesis and allocation of N to production of new leaves is poorly investigated and, as a consequence, species strategies are almost not documented.

Crop N and leaf growth

Whatever the relative impact of N on crop growth via leaf area and leaf and canopy photosynthesis, N supply does have a systematic and large effect on leaf growth. As illustrated in Fig. 3, it has been shown in several instances, that N supply increases the leaf area of plants and canopies to a greater extent than leaf and canopy photosynthesis (Robson and Deacon, 1978; Gastal and Saugier, 1986; MacDonald *et al.*, 1986). The increase in leaf area of plants and canopies is brought about by a large effect of N supply on the expansion of individual leaves and on branching, or tillering in grasses (Wilman and Pearse, 1984; Gastal and Lemaire, 1988; Trapani and Hall, 1996; Taylor *et al.*, 1993; Vos and Biemond, 1992; Vos *et al.*, 1996). The rate of leaf appearance and

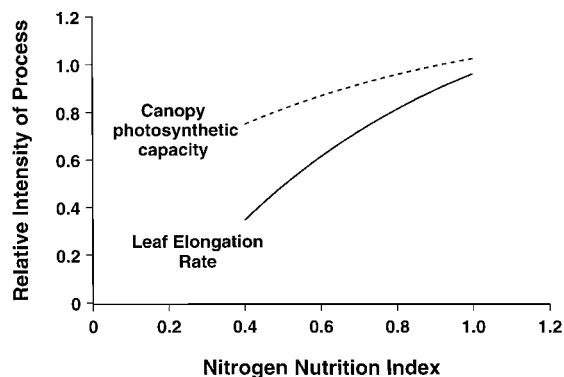


Fig. 3. Comparison of the sensitivity to nitrogen nutrition of leaf elongation and canopy photosynthetic capacity (canopy photosynthesis at a similar leaf area index for various N supply rates). (Redrawn from Gastal *et al.*, 1992, and Gastal and Bélanger, 1993.)

the duration of leaf expansion was little affected by N in many species (Gastal and Lemaire, 1988; Trapani and Hall, 1996; Taylor *et al.*, 1993; Vos and Biemond, 1992; Vos *et al.*, 1996). However, a number of other species do show a significant effect of N on the rate of leaf appearance (Cruz and Boval, 2000). Thus, the marked effect of N supply on leaf expansion and on branching appears a general response, whereas the effect on leaf appearance and leaf expansion duration is more species-specific.

In grasses, the reduction in leaf expansion due to a decreased N supply is often accompanied by an increase in fructans, both at the level of the whole plant and within leaf meristems (Volenc and Nelson, 1984), whilst in dicots starch often accumulates (MacDonald *et al.*, 1986; Paul and Stitt, 1993). The accumulation of non-structural carbohydrates in N-deficient plants suggests that carbohydrate supply is not the cause of the leaf growth reduction under low N supply, though this remains to be demonstrated definitively. Nitrogen supply alters the rates of cell division and cell expansion in growing leaves. In grasses, N supply greatly stimulates cell production rate, and the final cell length is little affected (MacAdam *et al.*, 1989; Gastal and Nelson, 1994; Fricke *et al.*, 1997). Whilst some studies have reported an increased cell elongation rate and a decreased duration of cell elongation in response to N supply (Gastal and Nelson, 1994; Fricke *et al.*, 1997), both processes appeared unaffected in other studies (MacAdam *et al.*, 1989; Gastal and Nelson, 1994). In all instances the impact of N on leaf expansion rate of grasses was related more to the effect of N on cell production than cell elongation rate. In dicots, early studies concluded that the impact of N supply on leaf growth was mostly due to an increased cell growth rate, because a larger final cell size was observed and also because N supply seemed to increase leaf water potential (Radin and Parker, 1979; Radin and Ackerson, 1981; Radin *et al.*, 1982). However, it was shown more recently that N supply does not significantly increase the turgor pressure of growing leaf tissue in grasses (Durand *et al.*, 1994; Fricke *et al.*, 1997), suggesting more an effect of N on wall expansion properties. Whether the response of leaf growth to N differs between grasses and dicots, as suggested earlier (Radin, 1983) remains an open question. It was recently shown in *Ricinus communis* that the relative impact of N on cell division and cell expansion depends on the developmental stage of the leaf (Roggatz *et al.*, 1999). A large effect of N on cell division was observed on this dicot species, similar to the observations on grasses, provided that N starvation was initiated early in leaf development, in the period of intense cell division (Roggatz *et al.*, 1999).

All the above elements underline that current understanding of the regulation of leaf growth in relation to N supply is extremely limited.

Nitrogen allocation to non-photosynthetic vegetative organs

As discussed above, much attention has been paid to the allocation of N to leaves, and even more specifically to lamina, within canopies. However, allocation of N to other vegetative tissues is also quantitatively important. Green leaf N content represented only 53% of shoot N in a lucerne crop (Lemaire *et al.*, 1992), and only 30% of shoot N in a wheat crop at the beginning of the grain-filling period (Grindlay *et al.*, 1995).

The leaf:stem ratio generally decreases as crop biomass increases (Lemaire *et al.*, 1992; Bélanger and McQueen, 1999; Bélanger and Richards, 2000). Therefore, a progressively greater proportion of C and N is allocated to the stem over the crop developmental period. In lucerne (Lemaire *et al.*, 1992) and reproductive ryegrass (F Gastal, unpublished data), the decrease in leaf:stem ratio over the growth period was accompanied by a much larger decrease in N concentration of stems than the limited decrease in N concentration of laminae reported earlier. As discussed earlier, in vegetative grasses where the stem is not developed, lamina bases contain a higher proportion of structural tissue and thus structural mass of lower N concentration, compared with lamina tips. Hence it is a common feature of both dicots and grasses, that an increasing proportion of shoot C and N is allocated to non-photosynthetic tissues during the growth of the crop, irrespective of whether this is achieved through alteration in the leaf:stem ratio or through changes in the proportion of photosynthetic and structural tissues within laminae.

The relative increase in the proportion of structural tissues is greater when plants are growing in dense canopies (Lemaire and Chartier, 1992; Lemaire and Gastal, 1997). Stem growth is enhanced under low blue light in dicots. In grasses, either a low level of light (Davies *et al.*, 1983; Wilson and Laidlaw, 1985; Casey *et al.*, 1999) or a reduction in the red/far-red ratio (Skinner and Simmons, 1993) at the leaf base, such as occurs during light competition, induces an increase in leaf growth and results in longer leaves with a higher cell wall content than shorter leaves (Duru *et al.*, 1999). There is growing evidence that increasing plant density leads to plant photomorphological reactions which determine to a large extent the observed changes in the allocation of C and N between photosynthetic and non-photosynthetic tissues. These considerations bring experimental support to the theory originally developed by Caloin and Yu (Caloin and Yu, 1984) and later by Charles-Edwards *et al.* (Charles-Edwards *et al.*, 1987), that the decline in shoot N concentration over the plant growth period, as observed in the relationship between critical N concentration and crop biomass, is determined by a decrease in the proportion of shoot material directly associated

with growth. Thus, the increase in leaf area during crop growth, achieved by building and positioning new leaves in the light, necessitates proportionally more structural tissues of low N content. The already mentioned trade-off between allocation of N to maintain photosynthetic activity of existing leaves, and allocation of N to build new leaf tissue in order to increase leaf area, is complicated by the additional cost in structural C and N.

Nitrogen supply also induces large changes in C and N allocation between roots and shoots. As discussed previously (Brouwer, 1962), increased N supply decreases the root:shoot ratio. Since this has been repeatedly verified in many studies, it will not be discussed further here, other than to mention that substantial variation between species in the intensity of the root:shoot response to nitrogen supply exists (Robinson, 1994). Root growth in response to N supply is also discussed in an earlier section of this paper.

Conclusion

Since soil N availability, N uptake and distribution, and finally crop growth are permanently interrelated during crop development and growth, the traditional view that crop N uptake and crop growth are either regulated by soil N supply or, alternatively, are regulated by crop demand, needs to be reconsidered and replaced by a more dynamic approach. The concept of critical N concentration has been developed extensively in the last decade. It allows the N status of crops to be precisely and dynamically quantified over their development, and thus represents a unique tool for the study of the various agronomical and ecophysiological aspects underlying the N-growth relationship. Critical N curves are now available on a number of major crops. On an ecophysiological point of view, researches conducted in the last decade have substantially improved current knowledge in several areas: response of root growth to local N supply; N partitioning between leaves of the canopy in relation to light environment and the consequences for plant and canopy photosynthesis; the allocation of N to non-photosynthetic organs, and particularly within shoots. Reviewing these recent advances in the context of a dynamic and integrated view of N uptake and distribution in crops also leads to the identification of a number of areas where current knowledge is particularly limited. The regulation of N uptake under heterogeneous soil N conditions, the regulation of leaf growth in relation to N supply and N uptake, and the regulation of N allocation between mature and growing leaves in relation to N supply, are among these areas where future research would improve an overall understanding of N uptake and distribution in plants and crops.

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