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Water deficit and nitrogen nutrition of crops. A review — Source link

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Published on: 01 Jul 2010 - Agronomy for Sustainable Development (EDP Sciences)

Topics: Deficit irrigation, Farm water, Irrigation, Nutrient management and Agriculture

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To cite this version:

Victoria Gonzalez-Dugo, Jean-Louis Durand, François Gastal. Water deficit and nitrogen nutrition of crops. A review. Agronomy for Sustainable Development, Springer Verlag/EDP Sciences/INRA, 2010, 30 (3), pp.529-544. 10.1051/agro/2009059. hal-00886493

Agron. Sustain. Dev. 30 (2010) 529–544
© INRA, EDP Sciences, 2009
DOI: 10.1051/agro/2009059

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Agronomy
for Sustainable Development

Review article

Water deficit and nitrogen nutrition of crops. A review

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(Accepted 15 October 2009)

Abstract – Among the environmental factors that can be modified by farmers, water and nitrogen are the main ones controlling plant growth. Irrigation and fertilizer application overcome this effect, if adequately used. Agriculture thus consumes about 85% of the total fresh water used worldwide. While only 18% of the world's cultivated areas are devoted to irrigated agriculture, this total surface represents more than 45% of total agricultural production. These data highlight the importance of irrigated agriculture in a framework where the growing population demands greater food production. In addition, tighter water restrictions and competition with other sectors of society is increasing pressure to diminish the share of fresh water for irrigation, thus resulting in the decrease in water diverted for agriculture.The effect of water and nutrient application on yield has led to the overuse of these practices in the last decades. This misuse of irrigation and fertilizers is no longer sustainable, given the economic and environmental costs. Sustainable agriculture requires a correct balance between the agronomic, economic and environmental aspects of nutrient management. The major advances shown in this review are the following: (1) the measurement of the intensity of drought and N deficiency is a prerequisite for quantitative assessment of crop needs and management of both irrigation and fertilizer application. The N concentration of leaves exposed to direct irradiance allows both a reliable and high-resolution measurement of the status and the assessment of N nutrition at the plant level. (2) Two experiments on sunflower and on tall fescue are used to relate the changes in time and irrigation intensity to the crop N status, and to introduce the complex relationships between N demand and supply in crops. (3) Effects of water deficits on N demand are reviewed, pointing out the high sensitivity of N-rich organs versus the relative lesser sensitivity of organs that are poorer in N compounds. (4) The generally equal sensitivities of nitrifying and denitrifying microbes are likely to explain many conflicting results on the impact of water deficits on soil mineral N availability for crops. (5) The transpiration stream largely determines the availability of mineral N in the rhizosphere. This makes our poor estimate of root densities a major obstacle to any precise assessment of N availability in fertilized crops. (6) The mineral N fluxes in the xylem are generally reduced under water deficit and assimilation is generally known to be more sensitive to water scarcity. (7) High osmotic pressures are maintained during grain filling, which enables the plant to recycle large amounts of previously assimilated N. Its part in the total grain N yield is therefore generally higher under water deficits. (8) Most crop models currently used in agronomy use N and water efficiently but exhibit different views on their interaction.

drought / nitrogen nutrition status / supply / demand / balance

Contents

1 Introduction 530
2 Quantification of plant water and nitrogen nutrition status 531
  2.1 Plant water status 531
  2.2 Crop and plant nitrogen status 532
3 Effect of water deficit on nitrogen nutrition dynamic 533
4 Effect of water deficit on plant nitrogen demand 534
  4.1 Growth of the whole-plant biomass 534
  4.2 Root shoot ratio and nitrogen demand 534

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5 Effect of water deficit on nitrogen supply . . . 534
5.1 Effect on soil N transformation processes . . . 534
5.2 Soil fluxes : transport of nitrogen to the roots, mass flow and diffusion . . . 535
5.3 Plant physiological processes involved in the definition of nitrogen supply . . . 535
6 Response of crop physiological functions involved in nitrogen nutrition to water deficit . . . 536
6.1 Nitrogen assimilation in plant tissues . . . 536
6.2 Effect on nitrogen movement through the xylem . . . 537
6.3 Remobilization of nitrogen to grains . . . 537
7 Concepts required for simulation models . . . 537
8 Conclusion . . . 538

1. INTRODUCTION

Water and N are the most limiting factors in agricultural production in most parts of the world, especially in arid and semiarid zones. Given current and future needs for high yields (Cassman, 2001; Sheehy, 2001), concerns are now being raised regarding the soil resources necessary to meet human needs. Traditionally, water and N have been overused in agriculture for decades, but this is no longer sustainable, considering the economic and environmental costs of these practices (Addiscott et al., 1991; Jury and Vaux, 2005). More than 55% of the increase in crop production, especially in emerging countries, comes from the use of chemical fertilizers, with N fertilizers being dominant (Li et al., 2009). However, N is also a significant pollutant that has a great impact on ecosystem deterioration (Galloway et al., 2008) and biodiversity (Stevens et al., 2004). Water scarcity, pollution and energy consumption are driving the maximization of water and N use in agriculture, in order to meet current and future demand while reducing resource requirements.

Climate change is an additional factor that increases uncertainty over the supply of resources (Asseng et al., 2009). Rainfall patterns are expected to change across the world (Giorgi and Bi, 2005), and for some regions, including most of Europe, droughts will be more frequent and severe (Easterling et al., 2000). This means that irrigation water will be more necessary than before to maintain production levels, and that crops will face water scarcity more often.

In situations where water availability cannot be assured, a plant can be subjected to a water deficit that may diminish growth. There are many physiological processes that are affected by water availability, mineral nutrition among others (Lemaire and Denoix, 1987; Onillon et al., 1995; Gonzalez-Dugo et al., 2005). As the major transport agent, and given its central role in biology, water determines the entire N biogeochemical cycle and, ultimately, its availability for plant production. The purpose of this work is to review the major advances in the assessment of the effect of water deficit on N nutrition.

The effect of water deficit on N nutrition has been the subject of considerable research at both plant (Morgan, 1984; Nicolas et al., 1985; Larsson, 1992; Matzner and Richards, 1996) and canopy (among others, Lemaire and Denoix, 1987; Cantero-Martinez et al., 1995; Onillon et al., 1995; Gonzalez-Dugo et al., 2005, Mistele and Schmidhalter, 2008) levels, but its involvement in a large number of interconnected metabolic processes makes it difficult to predict the effect of water deficit on plant N nutrition status. It is therefore necessary to consider the series of bio-physical and chemical processes to which N is subjected, in different chemical forms and through transfers between living organisms and abiotic components in an ecosystem.

N_2 fixation in leguminous plants is also known to be affected by water scarcity. Symbiotic fixation will not be considered within this work. For more information, see Streeter (2003) and Thomas et al. (2004).

During its life cycle, a plant may be subjected to a water deficit, a N deficit or a combination of both, thus co-limiting (Sadras, 2005) its productivity. The effects of water and/or N deficit on plant production therefore depend on their timing and intensity (Bradford and Hsiao, 1982; Nielsen and Halvorson, 1991). Irrigation and fertilizer application increase yield when soil water and N levels are limited. Due to increasing water shortages at the global level and groundwater pollution, while demand for food grows, it is essential to maximize the yield per unit water and N applied.

Crop N uptake has often been considered in relation either to soil availability (soil N supply approach) or to crop growth (N demand approach). It actually results from both (Gastal and Lemaire, 2002). Nitrogen absorption by crops is automatically reduced under dry conditions, even when mineral N is present in the soil colonized by roots (Gonzalez-Dugo et al., 2005). The absorption of N by roots requires the presence of water in the soil, as it is the agent that transports solutes to the soil-root interface (Garwood and Williams, 1967). Under water scarcity, N demand by plants is reduced, as growth rate is diminished. If the effect on N supply is greater than that on plant growth, the result will be a N deficiency. The implications of this demand/supply duality can be observed when different species exhibiting contrasted growth rates are compared under similar conditions (Gonzalez-Dugo et al., 2005). This deterioration of N nutrition also implies a reduction in growth in addition to water deficit–induced reduction. This series of direct and indirect (via N limitation) effects of water shortage on plant growth makes any quantification of the effect of water deficit on N nutrition a complex task. The correct assessment of nutrition status by indices and the use of physiology-based simulation models are therefore valuable tools for the quantitative assessment of direct and N-induced water effects on growth.

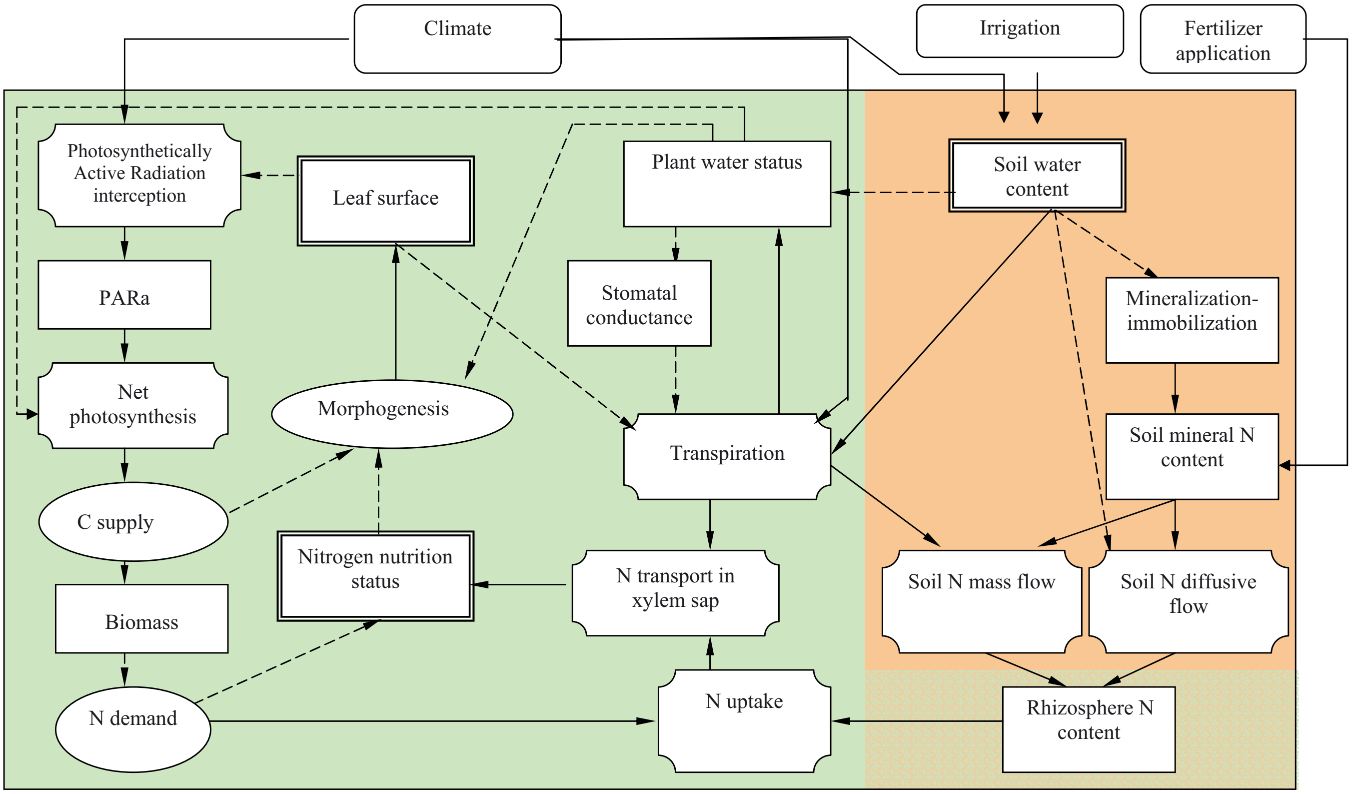

Figure 1. Conceptual framework of the principal processes involved in the response of crop N nutrition to water deficit. Plain arrows indicate fluxes (mass or energy), while dotted arrows indicate direct causal relationships.

The influence of water deficit on N nutrition status is at play at the level of the soil (through the availability of mineral N for root uptake) as well as at plant level. However, it is difficult to ascribe a ranking to any of these levels in terms of their effects because water availability for transpiration, carbon supply and growth potential all determine N demand, assimilation and distribution within the plant. These complex relationships are summarized in Figure 1, where the most important processes located in the soil and plant are shown. This review focuses on the principal processes affected. It first describes the main features of an operational definition of plant N nutrition status, in order to assess plant N demand correctly. It then analyzes the N biogeochemical cycle from the soil to its incorporation in the plant structure. Finally, some of the most used physiology-based simulation models are reviewed in order to analyze how the effect of water and N interaction on plant growth is modeled.

2. QUANTIFICATION OF PLANT WATER AND NITROGEN NUTRITION STATUS

2.1. Plant water status

The measurement of plant water status in terms of the water potential of leaves (ψ; MPa) directly generates a variable that is relevant to both water absorption and plant functioning, related specifically to the turgor pressure of cells (P; MPa):

$$\psi = P - \pi \qquad (1)$$

where π is the osmotic pressure of leaf tissues (MPa). The absorption of water into the plant, and its transpiration, are directly proportional to the fall in ψ values throughout the *soil plant atmosphere continuum*. This approach (Van den Honnert, 1948) has been widely validated and has proved its ability to explain most changes in plant water status in the field, because the main factors involved in water movements are fundamentally physical (Dixon and Joly, 1895; Philippe, 1966; Wei et al., 1999; Tyree and Cochard, 2003). Furthermore, physiological variables relevant to the plant (π and P) are directly related to the ratio between the actual water volume of the plant and its maximum volume (at full turgor and $\psi = 0$). The plant water status is hence best measured in most cases by the mean leaf water potential.

One of the main limitations for the assessment of water status using leaf water potential is that it is very time-consuming. Remote sensing-derived techniques are opening new avenues in assessing plant nutritional status (Berni et al., 2009). Thermal and multispectral information acquired by sensors onboard satellite or airborne platforms provides a sound basis for developing indices to assess plant water status, such as the Crop Water Stress Index (Idso et al., 1981; Jackson et al., 1981), which is closely related to the canopy temperature and stomatal conductance (Berni et al., 2009). Other indices have been developed from spectral information. The Photochemical Reflectance Index (Gamon et al., 1992), which is related to the xantophyll cycle, has demonstrated a strong relationship with water status and canopy temperature (Suarez et al., 2009). A major reason for the interest in these techniques is the possibility of remote measurement, which helps avoid time-consuming techniques, such as water potential or stomatal conductance, used for assessing water status at the field or farm level.

2.2. Crop and plant nitrogen status

The assessment of plant N nutrition status is far more complex than that of plant water status, because both in-soil and in-plant biological processes directly interfere with N availability and uptake, and even under optimum conditions, N concentration in the plant diminishes continuously during crop development (Van Dobben, 1962; Angus and Moncur, 1985; Van Keulen and Seligman, 1987). The cause of this decline is linked firstly to N dilution within the plant volume. Plant N is mainly located in metabolically active aerial plant parts, and is thus related more directly to plant surface than to plant volume. As a plant grows, the proportion (in weight) of structural and storage tissues, which are relatively poor in N, increases. As a consequence, the average plant N concentration diminishes (Greenwood et al., 1990; Lemaire and Gastal, 1997). At the crop level, the relationship between plant N content and its surface also results from the close relationship between the shoot N concentration and the incident solar irradiance (Hardwick, 1987; Gastal and Lemaire, 2002). Within the canopy, leaves exposed directly to solar radiation have the highest N concentration, which optimizes N use relative to carbon assimilation (Hirose and Werger, 1987; Hikosaka et al., 1994). Three-quarters of total reduced N in the leaf may be connected with photosynthesis (Field and Mooney, 1986), mostly in the form of RuBP carboxylase and chlorophyll. In order to measure plant N nutrition status, several indices have been designed in recent decades. Overman et al. (1995) developed a model where growth was related to fertilizer application. However, the actual amount of N available for the plant, including mineralized soil organic N, is not considered, making that approach difficult to extrapolate to different scenarios (Jeuffroy et al., 2002). In spite of their wide range of possible applications, indices considering soil N content only do not seem suited for assessing plant N status. Nitrogen concentration or uptake could not represent by itself the plant's N nutrition status, as it is directly related to plant biomass and growth rate (Lemaire and Gastal, 2009). In a controlled environment, it was shown that the relationship between N uptake (NO_3^- or NH_4^+) and the ionic concentration in soil solution followed a hyperbolic-type law with several kinetic phases (Rao and Rains, 1976; MacDuff et al., 1989; Tischner, 2000; Glass et al., 2002). Devienne- Barret et al. (2000) showed that such relationships also held true in the field. Meanwhile, Lemaire and Meynard (1997) pointed out that the N available for plant uptake is not only defined by the amount of mineral N contained in the rooting zone, but also by soil conditions defining root growth and activity.

At the crop level, Lemaire and Salette (1984) studied the relationship between shoot N content (in %) and dry matter content in tall fescue and cocksfoot plots cut to a stubble height of 5 cm. They defined a “critical N concentration” as the minimal N concentration required to achieve a maximal growth rate. Using the data obtained at several N fertilizer application rates, they showed that the critical N concentration was a function of aboveground biomass, which was statistically fitted to an allometric function:

$$N_c = a \cdot W^{-b} \tag{2}$$

where N_c is the critical N concentration (%) in the dry matter yield (W, in T ha^{-1}), and a and b are two parameters (equal to 4.8 and 0.36, respectively) for a tall fescue crop. Similar values were found in a number of other crop species (e.g. wheat: Justes et al., 1994; Mistele and Schmidhalter, 2008; pea: Ney et al., 1997; rape: Colnenne et al., 1998; potato: Bélanger et al., 2001; maize and sorghum: Greenwood et al., 1990; maize: Plénet and Lemaire, 1999). In all these species, the main difference was clearly related to the two metabolic pathways, C3 and C4 (Greenwood et al., 1990). According to this, the Nitrogen Nutrition Index proposed (I_{NN}, Eq. (3)) is the ratio between the actual shoot N concentration (N_o) and the critical value given for its shoot dry weight (Lemaire and Gastal, 1997).

$$I_{NN} = \frac{N_o}{N_c} \tag{3}$$

where N is non-limiting for growth when the Nitrogen Nutrition Index is larger than 1. The N Nutrition Index is subject to considerable inertia as it requires a significant quantity of biomass and it is difficult to keep accurate records over time, as the surface area required to measure yield is relatively large. This is a major drawback when trying to link rapid changes in water status to crop N status. Another limitation when determining the Nitrogen Nutrition Index is that it only applies to crop level and does not provide a direct and accurate estimate of the N status of individual plants.

At the plant level, it will be necessary to distinguish between the N nutrition status of different elements (species, populations or individual plants with different water status) within a complex crop, as in intercropping systems (e.g. in vine-grass systems, Celette et al., 2005) or in forage production. A solution to this problem was recently proposed by Farrugia et al. (2004), who found a linear relationship between the Nitrogen Nutrition Index (I_{NN}) and the N concentration of leaves directly exposed to incident radiation (N_{sup}), i.e., lamina at the top of the canopy:

$$N_{sup} = 3 \times I_{NN} + 0.97. \tag{4}$$

Duru (2004) fully confirmed this relationship in cocksfoot. With this method, the Nitrogen Nutrition Index can be determined rapidly, and it allows separate analysis of the N status of species growing together on the same plot, provided they

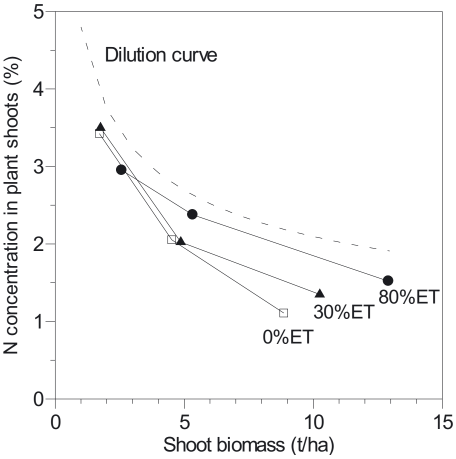

Figure 2. Relationship between shoot biomass and N concentration during the pre-anthesis period under four water treatments, ranging from 0 to 80% of the fully irrigated level (FI), with a N application rate of 210 kg N·ha^{-1}. The dotted line corresponds to the dilution curve of equation (2) for tall fescue and cocksfoot (Lemaire and Salette, 1984). Based on tabulated data from Alvarez de Toro (1987).

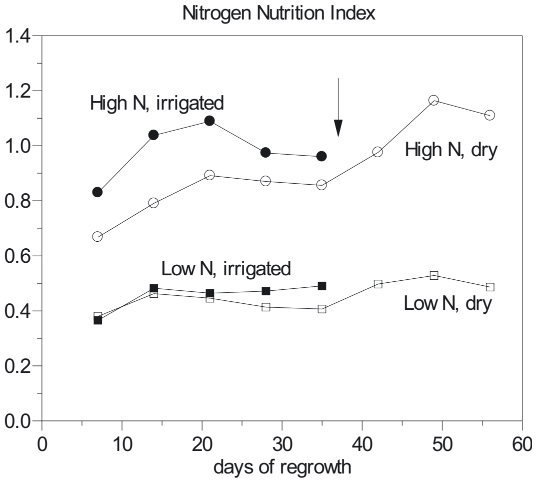

Figure 3. Changes over time in the Nitrogen Nutrition Index during summer regrowth of a tall fescue sward. Four treatments were studied: high (circles) and low (squares) N applications. Black and white symbols show the irrigated and dry treatments, respectively (After Onillon et al., 1995).

have some leaves in the top layer of the canopy. It also increases the possibility of assessing the N status of a crop in situations where its growth is very limited, as is often the case with water deficits. Other authors recently found a relationship between the Nitrogen Nutrition Index and the chlorophyll and polyphenol contents in wheat, which can be used as an indicator of the Nitrogen Nutrition Index (Cartelat et al., 2005; Rodriguez et al., 2009). Accurate tools are thus already available for the assessment of water and N nutrition status, which is a sine qua non condition for elucidating their interaction and its final effect on growth and development.

3. EFFECT OF WATER DEFICIT ON NITROGEN NUTRITION DYNAMIC

There is some evidence in the literature that shows how N status is altered by water deficit, both in the shorter and the longer term. Using the tabulated data generated by Alvarez de Toro (1987) during an irrigation experiment on sunflower, the relationship between shoot growth and N content during the pre-anthesis period was established (Fig. 3). From this work, we have selected three watering treatments (applying 0, 30 and 80% of evapotranspiration requirements, ET) receiving 210 kg N/ha. Despite the lack of any published references concerning the suitability of the critical N curve in sunflower, this figure clearly shows that for the same quantity of N applied to the soil, and with lower shoot biomass, especially on the last measurement date, N nutrition status declined under drier treatments (0% ET and 30% ET). A similar response was found with less fertilizer application, but the differences between irrigation regimes were smaller (not shown).

In tall fescue, Onillon et al. (1995) analyzed the effect of drought on the relationship between shoot growth and shoot N content from which the Nitrogen Nutrition Index could be computed (Fig. 2). Dry treatments generally exhibited lower Nitrogen Nutrition Index values than irrigated treatments. This effect was more pronounced when the amount of available N was higher. The authors found that in most cases, rewatering and the recovery of crop water status increased N status to values that were similar to those measured on irrigated plots. Gonzalez-Dugo et al. (2005) showed the variability in the resulting N nutrition status (established by means of the Nitrogen Nutrition Index) in two forage species displaying contrasting growth rate and root architecture (and sown on the same soil) when water and N were both limited. Italian ryegrass had a slower growth rate with a high percentage of fine roots in upper layers, while tall fescue showed a higher growth rate, but with thicker and deeper roots. Tall fescue was found to be more sensitive to water shortage-induced N deficiency, as its growth rate was higher and its root system performed less well in N acquisition. The importance of biomass and plant N remobilization in the inertia of N nutrition status as well as of the root system distribution was highlighted. The recovery capacity of Italian ryegrass (determined as the rate of increase in the Nitrogen Nutrition Index during a rewatering period) was thrice that of tall fescue.

Nitrogen-use efficiency (biomass produced per unit of N absorbed), which is related to the final Nitrogen Nutrition Index obtained at harvest and which may reflect the integrated impact, is also affected by water shortage. In wheat, Fan and Li (2001) found that N-use efficiency was increased by water deficit and diminished by the dose of N applied. Pirmoradian et al. (2004) reached the same conclusions in rice, but the effect was only significant at high fertilizer application rates. In that case, and with a N application of 80 kg N · ha^{-1}, physiological efficiency (kg grain produced · kg^{-1} N removed) doubled when 50% more water was applied. Gajri et al. (1993) found a marked interaction between N and water for yield, and dependence of water-use efficiency on the N rate and N-use efficiency on the water supply. The effect of water deficit on plant N recovery capacity and on N-use efficiency was reviewed by Aulakh and Malhi (2005).

4. EFFECT OF WATER DEFICIT ON PLANT NITROGEN DEMAND

4.1. Growth of the whole-plant biomass

It has been well established that water deficit reduces plant growth, primarily due to a reduction of the stomatal conductance that inhibits the C assimilation (Garwood et al., 1979; Bradford and Hsiao, 1982). Concerning yield, the stage at which drought occurs is critical; its effects are most pronounced if it takes place at an early stage. The first process affected by water deficit is foliar development and expansion (Fischer and Hagan, 1965; Bradford and Hsiao, 1982). As leaves are the vegetative organs that display higher N content during early developmental stages, N demand is also drastically reduced in early water deficits. Furthermore, during exponential growth, when the soil is not fully covered, drought restricts the active photosynthetic surface area, which causes a reduction in carbon assimilation and transpiration (Cowan, 1982; Durand et al., 1989) (see Fig. 1). When the leaf area index is below a value of approximately 3, the percentage of PAR absorbed to irradiated is below its potential maximum (Gosse et al., 1982; Durand et al., 1991; Akmal and Janssens, 2004). This also diminishes N needs (Nielsen and Halvorson, 1991), and may lead to a somewhat paradoxical situation where, for the same N uptake, an irrigated plant might experience N deficiency while a rainfed (and smaller) plant will maintain optimum nutrition status (Gonzalez-Dugo et al., 2005).

One source of complexity is that both N and water can affect leaf expansion and leaf photosynthesis simultaneously (Gastal and Saugier, 1989; Ghashghaie and Saugier, 1989, Durand et al., 1995; Jeuffroy et al., 2002) (Fig. 1), and their effects are intermingled. In tall fescue, experimental evidence suggested that water deficit did not alter the response of LER to N stress and vice versa (Durand, 1994). Under normal field conditions, such a reduction in photosynthesis is primarily a consequence of stomatal closure (Ghashghaie and Saugier, 1989). In the longer term, water deficit also induces N deficiency, that may further limit photosynthesis (Morgan, 1984; Lawlor et al., 1987; Ciompi et al., 1996; Arora et al., 2001). Photosynthetic rate is largely determined by the presence of RuBP carboxylase and chlorophyll content, both linearly related to leaf N content (Evans, 1989). Furthermore, Radin and Parker (1979) studying cotton plants and Broadley et al. (2001) studying lettuce demonstrated that soil N deficiency increased the sensitivity of stomata to water deficit, inducing lower leaf water potentials in a high transpiration regime, as measured in tall fescue (Onillon et al., 1995). Jacob et al. (1995) stated that the most important effect of N deficiency on plant water conductance occurs at the mesophyll level.

4.2. Root shoot ratio and nitrogen demand

The root/shoot ratio tends to increase with drought, largely due to a stronger effect of water deficit on shoot growth than on root growth (Sharp et al., 1988; Durand et al., 1989; Saab et al., 1990; Engels et al., 1994). In some cases, the root system may even continue to expand at very low water potential, whereas aboveground growth is completely halted (Wu et al., 1996). Because roots contain much lower concentrations of N than aboveground biomass, this change in the allocation pathway diminishes N needs. Measurements on roots are prone to major errors in the field (Pierret et al., 2005). Root mass changes under water deficit may be overestimated because of the restriction of root fragmentation and destruction by soil organisms, which depend on soil water content. However, some authors have found that the root growth of rice increased under water deficit (O'Toole, 1982; Ingram et al., 1994). An increase in root depth penetration has also been reported in rice (Mambani and Lal, 1983). By contrast, Yamauchi et al. (1996) observed a reduction in root growth as a result of drought. Engels et al. (1994) found that drought reduced root growth near the soil surface but enhanced it at lower levels. Onillon (1993) stated that the effect of water deficit on root dry weight was dependent on N fertilizer application. In any case, such positive effects on root growth may not necessarily ensure improved conditions for N nutrition because newly colonized root zones are often deeper than N-rich topsoil horizons.

5. EFFECT OF WATER DEFICIT ON NITROGEN SUPPLY

5.1. Effect on soil N transformation processes

Nitrogen transformation processes closely depend on water and its mobility in the soil. Among all the factors affecting soil nutrition, storage capacity and accessibility, soil texture, root depth and organic matter concentration deserve particular attention (Keller, 2005).

The size of soil NO_3^- and NH_4^+ pools reflects the balance between various fluxes which result from several soil processes (Fig. 4): plant N uptake, mineralization, immobilization, nitrification and losses to the atmosphere following denitrification and volatilization (Scholes et al., 1997, Lemaire et al., 2004). Mineralization, immobilization and nitrification are affected by temperature and soil water content (Pastor and Post, 1985; Gorissen et al., 2004; Lemaire et al., 2004). Smolander et al. (2005) showed that a drought lasting less than two months was not sufficient to destroy microbial biomass; its activity was diminished but recovered completely soon after rewetting. Although sensitive to water deficits, N mineralization by soil micro-organisms may indeed be more resistant than is sometimes suggested, partly because immobilization could be more sensitive to water deficits (Valé et al., 2007).

The response of microbial biomass, nitrification and mineralization during dry periods has been studied in various types of vegetation (Mazzarino et al., 1998 in the Patagonian steppe; Pulleman and Tietema, 1999 in *Pseudotsuga mensiezzii*; Schimel et al., 1999 in the Alaskan taiga; Fierer and Schimel, 2002 in perennial oak and *Bromus*; Kellilher et al., 2004 in pine forest, Smolander et al., 2005 in a Norwegian Picea forest). Westerman and Tucker (1978) showed that during a wet period, the soil mineral N content decreased because of the increase in immobilization by microorganisms and losses to the atmosphere. Rain pulses can thus enhance microbial activity without exerting any significant effect on plant growth and hence on N demand by plants (White et al., 2004). During dry periods, root death increases (Huang and Gao, 2000); the soil organic labile N pool may do so as well (White et al., 2004). Austin et al. (2004) demonstrated that mineralization was activated by a water pulse after a drought period. However, following a dry period, during which root and bacterial death increased the amount of soil organic matter, both the immobilization rate and nitrification increased after soil rewetting (Smolander et al., 2005). No general effect of drought on long-term soil mineral N availability can thus be expected from such a complex network. Furthermore, because of the large error inherent in the measurements of root compartments, and given the importance of the disturbances caused by drought in cropping systems, this topic continues to be a major area for research.

5.2. Soil fluxes: transport of nitrogen to the roots, mass flow and diffusion

Luxmoore and Millington (1971) indicated that the uptake of N and water may not occur throughout the entire root system. Using a system to inject nutrients at controlled depths in soil, the experiments carried out by Garwood and Williams (1967) proved that, as the soil became drier, N could be removed by a grass crop only when it was made available in deeper, moist soil horizons. Although other mechanisms might have been involved, their experiment was pioneering in suggesting that water flow influenced the local availability of N to roots. Indeed, insofar as N is dissolved in the soil solution, N uptake clearly depends on (i) water flows from the soil to the root system (Keller, 2005), and distribution of N and roots within the soil profile is essential, and (ii) ion diffusion fluxes in the rhizosphere.

Water in the soil solution is loaded with anions, cations and soluble organic molecules, transported to the roots by the stream produced by the transpiration demand, creating convective flow or "mass flow" (Fig. 1). Thus, the amount of N solutes reaching the root surface is dependent on the water flux and the N concentration of the soil solution. Any trait in the soil or root system that alters water extraction from the soil will thus directly determine the associated flow of ions to the root surface. Kovacs (2005) demonstrated the importance of mass flow to the simulation of plant N uptake, and its effect on maize production.

Because root N uptake is an active process, if the plant N uptake capacity is higher than the amount of N reaching the root, a N concentration gradient can be built up in the rhizosphere, with lower concentrations at the root surface (Porporato et al., 2003). This causes a diffusive flow, expressed as follows:

$$J = -D \cdot A \cdot \nabla c \quad (5)$$

where J ($\mathrm{mol \cdot s^{-1}}$) is the flux, and ∇c ($\mathrm{mol \cdot cm^{-3} \cdot cm^{-1}}$) the concentration gradient, D ($\mathrm{cm^2\,s^{-1}}$) the diffusion coefficient and A ($\mathrm{cm^2}$) the area for diffusion. As already noted, measurements of A are known to display large errors (Pierret et al., 2005). A is generally estimated after root length density. The D value also (empirically) reflects the reduction in the diffusion rate due to chemical reactions, and the tortuousness of the trajectory, the latter being related to the spatial distribution of water-filled soil pores (Barber, 1974). Diffusion is thus strongly dependent on soil properties and humidity. It is also sensitive to dispersion, which depends on the shape and orientation of soil pores. This is generally expressed using an additional dispersion coefficient. In order to simulate the diffusive flow, the root can be considered as a cylinder of a given radius surrounded by a concentric soil volume (Gardner, 1960). Diffusion to a single root depends, in the first instance, on the radius of the concentric soil cylinder that is explored by the root, which is a function of the distance to the next root. This can be related to the root length density (Van Keulen, 1981; Klepper and Rickman, 1990).

When water flow is weak, or if the solution concentration is low, diffusion increases in relation to mass flow (Passioura, 1963; Raynaud, 2004). This is thus the case in low fertility media (Williams and Yanai, 1996) or with low water availability. Using a theoretical model (de Wit and van Keulen, 1972), Van Keulen (1981) performed a series of simulations to compare the effects of mass flow rate, dispersion and root density on anion extraction from the soil. He showed that the anion extraction rate increased markedly when root density was doubled or when dispersion was set at nil.

The theoretical framework was hence well established by all these authors. However, the leap to accurate determination of N flow under field conditions is difficult due to our limited knowledge of functional root architecture (Pierret et al., 2005). However, there have been some promising advances in the analysis of root architecture (Doussan et al., 2003; Pierret et al., 2007).

5.3. Plant physiological processes involved in the definition of nitrogen supply

To date, simulation models and experiments performed in nutrient solutions with labeled N have been the only techniques available to analyze N uptake independently of soil water dynamics. Caution should thus be adopted when drawing any quantitative conclusions using these approaches. There is, however, evidence of the direct effects of water deficit on N uptake. Nitrogen uptake is an active process. Based on an analysis of root respiration, Bloom et al. (1992) showed that the amount of energy required to absorb 1 mol NO_3^- was equivalent to 1 to 2 adenosine triphosphates (ATP), or 0.16 to 0.32 mol CO_2. As for NH_4^+, Bloom et al. (1992) estimated that 0.33 mol CO_2 were needed to absorb and assimilate one mol of NH_4^+. An independent assessment of nitrate influx and efflux has been possible since the 1980s through the use of stable isotope labeling. Several transport systems for nitrate uptake have been found, operating at two different levels of soil concentration (Siddiqi et al., 1990) and with different affinities for nitrate. The high-affinity transport system is a low-concentration, saturable system. It reflects a strong ability for nitrate uptake at low concentrations in the soil solution, and it saturates between 0.2 and 0.5 $mmol.m^{-3}$ $[NO_3^-]$. This high-affinity system is subject to negative feedback regulation by root NO_3^- concentrations or certain products of NO_3^- assimilation (Siddiqi et al., 1990). The low-affinity and non-saturable transport system operates exclusively when the soil ion concentration is high, which may be a frequent occurrence under water deficit. This system has a linear relationship with soil nitrate concentrations and is only subject to negative feedback regulation after prolonged exposure to NO_3^- (Siddiqi et al., 1990). It may be related to a passive movement through specific NO_3^- channels, following an electrochemical potential gradient. Ammonium transport systems are similar to those of nitrate, as they also involve a low-capacity, high-affinity system and a passive transport system with high capacity and low affinity.

Studies of the effects of plant-soil water relationships on root N uptake have produced contrasting results (Bassiri-Rad et al., 1999). Nitrogen uptake can be considered as the minimum between N supply from soil and N demanded for growth. Some authors concluded that N uptake was independent of transpiration (Grubb, 1977; Schulze and Bloom, 1984; Gastal and Saugier, 1989; Hopmans and Bristow, 2002). Experiments analyzing the effect of the transpiration stream on N uptake during diurnal cycles reached similar conclusions, i.e., N uptake was found to be independent of transpiration (Triboi-Blondel, 1979; Bhat, 1982). During experiments carried out in nutrient solution with polyethylene glycol as an osmotic agent, Talouizite and Champigny (1988) indeed found an increase in nitrate uptake with short-term water deficit. Using ^{15}N-labeling, Matzner and Richards (1996) demonstrated that root capacity for N uptake diminished with a mild water deficit in *Artemisia tridentata*, but no further decrease was found when the drought stress was more severe. They stated that variations in the net effect of water deficit on N uptake might be correlated with the differing sensitivity of each transport system to water status. Buljovcic and Engels (2001) found a similar response in maize. In their experiment, the nitrate uptake capacity of excised maize roots fell to about 20% only when the soil water content decreased to 5% (w/w), corresponding to a soil water potential of about –3 MPa. During the same experiment, N uptake capacity was fully recovered after rewatering. These authors concluded that nutrient uptake from dry soil was primarily regulated by nutrient transport in the soil to the root surface. Using split-root experiments with polyethylene glycol and isotopic labeling, Larsson (1992) showed that N uptake in wheat was strikingly reduced with osmotic stress. This effect seemed to be more closely related to the water status of the shoot than to the root osmotic environment, which may have been the reason for the different results of all these experiments. N accumulation in the roots may also cause the inhibition of nitrate uptake (Larsson, 1992; González-Dugo, 2006).

Most of the physiological studies concerning the N uptake rate during water shortage periods have been done under controlled environments. Diouf et al. (2004) analyzed the effect of water deficit cycles on N uptake and N assimilation enzymes in the field by means of a plant N balance. There have been some attempts to assess the N uptake and allocation in the field, generally through the use of ^{15}N (Malagoli et al., 2005). However, the uncertainty about the size of the actual soil N pool due to N transformations under field conditions makes it difficult to make a quantitative assessment of N uptake by the plant, although it is a valuable tool for the analysis of the fertilizer recovery and the allocation pattern during plant ontogeny.

Thus, the processes that directly control N uptake under water deficit still need to be established, both at the molecular level (effect on transport system) and at the level of the whole plant.

6. RESPONSE OF CROP PHYSIOLOGICAL FUNCTIONS INVOLVED IN NITROGEN NUTRITION TO WATER DEFICIT

6.1. Nitrogen assimilation in plant tissues

Depending on the species, the assimilation of mineral N takes place in roots or shoots (Andrews, 1986), both exhibiting different energy costs. Gojon et al. (1994) suggested that the site of assimilation depended on the plant growth rate, with slow-growing species mainly assimilating via their roots, while fast-growing species assimilate nitrate in leaves. However, within a sample of eight herbaceous species exhibiting contrasted growth and assimilation rates, Scheurwater et al. (2002) demonstrated that assimilation systematically occurred in the leaves, irrespective of their growth rate.

The site of nitrate reduction may have an important effect on a plant's carbon budget. Plants that reduce nitrate in leaves could use the excess reducing power from photosynthesis, while those that reduce nitrate mainly in roots should obtain their reducing power from glycolysis and the oxidative pentose phosphate pathway (Scheurwater et al., 2002). As the energy cost of reducing nitrate in leaves is smaller than that in roots (Raven, 1985), in water deficit situations, plants that reduce nitrate in leaves are more efficient than those where the reduction takes place in roots.

Lawlor and Cornic (2002) stated that a water deficit could have a more marked effect on N assimilation than on the uptake process, as nitrate reductase activity diminished sharply, albeit in a reversible fashion, in line with low relative water content values. Other authors have also pointed out the particular sensitivity of nitrate reductase activity (Triboi-Blondel, 1978; Larsson et al., 1989; Larsson, 1992; Azedo-Silva et al., 2004; Correia et al., 2005).

6.2. Effect on nitrogen movement through the xylem

Dynamic variations in xylem sap composition result from differences in the transpiration rate and plant-internal nutrient relationships, which control the production of N compounds present in the xylem (Herdel et al., 2001; Peuke et al., 2001). Water shortage may thus have two different and opposite consequences regarding N flow. In the field, Bahrun et al. (2002) demonstrated that nitrate concentration in xylem sap in non-irrigated maize plants fell by more than 50% compared with irrigated control plants. Total nitrate flow was not measured in that experiment, but given the reduction in nitrate concentration and the decrease in stomatal conductance as a consequence of drought, it could be concluded that the net delivery of N to shoots was diminished. It is worth noting that in such a field experiment, the effect of water deficit on nitrate concentration is the result of cumulative effects on soil nitrate flow, nitrate uptake and the ratio between the decrease in nitrate and water uptake. The relationship between xylem flow and composition appears to be even more complex. It has been established that an increase in the solute concentration in xylem sap can reduce xylem hydraulic resistance (Zwieniecki et al., 2001). This would mean that for a given transpiration demand, water flow in the xylem may be enhanced if the solute concentration is increased. This is certainly valid when water availability is not limiting, but if plants are subjected to a water deficit and if an increase in solute concentration was the only consequence of a reduction in solvent volume, xylem sap flow would be diminished. In experiments performed in wheat, Larsson et al. (1989) showed that an increase in the osmotic pressure of nutrient solution increased xylem N concentration, although this increase did not compensate for the reduction in the transpiration rate. As a consequence, the delivery of nitrate to shoots decreased. By contrast, Nicolas et al. (1985) found in rain-fed wheat plants that the increase in N concentration in xylem sap compensated for the lower sap flux and that the amount of N reaching the shoots was maintained.

In sunflower plants grown under controlled conditions and in sandy loam-filled pots, Schurr and Schulze (1996) found that water deficit had no effect on xylem nitrate concentration. Indeed, under similar conditions, these levels even fell as the soil water content declined (Gollan et al., 1992). In that case, a restriction of N flow in the soil may have been involved. In another experiment in a controlled environment where transpiration and the nutrient supply were dissociated, Tanner and Beevers (2001) concluded that nutrient transport from roots to shoots was independent of transpiration. The two transpiration-independent water flows, i.e., the flux of water associated with volume expansion and Münch's counterflow in the phloem were found to ensure nutrient transport throughout the plant.

6.3. Remobilization of nitrogen to grains

For grain crops, N remobilization must also be taken into account, as most of the N that is present in grain has been taken up during the pre-anthesis period and thereafter remobilized from reserves or other organs. Grain number is set during flowering, so any limitation of crop growth rate during this period decreases grain number and yield in maize (Uhart and Andrade, 1995). Once grain number, and hence potential production, is established in the period from planting to seed set, carbon assimilation during seed filling and translocation of assimilates from reserves and senescing organs will set the final yield (Schnyder, 1993).

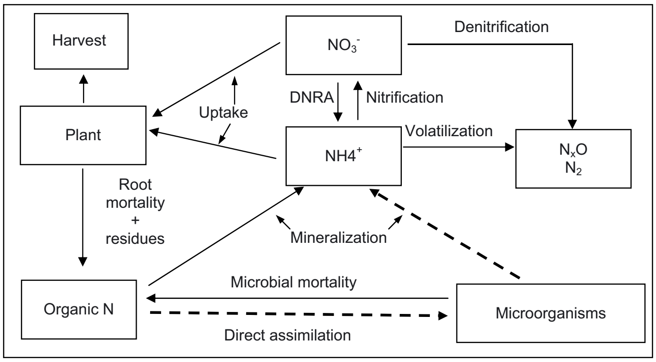

Figure 4. N cycle in the soil-plant-atmosphere system. Each process can be altered by the soil water regime. Dashed arrows show the processes that comprise net mineralization (After Lemaire et al., 2004).

Nitrogen assimilated during the pre-anthesis period is the main source of nitrogenous compounds for grain filling; the contribution of reserves to the final grain N ranged from 63 to 100% in wheat, 11 to 100% in soybean, 49 to 64% in sorghum and 41 to 69% in maize (Egli, 2004; Barbottin et al., 2005), depending on their capacity to store large amounts of C and N compounds in their vegetative organs before anthesis. The amount of N remobilized depends on the amount of N available and on the N remobilization efficiency. The N remobilization efficiency is high in situations of low N supply or low N availability (Barbottin et al., 2005).

Water deficit hastens leaf senescence (Palta et al., 1994); maintenance of green leaf area is therefore essential to grain filling and yield under drought. This should also alter the C flow to roots in order to maintain N absorption (Dreccer, 2005). Palta et al. (1994) showed that N remobilization efficiency was high in Mediterranean-like conditions, where plants are subjected to drought stress during the grain-filling period.

7. CONCEPTS REQUIRED FOR SIMULATION MODELS

Conceptual frameworks similar to that represented in Figure 1 have been converted into a series of quantitative equations linked together to build crop models. Those simulation models are valuable tools to gather the knowledge acquired by experimentation. Mechanistic models enable the synthesis of many experimental results in order to achieve a global knowledge of plant function. They also allow the extrapolation of

Table I. Revision of some daily time-step models and their interpretation of the effect of water and nitrogen interaction on biomass accumulation and leaf area formation.

Model	References	Biomass accumulation	LAI formation
Afrcwheat2	Porter, 1993	Water	Min (N, Water)
CERES-Maize	Jones and Kiriny, 1986	Min (N, Water)	Water
CropSim Wheat	Hunt and Pararajasingham, 1995	Min (N, Water)	Min (N, Water)
CropSyst	Stockle et al., 2003	Min (N, Water)	Water
Soygro	Sinclair et al., 1986	N*Water	N and water
STICS	Brisson et al., 2003	N*Water	Min (N, Water)
O'Leary and Connor	O'Leary and Connor, 1996	N*Water	N*Water

knowledge to different and future scenarios, a major requirement in the context of a continuously changing climate. Given the complexity of the interrelated processes considered here, models are relevant tools to discriminate between water- and N-related reductions in crop growth and development.

There is a large number of simulation models, appropriate for very different scales. Only some of the most used crop simulation models operating on a daily time step will be considered here to illustrate the different approaches to the effect of water and N interactions on crop growth and development.

In modeling, deficits are generally defined by means of reducing indices that go from 0 to 1. The definition of these indices results from empirical equations relating state variables that are affected by the deficit. Each model thus exhibits a choice of significant state variables and equations defining the indices.

In the models considered here, the first effect of soil or plant water status on N nutrition is found at the soil level (Stockle et al., 1994; O'Leary and Connor, 1996; van Ittersum et al., 2003; Singh et al., 2008). The amount of N that is available for plant uptake is calculated using the layers' water content and their contribution to total transpiration (van Ittersum et al., 2003).

For most models, more than one index related to a deficit are used for different processes with a contrasted sensitivity to constraints. CROPSIM-WHEAT, CROPSYST and the model developed by O'Leary and Connor define the water deficit using the ratio between actual and potential transpiration (Hunt and Pararajasingham, 1995; Stockle et al., 1994; O'Leary and Connor, 1996). CERES-Maize and AFRCWHEAT2 determine water deficit using a soil water balance (Jones and Kiriny, 1986; Porter, 1993). STICS considers the water available to roots above the permanent wilting point (Brisson et al., 2009).

Indices defining N deficit are generally calculated according to actual, minimum and maximum N content, in leaves, as in CROPSIM-WHEAT (Hunt and Pararajasingham, 1995) or in the aboveground biomass, as in AFRCWHEAT2 (Porter, 1993). STICS uses the Nitrogen Nutrition Index to assess N deficit (Brisson et al., 2009).

In general, biomass accumulation and leaf area formation are the processes that are typically noted as the most sensitive to these stresses. Some models use the most limiting factor, and therefore, the minimum between water and N stress indicator is used, underestimating the effect of the second stress. Other models consider that both processes interact in growth and development. Hence, both indices are considered. A summary of the most common models used, and how they account for water and N interaction in biomass development and leaf area formation, is given in Table I. Singh et al. (2008) demonstrated that CropSyst was better at predicting the influence of water and N interaction on biomass and yield formation, compared with CERES-Wheat.

The relative difference between the two approaches depends on the values of both indices. Let us consider the result of the difference ε between the minimum of these indices and their multiplication:

$$\varepsilon = \text{Min}\left(\text{w}_{\text{ater}}, \text{n}_{\text{itrogen}}\right) - \text{w}_{\text{ater}}{}^{*}\text{n}_{\text{itrogen}}$$

where w_{ater} and $\text{n}_{\text{itrogen}}$ are stress factors of water and N, respectively. ε is largest when both indices are close to 0.5 (Fig. 5). When one of these indices is close to 0 (very limiting factor), the relative weight of this index becomes important and hence the effect of the second factor is weak. On the contrary, when one index is close to 1, the main effect on the variable considered will be mainly ascribed to the second factor. The maximal difference occurs in the intermediary region, i.e. when both indices are close to 0.5. Under natural conditions and because of its intrinsic inertia, N stress could be maintained close to this value. But in dry seasons, drought stress often remains at low values, reaching optimal conditions only following rainfalls. It is therefore maintained within these values for short periods of time only. As a result, the difference in the simulation results obtained using one or the other approach rarely appears significant.

8. CONCLUSION

The analysis of the effect of water deficit on N nutrition is complex and requires a multiscale approach, from the membrane to the crop, and different media and their interfaces. The first and most important need is to separate growth-induced changes from the direct effects of water deficits. The main effect of water restriction is certainly a reduction in N demand due to the marked sensitivity of leaf area expansion. Nitrogen

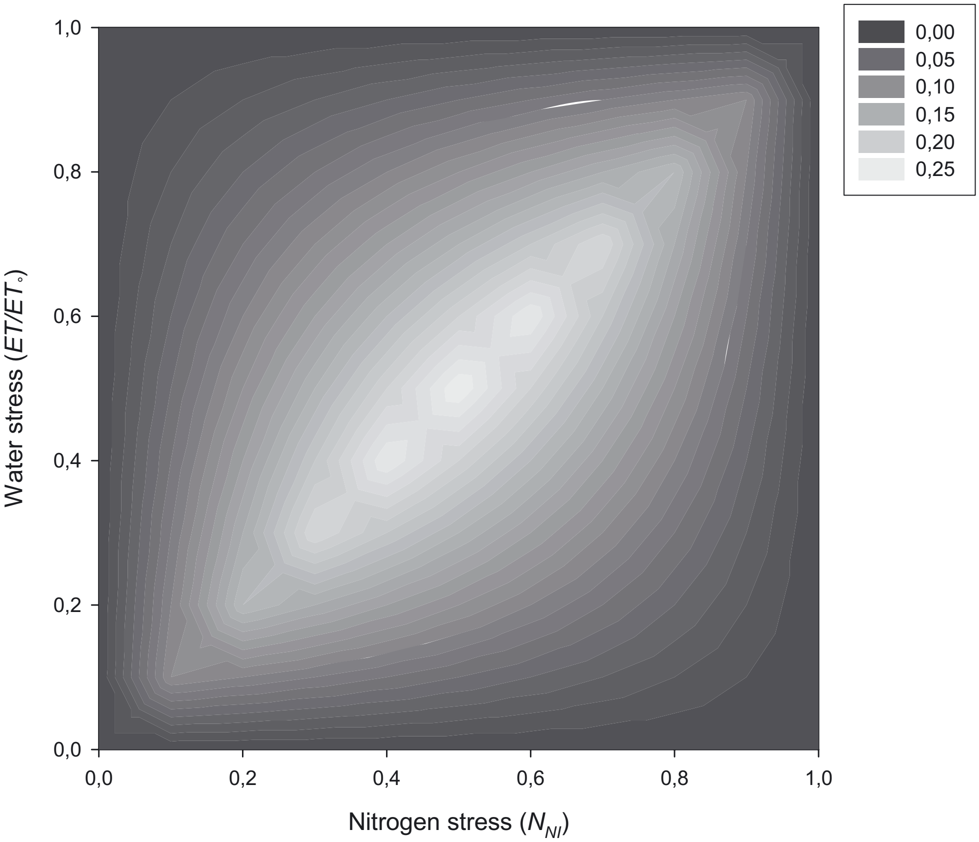

Figure 5. Difference (expressed by grayscale) between the minimum of water and nitrogen stress indices and the multiplication of both indices [Min (Water, N) – Water*N] in the space defined by both indices.

nutrition indices can reveal the processes that alter plant nutrition independently of its actual demand. Process-based crop growth simulation models must currently incorporate these concepts, either implicitly or explicitly. It is noteworthy, however, that they still do not take similar account of the interaction between N and water stress, thus reflecting the ongoing discussion concerning co-limitation analysis in crops. Indeed, some aspects remain poorly understood, especially concerning the establishment of the supply of N to meet plant needs.

Two areas in particular deserve further investigative efforts. Firstly, our lack of knowledge of the true extension of active root surface area is strongly detrimental to any attempt to clarify the mechanisms of N absorption. Secondly, our inability to determine the mineral N absorption rate in the field still remains a major obstacle. To clarify these points, and render fertilizer application methods more precise, greater efforts should be made to achieve a methodological breakthrough in these two areas.

Acknowledgements: The authors would like to thank Dr. Elías Fereres Castiel for his collaboration in the compilation of this paper. We also thank Dr. Jorge Alvarez de Toro. The anonymous reviewers are also acknowledged for their helpful comments that have improved this work. This research was supported by INRA, the Poitou-Charentes Region and the CNRS "ECosphère COntinentale" program, N#03CV114.

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