



Relationships between dynamics of nitrogen uptake and dry matter accumulation in maize crops. Determination of critical N concentration

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Abstract

The concept of critical nitrogen concentration ($\%N_c$) has been proposed as the minimum $\%N$ in shoots required to produce the maximum aerial biomass at a given time. Several authors have shown that $\%N_c$ declines as a function of aerial biomass accumulation (W) and the $\%N_c - W$ relationship has been proposed as a diagnostic tool of N status in different crops, excluding maize. From data obtained in five nitrogen fertilisation experiments in irrigated maize crops, 26 critical data-points were selected with a precise statistical procedure. An allometric relation was fitted and a critical $\%N - W$ relationship model is proposed in maize as:

$$\text{If } W < 1 \text{ t ha}^{-1} \quad \%N_c = 3.40$$

$$\text{If } 1 \text{ t ha}^{-1} \leq W \leq 22 \text{ t ha}^{-1} \quad \%N_c = 3.40 (W)^{-0.37}$$

The model is applicable to maize crop development between emergence and silking + 25 days. The model was tested and validated with data obtained in a network of 17 N fertilisation experiments conducted in France under contrasting pedoclimatic conditions. In only nine out of 280 data-points (3.2%), the plant N status was mispredicted when $\pm 5\%$ error around $\%N_c$ was allowed. A critical N uptake model (Nu_c , kg N ha⁻¹) is proposed as

$$Nu_c = 34 (W)^{0.63}$$

A comparison between Nu_c and N uptake observed in N treatments giving the maximal grain yields has shown that maize crops assimilate at least 30 kg N ha⁻¹ in a storage N pool at the silking stage. The significance of the critical $\%N - W$ and $Nu - W$ relationships is discussed in relation to theoretical models proposed in whole plant ecophysiology. Different relationships calculated between leaf area index and aerial biomass accumulation, and between N uptake and leaf area were consistent with previous results for other crops. This strengthens the interest of the critical $\%N - W$ relationship for use as diagnostic tool of nitrogen status in maize crops.

Introduction

Many studies show that plant nitrogen concentration decreases during the growth cycle in dense canopies. This is the result of two processes: (i) self-shading of leaves that induces a non-uniform leaf N content from

the top canopy layers with high N concentration to the shaded layers with low N concentration (Field, 1983; Hirose and Werger, 1987; Pons and Pearcy, 1994; Sinclair and Horie, 1989) and (ii) an increase in the proportion of plant structural and storage tissues with a lower nitrogen concentration, even when crops grow with non-limiting N supply (Caloin and Yu, 1984; Charles-Edwards et al., 1987). When this decrease of

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N concentration is only related to time, it leads to large differences according to different growing conditions for a given genotype.

Lemaire and Salette (1984) showed that plant N concentration in grasses growing with non-limiting N supply can be related to aerial dry matter accumulation by the equation:

$$\%N = \alpha(W)^{-\beta} \quad (1)$$

where W is the weight of aerial dry matter in t ha^{-1} and $\%N$ is the nitrogen concentration in shoots expressed in $\text{g } 100 \text{ g}^{-1}$ of dry matter weight. The coefficient α represents the plant $\%N$ for an aerial dry matter of 1 t ha^{-1} and the coefficient β characterises the pattern of decrease of $\%N$ during growth.

This relationship can be transformed by multiplying both sides of equation (1) by W . This leads to a relationship between cumulative shoot N uptake and aerial dry matter accumulation:

$$Nu = 10\alpha(W)^{1-\beta} \quad (2)$$

where Nu is cumulative N uptake in kg N ha^{-1} . The coefficient 10α represents the amount of N present in the shoots when aerial dry matter weight is 1 t ha^{-1} (the factor 10 converts the result to kg ha^{-1}) and $1 - \beta$ is the allometric ratio between N accumulation and dry matter accumulation in shoots.

These relationships allow the study of the dynamics of N uptake in relation to plant growth. Lemaire and Salette (1984) and Lemaire and Denoix (1987) have shown that, for grasses with a non-limiting level of N nutrition, it is possible to determine a constant relationship between $\%N$ and W (called the 'critical N curve') independent of the experimental conditions, and that below this curve, N availability becomes a limiting factor for dry matter growth. The critical $\%N - W$ relationship is based on the concept of critical plant $\%N$ ($\%N_c$), defined as the minimum N concentration in plants needed for maximum growth rate of the crop at a given time (Greenwood et al., 1991; Ulrich, 1952). Greenwood et al. (1990) generalized these relationships to various species and proposed two critical $\%N - W$ relationships for C_3 and C_4 species. These relationships were based on total biomass excluding fibrous roots, but including storage roots.

The critical $\%N - W$ relationship has been used to build a diagnostic tool for the N nutrition status of crop growth (Justes et al., 1994; Lemaire et al., 1989). However, to use the critical $\%N - W$ relationship in this way, it is necessary to determine the relationship for different crop species precisely. Justes et al. (1994)

proposed a precise statistical method for the determination of the data points corresponding to $\%N_c$. They determined and validated a critical $\%N - W$ relationship for winter wheat (*Triticum aestivum* L.), based on aerial biomass accumulation up to flowering stage. Colnenne et al. (1998) used the same methodology for the determination of critical $\%N_c$ in winter oilseed rape.

The aim of this study was (i) to determine and validate the critical $\%N - W$ relationship for maize (*Zea mays* L.) crops during vegetative and grain filling periods and (ii) to analyse the dynamics of N uptake as a function of aerial biomass accumulation and leaf area accumulation for vegetative growth and for ear growth during grain filling, in order to give a theoretical basis for N fertilisation management. These results obtained for maize crops are discussed in terms of the growth theory developed by Lemaire and Gastal (1997).

Materials and methods

Field experiments

Several N fertilisation experiments were conducted in France on irrigated maize crops. Experiments 1 to 5 (Table 1), cultivated with the same cultivar (cv Volga, Pioneer-France Maïs, index FAO 550) and in the same region (South-West of France), were used to determine a critical $\%N - W$ relationship. Data from a network of trials (17 site-years in France, nos. 6–22, Table 1) conducted by various research and technical organisations were then used to validate the relationship.

The rates of applied N fertilizer varied in the experiments (Table 1). In each experiment, one or two N rates were assumed to be non-limiting, while several rates were assumed to be limiting for maize at different growth stages. N-fertilizer (ammonium nitrate) was applied twice: 30 or 50 kg N ha^{-1} at sowing (from mid-April to the beginning of May according to the experimental conditions) and the remainder at the stage of six to eight visible leaves (beginning June). The N rate treatments were arranged in randomized block designs with three or four replications. The size of plots was greater than 100 m^2 (12 rows of maize at minimum, 0.8 m between the rows, 10 m in length).

All trials were conducted with optimal crop management in agreement with the practices advised in each location, in order to obtain the potential production (no limiting factor other than N). For example, on the experimental site of Onard, plant density was approximately $90\,000 \text{ plants ha}^{-1}$ and irrigation ranged

Table 1. Characteristics of the experimental field sites used

No.	Location*	Year	Soil texture Clay–Silt–Sand (%)	Cultivar	N rate treatments Applied N in kg N ha ⁻¹	Precipitation –Irrigation‡ (mm)
Experiments used to determine critical %N – W relationship						
1	Onard (40)	1991	5 – 16 – 79	Volga	30-100- <u>240</u> #	469 - 175
2	Onard-a (40)	1992	6 – 18 – 76	Volga	30-80-130-180- <u>230</u> -280	649 - 25
3	Onard-b (40)	1992	6 – 18 – 76	Volga	30-120-180- <u>240</u> -300	649 - 25
4	Onard (40)	1993	5 – 16 – 79	Volga	30-80-130- <u>180</u> -230-280	542 - 120
5	Pierroton (33)	1993	5 – 3 – 92	Volga	30-80-130- <u>180</u> -230-280	595 - 237
Experiments used to validate critical %N – W relationship						
6	Bergerac (24)	1993	15 – 27 – 58	Volga	30-80- <u>130</u> -180-230-280	630 - 17
7	Bergerac (24)	1994	15 – 45 – 38	Volga	0-90-140- <u>190</u> -240-290	446 - 90
8	La Côte St-André (38)	1993	17 – 39 – 44	Furio	22-80-130- <u>180</u> -230-280	925 - 110
9	La Côte St-André (38)	1994	17 – 39 – 44	Furio	22-80-130- <u>180</u> -230-280	438 - 210
10	La Jaillère (44)	1993	15 – 55 – 30	Déa	0-50- <u>100</u> -150-200-250	300 - 60
11	La Jaillère (44)	1994	15 – 55 – 30	Déa	0-50- <u>100</u> -150-200	356 - 80
12	Le Magneraud (16)	1994	12.1 - nc	Furio	0-70-110- <u>150</u> -190-230	395 - 270
13	Masseube (32)	1994	16 – 55 – 25	Volga	23-50-100- <u>150</u> -200-250	352 - 246
14	Meyenheim (68)	1993	12 – 25 – 61	Déa	0-50-100- <u>150</u> -200-250	366 - 237
15	Négrepelisse (82)	1993	11 – 27 – 62	Volga	0-50-100- <u>150</u> -200-250	565 - 125
16	Négrepelisse (82)	1994	11 – 27 – 62	Volga	0-50-100-150- <u>200</u> -250	455 - nc
17	Onard (40)	1990	6 – 18 – 76	Volga	50-120- <u>240</u>	347 - 175
18	Onard (40)	1994	6 – 18 – 76	Volga	50-90-140- <u>190</u> -240-290	344 - 225
19	Pierroton (33)	1994	5 – 3 – 92	Volga	30-80-130-180- <u>230</u> -280	503 - 321
20	Sainte-Livrade (47)	1994	8 – 12 – 79	Volga	0-145- <u>195</u> -245	344 - 230
21	Satolas (69)	1993	14 – 37 – 47	Volga	0-50-100-150- <u>200</u> -250	559 - 240
22	Satolas (69)	1994	16 – 32 – 50	Volga	0- <u>150</u> -200-250-300	514 - 180

* In parentheses, code number of French department.

‡ precipitation and irrigation between sowing and grain harvest.

nc, not communicated.

The underlined N rate corresponded to the optimal grain yield treatment: N_{opt} treatment.

between 25 to 175 mm, depending on the rainfall and crop evapotranspiration in each year. Weeds were controlled before sowing with 6 l ha⁻¹ of Alachlor (336 g l⁻¹) + Atrazine (144 g l⁻¹) and after maize emergence with Pyridate (45 %, 2 kg ha⁻¹).

Aerial biomass, leaf area index and samples analysis

Plant samples were collected every 7 – 14 days between emergence and silking stages, and at two to four sampling dates after silking up to silage or maturity stages. At each sampling time, aerial dry matter and N concentration were measured. The sample size was 12 – 15 plants collected in a 2-m long plot, depending on sowing density. The harvested plots were spaced out in such a way as to avoid being influenced by previous sample collections. The plants were

cut at the ground level. After determining the weight of 12 to 15 plants, five plants corresponding to average weight were selected and the dry matter was determined after oven-drying at 80°C during 72 h. After flowering stage, the plants were separated in two compartments: above-ground vegetative organs and ears (cobs+kernels). After grinding to a fine powder, N concentration in each compartment was determined using either the Kjeldahl method (wet digestion in H₂SO₄–H₂O₂, without specific reduction for nitrate) or the Dumas method (flash combustion with automatic nitrogen analyzer, including nitrate). The biomass and N uptake accumulations from emergence to silage stages were used. At the silage stage (around 30–35% dry matter in the whole plant), the aerial biomass accumulation and the N uptake reached the maximum values (Karlen et al., 1987; Plénet, 1995).

In the 1990–1993 Onard trials (experiments nos. 1, 2, 4 and 17, Table 1), the leaf area was measured at different sampling times. On each of 10–20 plants in some N treatments, the length and width of all visible leaves per plant were measured. The leaf area was calculated as $k \times \text{length} \times \text{width}$ with $k = 0.75$ for ligulate leaves and 0.50 for still unfolded visible leaves (Giauffret et al., 1991). Leaf area index (LAI, $\text{m}^2 \text{ leaf m}^{-2} \text{ soil}$) was calculated as the sum of green leaf area per plant \times plant density. The variation coefficients on LAI measured were ranged between 5 and 15%. Senescent leaves (if over half of its surface area was yellow or dry) were not taken into account in LAI.

Final grain yields were measured by harvesting 8–10 m of one or two rows from each plots at the grain maturity stage (30–32% moisture in kernels, 2 or 3 weeks after silage stage). Grain yields were adjusted to 150 g $\text{H}_2\text{O kg}^{-1}$ dry weight.

Data processing

The data processing has been described by Justes et al. (1994). For each experiment nos. 1–5 (Table 1) and on each sampling date, the aerial dry matter weight (W) measured in the different N treatments (three to six data-points) were compared with a Student's two-tail t -test at 10% level of probability in order to separate out two group of points.

Group (1): the non N-limiting growth treatment which is defined as a treatment for which a supplement of N application does not lead to an increase in aerial biomass (W), but which induces an increase of %N.

Group (2): the N-limiting growth treatment for which a supplement of N application leads to a significant increase in W .

The variation of %N with W was described using a bilinear relationship composed of (i) a vertical line corresponding to an increase of plant %N without variation in crop mass which refers to group (1) (the abscissa is equal to the mean of biomass which does not significantly vary across the N levels), (ii) an oblique regression line through the points corresponding to W increasing with %N increasing (group 2), where growth is limited by N nutrition. The critical %N was determined as the ordinate of the intersection of the two lines. This value (% N_c) and the corresponding value of W was introduced into a database for determining the parameters α and β of Eq. (1) by non-linear regression.

Among the measurement dates, we have used to determine one critical %N point, the data measure-

ments that had at least one N-limiting treatment and one non N-limiting treatment across the different N treatments. The data which did not satisfy this statistical criteria was not used to define the critical N curve.

When only three levels of N supply were applied, we have selected the measurement dates as the following procedure: (1) W of the lowest N rate was significantly different of W measured in the treatments with the two biggest N rates applied; (2) and W measured in the two biggest N rates were not significantly different.

To validate the critical %N – W relationship, the data of aerial biomass from the remaining experiments (nos. 6–22, Table 1) were analysed by ANOVA procedure at each date and for each experiment. In all experiments, the optimal N rate (N_{opt}) was selected. It corresponded to the treatment giving the optimum grain yield, i.e., grain yield statistically not different at $P_{0.10}$ of maximal grain yield generally obtained with the biggest N rate (N rate treatments underscored in Table 1). In all trials and at each sampling date, no statistical differences (LSD, $P > 0.10$) were observed between W measured in the N_{opt} treatment and W measured in the upper N rates. N treatments were considered as N-limiting when W was statistically different from the W_{opt} observed in the N_{opt} rate treatment (LSD, $P < 0.10$). We then calculated the number of data points that did not correspond to the model by the following procedure:

If $W < W_{\text{opt}}$, the number of outliers is given by %N $> \%N_c$ or %N $> (1.05\%N_c)$ or %N $> (1.10\%N_c)$

If $W = W_{\text{opt}}$, the number of outliers is given by %N $< \%N_c$ or %N $< (0.95\%N_c)$ or %N $< (0.90\%N_c)$

The comparison with values of % N_c increased or decreased by 5 or 10 % aided the detection of actual outliers and minimized the variability in data interpretation.

Results

Determination and validation of the critical %N – biomass relationship

The relationships between %N in the shoots and W , obtained in the six N treatments in 1992 at Onard (experiment no. 2, Table 1) from nine visible leaves stage to silking stage, are shown as an example (Fig. 1). The %N decreased for all treatments when the aerial biomass increased, the decrease being more rapid for

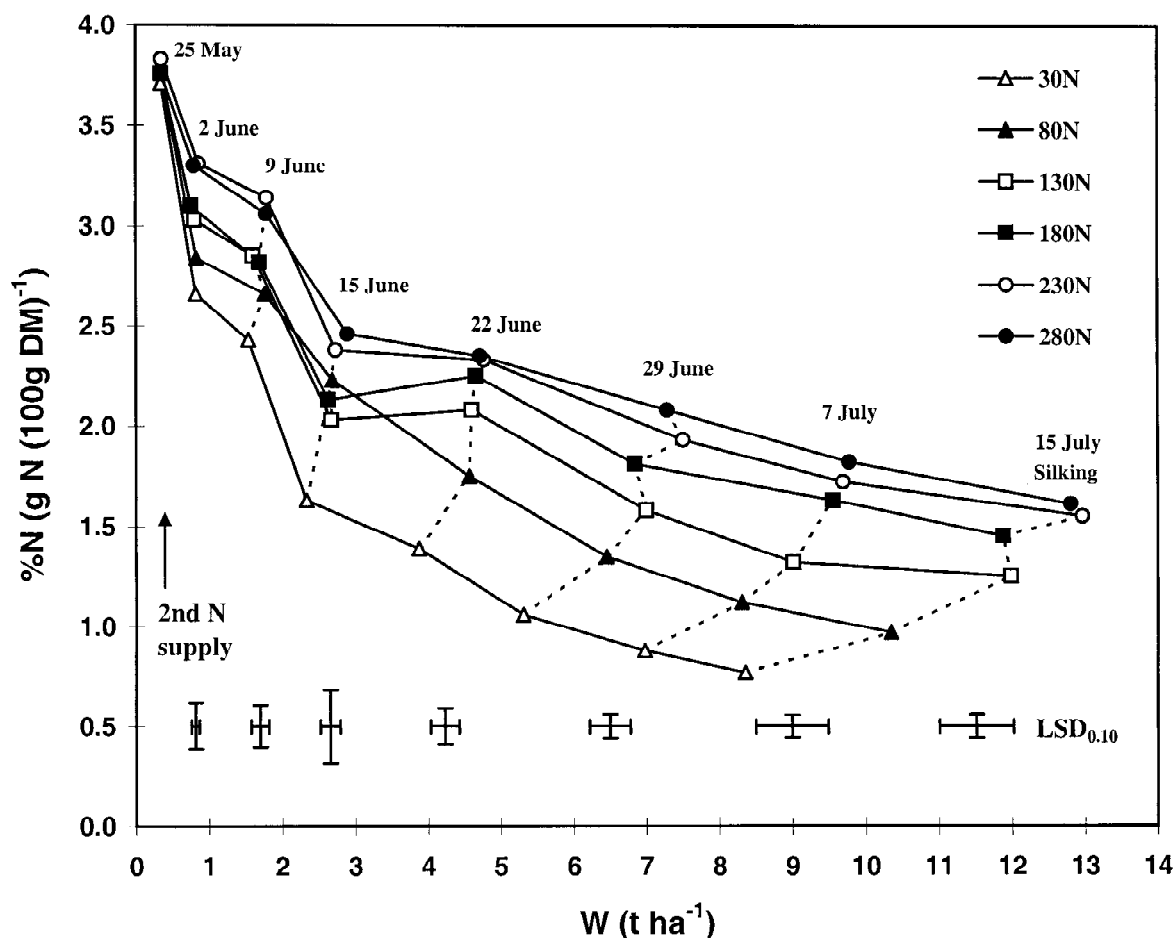


Figure 1. Relationships between the N concentration (%N) and aerial dry matter accumulation (W) of maize cv Volga during the period from emergence to silking stage, for six N treatments at Onard 1992 (experiment no. 2, Table 1). The six treatments received 30 kg N ha⁻¹ at the sowing stage (23 April 1992) and 0 (30N), 50 (80N), 100 (130N), 150 (180N), 200 (230N) and 250 (280N) kg N ha⁻¹ at the nine visible leaves stage (25 May 1992). Horizontal and vertical bars show least significance difference at $P_{0.10}$.

the lower N fertilizer rates. This figure shows the time course of N deficiency in the lowest N rate treatments: first, the shoot N concentration decreases while growth rate remains constant; then, the growth rate decreases.

Critical %N – W relationship

Among the 49 measurement dates (experiments nos. 1 – 5, Table 1), 26 sampling dates fulfilled the statistical criteria previously defined for evaluation of % N_c . Fig. 2 shows the % N_c and associated W value, determined by the intercept between oblique and vertical lines fitted through the data points for each sampling date during period between the emergence and the silking stages (17 values). Table 2 shows the values of % N_c

calculated during the entire crop development for the five field experiments: 17 % N_c values were obtained from nine to ten visible leaves to silking stages (0.95 – 12.5 t ha⁻¹) and nine values from post-silking to silage stages (13.4 – 26.0 t ha⁻¹). These critical points were converted to natural logarithms and fitted by linear regression (Fig. 3) in accordance with Eq. (1) which can be written:

$$\ln \%N = \ln \alpha + \beta \ln W \quad (3)$$

The linear regressions were fitted over three periods: emergence to silking stage, emergence to silking +25 days and emergence to silage stage. Fig. 3 highlights an acceleration in the decrease of %N with W

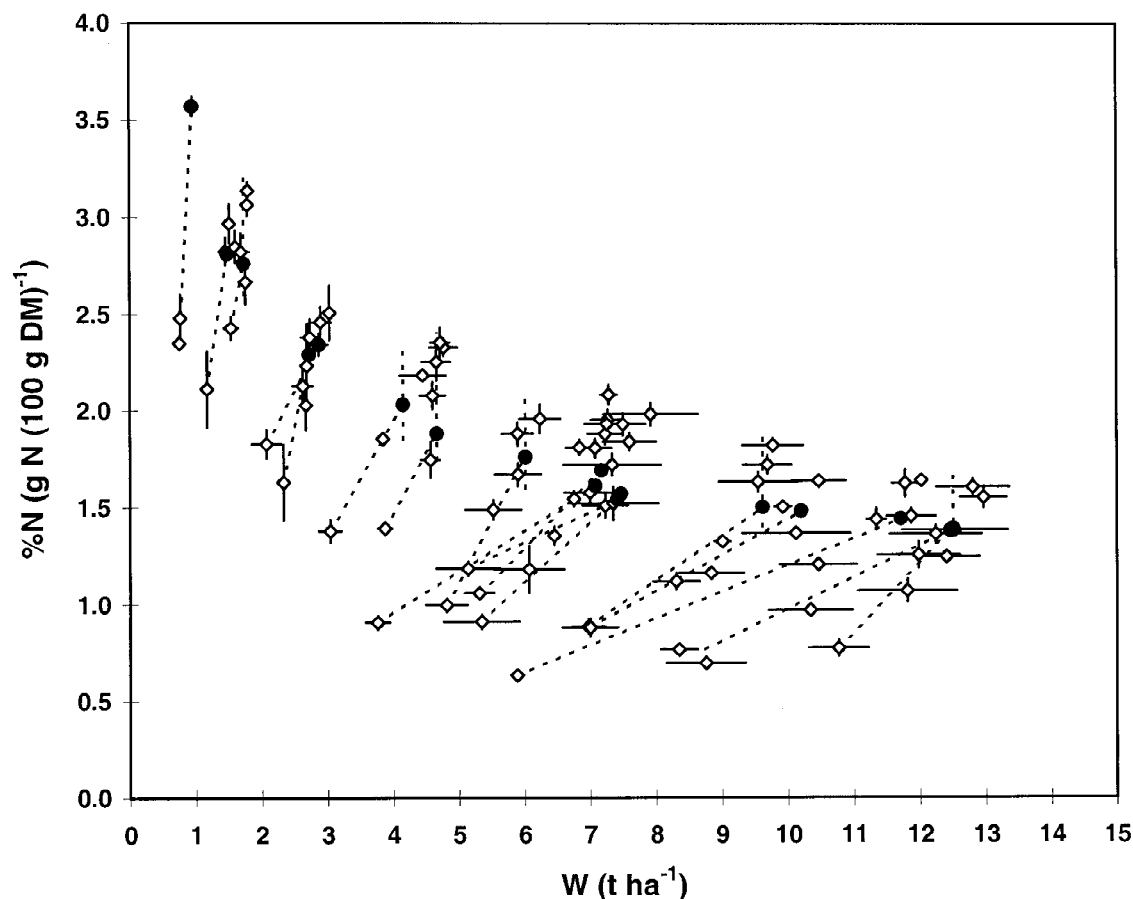


Figure 2. N concentration (%N) as a function of aerial biomass accumulation (W) in maize plants cv Volga under different N treatments during the period from emergence to silking stage in experiments 1 to 5 (Table 1). (\diamond) Values measured in the different N rate treatments (N1 to N3, N1 to N5, or N1 to N6 according to the experiment, see Table 1) at different dates; (\bullet) critical points ($\%N_c$) calculated at each date according to the method defined in the text. Horizontal and vertical bars show the standard error of the mean (four repetitions). The dotted lines represent the bilinear regressions between the N treatments at a given date in each experiment (see the text).

after 22 t ha^{-1} of aerial biomass, i.e., from silking stage+25 days onwards. To avoid bias in the parameter estimations caused by the log transformation, we fitted the model (Eq. (1)) to data normal scale by non-linear regression. Table 3 shows the regression statistics. The model accounted for 99% of the variance. The two parameters α and β were strongly correlated (-0.80). The parameters estimated for the three periods were not statistically different (confidence intervals), although the residuals were non-randomly distributed for the period from emergence to silage stages. Thus, we determined the critical $\%N - W$ relationship as the equation fitted to biomass values between 1 and 22 t ha^{-1} , i.e., the stages between nine to ten visible

leaves and silking+25 days. The parameter values so obtained were $\alpha = 3.40$ and $\beta = -0.37$.

However this relationship is not valid for $W < 1 \text{ t ha}^{-1}$ since its extrapolation for very low W gives N contents greater than those measured in young maize plants (for example, for 0.25 t ha^{-1} , $\%N = 5.70\%$). Because the N differences between treatments only started at the nine visible leaves stage in our experimental conditions, very few data were available for $\%N_c$ at young stages. Nevertheless, for $W < 1 \text{ t ha}^{-1}$, there is no competition for light and, as demonstrated by Lemaire and Gastal (1997), the $\%N$ decline with biomass accumulation for an isolated plant is small. Thus, as a first approximation, we can consider that $\%N_c$ remains constant and equal to 3.40% for young

Table 2. Critical N concentration ($\%N_c$, in g N (100 g DM) $^{-1}$) as a function of aerial dry matter accumulation (W , in t ha $^{-1}$) for two maize crop periods (emergence – silking and silking – maturity) calculated following the procedure defined in the text from experiments 1 to 5 (Table 1) conducted in South West of France with cv Volga

Experiments	Emergence – silking				Silking - maturity			
	DAE*	Stages	W (t ha $^{-1}$)	$\%N_c$	DAE	Stages	W (t ha $^{-1}$)	$\%N_c$ §
Onard 1991	56 62 68 75	13–14 L‡ 15 L 17 L 18 L	1.48 2.87 4.15 7.41	2.81 2.34 2.03 1.54	88	Silk.+ 15 days	13.43	1.23
Onard-a 1992	39 45 52 59 67 75	13 L 15 L 16–17 L 17–18 L Pre-silking Silking	1.73 2.72 4.66 7.17 9.62 12.50	2.76 2.29 1.88 1.69 1.50 1.39	87 99	Silk.+ 12 days Silk.+ 23 days	16.91 20.98	1.20 1.16
Onard 1993	33 60 75	10 L 18 L Silking	0.95 6.01 10.20	3.57 1.76 1.48	88 110	Silk.+ 13 days Silk.+ 35 days	14.77 21.16	1.26 1.02
Onard-b 1992	59 75	17-18 L Silking	7.08 11.71	1.61 1.44	87 101 132	Silk.+ 12 days Silk.+ 26 days Silage	17.81 21.52 25.15	1.17 1.05 0.99
Pierroton 1993	70 84	17-18 L Silking	7.47 12.46	1.57 1.38	133	Silage	25.98	0.95

* DAE, days after emergence.

‡L, visible leaf.

Table 3. Estimates of parameters α and β of the model $\%N_c = \alpha W^{-\beta}$ fitted with the critical data points (see Table 2) by a non-linear regression procedure for different periods of maize crop growth

Growth period	α parameter	β parameter	R^2 ‡	n	Correlation § α and β	Residual analysis
10 leaves to silking	$3.389 \pm 0.091^*$	-0.367 ± 0.019	0.990	17	-0.80	Randomly distributed
10 leaves to silking + 25 days	3.390 ± 0.080	-0.368 ± 0.015	0.991	22	-0.81	Randomly distributed
10 leaves to silage stage	3.405 ± 0.077	-0.373 ± 0.013	0.992	26	-0.81	Small bias when $W > 22$ t ha $^{-1}$

* confidence interval at $P > 0.95$.

‡ R^2 , % variance accounted.

§ Correlation between estimated parameters α and β .

plants until the crop mass reaches 1 t ha $^{-1}$ (emergence to 10 visible leaves stages). This value of 3.40% is close to the optimal N content in ear leaf blades (Jones, 1967; Loué, 1984; Plénet, 1995; Walworth et al., 1986).

Thus, for maize crops, the critical $\%N - W$ relationship can be described by the following two equations (Fig. 4):

$$\begin{aligned} \text{From 0 to 1 t ha}^{-1} & \quad \%N_c = 3.40 \\ \text{From 1 to 22 t ha}^{-1} & \quad \%N_c = 3.40(W)^{-0.37} \quad (4) \end{aligned}$$

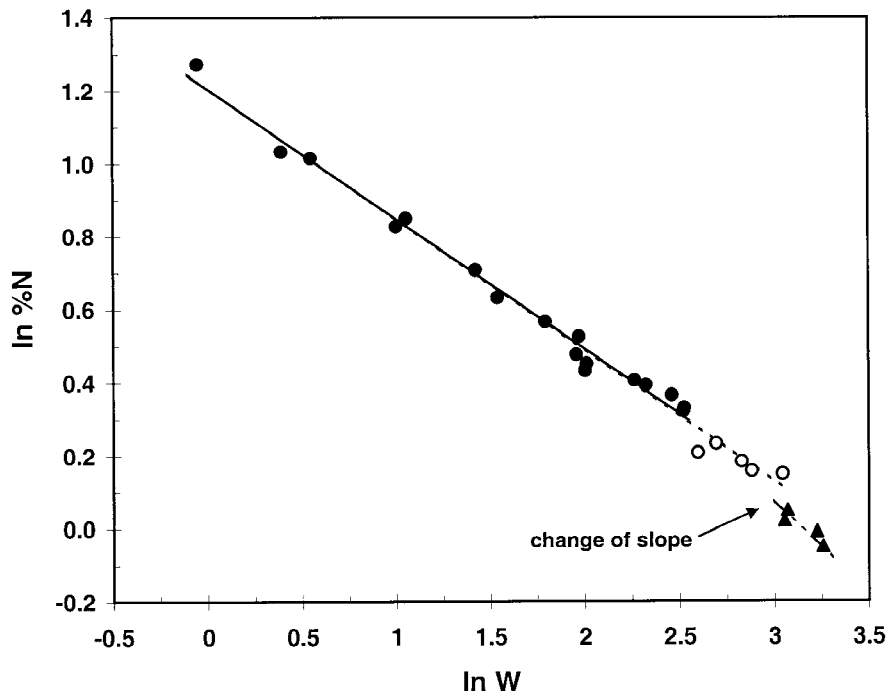


Figure 3. Relationships between the natural log of $%N_c$ ($\ln \%N_c$) and the natural log of aerial biomass ($\ln W$) for different stages of maize crops: (●) critical points and (—) linear regression for the period between 10 leaves stage and silking stage; (○) critical points and (----) linear regression from emergence to silking + 25 days; (▲) critical points and (-·-·-) linear regression from silking + 26 days to silage stage.

Validation of the critical $%N - W$ relationship

Data from 17 N fertilisation experiments (Table 1, experiment nos. 6 – 22) were used to test the validity of Eq. (4). The data were separated in two groups: N-limiting when W was significantly smaller than the W_{opt} measured in the N_{opt} treatment (LSD at $P < 0.10$), and N non-limiting when W was not significantly different from W_{opt} . Fig. 5 shows the results of this data analysis for maize cultivar Volga, and for two early maturity cultivars of maize (Déa and Furio) cultivated in northern conditions with potential yields lower than Volga. The N-limiting and non-limiting groups of data were well discriminated by the critical curve for all cultivars. To test the accuracy of the model, the number of data which did not correspond to the model was calculated following the procedure described in Methods (Table 4). The number of outliers was low for the Volga, Déa and Furio cultivars. In total, the number of cases where the model mispredicted the plant N status was low: 18 data out of 280 (6.4%) if $%N_c$ was the absolute reference, or nine data out of 280 (3.2%) if an uncertainty of $\pm 5\%$ around $%N_c$ was allowed. These results validated the critical $%N - W$

relationship in maize crops in different experimental and pedoclimatic conditions. The range of validity of this model is restricted to $0 - 22 \text{ t ha}^{-1}$ (emergence stage to silking+25 days). However, the model can be cautiously extrapolated to crop maturity for plant N diagnostics.

Fig. 5 shows a very large variability of N concentration for a given biomass in the studied experimental conditions. Two envelope curves were calculated for the pooled data from the two groups of cultivars:

$$%N_{\min} = 2.05(W)^{-0.56} \quad (5)$$

$$%N_{\max} = 6.30(W)^{-0.42} \quad (6)$$

For a given W , the observed $%N$ can vary by $\pm 70\%$ around the critical N concentration. The $%N_{\min}$ and $%N_{\max}$ curves might correspond to the limits of N concentration in maize (see discussion).

Critical N uptake

From the relationship $%N = \alpha W^{-\beta}$, the relationship between the amount of critical nitrogen uptake and the aerial biomass accumulation was determined. We

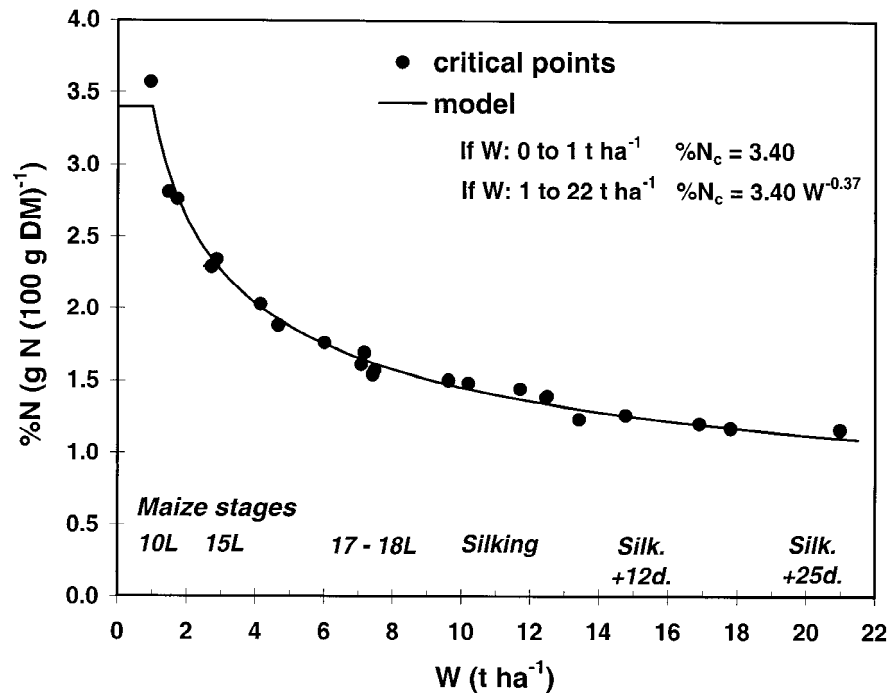


Figure 4. Relationship between critical N concentration ($\%N_c$) and aerial biomass (W) in maize crops for the period between emergence stage and silking + 25 days stage. See text for explanation of the model. Growth stages are given for irrigated maize crops in South West of France: 10L, 15L, 17–18L correspond to 10, 15, 17 or 18 visible leaves stages respectively.

obtained:

$$Nu_c = 34(W)^{0.63} \quad (7)$$

with Nu_c in kg N ha^{-1} and W in t ha^{-1} . The coefficient 34 (in kg N ha^{-1}) corresponds to the amount of N necessary to produce a crop biomass of 1 t ha^{-1} . The coefficient 0.63 ($= 1 - 0.37$) represents the ratio between the relative accumulation rate of nitrogen in aerial biomass ($dNu/Nudt$) and the relative growth rate (dW/Wdt).

The critical $Nu_c - W$ relationship is shown Fig. 6, along with the N uptake (Nu_{obs}) observed from emergence to maturity in the N_{opt} treatments in each of the 4 years of the Onard experiments. From silking stage onwards, the N uptake in vegetative organs (Nu_{veg}) and ears (Nu_{ear}) are shown (the latter by difference with the total N uptake) in the aerial parts of maize plants. The data for Nu_{obs} , corresponding to the dynamics of observed N uptake for maximal grain yields under our experimental conditions, were fitted using an asymptotic exponential curve:

$$Nu_{\text{obs}} = 270(1 - e^{-0.105W}) \quad (8)$$

with $R^2=0.99$, $df=27$, and a range of validity from 0 to 26 t ha^{-1} .

This curve of Nu_{obs} lies above the Nu_c curve from 2 to 22 t ha^{-1} of aerial biomass, i.e., from 14 visible leaves stage to silking+30 days stage.

An analysis was undertaken of the processes underlying the Nu_c and Nu_{obs} curves during the vegetative and reproductive growth periods.

Vegetative growth period: relationships with leaf area index

During vegetative growth, leaf area expansion may play a major role in N uptake. In the treatments close to critical data points, the leaf area index (LAI) was not always measured. Therefore, the data of N_{opt} treatments and of the lowest N rate treatments in the 1990–1993 Onard experiments (experiments nos. 1, 2, 3 and 17, Table 1) were used to establish the relationships between LAI and Nu from emergence to one week before the silking stage. During this period, Nu was linearly related to LAI (Fig. 7):

$$Nu = 28.9(\text{LAI}) \quad (9)$$

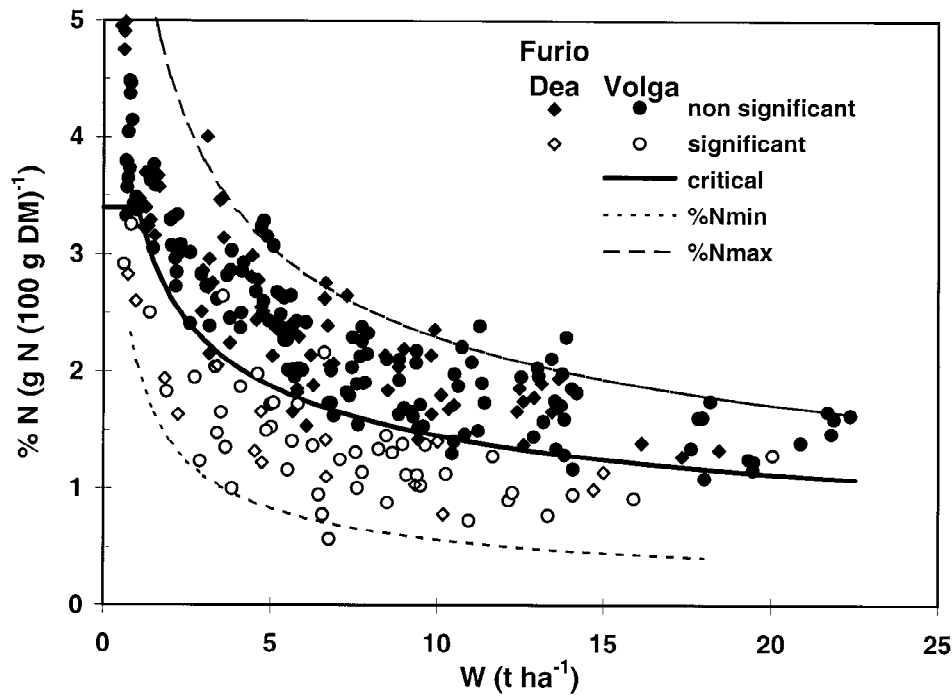


Figure 5. Relationships between N concentration (%N) and aerial biomass (W) for the experimental treatments described in Table 1 used to validate the critical %N – W relationship for two groups of maize crops: Volga cultivar and Déa – Furio cultivars. Non-significant, treatments where N was not statistically limiting for shoot growth; significant, treatments where N was statistically limiting for shoot growth; critical, critical %N – W relationship given by $\%N_c = 3.40(W)^{-0.37}$; $\%N_{\min}$ and $\%N_{\max}$, envelope curve (see text).

where N_u is N uptake in aerial biomass (kg N ha^{-1}), and LAI is leaf area index, $n=23$, $R^2=0.98$. This relationship implies that for a unit increment of LAI, maize tissues require an average of 29 kg N (or 2.9 g N m^{-2}) during vegetative growth. This value of 2.9 g N m^{-2} represents the quantity of total shoot N (leaves + stems) required to be assimilated per unit increment of LAI. The maximum LAI was reached around 1 week before the silking stage. After this date, the N_u increase was not related to LAI. In the N-limiting treatments, the relationship between N_u and LAI was a function of the intensity of N stress. In 1990, N deficiency was low and N_u was related to LAI with a slope quite similar to that observed in the N_{opt} treatment. In the other years, N deficiency was high and N_u in shoot was around 10 kg N LAI^{-1} when $\text{LAI} > 1.5$.

In parallel with the leaf area growth, allometric relationships (Fig. 8) between W and LAI were observed for the N_{opt} and N-limiting treatments in the 1990–1994 Onard experiments (experiments nos. 1, 2, 3 and 17, Table 1). Non-linear regressions were fitted to (i) all data between emergence and one week before the silking stage (W from 0.004 to 11 t ha^{-1}) and (ii) data

between the 10 visible leaf stage and 1 week before the silking stage (W from 1 t ha^{-1} , i.e., about $\text{LAI} = 1$) because N limitation only began at the 10-leaf stage.

When $0 < W < 11 \text{ t ha}^{-1}$

$$N_{\text{opt}} \quad \text{LAI} = 1.068(W)^{0.757} \\ n = 23, R^2 = 0.984 \quad (10)$$

$$\text{N-limiting} \quad \text{LAI} = 1.050(W)^{0.755} \\ n = 23, R^2 = 0.980 \quad (11)$$

When $1 < W < 11 \text{ t ha}^{-1}$

$$N_{\text{opt}} \quad \text{LAI} = 1.234(W)^{0.679} \\ n = 16, R^2 = 0.951 \quad (12)$$

$$\text{N-limiting} \quad \text{LAI} = 1.251(W)^{0.640} \\ n = 16, R^2 = 0.905 \quad (13)$$

with LAI in $\text{m}^2 \text{ leaf m}^{-2} \text{ soil}$ and W in t ha^{-1} . With all data, a slight bias was observed in the distribution of residuals (not shown) that indicated a more complex allometry. Thus, Fig. 8 only shows the non-linear regressions fitted with data where $W > 1 \text{ t ha}^{-1}$. In N_{opt}

Table 4. Number and frequency (*in italic>*) of data points which did not correspond to the model for two groups of maize cultivars used in the experimental sites in France

Groups of cultivars	Total number of data*	N-limiting [‡]				Non-N-limiting			
		Number of data	% N_c [¶]	1.05% N_c [¶]	1.10% N_c [¶]	Number of data	% N_c [§]	0.95% N_c [§]	0.90% N_c [§]
Volga	191	47	4 <i>8.5%</i>	3 <i>6.4%</i>	3 <i>6.4%</i>	144	10 <i>6.9%</i>	4 <i>2.8%</i>	0 <i>0%</i>
Déa - Furio	89	15	0 <i>0%</i>	0 –	0 –	74	4 <i>5.4%</i>	2 <i>2.7%</i>	1 <i>1.4%</i>
Total	280	62	4 <i>6.5%</i>	3 <i>4.8%</i>	3 <i>4.8%</i>	218	14 <i>6.4%</i>	6 <i>2.8%</i>	1 <i>0.5%</i>

* each data point is the mean of three or four repetitions.

[‡]N limiting, number of data where $W < W_{max}$ and non-limiting, number of data where $W = W_{max}$ at $P_{0.10}$.

[¶]When $W < W_{max}$ at $P_{0.10}$, number of data where $\%N > \%N_c$ or $(1.05\%N_c)$ or $(1.10\%N_c)$.

[§]When $W = W_{max}$ at $P_{0.10}$, number of data where $\%N < \%N_c$ or $(0.95\%N_c)$ or $(0.90\%N_c)$.

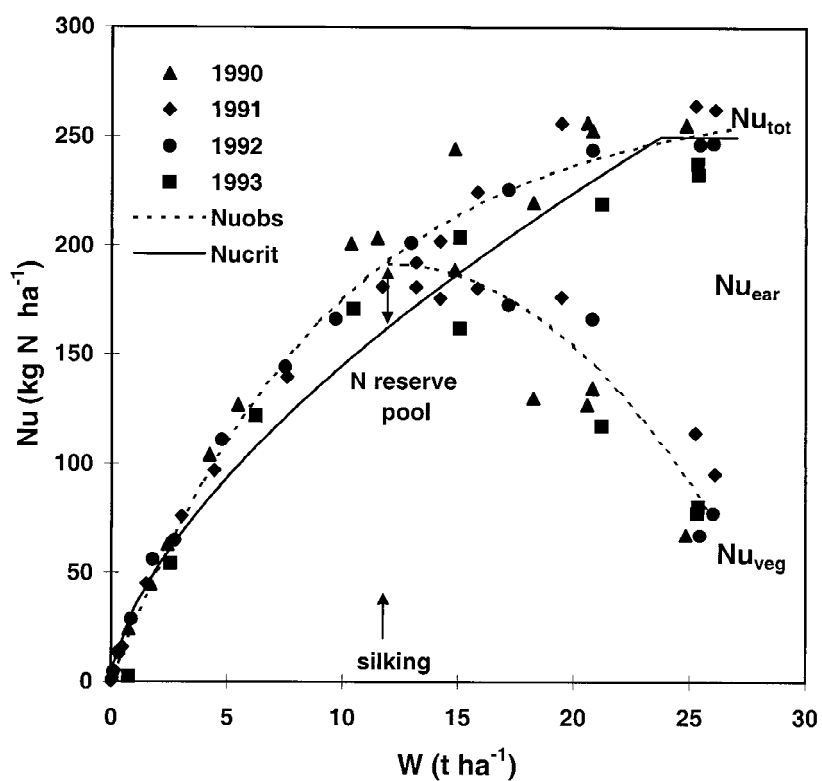


Figure 6. Relationships between N uptake by aerial biomass (Nu , in kg N ha^{-1}) and aerial biomass accumulation (W) in maize crops. (—) critical N uptake model, $Nu_c = 34 (W)^{0.63}$ from 0 to 24 t ha^{-1} , (---) N uptake observed for the N_{opt} treatments in the 1990–1993 Onard experiments during the entire crop development: $Nu_{obs} = 270 (1 - e^{-0.095W})$. From silking stage onwards, Nu_{obs} is decomposed into two components: N uptake in the vegetative organs (Nu_{veg}) and N uptake in the ears (Nu_{ear}), the sum being equal to Nu_{tot} .

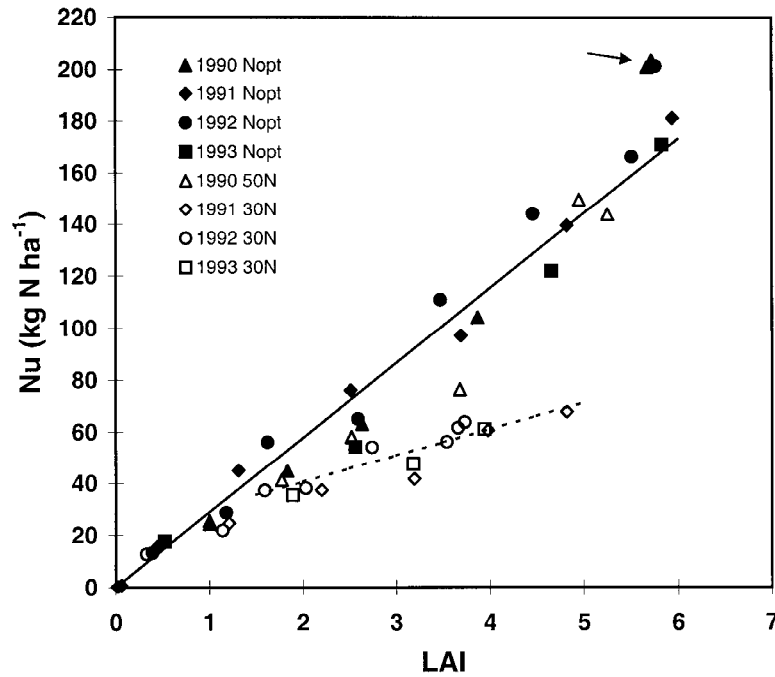


Figure 7. Relationship between the N uptake by aerial biomass (N_u) and green leaf area index (LAI, in m^2 leaf m^{-2} soil) in maize crops from emergence to 7 days before the silking stages for two groups of data: the non-N limiting treatments (N_{opt} treatments) and the N limiting treatments (30N or 50N treatments) in 1990–1993 Onard experiments. (—) linear regression fitted to the N_{opt} treatments, $N_u = 28.87$ LAI, $n = 23$, $R^2 = 0.98$; the data marked with an arrow are outside. (- - -) linear regression fitted to the N limiting treatments when LAI > 1.5, $N_u = 10.2$ LAI + 20.3.

treatments, the non-linearity of this relation (Eq. (11)) indicated that the plant must invest a greater proportion of its dry matter in supporting tissues (stems) as its leaf area developed. In the N-limiting treatments, the relationship observed between LAI and W was similar to that observed in the non-N limiting treatments. This confirms the robustness of this relationship and indicated that isometric growth between leaf area and plant mass was not strongly modified by N deficiency.

Reproductive growth period

From silking stage to maturity, the aerial biomass is made up of two main compartments: vegetative organs (leaves, stems, etc.) and reproductive organs (ears with grains). Table 5 shows the dry matter and the N uptake partitioning in maize at three growth stages: silking, silking+30 days and silage stages (means calculated in the N_{opt} treatments at Onard experiments). During this period, $N_{u_{\text{ear}}}$ was 173 kg N ha^{-1} , of which 113 kg N ha^{-1} ($= 190 - 77$) was remobilized from vegetative compartments and 60 kg N ha^{-1} was taken up from

the soil ($= 250 - 190$). At silking + 28 day stages, the maize crops had taken up 96% of $N_{u_{\text{tot}}}$ measured at the silage stage.

We had insufficient data to select critical points in the ears by the proposed statistical procedure. From data observed during the grain filling period under N_{opt} treatments in the Onard experiments (experiments nos. 1, 2, 3 and 17), we fitted a relationship between $\%N_{\text{opt,ear}}$ (% N in ear, $\text{g N (100 g ear)}^{-1}$) and W_{ear} (ear weight, t ha^{-1}) (Fig. 9):

$$\%N_{\text{opt,ear}} = 2.30(W_{\text{ear}})^{-0.25} \quad (14)$$

with 2.30 ± 0.37 , -0.25 ± 0.009 , $n=18$, $R^2=0.97$ and W_{ear} between 0.36 and 15.0 t ha^{-1} .

The %N decreased rapidly in the early period of ear growth which corresponded to the volume expansion process of the ear, i.e., cell division and cell expansion (from $3\%N_{\text{ear}}$ at 0.1 t ha^{-1} to $1.6\%N_{\text{ear}}$ at 4 t ha^{-1} ; from silking to silking + 25 days). Afterwards, $\%N_{\text{ear}}$ decreased slowly from $1.6\%N$ to $1.2\%N$ as W_{ear} increased from 4 to 15 t ha^{-1} . This means that an average of 14 kg N ha^{-1} was allocated to ears to

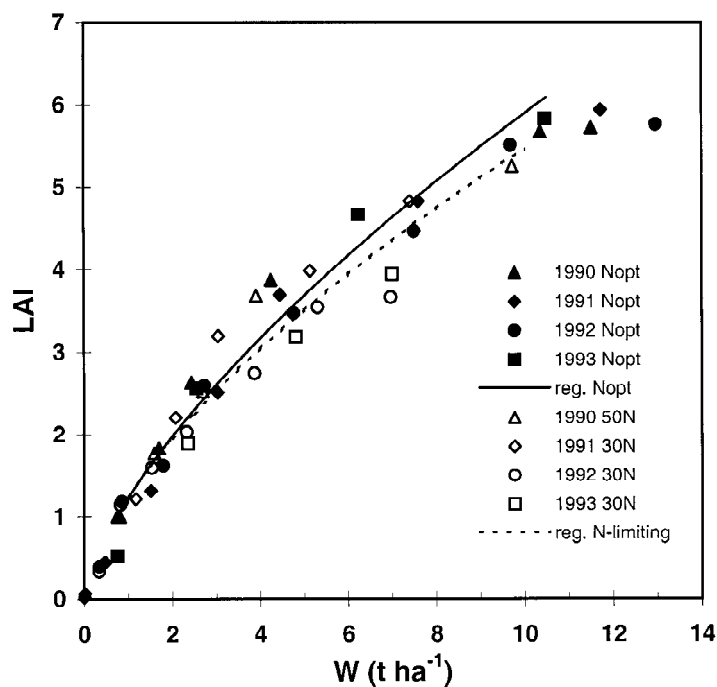


Figure 8. Relationships between green leaf area index (LAI, in $\text{m}^2 \text{ leaf m}^{-2} \text{ soil}$) and aerial biomass accumulation (W) in maize crops from emergence to 7 days before the silking stage in two groups of data: the non-N limiting treatments (N_{opt} treatments) and the N-limiting treatments (30N or 50N treatments) in 1990–1993 Onard experiments. The non-linear regression curves were fitted to the N_{opt} treatments: $\text{LAI} = 1.234 (W)^{0.679}$, $n = 16$, $R^2 = 0.95$ and the N-limiting treatments: $\text{LAI} = 1.250 (W)^{0.640}$, $n = 16$, $R^2 = 0.90$ for data between the 10 visible leaf stage ($W = 1 \text{ t ha}^{-1}$) and $W = 11 \text{ t ha}^{-1}$.

Table 5. Aerial dry matter weight (W) and N uptake (Nu) in different compartments of aerial parts of maize for three stages during reproductive period

Aerial compartments	Silking stage‡		Silking + 25 days stage		Silage stage	
	W (t ha^{-1})	Nu (kg N ha^{-1})	W (t ha^{-1})	Nu (kg N ha^{-1})	W (t ha^{-1})	Nu (kg N ha^{-1})
Vegetative	11.7 ± 0.4	190 ± 6	13.4 ± 0.5	148 ± 11	11.4 ± 0.4	77 ± 5
Ears	–	–	7.4 ± 0.7	92 ± 8	14.1 ± 0.2	173 ± 5
Total	11.7 ± 0.4	190 ± 6	20.8 ± 0.4	240 ± 7	25.5 ± 0.3	250 ± 4
% of silage stage*	46%	76%	82%	96%	100%	100%

Means (\pm standard error of mean) of data observed in N_{opt} treatments in 5 Onard experiments (experiments nos. 1, 2, 3, 4 and 17).

* % of data observed at silage stage (55 days after silking stage).

‡Silking stage was observed around 75 days after emergence stage.

accumulate 1 t ha^{-1} of ear dry matter during the main storage period for starch.

In parallel, during ear growth, the %N in vegetative organs (% N_{veg}) decreased (not shown). Despite the greater variability in % N_{veg} in comparison to % N_{ear} , a more rapid decrease in % N_{veg} was observed when W_{ear} reached $8\text{--}9 \text{ t ha}^{-1}$. At this stage, near silking

+ 28 days, the aerial biomass accumulation was approximately $21\text{--}23 \text{ t ha}^{-1}$. At maturity, % N_{veg} was 0.6–0.7%N. Thus, from silking to silking + 28 days, as a result of the different kinetics of N in the growing organs, the N decrease in the whole plant was similar to the %N decline before silking. The Nu_{ear} of 92 kg N ha^{-1} at silking + 28 days was the result of 50 kg N

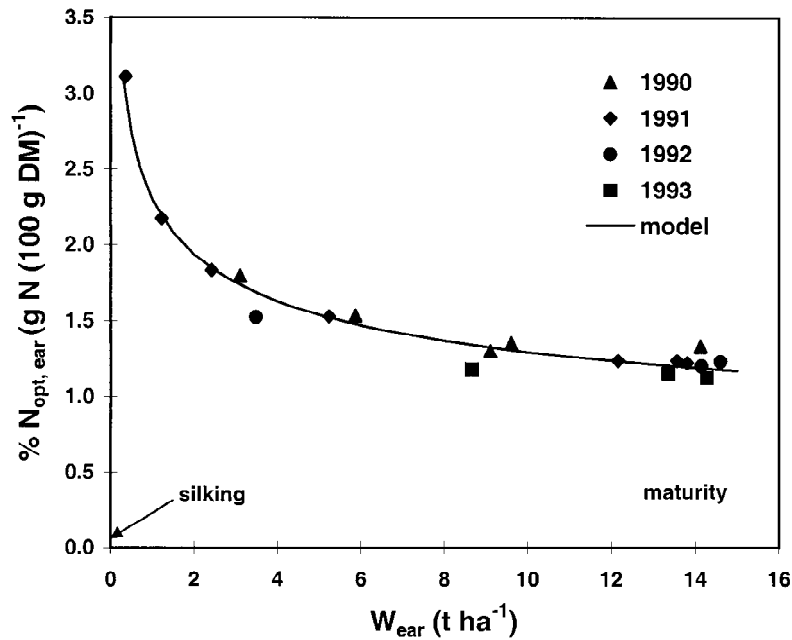


Figure 9. Relationships between N concentration in the ears ($\%N_{\text{opt, ear}}$) and ear dry matter accumulation (W_{ear}) during the grain filling period of maize in the N_{opt} treatments at Onard (experiments nos. 1, 2, 3 and 17, Table 1). (—) fitted allometric relationship: $\%N_{\text{opt, ear}} = 2.30 (W_{\text{ear}})^{-0.25}$ from 0.36 to 15 t $W_{\text{ear}} \text{ ha}^{-1}$.

ha^{-1} which was taken up from the soil and 42 kg N ha^{-1} which was remobilized from vegetative organs (Table 5). From silking + 28 days, the cessation of N uptake and the increase of N remobilization from vegetative organs (71 kg N ha^{-1}) to storage organs modified the $\%N - W$ relationship at the whole plant scale.

The extrapolation of Eq. (7) to values greater than 23 t ha^{-1} can be a problem because N accumulation never asymptotes while N absorption reaches its maximum before the silage stage (cf Fig. 6). The upper limit of validity of Eq. (7) has been fixed to silking+30–40 days ($N_{\text{uc}} = 250 \text{ kg N ha}^{-1}$ when $W = 24 \text{ t ha}^{-1}$). After this date, further N absorption from soil is very limited, and grain filling is mainly supplied by remobilization of N from leaves and stems. At the silking stage, the maize crops had taken up at least 30 kg N ha^{-1} more than that strictly needed for maximum instantaneous growth rate (Fig. 6, difference between N_{uc} and N_{obs} curves). Application of N fertilizer in the early crop period led to uptake of N in excess, which can be considered as an N reserve pool. In most cases tested, soil N availability at the end of the growing period was generally insufficient to supply crop N demand. A temporary 'luxury' uptake allowed the

crop to reach its potential growth. Thus, diagnosis of crop N nutrition status during the vegetative period must take into account the necessity of a N reserve pool (about 30 kg N ha^{-1}), because N applications late in season are not possible, except when N application can be associated with irrigation water. This N reserve is important, equivalent to 2.1 t ha^{-1} of grain yield (dry weight), assuming a final nitrogen concentration in the grain of 1.4% N (Cerrato and Blackmer, 1990; Plénet, 1995).

Discussion

The decline of critical $\%N$ is related to aerial biomass accumulation by an empirical allometric equation (Eq. (4)). This model has been validated in contrasting conditions of growth and development for maize crops. However, before using this empirical relationship as a diagnostic tool for the N nutrition status of maize crops, this relationship must be analyzed in terms of ecophysiological processes.

Analysis of the results based on a growth theory

To explain the critical %N – W relationship, we can use the conceptual model proposed by Caloin and Yu (1984) and developed further by Greenwood et al. (1991) and Lemaire and Gastal (1997). They assume that, during the vegetative growth period and for aerial organs, plant biomass can be divided into two compartments. One compartment called ‘metabolic’ is associated with metabolic activity such as photosynthesis, and has a high nitrogen concentration. The second compartment called ‘structural’ is associated with building the spatial architecture of plants. Structural tissues have a low nitrogen concentration. These two compartments are only conceptual entities. However, to a first approximation, we can consider that leaf tissues mainly correspond to the metabolic component and that stem support tissues mainly correspond to structural material. This would lead to proportionality between N uptake and leaf area expansion during the vegetative period. The hypothesis of proportionality between the amount of N accumulated and the green area of a crop has been proposed previously (Grindlay et al., 1993; Sylvester-Bradley et al., 1990; Lemaire et al., 1997a in lucerne). These authors found a constant N accumulation in shoot as a function of LAI, with a value of about 3 g N m⁻² of leaf area in wheat and lucerne crops under non-limiting N supply. Our results confirm the proportionality between the amount of N accumulated in the plant and its leaf area for maize crops before N accumulation occurs in storage organs. The constant value in maize (2.9 g N m⁻² leaf area) is very close to the value found for other crops.

In dense canopy, as the plant grows, the structural compartment increases more rapidly in comparison to isolated plants because competition for light requires plants to invest in greater proportion in supporting tissues. The proportion of metabolic/structural compartments rapidly decreases, similar to the decrease in the ratio of leaf area to aerial biomass (LAR, leaf area ratio) (Lemaire and Gastal, 1997). The ‘core-skin’ hypothesis developed by Hardwick (1987) assumes isometry between the active metabolic compartment, identified as energy exchange surfaces (scaling as leaf area, dimension 2), and biomass (plant size, dimension 3). According to this hypothesis, the LAI of a stand tends to increase in proportion to (W)^{2/3} in a dense canopy. In maize crops, our results show that the leaf area expansion is linked to growth mass by an allometric coefficient equal to about 0.68 (± 0.04) for the 1 t ha⁻¹ < W < 11 t ha⁻¹; this result supports

the assumption of Hardwick, even if a more complex allometry is observed when W values < 1 t ha⁻¹ are included in the regressions. Under maize N deficiency, the allometric coefficient was not statistically modified ($\beta = 0.64 \pm 0.05$). This result is similar to those obtained on three grass species in response to altered N regimes (McConnaughay and Coleman, 1998).

Several authors have shown that within dense canopies of different species, leaf nitrogen partitioning is non-uniform and a function of vertical light distribution (Charles-Edwards et al., 1987; Field, 1983; Hirose and Werger, 1987; Pons and Pearcy, 1994). In maize crops, we have shown that a relatively constant fraction of shoot N content occurred in leaves at the top of the canopy, despite the decrease of %N in the whole plant as aerial biomass increased (Lemaire et al., 1997c). The remobilization of metabolic leaf N from shaded leaves to well-illuminated leaves corresponds to an optimization of canopy photosynthesis. Thus, in dense canopies, N accumulation is not proportional to biomass accumulation. The combination of Eqs. (9) and (12) gives:

$$\begin{aligned} Nu &= 28.9 \times 1.234(W)^{0.679} \\ &=> Nu = 35.7(W)^{0.679} \end{aligned} \quad (15)$$

This equation is very similar to the empirical Eq. (7) which gives the critical Nu_c . Equation (15) was obtained from data obtained from N_{opt} treatments, whereas Eq. (7) was obtained from critical data-points. This might explain the small differences in the parameter values. Thus, the data obtained in maize crops suggest that the N accumulation rate in a dense canopy is proportional to the rate of increase of LAI during the vegetative growth period. However, as LAI tends to increase isometrically in relation to biomass, i.e., in proportion to (W)^{0.68}, the critical %N in plants decreases with biomass accumulation. Our data show that the allometric coefficient for the %N decline in maize plant (-0.37) is very close to the theoretical coefficient (-1/3) proposed by Hardwick (1987) and Lemaire and Gastal (1997).

In the early stage of growth, individual plants can be considered to be isolated, even in dense crops. In young plants, aerial biomass accumulation is mainly the result of leaf tissue expansion with a high N concentration. Plant growth is approximately exponential and the relative growth rate (RGR) is approximately constant. Under these conditions, internal nitrogen concentration is linearly related to RGR and exponential growth occurs only if internal nitrogen concentration is constant (Ågren, 1985; Ingestad, 1982).

In our model, the $\%N_c$ is constant from emergence stage to 10 leaves stage ($0 - 1 \text{ t ha}^{-1}$), in agreement with Ågren's theory. Nevertheless, Lemaire and Gastal (1997) demonstrated that even for isolated plants, exponential growth was an approximation and a small decline in $\%N$ was evident even for young plants. The value of $3.4\%N$ is close to the N concentration in leaves (Jones, 1967; Loué, 1984; Plénet, 1995; Walworth et al., 1986), but few values are available for young maize plants. We have analysed nitrogen by the Kjeldahl method without specific reduction of nitrate. In young plants, nitrate accumulation in shoots can be important and may explain the great variability in total N concentration. However, in growth chamber experiments, Khamis and Lamaze (1990) showed that maximal growth can be obtained in young maize plants with 3.4% reduced N (2.9 mg N/g^{-1} fresh weigh) and without nitrate accumulation in shoots.

In the critical $\%N - W$ relationship, $\%N$ decline occurs when $W > 1 \text{ t ha}^{-1}$ ($\text{LAI} > 1$). In wheat, $\%N$ declines when $W > 1.55 \text{ t ha}^{-1}$ (Justes et al., 1994). Greenwood et al. (1990) show for C_3 and C_4 species that $\%N$ decline starts when $W > 1 \text{ t ha}^{-1}$. However, it is difficult to determine exactly the limit between a constant $\%N$ and a $\%N$ decrease. This limit could be species dependent, because genotypic differences in RGR have been shown for isolated plants growing in non-limiting conditions (Poorter et al., 1990).

The great difference in the α values between C_3 species and maize is in agreement with results of various authors (Brown, 1978; Field and Mooney, 1983). The C_4 photosynthetic pathways have a higher photosynthetic nitrogen use efficiency (Anten et al., 1995; Greenwood et al., 1990) and have lower leaf N content (Sage and Pearcy, 1987), thus explaining the smaller $\%N$ in C_4 species.

After the silking stage, plant N dynamics can be separated into two periods. From silking to silking + 25 days, ear growth is mainly in volume, i.e., involving cell division and expansion of the grain and requiring a large N concentration (Tollenaar, 1977). Crawford et al. (1982) show that plant parts closely associated with the grain (the husk, cob and shank) act first as sinks (for 24 days) and then as sources of nitrogen after pollination. During this period (the lag phase), N uptake and remobilization from leaves and stem tissues sustain the N demand of developing tissues (Swank et al., 1982; Ta and Weiland, 1992). Consequently, the dynamic of $\%N$ decline in the whole plant is not disturbed. From 25 to 35 days after silking, plant N uptake has practically reached a maximum as shown

in Table 5 (Karlen et al., 1987; Plénet et al., 1992). The increase of starch deposition in grain (Boyer and Shannon, 1986; Prioul et al., 1990) and the deposition of major storage proteins (zein, glutelin) associated with carbon accumulation in the grain (Landry, 1984; Tsai et al., 1978) enhance N remobilization from stems and leaves, leading to a more rapid decline in whole plant $\%N$. However, because at this stage of growth the $\%N$ of grain is not very different from that of the vegetative parts in maize plants, the slope of the relationship between $\%N$ and whole plant biomass is only slightly modified, in contrast to grain legumes where high N concentration storage in grain slows the decrease in whole plant $\%N$ (Ney et al., 1997).

Variability of nitrogen concentration in plants

We observed a great variability in plant N concentration for a given value of aerial biomass in the validation experiments. N concentration can vary up to $\pm 70\%$ about $\%N_c$. Following Justes et al. (1994), we have fitted two envelope-curves. The $\%N_{\max}$ curve gives an estimation of maximum N accumulation in aerial biomass under field conditions. In this case, both growth and N uptake rates are maximum and N availability in soil is non-limiting. N absorption is then regulated by complex mechanisms involving a negative feedback effect from reduced N compounds transported to roots in the phloem (Lemaire et al., 1997b; Touraine et al., 1994). When soil N availability is high, N stored as nitrate and/or reduced N in leaf vacuoles and Rubisco (Millard, 1988), allows to sequester the nitrogen and reduces the amount of N recirculating to roots, so avoiding down regulation of N uptake (Lemaire and Millard, 1999). The finite limit to the amount of N that can be sequestered is difficult to establish because it is very linked to environmental conditions. For N_{opt} treatments in our experimental conditions, comparison of the observed N uptake with critical N uptake indicates N storage of at least 30 kg N ha^{-1} at the silking stage. The plant can remove the N stored to compensate for the decrease in external availability during grain filling. Thus, the ability of the plant to store N above the critical value $\%N_c$ could be an advantage under conditions of fluctuating soil N availability.

The $\%N_{\min}$ might be an estimate of N concentration in structural tissues, i.e., a minimum value from which relative growth rate becomes zero (Ågren, 1988). However, our N treatments did not induce N stress in the very early development stages. The

$\%N_{\min}$ curve probably overestimates the minimum N concentration in young maize plants. Above $4 \text{ t } W \text{ ha}^{-1}$, the minimum N concentration can be estimated by a horizontal line with a constant value near $0.7\% N$. This value is similar to that determined by Greenwood et al. (1991) in various crops and in wheat (B. Mary, in (Lemaire and Gastal, 1997)). This value of 0.7% is very close to the $\%N$ of the structural compartment estimated from the $\%N$ in vegetative organs at maturity ($\%N_{\text{veg}} = 0.6\text{--}0.7\%$).

Conclusions

The critical $\%N - W$ relationship for maize crops has been determined by fitting an empirical allometric equation, using a precise procedure to select critical data points. The resulting relationship is in agreement with theoretical models, thus underpinning its wider use as an indicator of maize crop N status. The critical $\%N - W$ relationship provides a useful link between N dynamics and plant growth. At present, a diagnostic on the plant growth can be realised by different potential crop growth models. The critical $\%N - W$ relationship provides an indicator of crop N status in the field at each growth stage, for use in the improvement of fertilisation management. In addition, integration of the critical $N_u - W$ relationship into crop growth models (Brisson et al., 1998) may allow the prediction of N demand in maize crops as a function of environmental conditions.

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