

# Genetic differences for nitrogen uptake and nitrogen utilisation efficiencies in winter wheat

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## Abstract

Due to economic and ecological factors, European agricultural practices are likely to go towards extensive systems with lower inputs of nitrogen (N) fertilisers. The objective of this study was to assess varietal differences for N use at two nitrogen levels. A set of 20 winter wheat (*Triticum aestivum* L.) genotypes was studied over 2 years in northern France on a deep loam soil without (N0) and with 170 kg ha<sup>-1</sup> N fertiliser (N+) as ammonium nitrate. Results were consistent on both years as the genotype × year or genotype × year × N level interactions were not significant. The genotype × N level interaction was highly significant except for total N utilisation efficiency (total above-ground dry weight/total above-ground N) and grain N concentration. The genotype × N level interaction for grain yield was mainly due to three contrasting genotypes: Cappelle, a cultivar from the 1940s, had the same yield at N0 and N+; Arche had a high yield at both N levels; and Récital had a high yield with added N and a very low one without N. The number of kernels/ear explained most of the variations of grain yield at N0 (48%) and N+ (80%), and of the interaction (67%). N uptake efficiency (total above-ground N/soil N supply) accounted for 64% of the variation in N use efficiency (grain yield/soil N supply), while at N0 and at N+ it accounted for only 30%. N utilisation efficiency (grain yield/total above-ground N) was then more important at N+ than at N0. Grain N explained most of total plant N variation at both N levels. The interaction for N use efficiency was best explained by the interaction of N uptake (63%). The applications of these results to a breeding programme to create varieties adapted to low-input management systems are discussed. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Winter wheat; Nitrogen utilisation efficiency; Nitrogen uptake efficiency

## 1. Introduction

Nitrogen (N) is one of the main inputs on winter wheat in high-input agricultural systems.

In a local survey of agricultural practices in northern France conducted in 1997, it represented 28% of the cost of inputs (Quiévreux, 1997). It is also responsible for an important part of agriculture-related pollution through leaching or denitrification (Mariotti, 1997). During at least the past 30 years, the nitrate content of water has increased in the intensive cropping area of France (Mary et al.,

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1997). To address both economic and ecological issues, plant breeders would have to release cultivars that minimise pollution risks and maximise farmers' revenue. Limited pollution risks could be achieved either with low fertiliser rates or cultivars that better absorb N. Concerning N, high revenue should be obtained with a maximum yield and quality per unit of N applied. Plant breeding programmes must produce varieties that absorb N more efficiently and use it more efficiently to produce grain. To obtain a high seed protein content and good quality, most of the absorbed N would have to be translocated to the grain before maturity.

Field experiments have shown that genetic variability for N uptake exists in small grains (Löffler et al., 1985; Van Sanford and MacKown, 1986; Fossati et al., 1993). Genotypic variation has also been reported for N utilisation efficiency expressed as the ratio of grain yield to total plant N (Cox et al., 1985; Van Sanford and MacKown, 1987; Dhugga and Waines, 1989; May et al., 1991). N uptake explains variation in grain yield more than N utilisation (Van Sanford and MacKown, 1987; Dhugga and Waines, 1989; May et al., 1991).

Moll et al. (1982), on corn (*Zea mays* L.), and Dhugga and Waines (1989), on hexaploid spring wheat and tetraploid spring wheat (*Triticum turgidum* L.), have shown that N uptake efficiency becomes more important than N utilisation efficiency in determining N use efficiency as soil N supply increased. However, Ortiz-Monasterio et al. (1997), for bread wheat, reported an inverse result. These studies were carried out in conditions where grain yields were low compared with northern France. Moreover, they did not address the genotype  $\times$  N level interaction, which was generally significant.

The objective of this study was to investigate the variability of N uptake and N utilisation efficiencies among winter wheat cultivars and to assess their relative importance in potentially high-yielding conditions.

## 2. Materials and methods

The experiment was conducted with 36 winter

wheat genotypes in 1993–1994 and with 30 genotypes in 1994–1995. Results presented here are from 20 genotypes common to both years. Except for VM014, a line from our plant-breeding programme, all the other genotypes are cultivars registered in France between 1946 and 1995 (Table 1). The cultivars were primarily chosen to ensure a wide range of heading dates. Two old cultivars, Cappelle and Etoile de Choisy, were chosen to see how they would perform at low N level compared with modern cultivars. They were registered in France in the late 1940s and Cappelle remained the most cultivated variety until the end of the 1960s. They were bred at a time when pesticides and chemical fertilisers were not commonly used and it could be assumed that they would do well at low N level.

Trials were sown on 8 October 1993 and 6 October 1994 at Estrées-Mons INRA experimental station (Somme, northern France). The soil, classified as a deep loam soil (Orthic Luvisol, FAO classification), contained an average of 19 g kg<sup>-1</sup> organic matter and was of pH 8.1. Soil samples were found to have 64 kg ha<sup>-1</sup> (7 February 1994) and 56 kg ha<sup>-1</sup> (8 February 1995) mineral N in the upper 120 cm profile. The experimental design was a randomised complete block design with three replications and a factorial combination of two N levels. Control plots received no N (N<sub>0</sub>), while fertilised plots (N+) were treated with 170 kg ha<sup>-1</sup> N as ammonium nitrate, one-half at tillering and one-half at the beginning of stem elongation. Two N levels only were applied as it is difficult to test more N levels within the frame of a plant-breeding programme with many different lines. The first N level (N+) was considered to be representative of current agricultural practices in the region of the present study. The second (N<sub>0</sub>) was an extreme condition not likely to occur on a farm, but it was chosen in order to maximise the probability to differentiate genotypes.

Each plot, consisting of six 5-m rows, 0.2 m apart, was sown at a density of 300 grains m<sup>-2</sup>. Following local agricultural practices, two growth regulators were sprayed to reduce the risk of lodging (762 g ha<sup>-1</sup> mepiquat chloride + 387 g ha<sup>-1</sup> ethephon and 1012 g ha<sup>-1</sup> chlormequat

chloride + 77 g ha<sup>-1</sup> choline chloride + 22 g ha<sup>-1</sup> imazaquin). Pesticide treatments were applied to achieve total control of parasites.

Dates to onset of stem elongation were recorded on one block for N+ as the number of days from planting until 50% of the plants reached 1 cm ear length stage (Kirby and Appleyard, 1984). Flowering dates were also recorded on one block for N+ as the number of days from planting until stamens were visible on 50% of the spikes. Before mechanical harvest with a plot combine, about 150 shoots were randomly cut at ground level on all six rows and then oven-dried at 80°C for 48 h.

These shoots were used to estimate thousand-kernel weight (TKW), number of kernels per ear, harvest index (HI), grain N concentration and straw + chaff N concentration. N concentrations were measured with a near-infrared reflectance analyser (Technicon InfraAlyzer 400; Technicon Instruments Corporation, Tarrytown, NY, USA)

calibrated against a Dumas procedure (Dumas, 1831). Grain dry weight was estimated as the sum of plot harvest plus grain weight of the shoot samples. Total above-ground dry weight and number of ears per square metre were computed from grain dry weight, HI, TKW and number of kernels per ear. Nitrogen harvest index (NHI) was calculated as grain N/total above-ground N.

N use efficiency for grain yield (NUE<sub>gdw</sub>) has been defined as grain dry weight/N supply. N supply is considered to be soil mineral N in the upper 120 cm profile measured in early February plus applied N. We did not take into account N that could be available deeper in the soil or that was released by mineralisation of organic matter after soil mineral N was measured. Grain N utilisation efficiency has been defined as grain dry weight/total above-ground N. In the same manner, total N utilisation efficiency, also termed as biological yield production efficiency by May et

Table 1  
Registration year, date to onset of stem elongation, flowering date, and plant height of 20 winter wheat varieties

Genotype	Abbreviation	Registration year	Onset of stem elongation (days from 1 January) <sup>a</sup>	Flowering date (days from 1 January) <sup>a</sup>	Plant height (cm) <sup>b</sup>
Arche	Arc	1989	80	153	85
Arminda	Arm	1977	91	160	93
Audace	Aud	1995	76	154	83
Camp Rémy	Cam	1980	86	157	88
Cappelle	Cap	1946	79	159	101
Déclic	Dec	1985	87	151	81
Etoile de Choisy	Eto	1950	72	145	99
Eurêka	Eur	1991	74	148	86
Génésis	Gen	1992	85	160	79
Promentin	Pro	1983	82	152	87
Récital	Rec	1986	78	148	77
Ritmo	Rit	1990	86	161	86
Sensor	Sen	1983	90	162	98
Sidéral	Sid	1990	71	148	85
Soissons	Soi	1987	83	150	80
Talent	Tal	1973	76	148	79
Thésée	The	1983	81	150	79
Trémie	Tre	1992	75	149	79
VM014	V14	–	83	159	79
Viking	Vik	1986	81	154	95

<sup>a</sup> Measured on one block on 2 years at N+ (170 kg N ha<sup>-1</sup>).

<sup>b</sup> Means over 2 years and two N treatments (0 and 170 kg N ha<sup>-1</sup>).

al. (1991) or biomass production efficiency by Ortiz-Monasterio et al. (1997), is defined as total above-ground dry weight/total above-ground N. Total above-ground N/N supply has been termed N uptake efficiency. N use efficiency for grain N yield (NUE<sub>gn</sub>) was defined as grain N/N supply.

Analysis of the contribution of the variation of component traits to the variation of the resultant trait was carried out as presented by Moll et al. (1982), Dhugga and Waines (1989). If  $Y_n$  is the log of a resultant trait and  $X1_n$ ,  $X2_n$  the logs of two component traits at the  $n$ th N level, then  $Y_n = X1_n + X2_n$ .  $\Sigma(X1_n Y_n)/\Sigma Y_n^2$  and  $\Sigma(X2_n Y_n)/\Sigma Y_n^2$  represent the net contribution of each component to the dependent trait both directly and indirectly through the other variables (Dhugga and Waines, 1989). We extended this analysis to the  $G \times N$  interaction in the same way. It was then possible to assess the contribution of the  $G \times N$  interaction of each component trait to the interaction of the resultant trait. The following analyses were carried out:

log(grain dry weight)

$$= \log(\text{number of ears per m}^2) \\ + \log(\text{number of kernels per ear}) \\ + \log(\text{TKW})$$

log(NUE<sub>gdw</sub>)

$$= \log(\text{N uptake efficiency}) \\ + \log(\text{total N utilisation efficiency}) + \log(\text{HI})$$

log(grain N)

$$= \log(\text{grain dry weight}) \\ + \log(\text{grain N concentration})$$

log(NUE<sub>gn</sub>)

$$= \log(\text{N uptake efficiency}) + \log(\text{HI})$$

When the genotype  $\times$  N level ( $G \times N$ ) interaction was significant for a character  $X$ , we computed the Wricke (1962) ecovalence ( $W_g^2$ ) of the genotype  $g$  as:

$$W_g^2 = \sum_{n=1}^N (X_{gn} - X_{g..} - X_{.n} + X_{...})^2$$

where  $n$  is the N level,  $X_{g..}$  the mean of genotype  $g$  over all N levels and years,  $X_{.n}$  the mean of N level  $n$  over all genotypes and years and  $X_{...}$  the general mean. The ecovalence (%) represents the part of the sum of squares of the interaction that may be attributed to a genotype.

### 3. Results

Analysis of variance showed significant differences among genotypes for all traits (Table 2). Although differences between the two different years were generally significant, results were consistent, as the year  $\times$  genotype interaction was significant only for TKW, HI and grain N concentration, and the year  $\times$  genotype  $\times$  N level interaction was never significant. Results will then be presented averaged over the 2 years. Differences between the two N levels were always significant except for number of kernels/ear. The  $G \times N$  interaction was significant for all traits except for total N utilisation efficiency and grain N concentration. All the traits for which this interaction was significant are represented in Figs. 1 and 2.

#### 3.1. Grain yield and yield components

Grain yield decreased from 799 g m<sup>-2</sup> on average at N+ to 584 g m<sup>-2</sup> at N0 (Fig. 1a). Computing the ecovalence showed that three cultivars, Cappelle, Récital and Arche, were responsible for about two-thirds of the  $G \times N$  interaction. Cappelle was the only genotype with no significant difference between its yield at the two N levels. Récital and Arche had no significantly different grain yield with added N, but exhibited a very different one without N. While Récital showed a very low yield without N, Arche had the best overall yield. In addition, Arche had, at N0, a significantly higher yield than Capelle and Etoile de Choisy at N+. Cappelle was very tall (Table 1) and even with the application of a chemical growth regulator, it

Table 2  
Analysis of variance (mean squares) of agronomic characteristics of 20 winter wheat genotypes cultivated for 2 years at two N levels<sup>a</sup>

Factor	Degrees of freedom	Grain dry weight (g m <sup>-2</sup> )	Number of ears per m <sup>2</sup>	Number of kernels per ear	Thousand kernel weight (g)	N uptake efficiency	N utilisation efficiency (g g <sup>-1</sup> N)	Harvest index	Grain N yield (g m <sup>-2</sup> )	Grain N concentration (%)	N harvest index
Year (Y)	1	104989**	3769 ns	7.4 ns	582.2**	3.12**	9.9**	0.363**	0.74 ns	0.414**	3340.8**
Genotype (G)	19	51556**	20790**	135.3**	177.0**	0.16**	10.2**	0.013**	10.6**	0.197**	51.7**
N level (N)	1	2755456**	1650780**	6.4 ns	283.0**	70.84**	316.9**	0.048**	1743.0**	3.678**	1328.9**
Y × G	19	2100 ns	5213 ns	10.5 ns	4.4*, **	0.02 ns	1.4 ns	0.001*	1.2 ns	0.017*	10.9 ns
Y × N	1	27906**	1519 ns	334.5**	0.0 ns	0.65**	11.5**	0.021**	17.2**	0.012 ns	120.2**
G × N	19	11520**	3293**	37.4**	4.9**	0.08**	1.0 ns	0.001**	2.2**	0.011 ns	13.2*
Y × G × N	19	1558 ns	6808 ns	8.7 ns							
Coefficient of variation (%)	0.8 ns	0.16 ns	1.2 ns	0.000 ns	0.6 ns	0.006 ns	9.6 ns				
		6.7	9.0	7.4	2.9	12.9	6.0	3.7	8.2	4.8	3.5

<sup>a</sup> ns, Not significant at  $P \geq 0.05$ ; \*, significant at  $P < 0.05$ ; \*\*, significant at  $P < 0.01$ .

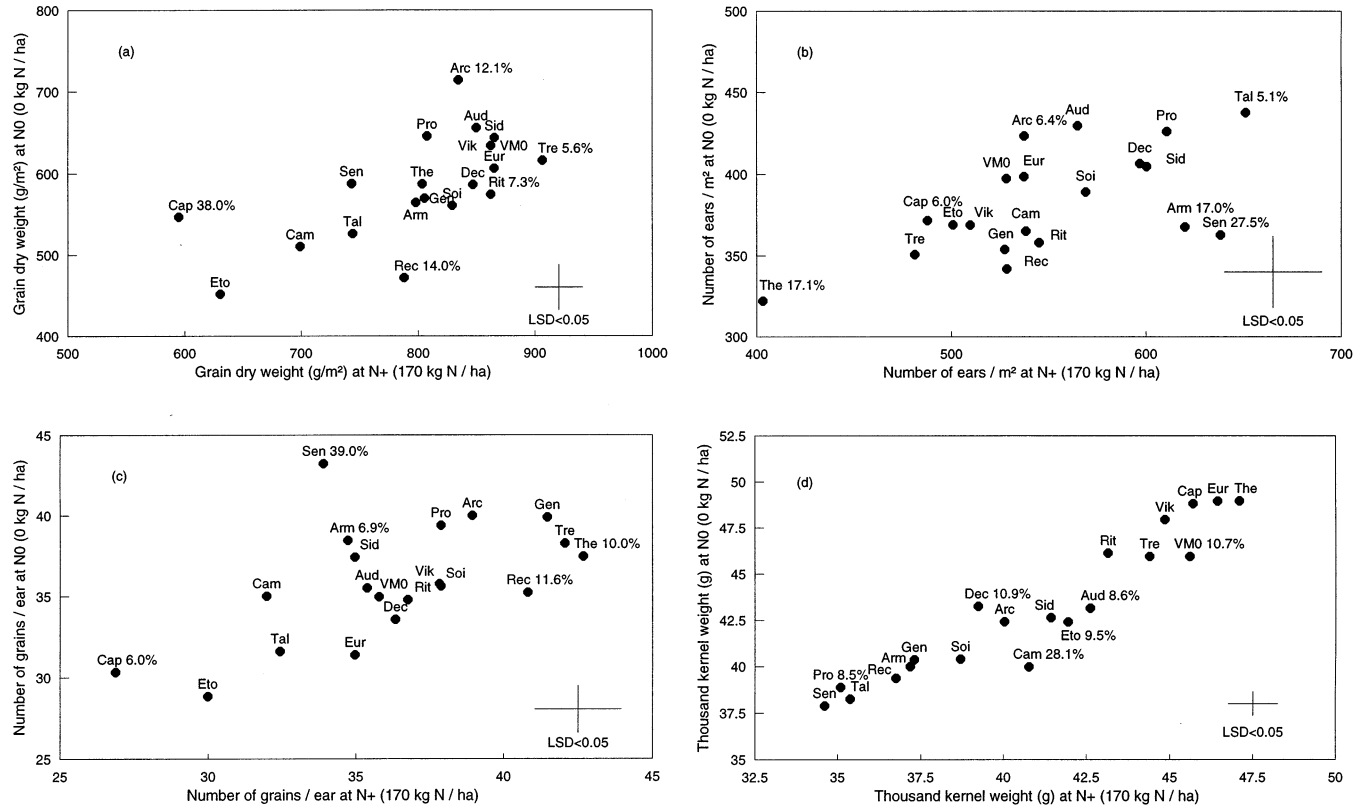


Fig. 1. Grain yields (a) and yield components (b, c, d) of 20 winter wheat genotypes grown at two N levels over 2 years. The contribution of each genotype to the G × N level interaction (ecovalence) was indicated when superior to 5%. The list of genotypes is presented in Table 1.

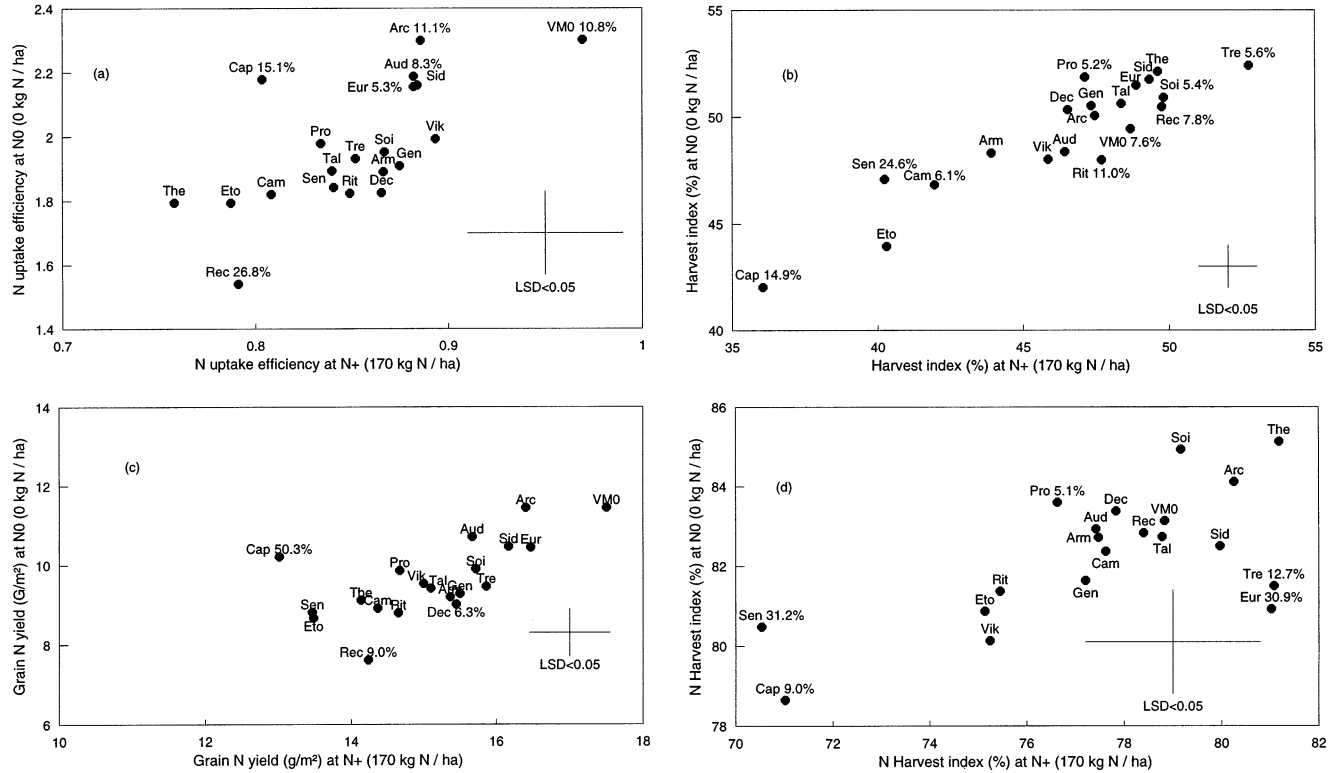


Fig. 2. N uptake efficiency (total above-ground N/N supply) (a), harvest index (b), grain N yield (c), and N harvest index (d) of 20 winter wheat genotypes grown at two N levels over 2 years. The contribution of each genotype to the  $G \times N$  level interaction (ecovalence) was indicated when superior to 5%. The list of genotypes is presented in Table 1.

was the only genotype that lodged on both years (data not shown).

The number of ears per m<sup>2</sup> (Fig. 1b) was the yield component that changed the most between N levels, values decreased, on average, from 549 at N+ to 382 ears m<sup>-2</sup> at N0. All cultivars had fewer ears at N0 than at N+. The cultivars with the highest ecovalence were Sensor, Thésée and Arminda. Sensor and Arminda were most affected by N deficiency, losing, respectively, 43 and 41% of their ears. Thésée had a very small number of ears m<sup>-2</sup> at both N levels.

The average number of kernels per ear (Fig. 1c) was not significantly different between N levels (35.8 kernels per ear at N0 and 36.1 kernels per ear at N+). The G × N interaction was, however, significant and while the grain number increased from N0 to N+ for Sensor, Cappelle and Arminda, it decreased for Thésée, Trémie, Récital and Eurêka.

TKW (Fig. 1d) was significantly higher at N0 (43.1 g) than at N+ (40.9 g). However, five genotypes, VM014, Audace, Etoile de Choisy, Sidéral and Camp Rémy, did not have increased TKW from N+ to N0. They were responsible for most of the G × N interaction. Déclic showed the highest increase in TKW from N+ to N0.

### 3.2. N use efficiency for grain yield and its components

The three components of N use efficiency are N uptake efficiency, total N utilisation efficiency and harvest index. N uptake efficiency (Fig. 2a) was higher at N0 (1.96) than at N+ (0.85). Four genotypes, Récital, Cappelle, Arche and VM014, were responsible of about two-thirds of the G × N interaction. Récital had a very low N uptake efficiency at both N levels, while Arche and VM014 ranked among the highest ones. Cappelle had a high N uptake efficiency without N and a low one with added N.

Total N utilisation efficiency ranged from 92.2 to 115.0 g g<sup>-1</sup> N at N0 and from 80.3 to 97.1 g g<sup>-1</sup> N at N+. The G × N interaction was not significant. Eurêka was the only genotype that showed no significant difference between the two N levels. Sensor had a significantly higher mean

than all the other genotypes except Viking and Ritmo. Talent had the significantly lower one except for VM014 and Soissons.

Mean harvest index (Fig. 2b) was significantly lower at N+ (46.3%) than at N0 (49.2%). However, six genotypes showed no significant differences between the two N levels: Trémie, Soissons, Récital, VM014, Ritmo and Audace. Sensor had the highest ecovalence as it was characterised by the highest increase between N+ and N0 for this component.

### 3.3. Grain N yield

Grain N yield (Fig. 2c) was higher at N+ (15.1 g m<sup>-2</sup>) than at N0 (9.6 g m<sup>-2</sup>) and the difference was significant for all cultivars. The breeding line VM014 had the highest mean at N+ and, along with Arche and Audace, the highest at N0. Cappelle represented one-half of the G × N interaction as it had a high grain N yield at N0 compared with N+.

Grain N concentration ranged from 1.50 to 1.92% at N0 and from 1.70 to 2.15% at N+. All the cultivars had a lower value at N0 and the G × N level interaction was not significant. The two old cultivars, Cappelle and Etoile de Choisy, had the highest mean concentrations.

Mean N harvest index (Fig. 2d) was significantly higher at N0 (82.3%) than at N+ (77.4%). The difference was, however, not significant for Trémie, Eurêka and Sidéral. The cultivar Sensor, which had the highest ecovalence, along with Cappelle, had the lowest NHI at N+.

### 3.4. Contribution of components to grain yield and grain N yield

The relative contributions of yield and N use efficiency components are presented in Table 3. At both N levels, the variation in number of kernels per ear explained most of the variation in grain yield, this part being higher at N+. Its G × N interaction also explained most of the interaction for grain yield. The variation for the number of ears explained one-third of the variation at N0 and one-third of the G × N interaction.



Table 3

Contribution of the components traits to the sum of squares of the resultant trait in 20 winter wheat genotypes grown over 2 years at each N level and for the genotype  $\times$  N level interaction

Resultant trait <sup>a</sup>	Component traits	N level		Genotype $\times$ N level interaction
		N0 (0 kg N ha <sup>-1</sup> )	N+ (170 kg N ha <sup>-1</sup> )	
Log(grain yield)	Log(number of ears per m <sup>2</sup> )	0.32	0.10	0.32
	Log(number of kernels per ear)	0.48	0.80	0.67
	Log(thousand-kernel weight)	0.21	0.10	0.01
Log(NUEgdw)	Log(N uptake efficiency)	0.64	0.31	0.63
	Log(total N utilisation efficiency)	0.15	-0.03	0.07
	Log(harvest index)	0.22	0.71	0.30
Log(grain N yield)	Log(grain yield)	0.85	1.13	1.11
	Log(grain N concentration)	0.15	-0.14	-0.11
Log(NUEgn)	Log(N uptake efficiency)	0.98	0.64	0.84
	Log(N harvest index)	0.02	0.34	0.15

<sup>a</sup> NUE, N use efficiency; NUEgdw = grain yield/N supply; NUEgn = grain N yield/N supply; N uptake efficiency = total above-ground N/N supply; Total N utilisation efficiency = total above-ground dry weight/total above-ground N.

N uptake efficiency accounted for more of the variation of N use efficiency for grain yield at N0 than at N+. It was the opposite for harvest index, while total N utilisation efficiency explained little of any variation. The G  $\times$  N interaction for N use efficiency was best explained by the interaction of N uptake, and then by the interaction of HI.

Grain yield explained most of the variation of grain N yield at N0 and N+ and also most of the G  $\times$  N interaction. N uptake efficiency explained all the variation of N use efficiency for grain N yield without N and two-thirds of it with added N. Its interaction explained also most of the interaction of this N use efficiency.

#### 4. Discussion

This experiment showed that varietal differences exist for grain yield without added N. With a mean yield of 5.8 t ha<sup>-1</sup>, however, N0 could be at least considered as a medium yielding condition. Even if plant breeders produce cultivars adapted to present European high yielding conditions, some of the modern varieties tested performed well in conditions where N was comparatively low. The old cultivar Cappelle,

bred in the 1940s when chemical fertilisers were not commonly used, showed a relatively high N uptake efficiency at N0 (Fig. 2), but it was possible to find modern cultivars with equivalent or better performances (Arche, VM014, Audace, Sidéral and Eurêka). Ortiz-Monasterio et al. (1997) estimated the genetic progress at different N levels with ten of CIMMYT's bread wheat cultivars bred in medium–high conditions (120–200 kg N ha<sup>-1</sup>). Comparing two N levels where lodging did not occur, they found that the genetic progress has been the same at N0, low N level, and N75, medium N level (they did not assess soil N supply but it was low).

As the G  $\times$  N interaction for grain yield was significant in our experiment, varieties behaved differently according to the N level. This is different from Austin et al. (1980) who found a strong positive correlation (+0.97) between yields measured on two experimental fields differing by their fertility with 12 genotypes forming a chronological series from 1908 on. They attributed this result to the system of variety production and evaluation, which is likely to produce varieties with a good yield level in all conditions. However, these varieties may not be the best adapted at low fertility level. Ceccarelli (1996) emphasised the importance of the optimal conditions to select for

low-input environments. He showed that lines selected for high yield in favourable environments yield more in medium to high yielding conditions than lines selected in less favourable conditions. They yield less, however, in the less favourable sites.

Grain yield is the final result of different steps that can be studied through the yield components. The stress we applied, an early and severe stress as no fertiliser was applied, had different effects on the three main yield components. While the mean number of ears per  $\text{m}^2$  decreased from  $\text{N}+$  to  $\text{N}0$ , the mean number of kernels per ear remained the same and the mean TKW increased. All cultivars had less ears per  $\text{m}^2$  at  $\text{N}0$  compared with  $\text{N}+$ . Sensor and Arminda had less ears than the others. They are two very late flowering varieties (Table 1) that were the latest to reach the stage of beginning stem elongation. Cultivar development timing may thus interact with the availability of N in the soil. As we did not monitor tillering, it was not possible to know whether N deficiency affected more tiller production or tiller survival. While the mean number of kernels per ear was the same at  $\text{N}0$  and  $\text{N}+$ , it increased for some and decreased for others. This was not directly related to the decrease in the number of ears per  $\text{m}^2$  even if Sensor and Arminda were among the varieties for which the number of kernels per ear increased from  $\text{N}+$  to  $\text{N}0$ . Récital had both lower number of ears per  $\text{m}^2$  and lower number of kernels per ear at  $\text{N}0$  than at  $\text{N}+$ . TKW was not higher for some cultivars at  $\text{N}0$ , although the number of kernels per  $\text{m}^2$  was always lower at  $\text{N}0$  compared with  $\text{N}+$ . For these lines, either they had reached their maximum TKW or N deficiency so altered the source, photosynthetic or storage capacity, that grain filling was hindered.

We showed that the  $\text{G} \times \text{N}$  interaction for grain yield was best explained by the interaction of the number of kernels per ear (Table 3). The number of kernels per ear is determined during a long period from the double ridge stage to anthesis. This is the result of the differentiation of spikelets and then florets, of which only a part will fully develop to be receptive at flowering. As we did not estimate the different components of the number of kernels per ear, we could not identify which

of these was more important. Competition within and between plants is likely to occur as tillering and stem elongation will also take place during this period.

N uptake efficiency data on Fig. 2a showed that at  $\text{N}0$ , more N was recovered at maturity than was present when residual soil N was measured (February). This N presumably originated mainly from organic matter N mineralisation. Differences between residual soil N in the upper 120 cm and total above-ground N at maturity were 50 and 63  $\text{kg N ha}^{-1}$  in 1994 and 1995, respectively. Like Moll et al. (1982), Dhugga and Waines (1989), Ortiz-Monasterio et al. (1997), our data showed that the contribution of N uptake efficiency and grain N utilisation efficiency were dependent on N level. In agreement with Ortiz-Monasterio et al. (1997), we found that N uptake efficiency accounted more for the variation in N use efficiency at  $\text{N}0$  than at  $\text{N}+$ . When grain N utilisation efficiency was further analysed, it was shown that HI was more important than total N utilisation efficiency in explaining the variation (Table 3), especially at  $\text{N}+$ . When N is rare, the ability to absorb N is certainly of paramount importance and would then be related to root characteristics. It may be hypothesised that differences for the ability to explore the soil or to absorb N existed in the material we tested. When N is not the limiting factor, N utilisation efficiency or harvest index have to be more determinant as N will be available for each genotype independent of the efficiency of their root system.

Ortiz-Monasterio et al. (1997) proposed selecting in medium–high fertility environments to improve for both low and high fertility conditions. They hypothesised that this will be true as they found that at this fertility level, both NUE and N uptake contributed to the variation of N use efficiency. In order to be so, the  $\text{G} \times \text{N}$  level interaction has to be low otherwise indirect selection will be inefficient. They found significant  $\text{G} \times \text{N}$  interactions for total N utilisation efficiency and harvest index but not for total nitrogen (they did not compute N uptake efficiency). In our conditions, the  $\text{G} \times \text{N}$  interaction for N uptake efficiency and harvest index was significant but not for total N utilisation efficiency. Our data

showed that the  $G \times N$  interaction for N uptake efficiency explained most of the variation of the interaction for grain yield.

As our data have shown that genetic variability exists for grain yield at low N level, a breeding programme is under way using, as parents, some of the cultivars investigated in this study. To take into account the  $G \times N$  interaction, field experiments are carried out at two N levels. The aim of this programme is to breed cultivars performing well under low input management systems. Resistance to lodging and common diseases will also be taken into account to limit the use of growth regulators and fungicides.

## References

- Austin, R.B., Bingham, J., Blackwell, R.D., Evans, L.T., Ford, M.A., Morgan, C.L., Taylor, M., 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *J. Agric. Sci., Camb.* 94, 675–689.
- Ceccarelli, S., 1996. Adaptation to low/high input cultivation. *Euphytica* 92, 203–214.
- Cox, M.C., Qualset, C.O., Rains, D.W., 1985. Genetic variation for nitrogen assimilation and translocation in wheat. II. Nitrogen assimilation in relation to grain yield and protein. *Crop Sci.* 25, 435–440.
- Dhugga, K.S., Waines, J.G., 1989. Analysis of nitrogen accumulation and use in bread and durum wheat. *Crop Sci.* 29, 1232–1239.
- Dumas, J.B.A., 1831. Procédés de l'analyse organique. *Ann. Chim. Phys.* 2, 198–213.
- Fossati, D., Fossati, A., Feil, B., 1993. Relationship between grain yield and grain nitrogen concentration in winter triticale. *Euphytica* 71, 115–123.
- Kirby, E.J.M., Appleyard, M., 1984. Cereal Development Guide. Arable Unit, National Agricultural Centre, Stoneleigh, Warwickshire, UK.
- Löffler, C.M., Rauch, T.L., Busch, R.H., 1985. Grain and plant protein relationships in hard red spring wheat. *Crop Sci.* 25, 521–524.
- Mariotti, A., 1997. Quelques réflexions sur le cycle biogéochimique de l'azote dans les agrosystèmes. In: Lemaire, G., Nicolardot, B. (Eds.), *Maîtrise de l'Azote dans les Agrosystèmes*, Reims, 19–20 Novembre 1996, Les Colloques n°83. INRA Editions, Versailles, France, pp. 9–22.
- Mary, B., Beaudoin, N., Benoit, M., 1997. Prévention de la pollution nitrique à l'échelle du bassin d'alimentation en eau. In: Lemaire, G., Nicolardot, B. (Eds.), *Maîtrise de l'Azote dans les Agrosystèmes*, Reims, 19–20 Novembre 1996, Les Colloques n°83. INRA Editions, Versailles, France, pp. 289–312.
- May, L., Van Sanford, D.A., MacKown, C.T., Cornelius, P.L., 1991. Genetic variation for nitrogen use in soft red  $\times$  hard red winter wheat populations. *Crop Sci.* 31, 626–630.
- Moll, R.H., Kamprath, E.J., Jackson, W.A., 1982. Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. *Agron. J.* 74, 562–564.
- Ortiz-Monasterio, J.I., Sayre, K.D., Rajaram, S., McMahon, M., 1997. Genetic progress in wheat yield and nitrogen use efficiency under four nitrogen rates. *Crop Sci.* 37, 898–904.
- Quiévreux, D., 1997. Réseau d'observation de parcelles de céréales. In: *Résultats de la Récolte 1997*. Chambre d'Agriculture de la Somme, Amiens, France.
- Van Sanford, D.A., MacKown, C.T., 1986. Variation in nitrogen use efficiency among soft red winter wheat genotypes. *Theor. Appl. Genet.* 72, 158–163.
- Van Sanford, D.A., MacKown, C.T., 1987. Cultivar differences in nitrogen remobilization during grain fill in soft red winter wheat. *Crop Sci.* 27, 295–300.
- Wricke, G., 1962. Über eine methode zur erfassung der ökologischen streubreite in feldversuchen. *Z. Pflanzenzücht.* 47, 92–96.