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The fate of labelled ^{15}N urea and ammonium nitrate applied to a winter wheat crop

II. Plant uptake and N efficiency

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Abstract

A field experiment was conducted on a winter wheat crop in Northern France with either ^{15}N-urea or ammonium nitrate, labelled either on NH_4 or on NO_3. The fertilizer was split between two dressings, one applied in early March and the second in mid-April, labelled separately. N uptake by the crop was measured at 8 successive times after each dressing. The N uptake efficiency of nitrate was higher than that of ammonium or urea over the whole growth cycle for both dressings. The RUC (Real Utilization Coefficient) reached a maximum at anthesis or even before anthesis, and decreased during the grain-filling period, indicative of N turnover in shoots. Thus the annual N use efficiency appeared highly dependent upon the date of measurement. At harvest, the contribution of soil N (residual N + mineralized N) to the crop was comparable to that from fertilizer, but the two pools were utilized at different periods.

Introduction

Most studies of fertilizer efficiency using ^{15}N-labelled nitrogen are restricted to balance-sheets at crop maturity. N fertilizer uptake efficiency had been defined by the Real Utilization Coefficient – RUC* – (Remy and Viaux, 1982). At harvest it generally held to be in the range 20–80%, the variability arising from the interaction between factors such as form of fertilizer, time of application, type of soil and climatic conditions (Machet *et al.*, 1987). The lower efficiency of ammonium and urea fertilizers compared to nitrate had often been attributed to soil volatilization losses. It could also be due to the potentially greater immobilization of the ammonium form by the soil microflora (Jansson, 1958). An understanding of the origin of the variations of N use efficiency and an ability to predict them are vital for improving N management during the cropping and intercropping periods.

$$*RUC = \frac{U_N \times e}{F \times e_o}$$

where U_N is the nitrogen uptake and e the isotopic excess in the plant at harvest, F the amount of fertilizer N applied and eo its isotopic excess.

It is also necessary to meet the needs of the crop throughout its growth and not merely at the end of the growth cycle. Kinetic studies of N transformation and plant uptake help understand the relative contribution of fertilizer and native N (Nielsen and Jensen, 1986). However such studies are still rare, partly because of the heavy experimental burden involved, partly because of the high cost.

The aim of the ^{15}N-labelled experiment described here was to characterize the dynamics of nitrogen uptake by a winter wheat crop, receiving ammonium nitrate or urea fertilizer, between N appli-

cation and harvest. The efficiency of the residual ^{15}N for the next crop (sugarbeet) had been determined and will be presented in another paper.

The experimental design has already been described, as have the corresponding data for changes in inorganic and organic nitrogen in the soil (Recous *et al.*, 1988a).

Methods

Analytical procedures for plant samples

The dry matter and nitrogen content of the above-ground parts of the plants expressed on an oven-dry basis, were measured on 12 successive occasions. At each date of sampling, the plants were carefully cut just above the soil surface from a 0.3 m^2 microplot so as not to disturb the soil, and subsequently washed free of soil and fertilizer N. At maturity plants were separated into (straw + chaff) and grain. The dry matter and nitrogen content of the roots were measured in the 0–10 cm layer at each time for sampling, in the 10–30 cm layer at four occasions, and on the whole profile (0–120 cm) at flowering. The soil cores were firstly sampled for determination of inorganic and organic nitrogen. The remaining soil (about 4, 7 and 4 kg of fresh soil for the 0–10 cm, 10–30 cm and 30–60-cm layers respectively) was used to evaluate the root content. Roots were removed from the soil cores after the soil had been dispersed for 12 hours with sodium metaphosphate (50 $g\,l^{-1}$) followed by copious washing on a 1-mm mesh sieve. Roots were separated from other plant residues by hand picking.

Shoot and root samples were dried at 80°C and finely ground to powder. Total nitrogen content and $^{15}N/^{14}N$ ratio were determined in a single determination using a flash combustion technique (Dumas method) with an automatic nitrogen analyser (Carlo Erba ANA 1400) connected with a mass spectrometer (VG SIRA 9).

Results

Production of dry matter and grain

The yields of dry matter are shown on Fig. 1. These were not significantly affected by the source of nitrogen at any date of sampling. However variability between plots was high (mean c.v. = 8.8%) owing to the small aera of the sampling microplots (0.3 m^2). That is why we used the mean dry matter data for the different fertilizer treatments at each date of sampling in our N calculations. High yields of above-ground dry matter for straw plus grain were obtained at harvest (18 t ha^{-1}). The grain yield (15% moisture content) averaged 10.4 t ha^{-1} and 6.6 t ha^{-1}, on fertilized plots (160 kg N ha^{-1} added) and control plots, respectively.

Root dry matter in the upper layers 0–30 cm increased up to flowering (Fig. 1). Due to the small amount of soil sampled, the variability on root mass was high (mean c.v. = 31%). No difference between the forms of fertilizer was found. The root profile made at flowering time indicated that more than half of the roots were located in the top 10-cm of soil and 20% in the 10–30 cm layer. If we consider that the weight of fine roots passing through the sieve was negligible (less than 1% of the total, according to Barraclough and Leigh, 1984), then root dry matter was about 1200 kg ha^{-1} at flowering time, equivalent to 10% of total dry matter. At this time there were no significant differences in total root dry matter between fertilized and control plots.

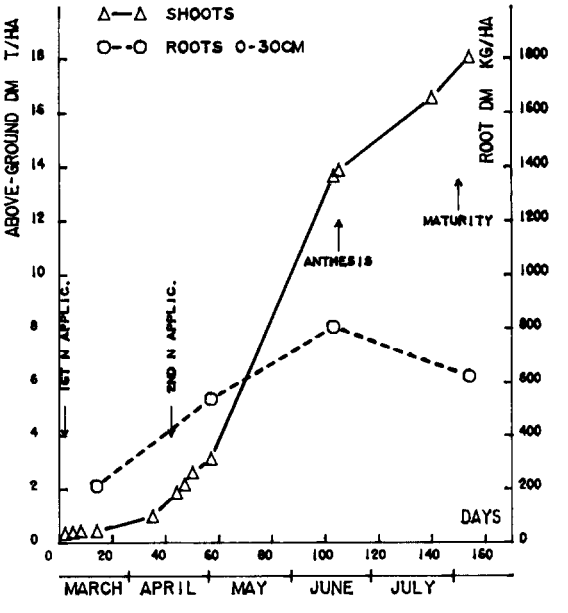

Fig. 1. Evolution of dry matter in shoots and roots (0–30 cm layer) during the growth cycle (mean of all fertilized).

Table 1. Shoot dry matter, shoot N uptake, grain yield and grain N, at harvest, for control (ON), urea and ammonium nitrate treatments (160 kg N ha^{-1}). Values in brackets are the standard errors on replicates

Treatment	Shoot Dry matter (t ha^{-1})	Shoot N uptake (kg ha^{-1})	Grain yield 85% DM (t ha^{-1})	Grain N (kg ha^{-1})
Control	13.0 (0.5)	95.9 (6.3)	6.6 (0.5)	67.6 (5.3)
Urea	18.0 (0.5)	164.7 (3.8)	10.4 (0.5)	128.4 (4.2)
NH_4NO_3	18.0 (0.5)	168.8 (11.0)	10.4 (0.4)	129.8 (8.4)

Table 2. Dry matter, net N uptake and RUC of wheat roots at three stages (mean of all fertilized treatments)

Stage	Dry matter (kg ha^{-1})	N uptake (kg ha^{-1})	N roots (% total uptake	RUC 1st dressing	RUC 2nd dressing
Tillering (day 14)	320[a]	4.6	18.0	ND	ND
Flowering (day 103)	1200	12.0	7.4	2.6[b]	1.1[b]
Maturity (day 154)	950[a]	10.0	6.0	1.4[b]	1.3[b]

[a] Dry matter was extrapolated on the 0–120 depth, on the basis of the root profile measured at flowering
[b] RUC were measured on roots from the 0–30 cm layer

Nitrogen content and total N uptake

The concentration of nitrogen in wheat above-ground tissues remained constant during tillering at about 50 mg g^{-1} for all fertilized treatments, irrespective of the form of application. Immediately after the second dressing (day 44), plants fertilized with urea contained 7% less N than the plants fertilized with ammonium nitrate, presumably because of the delayed uptake caused by urea hydrolysis. This difference becomes less after day 57. At harvest time N uptake by shoots averaged 86.0 kg ha^{-1} for unfertilized plots and 167.5 kg ha^{-1} for fertilized treatments, differences between urea and ammonium nitrate plots not being significant, neither for the total N offtake nor for the grain offtake (Table 1). The net uptake was equivalent to 17 kg N t^{-1} grain. It is well outside the usual N requirement for winter wheat which is close to 30 kg N t^{-1} grain (Remy and Viaux, 1982). In this experiment the nitrogen content of the grain was effectively very low (14.2 mg g^{-1}). It is noticeable that the net assimilation of N was nil between flowering and maturity, whereas the dry matter (above-ground parts) increased from 13.6 to 18.0 t ha^{-1}.

The roots contained 18% of total plant nitrogen at tillering, 7% at anthesis and 6% at maturity (Table 2). Although it has been shown that 1/3 to 2/3 of nitrate-N root content may be lost during the root separation procedure (Gonzales-Montaner, 1987), the greatest variability of root N measurements come from dry matter determination.

Assuming that the uptake of soil N is the same in the fertilized and unfertilized plots, the N uptake efficiency is given by the apparent utilization coefficient (AUC)*. This efficiency was 51% at harvest.

The course of N-fertilizer uptake

Fertilizer uptake was characterized by the real utilization coefficient (RUC) which is the proportion of the applied ^{15}N recovered in the shoots of the wheat crop. Figure 2 shows the uptake following the first application. During the first month the plant took more ^{15}N from the labelled nitrate fertilizer than from the ammonium fertilizer. At day 35, the RUC reached 60%, 38% and 32% for the plots $NH_4{}^{15}NO_3$, ^{15}N-urea and $^{15}NH_4NO_3$, respectively. By this time, all the mineral N remaining in the soil from the fertilizer was in the nitrate form. It accounted for about the same amount (17–20%) of the N applied, irrespective of the treat-

$$*AUC = \frac{U_N - U_o}{F}$$

where U_N and U_o is the nitrogen uptake in the fertilized and control treatments, respectively, and F the amount of fertilizer N applied.

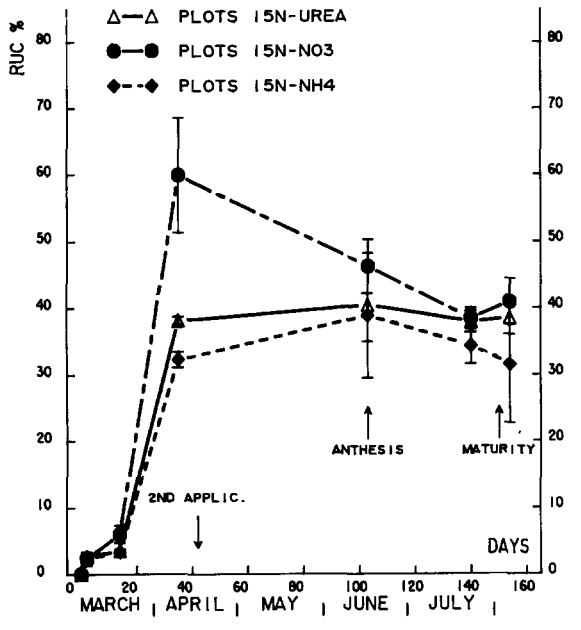

Fig. 2. Kinetics of N uptake efficiency of the first labelled N application, in shoots. Plots ^{15}N-NO_3 and ^{15}N-NH_4 received 50 kg N ha^{-1} as ammonium nitrate. Plots ^{15}N-urea received 50 kg N ha^{-1} as urea. Day 0 was the time of first application.

ment. The maximum uptake efficiency very likely reached a maximum after 35 days. Assuming that the uptake rate after day 35 was the same as during the 14–35 day period (until the complete depletion of the ^{15}N inorganic pool), and that the residual inorganic ^{15}N at day 35 was only subject to absorption by the crop and immobilization into soil organic matter, it can be calculated that the maximum RUC would be obtained around day 42 (date of second application) and would be respectively 74, 53 and 45% for the NH_4-$^{15}NO_3$, ^{15}N-urea and $^{15}NH_4$-NO_3 treatments. These are maximum values and must be reduced if losses occurred, particularly by denitrification.

In the labelled-NO_3 treatment there was a significant decrease of fertilizer-N in the tops prior to flowering, equivalent to 13.7% (s.e. = 5.4%) of the added ^{15}N. During the same period (35–105 d) the labelled organic N in soil increased markedly. The other two treatments showed a very different behaviour with small variations of the labelled plant (Δ*P) and soil organic matter (Δ*O) pools (Table 3). The sum Δ*P + Δ*O was remarkably constant, at 8% of ^{15}N applied. Finally, there was no significant difference in RUC between treatments at flowering and maturity. Between those two dates, there was a trend of decreasing RUC on 7 out of the 9 plots. The average decrease was 5.2% (s.e. = 5%).

The uptake of fertilizer-N was rapid after the second dressing; 29–31% of the urea and ammonium N, 25% of the nitrate N were found in the crop after two days, probably by foliar absorption. During the next 13 days, the extra ^{15}N uptake was equal to 11% (NH_4-$^{15}NO_3$), 4% (^{15}N-urea) and 3% ($^{15}NH_4$-NO_3). Again, preferential uptake of NO_3 was confirmed. The maximum ^{15}N uptake was recorded at flowering as 68% (NH_4-$^{15}NO_3$), 60% (^{15}N-urea) and 59% ($^{15}NH_4$-NO_3). Since the inorganic ^{15}N pool was thought to be depleted long before flowering, the peak of ^{15}N in the plant had probably been reached earlier, but cannot be evaluated. The nitrogen uptake efficiency decreased significantly from anthesis to maturity on the nine plots: the decrease averaged 6.9% of the ^{15}N added (s.e. = 3.3%). This shoot ^{15}N had not been transferred to the root system, since the amount of ^{15}N in the roots was itself lower at maturity than at flowering. The recovery of fertilizer N in the roots was in any case small (1–3%) for both dressings (Table 2).

Soil N and fertilizer N contribution

The course of total uptake and N uptake from the fertilizer and the soil pools are shown in Table 4. Uptake rates were very close for the urea and ammonium nitrate treatments, in spite of a slightly higher nitrogen uptake in the ammonium nitrate treatment after 47 days. In the days following each of the N applications – apart from the rapid foliar absorption of N-fertilizer between 42–44 day –, N fertilizer uptake rate was small and the crop took

Table 3. Variations of ^{15}N content in shoots (Δ*P) and in soil organic matter (Δ*O), between day 35 and day 103, for the first labelled application

Plots	Δ*P (%)	Δ*O (%)	Δ*P + Δ*O (%)
$NH_4{}^{15}NO_3$	−13.7	+22.4	+8.7
$^{15}NH_4NO_3$	+6.6	+1.7	+8.3
^{15}N-urea	+2.4	+5.2	+7.6

Table 4. N uptake of labelled and unlabelled N by wheat in above-ground parts

Treatment	Days	Fertilizer-N uptake				Soil N uptake	Total N uptake
		1st dressing		2nd dressing			
		kg N ha^{-1}					
Urea	2	1.3		–		16.4	17.7
	5	1.4		–		18.4	19.8
	8	1.5		–		19.9	21.4
	14	1.7		–		19.5	21.2
	35	19.0		–		30.7	49.7
	44	26.8[a]		32.8		33.3[a]	92.9
	47	26.8[a]		32.1		35.6[a]	94.5
	50	26.8[a]		33.0		44.2[a]	104.0
	57	26.8[a]		37.0		44.1[a]	107.9
	103	20.2		66.2		72.0	158.4
	140	18.9		55.0		71.7	145.6
	154	19.2		61.4		84.1	164.7
NH_4NO_3		*NO_3	*NH_4	*NO_3	*NH_4		
	2	0.6	0.6	–	–	15.7	16.9
	5	0.9	0.7	–	–	18.5	20.0
	8	1.0	0.8	–	–	20.1	21.9
	14	1.5	0.8	–	–	18.6	20.8
	35	14.9	8.0	–	–	27.7	50.6
	44	18.5[a]	11.3[a]	14.1	16.9	29.9[a]	82.8
	47	18.5[a]	11.3[a]	17.5	15.4	38.5[a]	101.2
	50	18.5[a]	11.3[a]	18.8	17.0	45.2[a]	110.8
	57	18.5[a]	11.3[a]	20.0	18.5	42.3[a]	110.6
	103	11.5	9.7	37.7	32.2	76.9	168.0
	140	9.5	8.5	31.4	27.8	80.8	158.0
	154	10.2	7.8	32.5	27.9	90.4	168.8

[a]Fertilizer and soil uptake were calculated for the 35–105 day period, assuming that the RUC reached its maximum value by day 42, and started to decrease after day 57

up nitrogen almost entirely from the native-N pool. These 'lag' phases were followed by a period of active uptake with nitrogen coming from soil and fertilizer N pools in comparable amounts. The soil contribution during the 35–105 day period was estimated, assuming that uptake was at its maximum at day 42 (see previous section) and that the decrease in RUC started after day 57. If these two hypothesis are wrong, the soil contribution will be underestimated by a maximum of 6 kg N ha^{-1}. During the grain-filling period (105–154 d), the net crop offtake remained constant. At the same time, a significant loss of nitrogen derived from the fertilizer took place, equivalent to 10.2 kg N ha^{-1} (s.e. = 3.9) (5.7% of 50 kg N ha^{-1} and 6.9% of 110 kg N ha^{-1}). If we suppose that nitrogen derived from fertilizer and from soil was equally subject to loss, the global loss between anthesis and maturity was 20.5 kg N ha^{-1}. Consequently there was a gross uptake of soil N of, at least, 20 kg N ha^{-1}.

The ratio atom % excess of the sample/atom % excess of N applied, called Ndff (Nitrogen derived from the fertilizer), give an independent estimate of the fertilizer contribution to plant N. At flowering time, this ratio (Table 5) showed that the second application of fertilizer N increased the proportion of N derived from fertilizer in the order shoots > roots 0–10 cm > roots 10–30 cm. In contrast, the contribution of the first dressing to these 3 compartments was about the same.

^{15}N recoveries

Total ^{15}N recovery is presented in Table 6. In spite of the care taken to distribute the fertilizer

Table 5. Ndff values for shoots and roots at flowering-mean of nine plots (^{15}N-urea, $^{15}NH_4$-$^{15}NO_3$ and NH_4-$^{15}NO_3$)

1st dressing			2nd dressing		
Shoots	Roots 0–10 cm	Roots 10–30 cm	Shoots	Roots 0–10 cm	Roots 10–30 cm
10.6 (2.1)	13.7 (2.3)	10.5 (3.9)	38.5 (3.2)	20.1 (2.3)	8.6 (2.2)

evenly, there was considerable variability in recovery of ^{15}N. The mean coefficients of variation were 16% for soil inorganic ^{15}N, 19% for soil organic ^{15}N and 11% for plant ^{15}N. No significant differences appeared between forms, for both applications. During the first 5 days after the first application, ^{15}N recovery averaged 105%. ^{15}N recovery fell to about 82% over the 8–35 day period. Only part of the ^{15}N deficit could be attributed to leaching of nitrate below 60 cm (see previous section), and labelled nitrate may have been denitrified. About 26% of the ^{15}N applied (13 kg N ha^{-1}) could not be accounted for at flowering time.

Immediately after the second dressing, a part of the fertilizer N was not recovered in plant and soil (0–10 cm). Transfers of nitrate below 10 cm could not be excluded, although it did not rain between the application (day 42) and day 50. The total recovery was approximatively constant until anthesis. At this date an average of 14% (15 kg N ha^{-1} of the ^{15}N applied) was not found in the soil-plant system. The lower recovery at final harvest is consistent with the occurrence of gaseous losses from shoots during the grain-filling period. Underestimation of certain compartments cannot explain the whole deficit: a 50% error on root mass estimation would represent at most 1% of ^{15}N applied. The KCl extracts contained some soluble organic ^{15}N which was measured at days 57 and 103; it averaged another 1% (Recous, 1988). Only traces of fertilizer N were found in the deeper layers at the end of the experiment, indicating that leaching was not involved. Denitrification seems to be the most probable process involved.

Discussion

Kinetics of fertilizer N use

These results enable us to describe the fate of

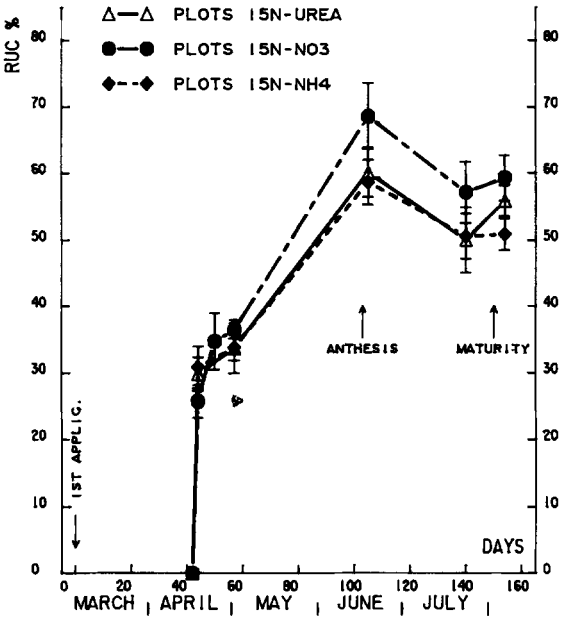

Fig. 3. Kinetics of N uptake efficiency of the second labelled N application in shoots. Plots ^{15}N-NO_3 and ^{15}N-NH_4 received 110 kg N ha^{-1} as ammonium nitrate; plots ^{15}N-urea received 110 kg N ha^{-1} as urea. Day 0 was the time of the first application (06/03/85).

nitrogen applied as urea or ammonium nitrate. The uptake kinetics clearly demonstrate that the fertilizer use efficiency by the above-ground parts of the crop (RUC) reached a maximum early, because of the rapid depletion of the labelled inorganic N pool (Recous *et al.*, 1988a), most of the fertilizer being used over a relatively short period. A similar pattern was observed by Nielsen and Jensen (1986) with spring barley and by Nannipieri *et al.* (1985) in a grass-legume association.

The ^{15}N uptake by the whole crop (roots + shoots) followed a very similar kinetics, since ^{15}N immobilization in roots was weak, *i.e.* 2.6% and 1.1% of each N application, at anthesis. This low ^{15}N recovery in roots was due to the small weight of roots, which represented 10% of the total dry matter at flowering. These data agree well with the calculations made from the paper of Barraclough and Leigh (1984), given a mean roots/(roots + shoots) ratio of 10.6% in June (8 experiments).

The maximum N use efficiency was followed by an important drop in the NH_4-$^{15}NO_3$ plots. This ^{15}N loss in shoots was fully recovered in the soil organic N (Table 3); therefore it was due to exudation of labelled plant compounds. In contrast, no

Table 6. Percentage recovery of fertilizer N in crop and soil. Values in brackets are the standard errors on replicates

Plots	Days	% ^{15}N applied					
		Volat. N	Soil N		Plant uptake		Total recovery fertilizer N
			Inorganic	Organic	Shoots	Roots	
First application							
^{15}N-urea	2[a]	0.2	91.3	4.5	2.6	ND	98.7 (12.8)
	5[b]	0.5	93.9	6.4	2.9	ND	103.7 (10.7)
	8[c]	0.8	71.2	8.9	3.0	ND	84.0 (6.9)
	14[c]	1.5	68.2	9.7	3.5	ND	83.0 (14.7)
	35[c]	1.5	20.2	20.7	38.1	ND	80.6 (13.6)
	103[d]	1.5	0.7	25.9	40.4	2.2	70.8 (8.8)
	154[d]	1.5	1.2	34.0	38.5	1.3	76.6 (7.5)
$NH_4{}^{15}NO_3$	2[a]	–	89.2	2.4	2.3	ND	94.1 (7.4)
	5[b]	–	116.4	2.3	3.6	ND	122.3 (13.2)
	8[c]	–	73.7	5.2	3.8	ND	82.8 (11.2)
	14[c]	–	77.2	5.5	6.0	ND	88.7 (9.9)
	35[c]	–	18.0	9.6	59.9	ND	87.6 (13.0)
	103[d]	–	0.9	32.1	46.2	3.0	82.2 (5.8)
	154[d]	–	1.0	29.3	40.9	1.5	72.7 (6.4)
$^{15}NH_4NO_3$	2[a]	0.1	107.5	4.9	2.4	ND	115.0 (10.5)
	5[b]	0.2	94.5	4.6	2.9	ND	102.2 (11.4)
	8[c]	0.4	70.3	7.0	3.2	ND	81.0 (4.1)
	14[c]	0.7	79.2	8.8	3.3	ND	92.0 (15.0)
	35[c]	0.7	15.1	26.2	32.3	ND	74.4 (6.2)
	103[d]	0.7	0.7	27.9	38.8	2.5	70.7 (15.0)
	154[d]	0.7	0.8	34.2	29.8	1.3	66.9 (13.7)
Second application							
^{15}N-urea	44[a]	0.2	44.0	4.0	29.8	ND	83.3 (8.0)
	47[a]	0.5	39.4	9.0	29.3	ND	82.0 (2.1)
	50[a]	0.8	33.8	11.5	30.0	ND	82.2 (6.0)
	57[c]	1.5	33.6	20.7	33.8	ND	89.7 (10.8)
	103[d]	1.5	1.5	22.3	60.3	1.4	87.1 (4.2)
	154[d]	1.5	0.8	21.5	56.0	1.1	80.4 (4.2)
$NH_{4}{}^{15}NO_3$	44[a]	–	61.7	1.8	25.6	ND	91.2 (1.8)
	47[a]	–	53.0	3.1	31.8	ND	88.8 (9.9)
	50[a]	–	53.0	5.3	34.6	ND	95.6 (4.3)
	57[c]	–	47.1	8.0	36.4	ND	91.1 (15.6)
	103[d]	–	1.0	15.0	68.4	1.1	85.6 (5.6)
	154[d]	–	0.6	16.7	59.1	1.2	78.6 (4.2)
$^{15}NH_4NO_3$	44[a]	0.1	49.3	5.6	31.0	ND	88.9 (6.0)
	47[a]	0.4	50.4	15.2	28.2	ND	96.4 (6.6)
	50[a]	0.6	36.2	16.4	31.1	ND	87.1 (2.1)
	57[c]	1.0	36.8	22.4	34.0	ND	94.3 (11.0)
	103[d]	1.0	0.7	31.2	59.0	1.0	93.2 (2.5)
	154[d]	1.0	0.8	28.0	51.2	1.6	82.7 (2.4)

a, b, c, d indicate that 0–10 cm, 0–30 cm, 0–60 cm and 0–120 cm layers were sampled, respectively
e: total recovery also includes the ^{15}N found in plant washings

similar ^{15}N exudation was observed in the other two treatments. However, if we consider that $^{15}NH_4$-NO_3 and NH_4-$^{15}NO_3$ treatments are ^{14}N replicates, we must conclude that an exudation of unlabelled N compounds took place in the $^{15}NH_4$-NO_3 plots (and probably in the ^{15}N-urea plots as well).

We hypothesized that the plant NO_3 pool could have been involved in the exudation. Measurements made at day 35, indicated that the concentra-

tion of nitrate in shoots was 2900 mg N kg^{-1} DM (s.e. = 200), irrespective of the treatments, representing 2.9 kg NO_3-N ha^{-1} at this time. The amounts of $^{15}NO_3$ were 4.04 (s.e. = 0.16), 2.73 (s.e. = 0.10) and 2.76 (s.e. = 0.14)% ^{15}N applied, for NH_4-$^{15}NO_3$, $^{15}NH_4$-NO_3 and ^{15}N-urea, respectively. The $^{15}NO_3$ pool was significantly greater in the NH_4-$^{15}NO_3$ treatment as expected, but it could not explain the whole labelled exudation. However the plant NO_3 hypothesis cannot definitely be excluded regarding that the actual time of exudation was not known and the turnover time of the nitrate pool in shoots is only a few days (Gonzalez-Montaner, 1987).

The RUC decreased during the grain-filling period, and very probably before flowering time. This means that a quantitative loss of previously-assimilated nitrogen occurred, although root absorption remained active until harvest. This was also observed by Boniface *et al.* (1979) and Smith *et al.* (1983). Possible pathways of N losses in tops have been reviewed by Wetselaar and Farquhar (1980). Since negligible mechanical losses were recorded in our experiment, the nitrogen turnover in shoots must be associated with translocation of N to the root system followed by exudation into the soil, and/or gaseous losses by volatilization from the canopy. Losses by ammonia volatilization have been shown to occur (O'Deen and Porter, 1987, Farquhar *et al.*, 1983, Hooker *et al.*, 1980). Using micrometeorological techniques, Harper *et al.* (1987) found that a net amount of 7 kg N ha^{-1} was lost during the senescence of wheat.

If the sampling schedule was well suited for assessing the kinetics of N transformations in the soil, it was less satisfactory for following N uptake by the crop. There was a sampling gap between early uptake and flowering time. In another investigation made with a regular time-step, it was found that N losses took place rather suddenly after anthesis (Mary *et al.*, 1987). Measurements of fertilizer-N efficiency by winter wheat are thus highly dependent upon the time or the growth stage selected for evaluation of recovery. The data obtained indicate that, in many cases, RUC values measured at harvest, as done in most ^{15}N studies, underestimate the potential fertilizer N uptake efficiency. Conversely the plant must not be considered simply as an accumulative sink for nitrogen.

Comparison of urea, ammonium and nitrate as sources of nitrogen

The higher N uptake efficiency of nitrate *versus* ammonium and urea had been often reported (Broadbent and Nakashima, 1968; Dev and Rennie, 1979; Guiraud *et al.*, 1986; van Lierop and Tran, 1980; Powlson *et al.*, 1986). This was observed over the whole sampling period in our experiments. Differences between forms increased until anthesis. Later on, mechanisms which occurred at the end of the growth cycle, erased part of these differences: losses seemed to be more important when previous uptake was high. The fate of urea appeared to be very similar to that of the ammonium part of ammonium nitrate. Hydrolysis, characterized by a 'delay effect' and by a temporary rise of soil pH (Connolly *et al.*, 1980; Rachpal-Singh and Nye, 1984), did not significantly affect microbial immobilization and plant uptake.

Two processes are probably involved in differentiation between forms of N:

- The plant depletes the nitrate pool in preference to the ammonium pool (while both pools are present in large amounts). This could be the consequence of a higher uptake rate of roots for nitrate-ion. This explanation is however in conflict with physiological studies performed in the laboratory (Lewis *et al.*, 1985; McDuff *et al.*, 1985). Another explanation could be the differential localization of NH_4 and NO_3 ions in the soil profile after nitrogen application, and the ability for nitrate-ion to be carried by mass-flow.
- Simultaneously, the NH_4 pool is preferentially immobilized by the heterotrophic microflora, as observed, limiting, *in fine* the availability of nitrogen applied as urea or ammonium.

^{15}N balance

The ^{15}N recoveries obtained ranged from 71% to 94% at anthesis. These values are not fully satisfactory if we consider that much attention had been paid to sampling and analysis. However they are in the range observed in other field studies. A 80–85% recovery was reported by Olson and Swallow (1984) in a 5 years experiment. Powlson (1987) found a mean recovery of 81% on 12 winter wheat

trials. These deficits were mainly attributed to denitrification in the soil. In our experiment, nitrate and ammonia losses from the soil and the crop seemed to be responsible for the ^{15}N deficit.

Soil and fertilizer N dynamics

We observed that fertilizer N was used by the crop over a relatively short period, whereas the absorption of soil N was effective throughout the growth cycle. Apparent and real efficiencies were similar at harvest (RUC = 49%, AUC = 51%), so that N uptake from the soil inorganic pool was similar for both unfertilized and fertilized treatments. In other words, the added N had not been involved in pool substitution with soil N and no measurable 'added nitrogen interaction' (ANI, as defined by Jenkinson *et al.*, 1985) occurred. This could be expected since inorganic N was present in soil in relatively small amounts at the time the fertilizer was applied, and little fertilizer N moved below 10 cm. This absence of interaction is often observed (Machet *et al.*, 1987, Nielsen *et al.*, 1987) and was discussed by Hart *et al.* (1986), and by Powlson *et al.* (1986).

These conditions of differential availability of fertilizer and soil N in time and space are contrary to the assumption made by Fried and Dean (1952) in calculating 'A' values. It is therefore irrelevant to assess gross mineralization by this method, using the real utilization coefficient (RUC) for soil N, as pointed out by Remy (1985). Gross processes must be approached by modelling the fluxes of N and ^{15}N through the various compartments being examined over a series of short time steps.

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