

Interactions between decomposition of plant residues and nitrogen cycling in soil

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Abstract

The processes of N mineralization and immobilization which can occur in agricultural soils during decomposition of plant residues are briefly reviewed in this paper. Results from different incubation studies have indicated that the amounts of N immobilized can be very important and that the intensity and kinetics of N immobilization and subsequent remineralization depend on the nature of plant residues and the type of decomposers associated. However, most of the available literature on these processes refer to incubations where large amounts of mineral N were present in soil.

Incubations carried out at low mineral N concentrations have shown that the decomposition rate of plant residues is decreased but not stopped. The immobilization intensity, expressed per unit of mineralized C, is reduced and N remineralization is delayed. Nitrogen availability in soil can therefore strongly modify the MIT kinetics (mineralization-immobilization turnover) by a feed-back effect.

The mineralization and immobilization kinetics have been determined in a two-years field experiment in bare soil with or without wheat straw. Mineralization in plots without straw seemed to be realistically predicted by accounting for variations in soil temperature and moisture. Immobilization associated with straw decomposition was clearly shown. It was increased markedly by the addition of mineral N throughout decomposition. It is concluded that mineral N availability is an important factor controlling plant residues decomposition under field conditions. A better prediction of the evolution of mineral N in soil may therefore require description and modelling of the respective localization of both organic matter and mineral N in soil aggregates.

Introduction

The use of ¹⁵N tracers in incubation studies has clearly demonstrated that mineralization and immobilization processes of nitrogen, can take place simultaneously in soil (Bjarnason, 1988; Jansson and Persson, 1982; Kirkham and Bartholomew, 1954). Microbial immobilization of mineral N frequently occurs whereas (positive) net mineralization is found in soil (Hart et al., 1994; Recous et al., 1992). Conversely, the isotopic dilution of mineral ¹⁵N shows that ammonification continues even when N immobilization is the dominant process (Bjarnason, 1988; Mary and Recous, 1995). The existence of the two processes is particularly obvious during the initial decomposition of all

plant residues in spite of their diversity going from rhizodeposits produced during plant growth to unharvested plant parts (coming either from mature crops or young crops like cover-crops). However, most of these results have been established under laboratory conditions and it is not precisely known to what extent they can be extrapolated to field conditions. Answering this question is one of the present challenges : are the 'mechanistic' C and N models realistic enough to predict the evolution of mineral N in agricultural fields ? For example, these models often predict that gross rates of mineralization and immobilization are much higher than net rates (Houot and Chaussod, 1991; Paul and Juma, 1981). This paper first reviews the effect of decomposition processes on N transformations. It presents results from a field experiment

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Table 1. Maximum net immobilization of soil mineral N and microbial assimilation of nitrogen measured during decomposition of various plant residues in incubation studies at 25 °C

Plant material	C/N	N/C	Net immobilization (mg N g ⁻¹ C)	Microbial assimilation (mg N g ⁻¹ C)
Wheat leaves ^d	13	76	0	48
Maize roots ^a	14	72	19	66
Rye roots ^b	28	36	23	-
Wheat roots ^d	34	29	27	50
Rye grass roots ^b	51	19	24	-
Root mucilage ^a	64	16	72	88
Wheat straw ^c	100	10	28	32
Maize straw ^d	130	8	27	-
Glucose ^a	∞	0	61	61

^a Data from Mary et al. (1993).

^b Data from Mary (1988).

^c Data from Robin (1994).

^d Unpublished data.

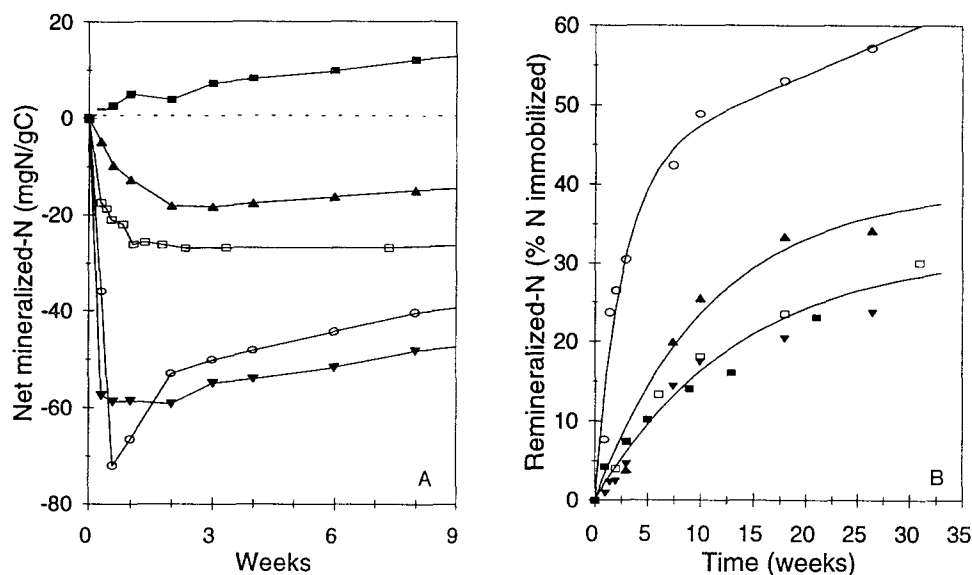


Figure 2. A. Kinetics of net mineralization resulting from the decomposition of different plant residues in laboratory experiments at 25 °C. Net mineralization is calculated by difference with an unamended soil. B. Kinetics of N remineralization during the decomposition of different plant residues in laboratory experiments at 25 °C. Net remineralization is calculated by difference with the unamended soil and expressed as % of maximum N immobilized. Day 0 is the time of maximum immobilization. ■ wheat leaves, ▲ maize roots, ○, root mucilage, ▼ glucose, □ maize straw. Data from ^a Mary et al. (1993), ^b Recous (1994), ^c Mary, unpublished results.

mine the exact fate of added residue-N and quantify microbial N assimilation.

Tracing soil mineral N or/and residue-N pools with ¹⁵N can be done by measuring the variations in the N and ¹⁵N mineral pools or N and ¹⁵N organic pools (soil biomass) and by using calculations based on the isotopic dilution technique (Barraclough, 1991; Davidson et al., 1991; Kirkham and Bartholomew, 1954; Nishio

et al., 1985). This allows to describe the dynamics of gross N mineralization and immobilization after residue incorporation (Jensen, 1994a, c; Ocio et al., 1991; Recous et al., 1995; Sorensen, 1981). The use of 'paired' ¹⁵N treatments such as those suggested by Bjarnason (1988) and Barraclough (1991), combining ¹⁵N-NH₄⁺ and ¹⁵N-NO₃⁻ applications, has been shown useful to assess simultaneously several N transforma-

tion rates and to improve the accuracy of N immobilization rate determinations. A similar approach can be adopted with plant residues, using combined treatments identical in total amount of added N and C but differing only in the N pool being labelled (^{15}N residues + ^{14}N mineral and ^{14}N residues + ^{15}N mineral). It could be fruitfully associated with improved methods of calculation like numerical techniques and optimization routines (Mary and Recous, 1994; Myrold and Tiedje, 1986; Wessel and Tietema, 1992). These tracing techniques are promising to better evaluate the various N fluxes (Fig. 1) and the confidence intervals for each of them, although they require very accurate data.

The N fluxes which do not enter the mineral N pool, i.e. direct assimilation of residue-N (j) and re-assimilation during biomass-N recycling (a), in fact escape quantification by the isotopic dilution technique. Evaluation of the direct assimilation of residue-N can be done by measuring the mean isotopic ^{15}N excess of the mineral N immobilized and that of the newly-formed biomass N (Mary et al., 1993). Using this method, we found that the net microbial assimilation ($i+j$) was much less variable between residues than net immobilization (Table 1). This suggests that direct assimilation of N may represent a significant part of microbial N assimilation and that this flux can explain a large part of the differences found in net N immobilization, particularly for residues rich in N. However, some differences in microbial assimilation still exist, probably arising from the nature of the decomposing microflora. These differences can be explained if we consider that fungi are mainly responsible for the decomposition of cellulose and lignin while bacteria are the main decomposers of soluble compounds and that the C/N ratio of the former is larger than that of the latter.

In the case of cereal straw which has a low N content, net immobilization is not very different from microbial assimilation. It is then easier to compare results reported in the literature. The calculations obtained from different experiments performed under laboratory conditions indicate a narrow range of N immobilization values : between 26 and 31 mg N g⁻¹C decomposed (Table 2). The lowest values observed by Reinertsen et al. (1984) and Bakken (1986) are likely to result from a limited availability of soil mineral N in these experiments. This suggests that the relationship between C decomposed and N immobilized can be markedly altered by the availability of N. This will be discussed in the second part of this paper.

Table 2. Maximum immobilization of soil mineral N measured during decomposition of wheat straw under laboratory conditions (values in mgN per g of added carbon)

Authors	Immobilized-N (mg N g ⁻¹ C)
Simon (1960)	28.5
Guiraud (1984)	30.8
Reinertsen et al. (1984)	18.0 ^a 27.0 ^b
Bakken (1986)	15.1
Nieder and Richter (1986)	25.8
Robin (1994)	27.4

^a Without N.

^b With mineral N.

The remineralization kinetics, i.e. the rate of release of previously assimilated N, seems to be depending also on the type of substrate (Fig. 2B). Again one can hypothesize that the differences in remineralization rates between substrates arise from the nature of the decomposing microflora involved in the primary decomposition. For example, the rapid release of immobilized N observed during decomposition of root mucilage could be associated with a rather specific bacterial population, decaying rapidly (Mary et al., 1993). The remineralization rate decreased rapidly with time for all types of residues. The cumulative remineralization was always partial, confirming the results of many experiments done under laboratory or field conditions (Azam et al., 1985; Denys et al., 1990; Jensen, 1994b; Müller and Sundmann, 1988; Seligman et al., 1986).

Although the mechanisms of joint C and N evolution are well understood, there are still difficulties in generalizing existing data to other types of residues and in establishing stable relationships between C and N fluxes. The difficulties arise from :

- the rapid occurrence of biomass recycling process which, after a few days, can lead to the calculation of net rather than gross fluxes,
- the interaction between added N (mineral and organic) and native soil N which yields substitution effect during immobilization-mineralization turnover (Jenkinson et al., 1985), as shown by Bjarnason (1988), Fox et al. (1990), Ocio et al. (1991), Azam et al. (1993).
- the very different time-steps of investigation (day to year) in the literature and the relatively few data combining C and N evolution.

Table 3. Net immobilization of soil mineral N calculated during decomposition of wheat straw under field conditions

Straw added (kg ha ⁻¹)	N/C (mg Ng ⁻¹ C)	Period of calculation	Net immobilization		References
			(mg N g ⁻¹ C)	(kg N ha ⁻¹)	
3000	12.5	1 year	33.0	40	Powlson et al. (1985)
10000	20.8	14 days	11.5 ^a	50 ^a	Ocio et al. (1991)
			20.7 ^b	90 ^b	
8000	8.0	1 year	11.5–13.0 ^a	39–44 ^a	This work
			24.3–32.0 ^b	82–108 ^b	

^a Without N.^b With mineral N.

Quantification under field conditions

The intensity and kinetics of N mineralization and immobilization processes therefore seem to be satisfactorily characterized and understood in experiments performed under laboratory conditions. In contrast, the importance of these processes under field conditions is still poorly known. The scarcity of the available data results from two main difficulties : i) the heterogeneity of mineral N distribution in soil and ii) the interference of several other processes (nitrate movement in soil, root absorption, volatilization and denitrification, ...). In order to test the possibility of extrapolating laboratory results to field conditions, we have attempted to determine the kinetics of net N mineralization during two field experiments.

Methods

The two field experiments were carried out in Northern France in 1990–91 and 1991–92, comparing C and N transformations in a bare soil with or without wheat straw incorporated. Full details of the experiments are given by Darwis (1993). The experiments began after wheat harvest every year and were done on a loamy soil (18% clay, 70% loam; 8% sand; 4% stone, 0.11% organic N; 1.0% organic C; pH_{H₂O} 8). Mature straw (C:N=125) was added at a rate of 8000 kg DM ha⁻¹ and incorporated by rotavator or disk ploughing. Water and mineral N content in soil were measured over 10–12 months at 3–4 weeks intervals up to 150 cm depth. Straw decomposition was assessed by measuring residual coarse straw in the top soil (fraction > 1 mm).

Net N mineralization was calculated from the measurements of mineral N in the soil profiles, as indicated previously. It was assumed that the nitrogen losses by volatilization and denitrification were small and compensated by atmospheric deposition (which represents

about 12 kg N ha⁻¹ yr⁻¹). The rate of net mineralization was taken equal to the rate of accumulation of mineral N in the soil profile (0–150 cm), except during water drainage periods where the N leached out was added to the accumulated N. Leaching was calculated by using a model derived from Burns' model (1976) which has been found to be valid in loamy soils (Khanif et al., 1985).

The effect of possible deficiencies in soil mineral N on straw decomposition was investigated during the second experiment by adding two treatments : one receiving 180 kg NO₃⁻-N ha⁻¹ splitted in 6 times, and one receiving 330 kg NO₃⁻-N ha⁻¹ splitted in 11 times (after each soil sampling). In the latter treatment, each application of 30 kg N ha⁻¹ was ¹⁵N-labelled (atom% excess = 20.1%). Mineral and organic ¹⁵N were measured on the 0–5, 5–10, 10–15 and 15–20 cm layers. Gross N immobilization was calculated using the enrichment isotope technique (Davidson et al., 1991; Mary and Recous, 1995).

The effect of soil temperature and water content on N mineralization was taken into account using a method derived from that of Andr n and Paustian (1987). A 'normalized' time (equivalent to Q_{sum} in their work) was calculated as follows :

$$t_{\text{normalized}} = t_{\text{real}} \cdot f(T) \cdot g(\psi)$$

where $f(T)$ is a correction factor due to soil temperature, $g(\psi)$ is a reduction factor due to soil water potential. The factor $f(T)$ is a multi-exponential function of temperature. It is set at 1 at a conventional temperature of 25 °C. The rate constants (or coefficients Q₁₀) were those found by Recous (1995) in soils amended with maize residues and control soils. They vary according to the temperature range. The effect of soil moisture on N mineralization is described as an exponential function of soil water potential as proposed by Andr n et

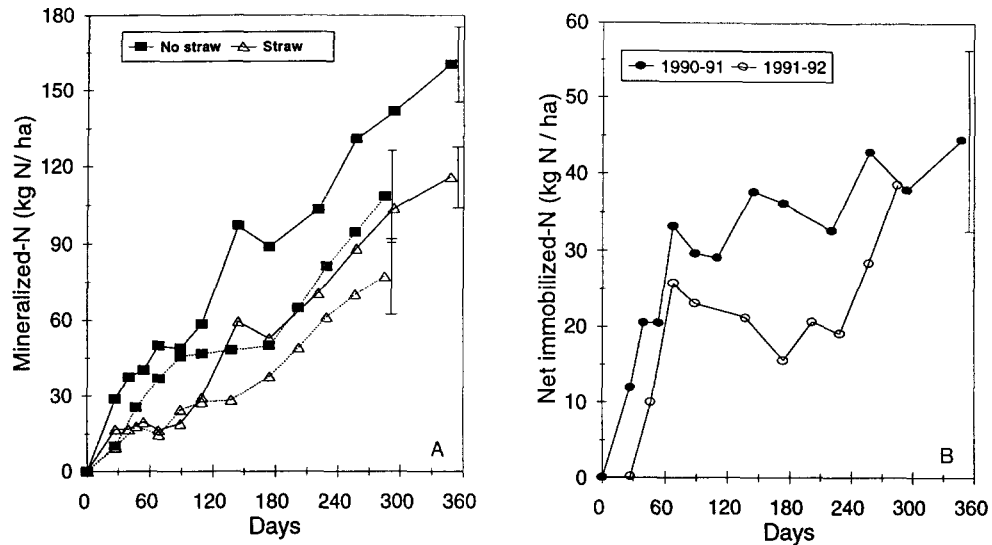


Figure 3. A Kinetics of net mineralization in a bare soil with (Δ) and without (\blacksquare) straw incorporated (8 t DM ha^{-1}), during two field experiments. First year : 07.26.1990 to 07.09.1991 (solid lines). Second year : 08.29.1991 to 06.09.1992 (dashed lines). Day 0 is the time of straw incorporation. Vertical bars indicate the mean standard deviation. B. Kinetics of net immobilization of mineral N due to straw decomposition during two field experiments (calculated from Figure 3A).

al. (1992). The combined effect was calculated as the product of the two terms, assuming that there were no interactions between temperature and moisture. The cumulative normalized time was calculated by summing each normalized day. This approach enables to compare field experiments differing in climatic conditions to laboratory experiments conducted under constant conditions of temperature and moisture.

Results

The calculated net mineralization for the two years and the two treatments (with or without straw) is shown in Figure 3A. Each point is the mean of six measurements ($3 \text{ replicates} \times 2 \text{ soil tillage treatments}$) since the two modes of tillage (rotavator and disk ploughing) gave very similar results (the differences were never significant and randomly distributed with time). The accuracy of calculation of net mineralization mainly depends on the variability of mineral N distribution in soil and the validity of N leaching estimates. The average standard deviation on mineral N measurements was 12 and 16 kg N ha^{-1} for the years 1990–91 and 1991–92 respectively, corresponding to a similar coefficient of variation of 16%. Concerning leaching, the water balance indicated that the period of water drainage (below 150 cm) essentially took place in winter period (approximately between days 140 and 240). The model indicated that the amount of nitrate leached out varied from 9 to 16 kg N ha^{-1} during the first year and 3 to 14 kg N ha^{-1} during the second year. Leaching was therefore

relatively small compared to the amount of N accumulated in soil, indicating that inaccuracies in the leaching model outputs would not affect the calculations of net mineralization.

In the bare soil without straw, net mineralization reached $160 (\pm 21) \text{ kg N ha}^{-1}$ after almost one year (348 days) in 1990–91 and $116 (\pm 22) \text{ kg N ha}^{-1}$ after 285 days in 1991–92. The mineralization was slower during the second year. Cumulative mineralization for both years was slightly higher than the reported values for similar pedoclimatic conditions : between 80 and $124 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Hofman, 1988). The higher net mineralization in our experiments could be attributed to a lower immobilization due to the fact that a larger part of the readily decomposable carbon (wheat straw, stubble and chaff) had been removed.

Net mineralization was lower in the plots where wheat straw (8 t ha^{-1}) had been incorporated (Fig. 3A). The net N immobilization associated with straw decomposition was calculated by difference (Fig. 3B). The fluctuations in the kinetics were probably due to the relatively large inaccuracy inherent to the method of calculation. However, it appears that the kinetics consisted of a rapid immobilization phase after straw incorporation (in summer and autumn) followed by a slower immobilization phase in winter and spring. No apparent remineralization occurred, even one year after straw incorporation in soil. These results are consistent with our laboratory experiments. Net immobilization reached $44 (\pm 16)$ and $39 (\pm 9) \text{ kg N ha}^{-1}$ at the end of

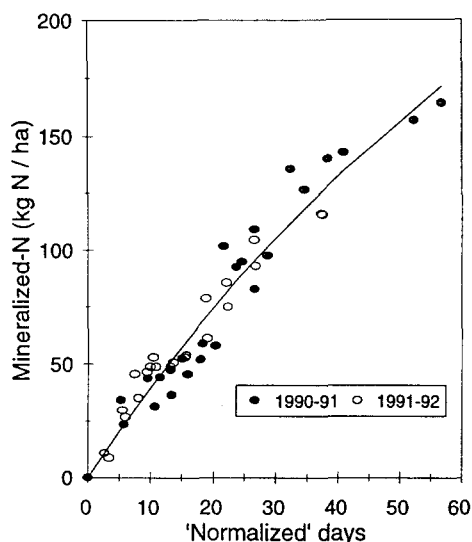


Figure 4. Evolution of net mineralization in a bare soil without straw versus 'normalized' time (equivalent days at 25 °C and optimum water potential)

the 1990–91 and 1991–92 experiments, respectively. This corresponds to 13.0 and 11.5 mg N g⁻¹ added C. These values are in the lower range of previously reported estimates of net immobilization under field conditions, although those were variable and made at very different times (Table 3).

The two one-year experiments performed under our field conditions have represented 59–74 days of 'normalized' time (equivalent time at 25 °C temperature and optimal water conditions), corresponding to 16–20% of the real time. When the normalized days were substituted to real days, the differences in the kinetics of net mineralization observed between the 2 years in the plots without straw disappeared (Fig. 4). Furthermore, net mineralization could be fitted to a first order kinetics, similar to what can be found during incubation tests like those from Stanford and Smith (1972):

$$N_m = N_o \cdot (1 - e^{-k \cdot t})$$

The best fit (calculated by non-linear regression procedure) was obtained for the following parameters : $N_o=340$ kg N ha⁻¹ and $k=0.087$ week⁻¹. The fit was satisfactory : $r^2=0.949$ ($n=50$) and unbiased. However, each of these parameters could not be precisely determined since both were strongly correlated, in agreement with previous observations concerning mineralization kinetics in incubation studies (Dendooven, 1990). Indeed, a slightly less good fit was found when assuming that all organic nitrogen was 'potentially mineralizable N' : $N_o=3950$ kg N ha⁻¹ and $k=0.0062$ week⁻¹ ($r^2=0.928$). The product $k \cdot N_o$

which can be much more precisely assessed was equal to $7.0 (\pm 0.4)$ mg N kg⁻¹ soil week⁻¹ for the arable layer in these normalized conditions. Previous laboratory experiments using the incubation method of Stanford and Smith (1972) at 35 °C had indicated that the $k \cdot N_o$ values were around 9.5 mg N kg⁻¹ soil week⁻¹ in this type of soil (Mary and Rémy, 1979; Mary, 1988). If we consider a temperature coefficient $Q_{10}=1.8$ in the range 25–35 °C (Campbell et al., 1981; Stanford et al., 1973) the $k \cdot N_o$ found in the field would be $7.0 \times 1.8=12.6$ mg N kg⁻¹ soil week⁻¹ at 35 °C. Apparently, laboratory results would underestimate field mineralization by 25%. However, the unaccounted mineralization may have originated in the soil below the plough layer. The amount of organic N in the 30–60 cm layer still represents about 30% of the organic N in the 0–30 cm layer and may easily have been the source of the extra N mineralized. Therefore it seems safe to conclude that a reasonable agreement was found between field and laboratory results in plots without straw.

The kinetics of net N immobilization in the soils where straw was incorporated also were not significantly different between the two years, when the time was expressed in 'normalized' days (Fig. 5A). The kinetics also presented an exponential shape : the maximum net immobilization was calculated at 51 kg N ha⁻¹, the rate constant at 0.031 day⁻¹. The immobilization of soil mineral nitrogen was clearly correlated with C decomposition, since the residual straw-C (fraction > 1 mm) decayed exponentially with a rate constant ($k=0.027$ day⁻¹) almost equal to the rate constant of N immobilization (Fig. 5B). This would indicate a ratio of immobilized N : decomposed C close to 6.5 kg N t⁻¹ straw decomposed, corresponding to about 15 mg N g⁻¹ C decomposed. This value is much smaller (around 50% less) than the N immobilization potential which has been found in laboratory incubations when mineral N is not a limiting factor of decomposition (Table 2). This suggests that soil mineral N (or more generally N available to soil microorganisms) could have limited the rate and the intensity of N immobilization in the field. This hypothesis is examined below.

Control of C decomposition by inorganic N availability

Characterization

The fact that nitrogen availability can be a limiting factor for microorganisms in soil responsible for decomposition process has been established for a long time

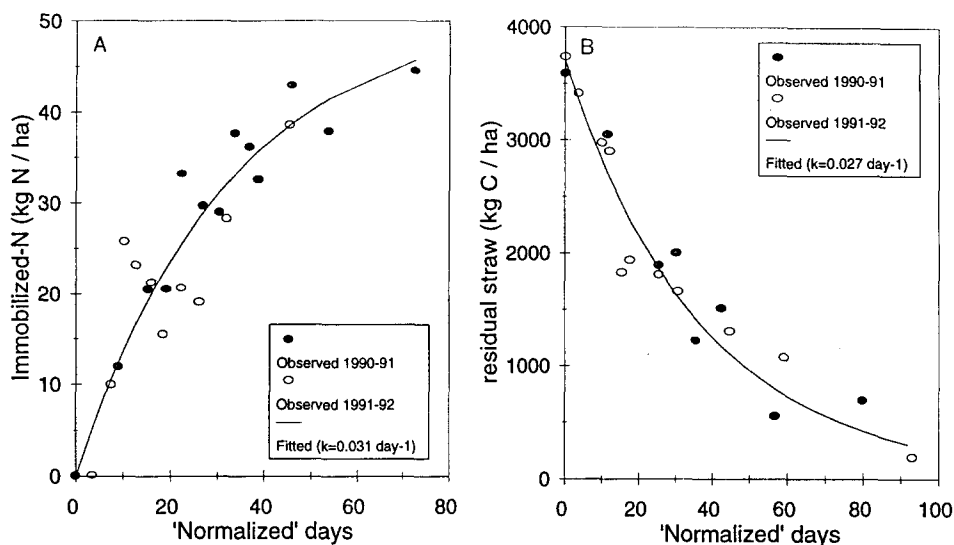


Figure 5. A Evolution of net immobilization of soil mineral N due to straw decomposition versus 'normalized' time. B. Evolution of residual straw C (fraction > 1 mm) measured in the field experiments versus 'normalized' time.

for various types of plant residues. This result is not surprising since the N:C ratio of soil microorganisms are greater than those of most plant residues (Swift et al., 1979) and therefore the external source of N can be rapidly exhausted.

The effect of N on the decomposition of carbon compounds was assessed in numerous investigations under laboratory conditions mainly by varying the initial C:N ratio of the soil+residue system by one of the following procedures: i) incubating one type of residue containing different amounts of nitrogen, ii) adding different amounts of mineral N in soil, and iii) using different types of residues with different initial N contents. The effect of N availability on C decomposition was assessed mainly by monitoring the rates of CO₂-C evolution over short or long time intervals. The results obtained have been quite variable as mentioned in Fog's review (1988), the variability depending mainly on the nature of the residue and the time scale used to evaluate the effect of added N. It has been shown also that the effect of N addition can be non-uniform during the decomposition process (Knapp et al., 1983). Cochran et al. (1988) concluded that the different C pools which co-exist in a residue create different responses to N addition: the addition of nitrogen clearly enhanced the initial rate of decomposition of the soluble fraction even though the N content of this fraction is high (Reinertsen et al., 1984; Bremer et al., 1991), but its effect can be less important, sometimes nil or even negative, in the later stages of decomposition (when the more recalcitrant com-

pounds are decomposing). In the long term, the humification process would be modified by N availability in terms of amount and quality of the humified products formed (Lueken et al., 1962; Fog, 1988). The complex interactions between N and type of residues, type of decomposers and chemical reactions during humification have been described in Fog's review (1988).

C and N relationships at low and high N levels

If the effect of N addition on straw decomposition has been clearly demonstrated, at least in the short term, little information exists on the C and N relationships during decomposition at different levels of N availability. The results obtained by Reinertsen et al. (1984), Bakken (1986) and Ocio et al. (1991) indicate that the C and N relationships can be modified at low N concentrations. Parker (1962) had already suggested that this could occur under field conditions.

The effect of N availability on the C and N relationships during decomposition of maize residue was investigated at five different levels of initial N content in soil after addition of ¹⁵NH₄ ¹⁵NO₃ (Recous et al., 1995). For the two initial lowest levels of mineral N (6 and 18 mg N g⁻¹ added C), the disappearance of inorganic N in soil due to microbial immobilization caused a marked decrease of the C mineralization rate. For the three other initial levels of mineral N (35, 47 and 59 mg N g⁻¹ added C), the immobilization process depleted only a part of the soil mineral N content. The kinetics of C mineralization were identical in these three treat-

ments as were the kinetics of net N immobilization. The ratio between net immobilized N and decomposed C was calculated in each of the five treatments at times corresponding to the same degree of decomposition. For instance, when the mineralized C reached 30% of the added C, the ratio was identical for the three unlimited N treatments, and was equal to $28.6 \pm 1.3 \text{ mg N g}^{-1}$ added C whereas it was only 19.5 and 8.8 mg N g^{-1} added C for the two lowest N levels. From these results it was concluded that there was no 'luxury' consumption of nitrogen by microorganisms at high N levels and that microbial N assimilation (flux $i+j$) per unit of decomposed C was reduced at low N availability. Several processes may explain such results: i) the modification of microbial succession (Bremer et al., 1991; Fog, 1988; Park, 1976), ii) the adaptation of the internal N content of fungi (Bremer et al., 1991; Levi and Cowling, 1966) and iii) the modification of C and N metabolism (energy allocated to growth or to maintenance). Other hypotheses concern the re-use of internal N (Bremer et al., 1991; Cowling and Merrill, 1969) and the acceleration of biomass recycling (Robin, 1994).

Control at field scale

Most of the reported experiments about the effect of N limitation on organic matter decomposition were conducted under laboratory conditions with ground residues well mixed to sieved soils. It was assumed that N and C were homogeneously distributed and equally available in each soil microsite throughout the whole period of incubation. This allowed to establish potential relationships between C and N under 'optimal' conditions, i.e. in which soluble C and N movements would not influence microbial activity. The conditions under which the availability of N would control the decomposition of C could be very different in intact soil cores and a fortiori under field conditions.

We have attempted to evaluate the effect of N availability on N immobilization in the previously described field experiment after straw incorporation (1991–92). The results are presented in Figure 6. Net immobilization was calculated similarly in the treatment N_0 without addition of mineral N (presented earlier, Fig. 3B) and in the treatment N_{180} which received $6 \times 30 \text{ kg N ha}^{-1}$. Net immobilization was clearly stimulated during each 3 to 4 weeks period following each application of mineral N. There was a trend for a decrease in net immobilization in both treatments during winter (between normalized days 12 and 24). The decrease

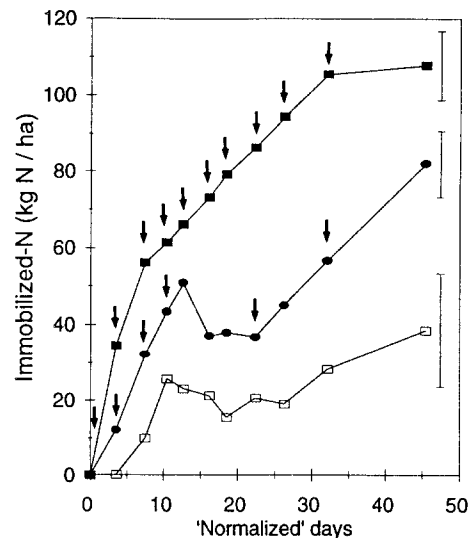


Figure 6. Evolution of N immobilization associated to straw decomposition versus 'normalized' time, with and without addition of mineral N. The arrows indicate the applications of NO_3^- (30 kg N ha^{-1}). The curves represent net immobilization in treatments N_0 and N_{180} and gross immobilization in treatment N_{330} .

appears to be in apparent contradiction with laboratory results which showed that net remineralization did not happen before most of the straw had decomposed (this condition was not achieved yet in the field). However, it can be observed that the decrease (or the stabilization) in net immobilization occurred when the amounts of soil mineral N were smallest: the average amounts of mineral N present in the straw layer during this period were 4 and 7 kg N ha^{-1} in treatments N_0 and N_{180} respectively, compared to 6 and 22 kg N ha^{-1} during the 0–12 days period and 14 and 40 kg N ha^{-1} during the 24–39 days period.

Gross immobilization was calculated in the treatment N_{330} which received the highest rate of mineral N: $11 \times 30 \text{ kg N ha}^{-1}$. The kinetics of gross immobilization was close to what was found in laboratory incubations. The immobilization rate was high at the beginning of decomposition and declined regularly thereafter without reaching zero. The average amount of mineral N in the straw layer of this treatment remained always higher than 17 kg N ha^{-1} , even during the 12–24 days period. At the end of the experiment (day 285 or normalized day 46), net immobilization reached $44 (\pm 21)$ and $82 (\pm 7) \text{ kg N ha}^{-1}$ in the N_0 and N_{180} treatments; gross immobilization in the N_{330} treatment reached $108 (\pm 11) \text{ kg N ha}^{-1}$. These figures represent 13.0, 24.3 and 32.0 mg N g^{-1} added C respectively, the latter value being equal to the immobilization potential found with straw in incubation studies. These results

demonstrate that the availability of N in soil can control (slow down) the decomposition process and strongly reduce the N immobilization potential of plant residues (Table 3).

This effect is not properly accounted for by the present 'mechanistic' simulations models describing C and N transformations. In these models, mineral N is generally supposed to control decomposition by a switch function acting only on the decay rate of the C pool involved, when the amount of mineral N goes down a value close to 1 mg N kg⁻¹ soil (Paul and Juma, 1981; Van Veen et al., 1984). An improved parameterization is necessary which will lead to reduce the importance of simulated immobilization rates.

Several authors have clearly demonstrated the interactions between N availability and parameters like residue size and residue placement. For example, the decomposition of residues left at the soil surface as a mulch can be enhanced by N addition while the rate of decomposition of the same residues well mixed in the upper soil layer may not be modified by the N treatment (Bremer et al., 1991; Parker, 1962; Schomberg et al., 1994).

A second important aspect concerns the localization of C in the soil. It has been shown that the distribution as well as the size and composition of the residues left at the soil surface and in the soil after harvesting and tillage operations are very heterogeneous. For example, the amount of straw left at the soil surface after combine harvesting may vary between 3 and 16 t DM ha⁻¹ (Machet, pers. comm.). This implies that under normal agricultural conditions, the soil will present sites with large amounts of residues to be decomposed and others containing small amounts of decomposable C. In the former case the N availability will very probably limit the decomposition process while the decomposition can be optimal in the latter. In the previous example, the N immobilization potential in zones containing 16 t DM ha⁻¹ would represent about 210 kg N ha⁻¹. Such an important amount of N cannot be found in the vicinity of straw environment during a one-year decomposition period. Our conclusions are contradictory with Bremer et al. (1991) who stated that microbial activity is unlikely to be limited by nitrogen under field conditions.

At the local scale, an interaction may occur with physical soil parameters (soil texture, water content). The local demand for nitrogen during decomposition could be supplied instantaneously or not, as a function of the rate of diffusion of nitrogen from the surrounding soil, even though the amount of N is high in the soil.

In the rhizosphere, this could be the more important factor, if we consider that mucilages can be shed at a much faster rate than mineral nitrogen can diffuse to the root surface.

Furthermore, the rapid transport of N from the arable to the deeper layers occurs during rainfall events, and may limit the availability of N in the upper layer where residues are incorporated, even though N mineralization remains active. This situation was clearly shown in our experiments during the autumn (Darwis, 1993).

Conclusion

Although basal mechanisms involved during organic residue decomposition have been clearly indentified, there are still difficulties to predict C and N evolution during the decomposition of plant residues, especially under field conditions. It is necessary to improve the combined description of C and N transformations and the quantification of total assimilation of N (gross immobilization, direct assimilation of organic N compounds and N recycling).

The effect of straw addition on N transformations was studied under field conditions. The intensity of N immobilization was generally smaller than under laboratory conditions, probably because N availability was limiting decomposition. The N immobilization potential associated with the decomposition of most plant residues must be compared to N availability in the soil layers where residues are incorporated. The immobilization potential is very high and probably often higher than available mineral N. Therefore plant residue decomposition could be frequently controlled by N. Under limiting N conditions, immobilization last longer but with lower rate. This could explain the relatively high immobilization potential measured with ¹⁵N (Recous et al., 1992; Schimel et al., 1989).

According to this hypothesis, the distribution of plant residues and nutrients (N) would be important to account for and would explain a large part of the variability of mineral N distribution in soil. Mono-dimensional models appears to be insufficient to predict the mean amount of mineral N in soil. Studies of the effects of soil structure, plant residue localization and nitrate movement between aggregates on C and N transformations are necessary.

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