Microbial immobilization of ammonium and nitrate in relation to ammonification and nitrification rates in organic and conventional cropping systems

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Received 26 February 2002; received in revised form 17 September 2002; accepted 25 September 2002

Abstract

Agricultural systems that receive high or low organic matter (OM) inputs would be expected to differ in soil nitrogen (N) transformation rates and fates of ammonium ($\text{NH}_4^+$) and nitrate ($\text{NO}_3^-$). To compare $\text{NH}_4^+$ availability, competition between nitrifiers and heterotrophic microorganisms for $\text{NH}_4^+$, and microbial $\text{NO}_3^-$ assimilation in an organic vs. a conventional irrigated cropping system in the California Central Valley, chemical and biological soil assays, $^{15}$N isotope pool dilution and $^{15}$N tracer techniques were used. Potentially mineralizable N (PMN) and hot minus cold KCl-extracted $\text{NH}_4^+$ as indicators of soil N supplying capacity were measured five times during the tomato growing season. At mid-season, rates of gross ammonification and gross nitrification after rewetting dry soil were measured in microcosms. Microbial immobilization of $\text{NO}_3^-$ and $\text{NH}_4^+$ was estimated based on the uptake of $^{15}$N and gross consumption rates. Gross ammonification, PMN, and hot minus cold KCl-extracted $\text{NH}_4^+$ were approximately twice as high in the organically than the conventionally managed soil. Net estimated microbial $\text{NO}_3^-$ assimilation rates were between 32 and 35% of gross nitrification rates in the conventional and between 37 and 46% in the organic system. In both soils, microbes assimilated more $\text{NO}_3^-$ than $\text{NH}_4^+$. Heterotrophic microbes assimilated less $\text{NH}_4^+$ than $\text{NO}_3^-$ probably because $\text{NH}_4^+$ concentrations were low and competition by nitrifiers was apparently strong. The high OM input organic system released $\text{NH}_4^+$ in a gradual manner and, compared to the low OM input conventional system, supported a more active microbial biomass with greater N demand that was met mainly by $\text{NO}_3^-$ immobilization.

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Keywords: Microbial ecology; $^{15}$N isotope pool dilution; Agroecology

1. Introduction

Agricultural systems vary in important ways with respect to nitrogen (N) and carbon (C) cycling. Systems that receive high organic matter (OM) inputs have greater labile C pools, greater microbial activity and greater soil N supplying power compared to systems that receive only mineral fertilizer (Gunapala and Scow, 1998; Kramer et al., 2002). Many studies have focused on fates of N inputs during one or more growing seasons, and many chemical and biological soil assays have been developed to predict N availability to crops (Bundy and Meisinger, 1994). Less is known about the actual rates of short-term microbial N transformations in systems that differ in C availability and soil N supplying capacity. Agricultural soils that differ in OM inputs would be expected to differ in rates of soil N transformations, competition for ammonium ($\text{NH}_4^+$) by immobilizers and nitrifiers, and fates of nitrate ($\text{NO}_3^-$).

Ammonium has been found to be the preferred form of N for assimilation by microbes in many cultivated soils (e.g. Azam et al., 1993). Nevertheless, nitrification is often considered the major fate of $\text{NH}_4^+$ in agricultural soil (Robertson, 1997), where $\text{NH}_4^+$ is usually present in low concentrations ($<2 \mu g \text{NH}_4^+\text{N g}^{-1}\text{soil}$) compared to $\text{NO}_3^-$. In some agricultural soils, no $\text{NO}_3^-$ immobilization has been observed (Shi and Norton, 2000), while in others, $\text{NO}_3^-$ immobilization was recorded after 1–4 weeks (Schimel, 1986) or several months (Kissel and Smith, 1978). Carbon inputs often increase $\text{NO}_3^-$ immobilization (Recous et al., 1990). In most investigations comparing $\text{NO}_3^-$ and $\text{NH}_4^+$ assimilation in cultivated soils, N is applied in concentrations of $\geq 50 \mu g \text{N g}^{-1}\text{soil}$, and microbial N immobilization in soils that do not receive concentrated N inputs has

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PII: S0038-0717(02)00233-X
been less studied. A better understanding of inorganic N immobilization by microbes in differentially managed cropping systems is important since timing of inorganic N release and crop N uptake are not always synchronized, thus leading to potential N loss and environmental degradation (Robertson, 1997; Matson et al., 1997).

Drying and rewetting of soil, as it occurs in irrigated systems, may also affect the rates of production and consumption of NH$_4^+$ and NO$_3^-$. Increased net N mineralization upon rewetting air-dry soils has been demonstrated (Sparling and Ross, 1988; Appel, 1998). Nitrification activity, on the other hand, has been shown to either respond quickly to increased moisture (Davidson et al., 1993), to increase over 1–4 d after rewetting (Venterea and Rolston, 2000a), or to be inhibited by repeated drying and wetting (Franzluebbers et al., 1994). Simultaneous measurement of gross rates of ammonification and nitrification, combined with measurements of microbial N immobilization after rewetting dry soil could show relationships between production and consumption of inorganic N during key periods of crop N uptake or potential N loss.

The $^{15}$N isotope pool dilution approach is well suited to measure short-term N transformations (Hart et al., 1994), but spatial variability of inorganic N concentrations, especially in agricultural soils (Wolt, 1994), can make this method unfeasible. To reduce variability of inorganic N concentrations, sieving and mixing agricultural soil has often been used (e.g. Myrold and Tiedje, 1986). Sieving can increase mineralization rates (Ross et al., 1985; Calderón, 1993), to increase over 1–4 d after rewetting (Venterea and Rolston, 2000a), or to be inhibited by repeated drying and wetting (Franzluebbers et al., 1994). Simultaneous measurement of gross rates of ammonification and nitrification, combined with measurements of microbial N immobilization after rewetting dry soil could show relationships between production and consumption of inorganic N during key periods of crop N uptake or potential N loss.

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We compared two irrigated cropping systems in California’s summer-dry Central Valley that receive different types and amounts of C and N inputs to investigate the differences in soil N supplying capacity, short-term NH$_4^+$ availability, and microbial N immobilization patterns. The objectives of this study were to: (i) monitor soil N supplying capacity during a cropping season; (ii) measure rates of gross mineralization, gross nitrification, and microbial immobilization of inorganic N after rewetting dry soil; (iii) evaluate two methods, sieving and leaching, to minimize variability of soil NO$_3^-$ concentrations, a prerequisite for using the $^{15}$N isotope pool dilution technique.

### 2. Materials and methods

#### 2.1. Field site

Our study site was the University of California Davis Long Term Research on Agricultural Systems (LTRAS) project in Yolo County, CA, where since 1993 several cropping systems have been maintained in six randomized replications of 60 m × 60 m plots on the same soil types. We sampled soils of an organically and a conventionally managed system (Table 1). The inputs in the organically managed tomato–corn rotation were a winter legume cover crop, animal manure (composted poultry litter), and harvest residue. Average N inputs from cover crop and manure were 350 kg ha$^{-1}$ yr$^{-1}$. An additional 40 kg N ha$^{-1}$ yr$^{-1}$ was returned to the soil as harvest residue. Dry matter inputs in the conventionally managed tomato–wheat rotation consisted of harvest residue and fertilizer. Each crop received 165 kg N ha$^{-1}$ as granular inorganic fertilizer or urea, in two applications each. Approximately 20 kg N ha$^{-1}$ yr$^{-1}$ was returned to the soil as harvest residue. Both systems were furrow-irrigated. The soil types were Yolo silt loam, a fine-silty, mixed, non-acid, thermic Typic Xerorthent and Rincon silty clay loam, a fine montmorillonitic, thermic Typic Haploxeralf.

#### 2.2. Potentially mineralizable N and inorganic N pools

During the 1999 tomato growing season, we sampled three replicates of each system on the following dates: May 24, June 7, July 1, July 23, and August 19. On each date, a composite sample was collected consisting of 30 cores (2 cm diameter, 0–15 cm depth) taken in diagonal patterns across each plot. An equal number of cores was taken 15, 30, and 45 cm from the centerline of the tomato beds. To avoid the confounding effects of extremely high inorganic N concentrations, the fertilizer bands (7.5 and 23 cm from the centerline) were not sampled.

On each sampling day, three 7 g subsamples of the well-mixed composite samples were extracted with 2 M KCl at a liquid/soil ratio of 5:1. The samples were shaken for 1 h on a reciprocating shaker, centrifuged, and the supernatant was collected. The rest of the soil was air-dried for about 3 d and sieved (2 mm) to standardize assay conditions between sampling dates. To determine potentially mineralizable N

<table>
<thead>
<tr>
<th>Table 1</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Soil characteristics and average yearly inputs of organic (tomato/corn/legume cover crop) and conventional (tomato/wheat) systems at LTRAS.</strong> Bulk density was measured at midseason. Values are means ($n = 3$)</td>
</tr>
<tr>
<td>Management type</td>
</tr>
<tr>
<td>PH (H$_2$O 1:1)</td>
</tr>
<tr>
<td>CEC (meq 100 g$^{-1}$ soil)</td>
</tr>
<tr>
<td>Sand (%)</td>
</tr>
<tr>
<td>Silt (%)</td>
</tr>
<tr>
<td>Clay (%)</td>
</tr>
<tr>
<td>Bulk density 0–7.5 cm (g cm$^{-3}$)</td>
</tr>
<tr>
<td>Bulk density 7.5–15 cm (g cm$^{-3}$)</td>
</tr>
<tr>
<td>Organic C (g kg$^{-1}$)</td>
</tr>
<tr>
<td>Organic N (g kg$^{-1}$)</td>
</tr>
<tr>
<td>C/N ratio</td>
</tr>
<tr>
<td>Dry matter inputs (Mg ha$^{-1}$ yr$^{-1}$)</td>
</tr>
<tr>
<td>N inputs (kg N ha$^{-1}$ yr$^{-1}$)</td>
</tr>
</tbody>
</table>
The (15NH₄)₂SO₄ (99% ¹⁵N) solution was 1.02 mM, cores were removed using beveled PVC pipe sections. Eighty cores were taken from random locations within three covered with perforated parafilm. Soil water potential (C_w) left undisturbed and NO₃ was brought to field capacity. The other half of the samples were four cores comprising a cluster through a 2 mm mesh. The soils with a pressure plate apparatus. Generated for the organically and conventionally managed Kjeldahl procedure to eliminate NO₃. The additions increased 3.50 mM for the leached and sieved samples, respectively. The MBN extracts biomass N (MBN) by the 1 d chloroform-fumigation 24 h, 50 g of soil was used for determination of microbial extraction method (Brookes et al., 1985). The MBN extracts and 0.5 M K₂SO₄ blanks were digested, using a modified Kjeldahl procedure to eliminate NO₃ interference (Wyland et al., 1994). All extracts were analyzed for NO₃⁻ and NH₄⁺ on a Lachat flow injection analyzer. The unfumigated soil samples provide a measure of dissolved organic N (DON). A small amount of soil was used for moisture determination (0 and 24 h).

To prepare the samples and blanks for ¹⁵N analysis, diffusion techniques were used (Brooks et al., 1989; Stark and Hart, 1996). As NH₄⁺ concentrations in the 24 h KCl extracts in the ¹⁵N pool dilution experiments were low, some of the samples with similar concentrations of NH₄⁺ were pooled for the diffusion procedures. The mass and isotopic composition of N due to Devarda’s alloy contamination (Sigman et al., 1997) were measured several times by combusting a single tin capsule containing ten filter disks (each from one diffused blank). Isotope ratios were determined by an Europa Integra mass spectrometer (PDZ Europa Ltd, Cheshire, UK) at the UC Davis Stable Isotope Facility.

Gross ammonification, nitrification (n), and consumption rates of NH₄⁺ (C_NH₄) and NO₃⁻ were calculated according to Kirkham and Bartholomew (1954). Immobilization of NH₄⁺ and NO₃⁻ by microbes was estimated from consumption rates by assuming that gaseous N losses and other possible fates of inorganic N were negligible. Microbial immobilization of NH₄⁺ (I_NH₄) was estimated as

\[ I_{\text{NH}_4} = C_{\text{NH}_4} - n. \]

(1)

MBN was calculated by subtracting NH₄⁺-N in the digested non-fumigated sample from the NH₄⁺-N in the digested fumigated sample. All MBN data are expressed as the flush of N after fumigation with no conversion factor to account for the incomplete recovery of MBN. Immobilization of NO₃⁻ or NH₄⁺ (I_NO₃,NH₄) was also calculated from ¹⁵N recovery in microbial biomass, as

\[ I_{\text{NO}_3,\text{NH}_4} = \frac{\left( N_{\text{fum}} \times \frac{Ae_{\text{fum}}}{100} \right) - \left( N_{\text{non-fum}} \times \frac{Ae_{\text{non-fum}}}{100} \right)}{Ae_{\text{NO}_3,\text{NH}_4}} \]

(2)

where \( N_{\text{fum}} = \mu g \text{ NH}_4^+\text{-N g}^{-1}\text{ soil in digested fumigated samples}, N_{\text{non-fum}} = \mu g \text{ NH}_4^+\text{-N g}^{-1}\text{ soil in digested non-fumigated samples}, Ae_{\text{fum}} = \text{at.\% excess} \text{ ¹⁵N in extracts of fumigated samples}, Ae_{\text{non-fum}} = \text{at.\% excess} \text{ ¹⁵N in extracts of non-fumigated samples}, and Ae_{\text{NO}_3,\text{NH}_4} = \text{average at.\% excess} \text{ ¹⁵N of soil NO}_3^- \text{ or NH}_4^+ \text{ calculated as } (\text{at.\% excess} \text{ ¹⁵N at 0 h} + \text{at.\% excess at 24 h})/2.

To evaluate the sieving and leaching pretreatments, the coefficient of variation (CV) of NO₃⁻ concentrations was determined in pairs of cores from the same location in the field. Pairs (at 0 or 24 h) consisted of cores injected with either ¹⁵NO₃⁻ or ¹⁵NH₄⁺. The known mass of the ¹⁵N added as label was subtracted, if necessary. The mean of all CVs of sieved and leached pairs was then calculated.

The data were analyzed as a split plot design with soil management type as the main plot effect and sampling date for field measurements or laboratory treatments as subplots. To test simple effects within soil management type,
Duncan’s multiple range test and Fisher’s protected LSD were used. In the text, means ± standard errors (SEM) are reported.

3. Results

3.1. Field measurements: seasonal changes in soil N supplying capacity

Both indicators of soil N supplying capacity, PMN and hot minus cold KCl-extracted NH$_4^+$, were about twice as high in the organically managed soil compared to the conventionally managed soil ($P < 0.0001$) (Fig. 1). In both soil management types, PMN declined by about 60% during the course of the growing season. In the organically managed soil, mean hot minus cold KCl-extracted NH$_4^+$ decreased by about 21% between May 24 and August 19 measurements, but there was no change in the conventionally managed soil. In contrast to the soil N availability indices, inorganic N pools did not differ between farming practices. Mean NH$_4^+$ concentrations were low (<1–2 µg NH$_4^+$-N g$^{-1}$ soil) on all five sampling occasions, including the 1 July sampling that took place 3 weeks after the (NH$_4$)$_2$SO$_4$ sidedress application in the conventionally managed soil. Mean NO$_3^-$ concentrations in these composite samples were variable, but were not different between dates.

3.2. $^{15}$N pool dilution and inorganic N immobilization

Total recovery of the applied $^{15}$N label was 107.1 ± 6.2% for NO$_3^-$, and 80.9 ± 1.0% for NH$_4^+$. In the samples labeled with $^{15}$NO$_3^-$, virtually no $^{15}$N was found in excess of natural abundance as NH$_4^+$. The average soil water potential ($\Psi_{soil}$) in the four treatments ranged from $-0.1$ to $-0.3$ MPa, with no differences between the two soil types. There was a weak positive correlation between gravimetric water content ($w$) and gross ammonification rates ($r^2 = 0.19, P < 0.05$) in the organically managed soil, but regressions of nitrification rates on $w$ and of gross ammonification rates on $w$ in the conventionally managed soil were not significant.

Production and fate of NH$_4^+$ at 12 and 120 h after rewetting were summarized for the organic and conventional system by pooling the results of leached and sieved samples (Fig. 2(a)); see below for a comparison of these two pretreatments. The means of corresponding upper (0–7.5 cm) and lower layer (7.5–15 cm) samples were considered experimental units. Mean N transformation rates in each soil type and treatment did not differ between layers (t-tests, $P > 0.05$). Gross nitrification data of the sieved samples at 12 h after rewetting from the organic soil were not included due to the high propensity for negative values (Fig. 3). Pooling the data for pretreatment and layers in this manner highlighted the major trends by reducing variability. Gross ammonification rates were significantly higher in the organically than in the conventionally managed soil, but gross nitrification rates were similar in the two soils (Fig. 2(a)). Gross nitrification rates did not differ from gross ammonification rates in either soil. Time
since rewetting neither affected mean gross ammonification rates nor mean gross nitrification rates.

MBN was higher in the organically than in the conventionally managed soil \((P < 0.0001)\) (Table 2). In both soils at 12 and at 120 h after rewetting, microbes assimilated significantly more NO\(_3^-\) \((^{14+15}\text{N}-\text{N})\) than NH\(_4^+\) \((^{14+15}\text{N}-\text{N})\) based on \(^{15}\text{N}\) recovery in the microbial biomass (Fig. 2(a)). Mean microbial immobilization rates of NH\(_4^+\) and NO\(_3^-\), as calculated from gross consumption rates, showed the same trend, but there were no differences statistically because of large standard errors (Fig. 2(b)). Using \(^{15}\text{N}\) recovery in MBN, the estimated net microbial NO\(_3^-\) assimilation rate in the conventionally managed soil was between 32 and 35% of gross nitrification rates; in the organically managed soil, the estimated net assimilation rate of NO\(_3^-\) was between 37 and 46% of gross nitrification rates. Net estimated NO\(_3^-\) assimilation per day relative to the respective mean NO\(_3^-\) pools was 2–4% in the conventional and 5–6% in the organic system. Estimated net NH\(_4^+\) assimilation per day relative to the respective mean NH\(_4^+\) pools was 19–24% in the conventionally, and 30% in the organically managed soil.

DON was significantly lower in the leached samples than in the sieved samples \((5.7 \pm 0.3 \mu g\) N g\(^{-1}\) soil vs. \(6.8 \pm 0.4 \mu g\) N g\(^{-1}\) soil, respectively; \(P < 0.01\)), but mean gross ammonification rates of sieved and leached samples in soils of both management types were not different \((t\text{-test}; P > 0.05)\). Leaching was more effective at reducing variability of initial NO\(_3^-\) concentrations than sieving, and therefore, more consistent nitrification rates were obtained in the leached samples (Fig. 3). The mean CV of NO\(_3^-\) concentrations for leached pairs was 9 vs. a mean CV of 21 for sieved pairs. About 45% of the gross

Table 2

<table>
<thead>
<tr>
<th>Experiment</th>
<th>NH(_4^+), 12 h</th>
<th>NO(_3^-), 12 h</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(\mu g) N g(^{-1}) soil</td>
<td></td>
</tr>
<tr>
<td><strong>Conventional</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(t_0)</td>
<td>1.26 \pm 0.19</td>
<td>0.76 \pm 0.05</td>
</tr>
<tr>
<td>(t_{24,\text{h}})</td>
<td>0.62 \pm 0.15</td>
<td>0.27 \pm 0.01</td>
</tr>
<tr>
<td>MBN(_{24,\text{h}})</td>
<td>11.45 \pm 1.14</td>
<td>23.31 \pm 1.01</td>
</tr>
<tr>
<td><strong>Organic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(t_0)</td>
<td>0.60 \pm 0.03</td>
<td>0.64 \pm 0.04</td>
</tr>
<tr>
<td>(t_{24,\text{h}})</td>
<td>0.24 \pm 0.04</td>
<td>0.27 \pm 0.05</td>
</tr>
<tr>
<td>MBN(_{24,\text{h}})</td>
<td>10.12 \pm 0.78</td>
<td>19.92 \pm 1.20</td>
</tr>
<tr>
<td><strong>Conventional</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(t_0)</td>
<td>10.53 \pm 1.20</td>
<td>12.10 \pm 1.40</td>
</tr>
<tr>
<td>(t_{24,\text{h}})</td>
<td>12.59 \pm 2.08</td>
<td>12.51 \pm 1.08</td>
</tr>
<tr>
<td>MBN(_{24,\text{h}})</td>
<td>10.58 \pm 1.26</td>
<td>23.67 \pm 1.27</td>
</tr>
<tr>
<td><strong>Organic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(t_0)</td>
<td>11.89 \pm 1.60</td>
<td>14.31 \pm 0.10</td>
</tr>
<tr>
<td>(t_{24,\text{h}})</td>
<td>11.45 \pm 1.83</td>
<td>15.16 \pm 1.54</td>
</tr>
<tr>
<td>MBN(_{24,\text{h}})</td>
<td>10.95 \pm 1.17</td>
<td>22.05 \pm 1.40</td>
</tr>
</tbody>
</table>
nitrification rates obtained using sieved soil were negative whereas 8% of those rates were negative among the leached samples.

4. Discussion

PMN, hot minus cold KCl-extracted NH$_4^+$ and $^{15}$N isotope pool dilution experiments all demonstrated the greater soil N supplying capacity, and therefore greater NH$_4^+$ availability, of the organic compared to the conventional system. The most striking results were that under both management types, microbes assimilated more NO$_3^-$ than NH$_4^+$ and that microbial NO$_3^-$ immobilization rates were substantial compared to gross nitrification rates.

4.1. Soil N supplying capacity

In both soils, PMN declined as the tomato season progressed. Lower values of PMN in the second half of the growing season in similar cropping systems were also reported by Gunapala and Scow (1998). The decline in PMN could be due to a decrease in MBN or a diminishing pool of easily mineralizable non-living OM. In anaerobic incubation, killed aerobic microorganisms may be the most important part of the organic substrate being mineralized. In a range of forest soils, there was a strong correlation between the amount and isotopic composition of the NH$_4^+$ produced by anaerobic incubation and MBN measured via chloroform fumigation-incubation (Myrold, 1986), suggesting that those two N pools are largely identical. In agricultural soils such correlations have not always been found (Drinkwater et al., 1996), perhaps because different types of C and N inputs and removals affect substrate composition. In both our soils, concentrations of MBN and PMN were similar, when both were measured in late July, supporting the idea that NH$_4^+$ released by anaerobic incubation is mostly microbial N. In this study, PMN as an indicator of relative N availability showed a clear difference between organic and conventional farming practices. However, PMN provided no information on actual rates of NH$_4^+$ release, the fate of this newly released NH$_4^+$, or the extent of recycling of inorganic N via microbial biomass. The results of the $^{15}$N experiments, which complement the PMN measurements, suggest a very dynamic role of MBN and highlight the importance of microbial N immobilization that is taking place simultaneously with inorganic N production.

While PMN as a biological assay measures the release of NH$_4^+$ from various easily mineralizable N fractions, hot KCl releases NH$_4^+$ from only certain organic N compounds whose chemical nature is mostly unknown (Gianello and Bremner, 1986; Curtin and Wen, 1999). In neither soil did changes in PMN closely parallel changes in hot minus cold KCl-extracted NH$_4^+$. By 19 August, concentrations of hot minus cold KCl-extracted NH$_4^+$ and PMN were no longer different in either soil. At that time, whether the NH$_4^+$ released by the two assays was of the same origin is not known.

In contrast to the soil N availability indices, inorganic N concentrations provided no information on actual NH$_4^+$ availability since NH$_4^+$ concentrations were always low except in the fertilizer band, where concentrations reach up to 1000 μg NH$_4^+$-N g$^{-1}$ soil (Frederick and Broadbent, 1965).

4.2. Rates of soil N transformations

Nitrate immobilization by heterotrophic microbes and N process rates were greater under organic than conventional practice although gross nitrification rates were not statistically different between the two soils due to the large variability of the data. In general, gross nitrification rates plus NH$_4^+$ immobilization rates approximately added up to gross ammonification rates. Gross nitrification rates in the 12 h treatment of the conventionally managed soil were twice as high as gross ammonification rates probably because mean background NH$_4^+$ concentrations in those samples were twice as high as in the other treatments (Table 2). Thus, during that 24 h incubation, residual and freshly produced NH$_4^+$ were apparently nitrified, and presumably, nitrification rates would not have exceeded ammonification rates over the longer term.

An important result of this study was the high NO$_3^-$ immobilization rates relative to the gross nitrification rates. Nitrate immobilization rates approaching gross nitrification rates have been reported for grassland and forest soils (Stark and Hart, 1997; Hatch et al., 2000), which, in contrast to agricultural soils, are considered N rather than C limited. Although in both soils microbial NO$_3^-$ immobilization was substantial, suggesting an important function of microbes in controlling NO$_3^-$ concentrations, there were nevertheless sizable standing pools of NO$_3^-$ throughout the growing season possibly because soil C limited NO$_3^-$ immobilization in both systems, and NO$_3^-$ availability exceeded plant N demand.

In these soils, heterotrophic microbes assimilated less NH$_4^+$ than NO$_3^-$ probably because NH$_4^+$ concentrations were low and the spatial distribution of NH$_4^+$ may not have been uniform due to diffusional limitations. Concentrations of NO$_3^-$, on the other hand, were much higher and the physical constraints to its distribution are lower (Tinker and Nye, 2000). Low concentrations of NH$_4^+$ only partially inhibit NO$_3^-$ assimilation by microbes (Rice and Tiedje, 1989). Moreover, NH$_4^+$ may have disappeared completely from some microsites in the soil because of nitrification. The fact that microbial NH$_4^+$ assimilation rates were similar in the two soils, even though gross ammonification rates were much higher in the organically than the conventionally managed soil, seems to indicate strong competition for NH$_4^+$ between nitrifiers and N immobilizers. Thus, NO$_3^-$ was likely
more available to microbes. If microbial immobilization of inorganic N is expressed relative to source pool sizes, as suggested by Low et al. (1997), NH$_4^+$ immobilization in both soils was at least five times greater than NO$_3^-$ immobilization, lending support to the widely held notion that NH$_4^+$, being in the reduced state, is the preferred N form for assimilation by microbes (Paul and Clark, 1996).

It is unlikely that the addition of K$^{15}$NO$_3$ stimulated microbial NO$_3^-$ immobilization since NO$_3^-$ concentrations in the isotope pool dilution experiment were similar to those encountered in the field. Nitrate consumption rates tended to be higher than our estimated rates of microbial NO$_3^-$ immobilization. Using a correction factor to convert the 1 d fumigation N-flush ($F_N$) to MBN, e.g. $F_N/0.54$ (Shen et al., 1984; Brookes et al., 1985), would also increase the rate of NO$_3^-$ immobilization. Thus, our estimates of microbial NO$_3^-$ assimilation based on $^{15}$N recovery in MBN are conservative. Microbial assimilation of NH$_4^+$ may have been stimulated because the ambient NH$_4^+$ pools were approximately doubled by the application of the $^{15}$N label. In addition, our estimates of microbial NH$_4^+$ immobilization could be inflated because some of the $^{15}$N measured in the microbial biomass may have been taken up as NO$_3^-$.

It appears that microbial demand for N as a result of C availability, the spatial distribution of NH$_4^+$ and NO$_3^-$, and competition by NH$_4^+$ oxidizers must all be considered factors that determine the magnitude and proportion of NH$_4^+$ and NO$_3^-$ assimilation by microbes. Because NH$_4^+$ and NO$_3^-$ concentrations in the microcosms were similar as in the field, where heterotrophic microbes face additional competition for NH$_4^+$ by roots, our results indicate that in some agricultural soils, microbial NO$_3^-$ immobilization may be greater than NH$_4^+$ immobilization.

Time elapsed since rewetting had no effect on ammonification or nitrification rates in either soil management type. Two weeks of air-drying may not have caused a flush of mineralization (Sparrling and Ross, 1988) large enough to be observed in this experiment, or alternatively, the 5 d period at high water potential was possibly not long enough for mineralizable substrate depletion (Appel, 1998; Pullman and Tietema, 1999) to occur. Nitrification activity was not impeded by prior soil drying.

4.3. Organic vs. conventional management

The high OM inputs in the organic system resulted in greater N supplying capacity well into the growing season, when N demand by plants is still high (Jackson and Bloom, 1990), compared to the low OM input conventional system. Nitrification appears to be the major fate of NH$_4^+$ in both systems. Measuring short-term rates of production and consumption of inorganic N highlighted the differential importance of recycling of NO$_3^-$ in these systems. Microbial NO$_3^-$ immobilization was unexpectedly high and, expressed as a percentage of gross nitrification rates, greater in the organic compared to the conventional soil. Highly concentrated inorganic N inputs can have detrimental environmental impacts (Matson et al., 1997; Venterea and Rolston, 2000b). Our data suggest that high OM inputs as an alternative resulted in a gradual release of inorganic N. Moreover, the greater C availability in the organic system apparently supports a more active microbial biomass with greater N demand, thus promoting immobilization and recycling of NO$_3^-$. The challenge in managing high OM input systems may well be in balancing C and N inputs to prevent a build-up of large standing NO$_3^-$ pools, yet avoiding high rates of microbial N immobilization during peak periods of crop N demand.

Acknowledgements

We thank R. Venterea and two anonymous reviewers for their critical comments on earlier versions of the manuscript, D. Harris for the $^{15}$N mass spectrometer analyses, and A. Clymo and I. Ramirez for technical assistance. Funding for this research was provided by the USDA-NRI Soils and Soil Biology Program, grant number 2000-00991, and the Kearny Foundation of Soil Science, grant number 97-D-24.

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