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Significance of Enzyme Activities in Soil Nitrogen Mineralization

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This study was undertaken to assess the relationship between nitrogen (N) mineralization in soils treated with eight lime application rates, with four field replications, and the activities of six amidohydrolases involved in N cycling and four glycosidases involved in carbon (C) cycling in soils. Nitrogen mineralization was studied at 20 or 30 °C for 20 weeks, and with the exception of N-*aceyl-β-D-glucosaminidase (NAGase; EC 3.2.1.30) activity, which was assayed at both temperatures, the enzyme activities were assayed at 30 °C at their optimal pH values. Results showed that among the eight enzyme activities studied, NAGase activity was the most significantly correlated with the cumulative amounts of N mineralized in 32 soil samples at 20 °C (*r *= 0.87***) and at 30 °C (*r *= 0.95***). The cumulative amounts of N mineralized at 30 °C were also significantly correlated with arylamidase and L-aspartase activities, with* r *values of 0.61*** and 0.52**, respectively. Because NAGase activity is involved in both N and C cycling, the cumulative amounts of N mineralized at 30 °C were also significantly correlated with the activities of β-glucosidase (*r *= 0.80***) and β-galactosidase (*r *= 0.58***). Activities of other N enzymes that were significantly correlated with the cumulative amounts of N mineralized at 30 °C in 20 weeks were those of L-asparaginase (*r *= 0.61***), urease (*r *= 0.57***), amidase (*r *= 0.54**), and L-glutaminase (*r *= 0.41*). It seems that the activity of NAGase can be used as an index of N mineralization in soils.*

Keywords *N*-Aceyl-β-D-glucosaminidase, amidohydrolases, glucosidases, organic matter, organic N

Introduction

Organic nitrogen (N) in soils consists of a variety of compounds including amino acids, which are associated with proteins and peptides, and amino sugars, which are associated with chitin in soils. After acid hydrolysis, those comprise 30–45% and 5–10% of total organic N in soils, respectively (Stevenson 1994). Studies on the amino acid composition of soil organic matter showed that 13 amino acids identified in extracts of 10 Iowa surface soils ranged from 32 to 50%, expressed as percentages of total organic N extracted, and that those of surface soils of two sites under different cropping systems in Iowa varied among the crop rotations at the two sites (Senwo and Tabatabai 1998). The chemical nature of a large fraction (30–55%) of the

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organic N in soils is still unknown (Stevenson 1994). Thus, in soils, the substrates that participate directly or indirectly in the ammonification and nitrification processes are of different origins and chemical classes and are present in different microenvironments. Similarly, hydrolases, oxidases, deaminases, and lyases enzymes, which act on those substrates, may originate directly from various plant, animal, or microbial sources (Ladd and Jackson 1982; Tabatabai 1994). Therefore, studies of enzyme activities should provide insight into biochemical processes in soils by which N is mineralized. Such assays, if successful, can be used as sensitive biochemical indexes. Enzyme activities have also been suggested as early indicators of changes in soil properties induced by soil management processes, because of their rapid response to change in management practices, their relationship to soil biology, and ease and accuracy of their assay (Powlson, Brookes, and Christensen 1987; Dick 1994). A highly significant correlation between soil microbial biomass and gross N mineralization has been reported (Madison et al. 1998), and microbial biomass of soils was suggested as a predictor of net N mineralization (Burton and McGill 1992). Other studies have suggested that enzyme activities can be used as indexes of soil fertility (see Skujins 1967), but little information is available to support such conclusions. A study on the characterization of the active N pools in soils under different cropping systems, however, suggested that N mineralization in soils is predominantly controlled by biochemical processes such as enzyme activities other than the overall microbial activity (Deng, Moore, and Tabatabai 2000). That study also reported a significant correlation between active N pools and amidase activity, which plays an important role in N mineralization in soils.

N-Acetyl-β-D-glucosaminidase (NAGase, EC 3.2.1.30) is the enzyme that catalyzes the hydrolysis of *N*-acetyl-β-D-glucosamine residue from the terminal nonreducing ends of chitooligosaccharides. This enzyme is also classified as β-hexoaminidase (EC 3.2.1.52) by the International Union of Biochemistry because it cleaves the amino sugar *N*-acetyl-β-D-galatosamine (Webb 1984). The NAGase is involved in chitin degradation in soils. Studies by Ekenler and Tabatabai (2002) showed that NAGase activity is significantly correlated with organic carbon (C) and N, with microbial biomass C and N, and with the cumulative amounts of N mineralized at 30 °C during 24 weeks of incubation of 36 and 44 surface soils from two sites under different cropping systems sampled in 2 years. Those results suggested that the NAGase enzyme may play a major role in N mineralization. This finding is important because this enzyme activity could be a rate-limiting step in organic N mineralization in soils by producing *N*-acetyl-D-glucosamine, which in turn is mineralized to ammonium (NH_4^+), which is then nitrified under aerobic conditions. Other studies evaluating the relationship between this enzyme activity and N-mineralization indexes (used to predict plant-available N) in soils from six agroecological zones of the north central region of the United States showed that the amounts of N mineralized by all the biological and chemical indexes studied were significantly correlated with NAGase activity, with r values ranging from 0.86 ($P < 0.001$) for the amounts of N mineralized in rewetted, air-dried soils incubated under anaerobic conditions to 0.47 ($P < 0.001$) for the amounts of N mineralized in soils incubated under aerobic incubation. The r values of the relationships between the NAGase activity and the other biological and chemical indexes studied were within this range. The amounts of inorganic N released by the N-mineralization indexes, with the exception of those under aerobic incubation, were significantly ($P < 0.001$) correlated with organic C and total N of soils, with r values ranging from 0.65 ($P < 0.001$) to 0.78 ($P < 0.001$) and from 0.62 ($P < 0.001$) to 0.80

($P < 0.001$) for organic C and total N, respectively (Ekenler and Tabatabai 2004a). Because both enzyme activities and N mineralization are affected by soil pH, the objective of this study was to assess the relationship between the amounts of N mineralized in field-moist soils incubated under aerobic conditions for 20 weeks and the activities of the enzymes involved in hydrolysis of N-containing native organic compounds in soils and urease activity.

Materials and Methods

Experimental Design

The soil used was a Kenyon loam (fine-loamy, mixed, mesic Typic Hapludoll). The experimental site was established in 1984 at the Northeast Research Center in Nashua, Iowa. Agricultural limestone from a local quarry was broadcast the first year at the following rates: 0, 1120, 2240, 4480, 6720, 8960, 13440, and 17920 kg effective calcium carbonate equivalent (ECCE) ha^{-1}. Treatments were arranged in a randomized complete block design with four replicates. The size of each field plot was 6 × 15 m. Corn (*Zea mays* L.) and soybean (*Glycine max* L.) were grown in alternate years, with periodic applications of fertilizers to maintain high levels of N, phosphorus (P), and potassium (K).

Sampling and Laboratory Analyses

Surface soil samples (0 to 15 cm) were taken after corn harvest from all field replicates (32 samples), 7 years after lime application, by pooling six to eight cores (7.6 cm in diameter). The samples were passed through a 2-mm mesh sieve, and a portion of each sample was air dried for 48 h at room temperature (22 °C) and ground to pass a 2-mm sieve, a portion of which was ground to pass an 80-mesh (180-μm) sieve. Organic C was determined by the Mebius method (1960), and total N was determined by a semi-micro-Kjeldahl method (Bremner and Mulvaney 1982) on the <180-μm samples. The pH values were measured on the <2-mm air-dried samples by using a glass combination electrode [soil: 0.01 *M* calcium chloride ($CaCl_2$) ratio, 1:2.5]. With the exception of NAGase activity, which was assayed at 20 °C and 30 °C (the reason is given later), the other enzyme activities were assayed at 30 °C on the <2-mm field-moist samples at their optimal pH values in duplicates with one control and are expressed on a moisture-free basis. The assay methods used and the reactions involved were previously summarized by Senwo and Tabatabai (1996), Acosta-Martinez and Tabatabai (2000a, 2000b), and Parham and Deng (2000). Moisture was determined from loss in weight after drying at 105 °C for 48 h. When not in use, the field-moist samples were stored in plastic bags at 4 °C.

Nitrogen Mineralization

Nitrogen mineralization was studied as described by Deng and Tabatabai (2000) and Deng, Moore, and Tabatabai (2000). The protocol involved incubating (in duplicates) a mixture of field-moist soil (20 g on an oven-dried basis) and an equal weight of acid-washed silica sand (<20 mesh). The soil and sand were mixed thoroughly after being moistened with fine spray of deionized water to obtain a homogenous mixture and prevent aggregation during transfer to a leaching tube

(3.5 cm in diameter and 15 cm long), and the mixture was retained by means of a glass wool pad and a layer of silica sand. A thin (ca. 5 mm) glass wool pad was placed over the soil–sand mixture to prevent displacement of the soil when solution was poured over the mixture. The leaching tube was placed on a 250-mL suction flask, and the mineral N initially present was removed by leaching with 100 ml of 5 mM calcium chloride ($CaCl_2{\cdot}2H_2O$). Suction of 6 kPa (60 cm Hg) was applied to remove the excess water. The tube was covered with a piece of plastic film with a single hole (0.5 cm in diameter) for aeration and placed in an upright position in a 20 °C or 30 °C incubator. The N mineralized during incubation was removed by leaching with 100 mL of 5 mM $CaCl_2{\cdot}2H_2O$ every 2 weeks for up to 20 weeks. The volume of the leachate was adjusted to 100 mL, and aliquots of the leachate were analyzed for ammonium (NH_4^+)-N and [nitrate (NO_3^-) + nitrite (NO_2^-)]-N by steam distillation and NO_2^--N by the colorimetric method of Griess-Ilosvay (Keeney and Nelson 1982; Mulvaney 1996).

Statistical Analyses

Statistical analyses were performed by the general linear model procedure of the SAS system (Barr et al. 1976). For all data points shown in Figures 1–5, the differences between the duplicate values obtained in the analyses or assays were smaller than the symbol size.

Results and Discussion

Nitrogen mineralization in soils is affected by various factors such as organic N, C/N ratio, pH, moisture content, and temperature. To demonstrate the relationship

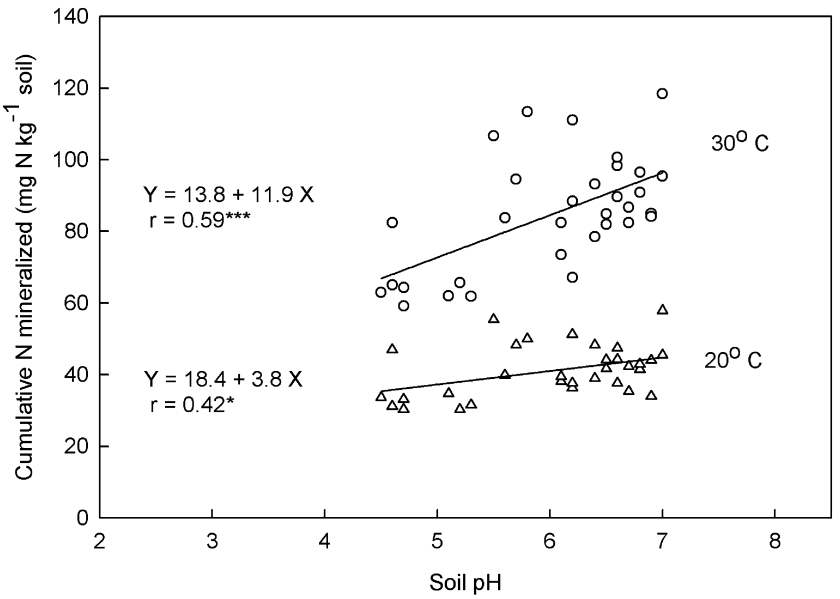

Figure 1. Relationships between soil pH and the cumulative amounts of N mineralized during 20 weeks of incubation at 20°C and 30°C.

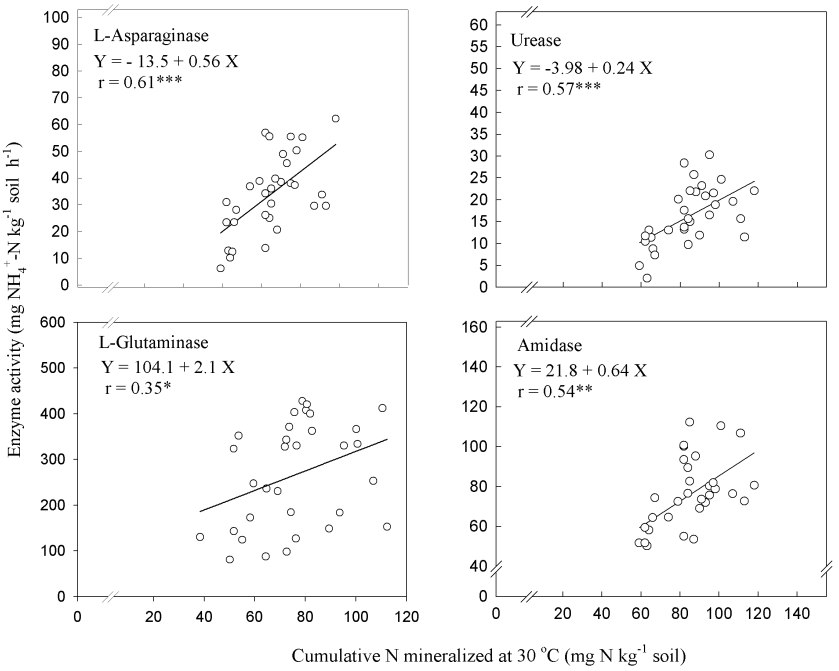

Figure 2. Relationships between the cumulative amounts of N mineralized during 20 weeks of incubation at 30°C and the activities of L-asparaginase, urease, L-glutaminase, and amidase assayed at the same temperature.

between N mineralization and the activities of the enzymes involved in this process, it is essential that percentages of organic C and N remain constant, but the pH values may vary. Results showed that, in general, the means of soil pH were significantly increased after 7 years of lime application, from 4.9 in the control to 6.9 in the plots treated with the greatest rate of lime application (Table 1). Temperature and

Table 1. Effect of lime application rates on the soil pH, organic C, and organic N

Lime application rate (kg ECCE[b] ha^{-1})	pH[a]	Organic C ($g\,kg^{-1}$ soil)	Organic N ($g\,kg^{-1}$ soil)
0	4.6–5.5 (4.9)[c]	14.2–15.6 (15.0)	1.2–1.4 (1.3)
1120	4.7–5.8 (5.1)	14.7–15.3 (15.0)	1.3–1.3 (1.3)
2240	5.1–6.2 (5.7)	14.8–17.2 (15.0)	1.2–1.4 (1.3)
4480	5.3–6.5 (6.1)	15.1–15.6 (15.3)	1.3–1.3 (1.3)
6720	6.1–6.7 (6.4)	14.7–15.8 (15.2)	1.2–1.4 (1.3)
8960	6.4–6.8 (6.6)	15.3–16.5 (15.8)	1.3–1.5 (1.4)
13440	6.2–6.9 (6.6)	14.9–16.0 (15.3)	1.3–1.4 (1.3)
17920	6.7–7.0 (6.9)	14.5–16.3 (15.1)	1.2–1.4 (1.3)
LSD ($P < 0.05$)	(0.5)	(NS)	(NS)

[a]Soil/0.01 M $CaCl_2$ solution ratio, 1:2.5.
[b]ECCE, effective calcium carbonate equivalent.
[c]Values in parentheses are averages of soil samples from four replicated field plots.

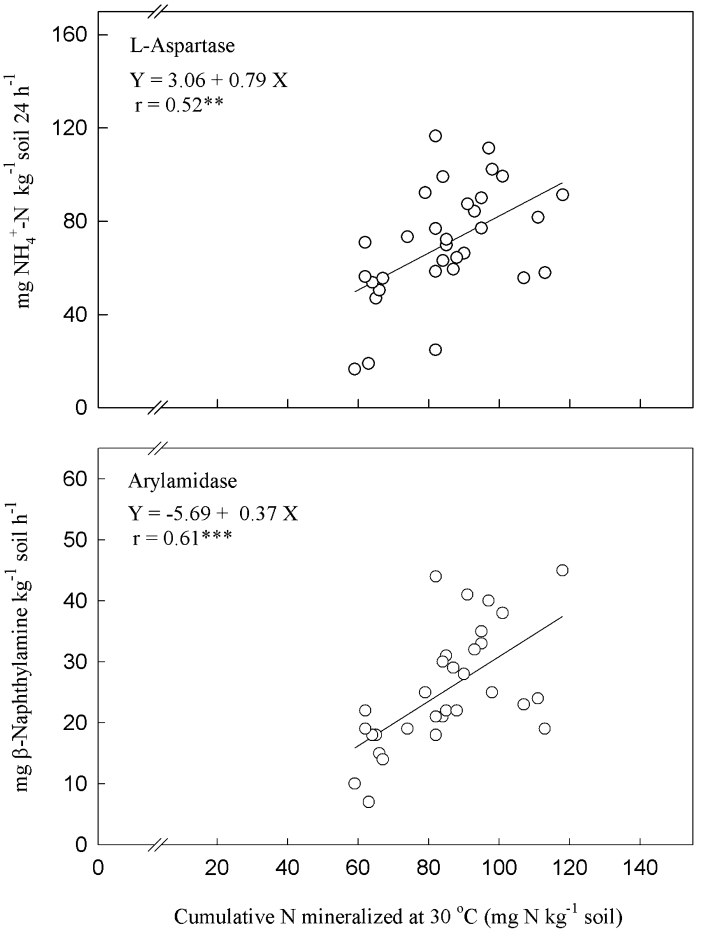

Figure 3. Relationships between the cumulative amounts of N mineralized during 20 weeks of incubation at 30°C and the activities of L-aspartase and arylamidase assayed at the same temperature.

moisture were controlled during incubation. The C/N ratio was about constant because the experiment was conducted on a single soil type and series.

Effect of pH

The cumulative amounts of N mineralized at both 20 °C and 30 °C varied among the soil samples of the four replicated field plots at each lime application rate. This presumably was due to the variability (spatial variability) among the soils of the replicates in pH and organic C and N (Table 1). The amounts of N mineralized in soils, however, were linearly and significantly correlated with soil pH (Figure 1). The correlation coefficients (r values) were 0.42 ($P < 0.05$) and 0.59 ($P < 0.001$) at 20 °C and 30 °C, respectively. Recent work showed that the activities of 16 enzymes, including those involved in this study, increased with soil pH (with the exception of acid phosphatase activity, which decreased with pH in limed agricultural soils) and that liming significantly increased the specific activities of the enzymes

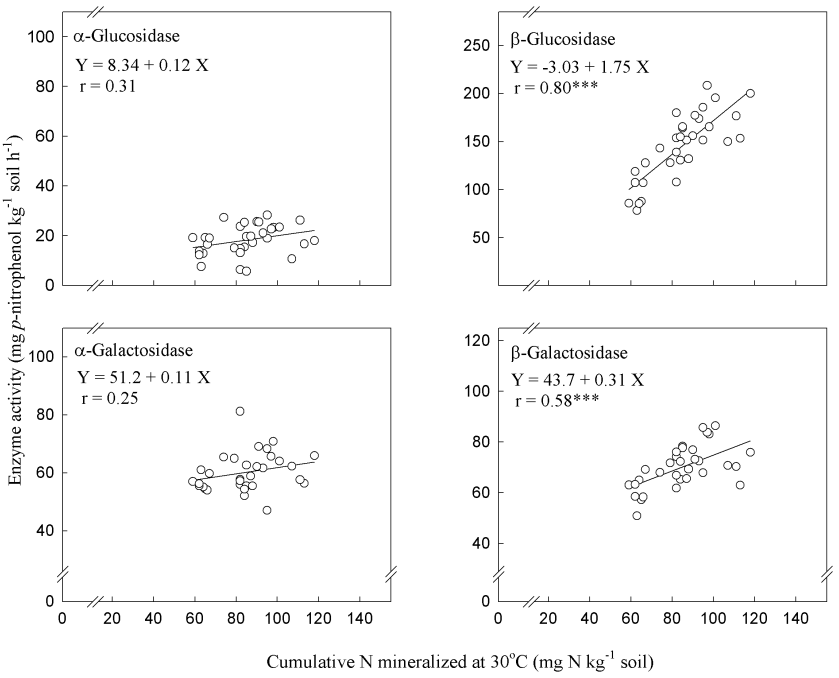

Figure 4. Relationships between the cumulative amounts of N mineralized during 20 weeks of incubation at 30°C and the activities of α-glucosidase, *β*-glucosidase, α-galactosidase, and *β*-galactosidase assayed at the same temperature.

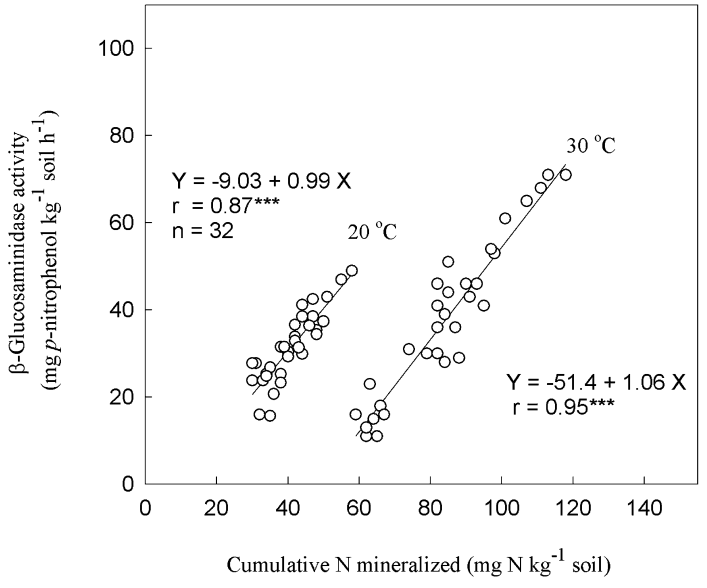

Figure 5. Relationships between the cumulative amounts of N mineralized during 20 weeks of incubation at 20°C or 30°C and the *β*-glucosaminidase activity assayed at the same temperatures.

(Acosta-Martinez and Tabatabai 2000a; Ekenler and Tabatabai 2002, 2004b). Expressed as percentages of the total organic N of soils, the cumulative amounts of N mineralized ranged from 2.7 to 3.4% at 20 °C incubation and from 5.8 to 7.5% at 30 °C incubation (Senwo and Tabatabai 2005). Early work showed that liming soils to higher pH values did not affect N-mineralization rate (Dancer, Peterson, and Chesters 1973). Other studies involving 40 Canadian acid soils (pH 4.0–5.6), however, showed that the cumulative amounts of N mineralized increased twofold during a 4-week incubation when the pH was increased to 6.7 by liming; this effect was not permanent because no enhancement of N mineralization was observed 1 to 2 years after liming (Nyborg and Hoyt 1978). The soils used in our study were limed 7 years before sampling. Throughout the 20 weeks of incubation, no significant concentration of NO_2^--N or NH_4^+-N could be detected in the soil leachates at any pH value. This was expected because the former is not stable at the pH values used, and the latter accumulates only when pH values fall as low as 4 where nitrification is inhibited (Cornfield 1952, 1953; Fu, Xu, and Tabatabai 1987). In addition, nitrification rates increase with increasing pH (Senwo and Tabatabai 2005). Because the response of N mineralization at 20 °C to soil pH was much less than that at 30 °C, as is evident from the slope of the regression lines, the enzyme assays, with the exception of NAGase activity, were performed only at 30 °C. Because NAGase activity at 30 °C was extraordinarily and significantly correlated with the amounts of N mineralized at 30 °C, we also examined this relationship at 20 °C.

Activities of Amidohydrolases and Arylamidase

Because several enzymes are involved in hydrolyzing nitrogenous compounds in soils, we evaluated the relationships between the cumulative amounts of N mineralized over 20 weeks of incubation and the activities of amidohydrolyses or arylamidase (Figures 2 and 3). Results showed that the activities of L-asparaginase, urease, L-glutaminase, amidase, L-aspartase, and arylamidase were significantly correlated with the cumulative amounts of N mineralized at 30 °C. The r values of those relationships ranged from 0.35 ($P < 0.05$) for L-glutaminase to 0.61 ($P < 0.001$) for L-asparaginase and arylamidase, suggesting the involvement of those enzymes in hydrolyzing the specific amino acids released from soil organic matter. Other studies have shown significant correlation between amidase, asparaginase, urease, dipeptidase, and protease activities and N mineralization (Burton and McGill 1992; Burket and Dick 1998; Zaman et al. 1999; Deng, Moore, and Tabatabai 2000). Other recent work showed that the annual means of arginine ammonification values were correlated with gross N-mineralization values in four different agricultural fields in Denmark (Bonde et al. 2001). Although the activities of those enzymes can be used as indexes of N mineralization, the relatively low magnitude of the correlation coefficients (r values) suggests that they do not provide very reliable indexes.

Glycosidase Activities

A variety of microbially derived amino sugars occur as their *N*-acetyl derivatives in soils. Among those, glucosamine, galactosamine, and muramic acid predominate (Ladd and Jackson 1982). Because several glycosidases are involved in hydrolysis of organic N compounds in soils, we evaluated the relationships between the

cumulative amounts of N mineralized at 30 °C during 20 weeks of incubation and the activities of α- and β-glucosidases and α- and β-galactosidases assayed at 30 °C. Results showed that only the activities of β-glucosidase and β-galactosidase were significantly correlated with N mineralization, with r values of 0.80 and 0.58 ($P < 0.001$), respectively (Figure 4). Among the glycosidases studied, the activity of NAGase was the most significantly correlated with the cumulative amounts of N mineralized both at 20 °C and 30 °C (Figure 5; the enzyme activity was assayed at the same temperatures), with r values of 0.87 and 0.95 ($P < 0.001$), respectively. The slopes of the regression lines were about the same (ca. 1), suggesting that the activity of this enzyme can be used as an index of N mineralization within the range of temperatures specified. These results support our earlier report (Ekenler and Tabatabai 2002) on the significant correlation between the amounts of N mineralized in surface soils of two sites under different cropping systems in Iowa during 24 weeks of incubation at 30 °C and the activity of NAGase assayed at 37 °C, with r values of 0.84 and 0.79 ($P < 0.001$), respectively. This finding is significant because recent studies by Ekenler and Tabatabai (2004a) showed that the amounts of N mineralized, as measured by several biological and chemical availability indexes, were significantly correlated with NAGase activity of 56 surface soils from six agroecological zones of the north central region of the United States. The r values were 0.73 and 0.76 ($P < 0.001$) for the amounts of NH_4^+-N released by steam distillation with phosphate–borate buffer (PO_4-B_4O_7, pH 11.2) for 4 and 8 min, respectively; 0.69 and 0.74 ($P < 0.001$) for the amounts of NH_4^+-N released with a solution containing sodium borate ($Na_2B_4O_7$, pH 11.5) for 4 and 8 min, respectively; 0.47 ($P < 0.001$) for the amounts of N produced under aerobic incubation; 0.80 ($P < 0.001$) for the amounts of inorganic N produced by incubation under anaerobic conditions of field-moist soils; and 0.86 ($P < 0.001$) for anaerobic incubation of rewetted air-dried soils. From the results reported in Figure 5 and the highly significant linear relationships between the results obtained by the chemical and biological indexes stated previously and the activity of this enzyme in soils, it is clear that NAGase hydrolyzes the same N bonds that are susceptible to hydrolysis under aerobic conditions and that NAGase activity can be used as an index of mineralizable N in soils.

Conclusions

The results support the views that increasing soil pH by liming increases enzyme activities, which in turn increase N mineralization, and that NAGase activity can be used as a reliable index of N mineralization in soils.

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