

# Effect of plant materials on microbial transformation of amino sugars in three soil microcosms

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**Abstract** Amino sugars, being predominantly of microbial origin, can help elucidate the role of microbes in carbon and nitrogen cycling in soils. However, little is known about the microbial degradation and synthesis of soil amino sugars as affected by plant-derived organic materials. We conducted a 30-week microcosm study using three soils amended with soybean leaf or maize stalk to investigate changes in the amounts and patterns of amino sugars over time. The total soil amino sugar content initially increased during the incubation, but later decreased. Amino sugar content of soil amended with maize stalk peaked at an earlier time than it did for soybean leaf, suggesting nutrient quantity and substrate composition influence microbial transformation. Temporal dynamics of the proportion of total soil amino sugar to organic matter after plant material addition conformed to parabolic models ( $r > 0.8$ ;  $p < 0.01$ ), which tended to converge over time. The models predicted that the proportions would ultimately approach the initial values as determined before amendment. These findings suggest that soil organic matter has the ability to maintain a baseline steady-state level of amino sugars, and support the

interpretation of soil amino sugar reservoir as two components: the Stable Pool (SP) and the Transition Pool (TP).

**Keywords** Amino sugar · Microbial residue · Plant material · Microbial transformation · Pool

## Introduction

Plant litter is a primary nutrient source for saprophytic microbiota in soils, and its quantity and properties strongly influence the formation and humification of soil organic matter (SOM) in terrestrial ecosystems (Swift et al. 1979; Scholes et al. 1997; Kögel-Knabner 2002). Soil microbial biomass represents a significant compartment of terrestrial carbon, and its residues are important parent materials for humus formation (Haider 1992; Kögel-Knabner 2002). Growth of the microorganisms responsible for genesis and cycling of humic substances is influenced by carbon (C) and nitrogen (N) availability in the decomposing plant residues (Balsler 2005). During plant residue decomposition, a fraction of the plant C and N is assimilated into the microbial biomass, rendering it largely inaccessible to further biological transformation. The assimilated C and N may remain unavailable to the plant and decomposer community for an appreciable time after microbial death (Jansson and Persson 1982). Little is known, however, about the fate of the C and N in the dead microbial cells.

Soil amino sugars are predominantly of microbial origin (Parsons 1981; Stevenson 1982) and are relatively stable over time (Chantigny et al. 1997). The relative representation of different structural classes of amino sugars can be used to differentiate between fungal and bacterial residues in soils (Guggenberger et al. 1999; Glaser et al. 2004).

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**Table 1** Soil physical and chemical properties

Soil type	OM g kg <sup>-1</sup>	Total N g kg <sup>-1</sup>	C/N ratio	Alkali soluble N mg kg <sup>-1</sup>	Available P mg kg <sup>-1</sup>	Available K mg kg <sup>-1</sup>	pH (H <sub>2</sub> O) value 1:2.5
Red soil	14.7 <sup>a</sup>	1.07 <sup>a</sup>	7.18 <sup>a</sup>	96.4 <sup>a</sup>	0.09 <sup>a</sup>	188.2 <sup>a</sup>	5.5 <sup>a</sup>
Brown soil	19.6 <sup>b</sup>	1.21 <sup>b</sup>	8.28 <sup>b</sup>	108.5 <sup>b</sup>	0.07 <sup>a</sup>	85.1 <sup>b</sup>	6.0 <sup>b</sup>
Black soil	24.4 <sup>c</sup>	1.52 <sup>c</sup>	8.23 <sup>ab</sup>	135.7 <sup>c</sup>	0.15 <sup>b</sup>	63.7 <sup>c</sup>	6.1 <sup>b</sup>

Letters indicate significant differences among three soil types at the 0.05 probability level. OM represents organic matter.

Understanding the fungal and bacterial contributions to microbial residues can further provide insights into how these organisms govern C and N cycling in soil (Amelung 2001; Simpson et al. 2004). The approach is based on existence of several distinct variations on the molecular structure of amino sugars, with two of them representative of bacteria and one of fungi (Nannipieri et al. 1979; Parsons 1981).

Amino sugars are rapidly synthesized during microbial immobilization of inorganic N (McGill et al. 1973), regardless of the type of organic material added to soil (Sowden 1968). Lowe (1973) found that the amino sugar content of forest soils increases with respect to humification. Dai et al. (2002) showed that the level of amino sugar N, as a proportion of total N, remains constant or increases with time in arctic soil microcosms. Amelung et al. (2001) used amino sugars to investigate the fate of microbial residues during beech leaf (*Fagus sylvatica* L.) litter decomposition; however, their experiment was confined only to pure minerals and plant litters (not real soil). Little is known about the time scale at which amino sugars respond to introduced plant materials in soils.

The objective of this study was to investigate the effects of plant materials on fungal and bacterial transformation processes in soils. We conducted a series of incubation experiments in which four amino sugars were monitored over time in the presence and absence of added plant materials. Galactosamine (GalN) and muramic acid (MurA) were used as markers for bacterial cell wall residues and glucosamine (GluN) was used as a marker for fungal cell wall residues. Mannosamine (ManN) was consulted as a cumulative index of amino sugar, as the extent to which it owes its origin to bacteria or fungi is presently unclear.

## Materials and methods

### Soil and plant materials

We selected an oxisol (red soil), an alfisol (brown soil) and a mollisol (black soil) for our study. All three soils lacked appreciable carbonate content (permitting the assumption that all soil C was organic). Red soil samples were obtained from the Experimental Station of Jiangxi Agricultural University, Jiangxi, China (28°46' N, 115°50' E, ~65 m a.s.l.); brown soil samples from the Shenyang Experimental Ecology Station of the Chinese Academy of Science, Shenyang, China (41°31' N, 123°24' E, ~31 m a.s.l.); and black soil samples from Gongzhuling, Jiling, China (43°36' N, 124°40' E, ~206 m a.s.l.). The soils were sampled from 0 to 20 cm depth, air-dried, sieved and homogenized using a 1-mm mesh and subsequently stored in cool, dark conditions. The C, N, phosphorus, and potassium content as well as pH were determined for each (Table 1).

Soybean leaves [*Glycine max* (L.) Merr.] and maize stalks (*Zea mays* L.) were harvested, air-dried, cut into pieces of approximately 2 mm<sup>2</sup>, and analyzed for C, N, amino sugar content (Table 2). Amino sugars initially detected in plant materials were likely produced by the soil and epiphyllous microbial communities before sample collection, as all previous studies demonstrate that plants do not synthesize amino sugars in significant amounts (Parsons 1981; Stevenson 1982).

### Microcosm design

Soils were amended with plant material to a ratio of one part plant material to 25 parts soil by mass, and then distributed among individual plastic pots (approximately 1,000 ml). Purified water was added to approximately 25%

**Table 2** Properties of soybean leaf and maize stalk

Plant material	Total C g kg <sup>-1</sup>	Total N g kg <sup>-1</sup>	Total S g kg <sup>-1</sup>	C/N Ratio	Total A.S. µg g <sup>-1</sup>	GluN µg g <sup>-1</sup>	ManN µg g <sup>-1</sup>	GalN µg g <sup>-1</sup>	MurA µg g <sup>-1</sup>
Soybean leaf	442.5	9.08	3.19	48.73	328	234.5	16.0	26.0	51.5
Maize stalk	416.0	14.38	3.87	28.93	2340	1701.5	200.5	192.5	245.5

A.S. amino sugars, *GluN* glucosamine, *ManN* mannosamine, *GalN* galactosamine, *MurA* muramic acid

of the air-dried soil weight. The assembled microcosms were covered with perforated plastic lids (nine holes, each approximately 4 mm in diameter) to ensure air circulation while minimizing water loss, and incubated at 25°C to optimize microbial utilization of organic substrates. Soil moisture was maintained by weight with regular watering to a constant weight. Soils without added plant material were incubated in parallel to serve as controls. To stimulate microbial growth,  $\text{KH}_2\text{PO}_4$  (40 mg P  $\text{kg}^{-1}$  soil) was added into each pot at the start of the incubation, and  $(\text{NH}_4)_2\text{SO}_4$  (40 mg N  $\text{kg}^{-1}$  soil) was added at 1, 3, 6, 9, 12, and 15 weeks. Three replicates from each treatment were sampled after 0, 1, 3, 6, 9, 12, 15, 21, and 30 weeks of incubation. Samples were air-dried and milled to <0.25 mm before analysis.

### Chemical analysis

Total C and N content were determined for dry soils using a Vario EL C/N/S analyzer (Elementar, Germany). Measurement was based on combustion of dry sample material and quantitation of  $\text{CO}_2$  and  $\text{N}_2$  evolved using thermal conductivity detection. Total SOM was estimated from soil organic carbon (SOC) by multiplying by 1.724.

The four individual amino sugars (GluN, ManN, GalN, and MurA) were quantified using gas chromatography (GC) after conversion to aldonitrile acetates per the method of Zhang and Amelung (1996). Soil samples were hydrolyzed with 6 M HCl at 105°C for 8 h, followed by filtration and neutralization of the liquid phase. The supernatant was lyophilized, and the amino sugars were recovered from the residue by washing with methanol. Amino sugars were transformed into aldonitrile derivatives for analysis by GC (Agilent 6890A Tech, USA) equipped with an HP-5 (25 m×0.32 mm×0.25  $\mu\text{m}$ ) fused silica column and flame ionization detector. Amino sugars were quantified relative to the internal standard myo-inositol, which was added to the samples before purification. Recovery efficiency was monitored using the surrogate standard methyl-glucamine, which was added before derivatization. Total amino sugar content was calculated as the sum of the four individual amino sugars (Amelung 2001; Solomon et al. 2001).

### Statistical analysis

C/N ratios, total amino sugar concentrations, and ratios of individual amino sugars were compared across soil types (red soil, brown soil, and black soil) at each sampling time using a one-way analysis of variance (ANOVA). Treatment groups (soybean leaf or maize stalk) within each soil type were also compared using a one-way ANOVA. A post hoc separation of means by least significant difference (LSD)

was performed in cases where main effects were significant at  $P<0.05$ . A multiple-comparisons test was used to determine the significance of differences among C/N ratios, total amino sugar concentrations and amino sugar ratios sequentially, along with a post hoc separation of means by LSD ( $P<0.05$ ). Curvilinear regressions were used to model relationships between amino sugar to organic matter ratios and time, with coefficients of determination ( $r^2$ ) indicating goodness of fit. Statistical analyses were performed with the SPSS (SYSTAT Software) software for Windows, and regression analyses and figure preparations were accomplished using Microsoft Excel and Sigma Plot (SYSTAT Software).

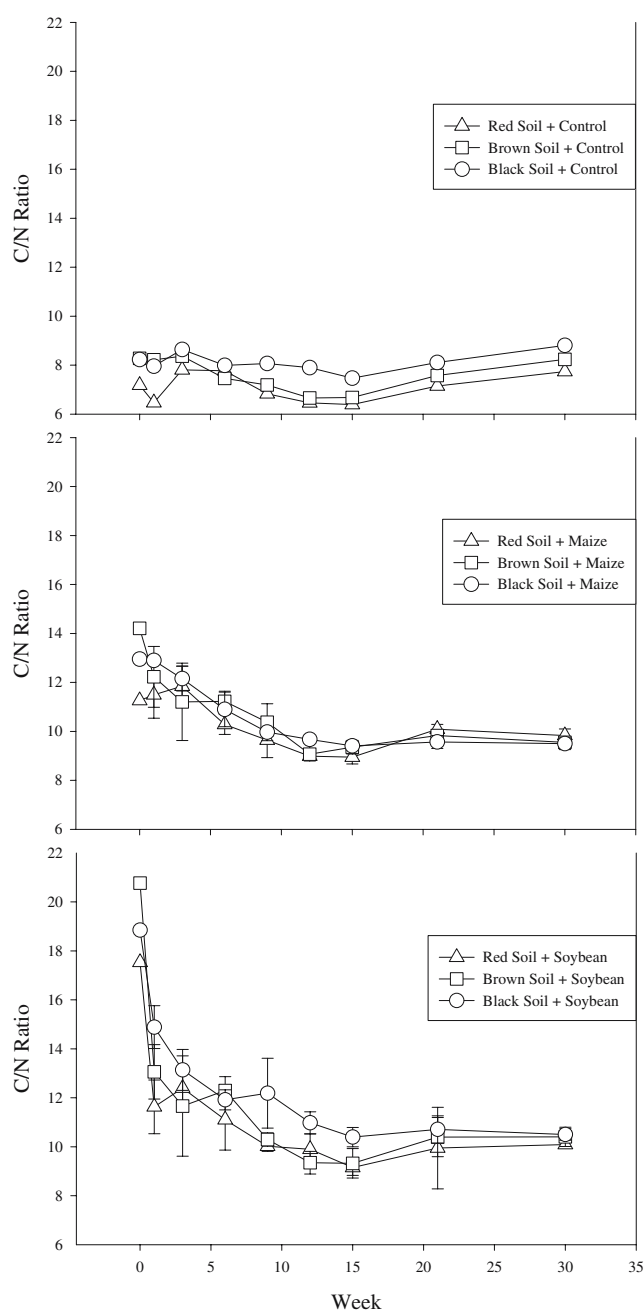
## Results and discussion

### Plant material mineralization and decomposition

Soil C/N ratios (Fig. 1) and organic C (data not shown, Liang 2003) decreased over time in microcosms amended with plant materials. These observations were potentially a consequence of microbial turnover of organic C. Relatively stable C and C/N ratios in unamended controls over time indicate the microbial community remained less active in the absence of added organic material.

Addition of soybean leaf or maize stalk to soil significantly influenced the organic C and C/N ratios. After a 30-week incubation, soils amended with soybean leaves or maize stalk, respectively, lost amounts of initial organic C equal to 40 or 14% for red soil, 46 or 27% for brown soil, and 37 or 20% for black soil. C/N ratios decreased over time in amended soils, especially in those to which soybean leaves were added (Fig. 1). As soybean leaves have a C/N ratio approximately twice that of maize stalk, but a similar C content to maize stalk (Table 2), it is reasonable to suppose that adding organic material of high C/N ratio increased competition for N within the microbial community at the early stage of incubation, thereby inducing the more rapid decline in C/N ratio observed in soybean-leaf-amended soil. C/N ratios of the amended soils gradually declined toward 10:1, the approximate C/N ratio of the unamended soils after the 30-week incubation. The slight increase in C/N ratio observed after 15 weeks probably resulted from cessation of inorganic N [ $(\text{NH}_4)_2\text{SO}_4$ ] inputs.

Our observations (C mass loss and C/N decline) suggest that some of the added plant material was mineralized during decomposition, and that some of it was either unaltered or incorporated into the soil microbial biomass. Previous studies suggest that substantial amounts of substrate C and N are assimilated into the living soil microbial biomass and subsequently stabilized in dead microbial residues, and that these nonliving residues represent a significant soil energy and nutrient reservoir (Gregorich



**Fig. 1** Changes in soil C/N ratios during incubation of soils amended with soybean leaf or maize stalk. Error bars represent the standard deviation of three replicates

et al. 1991; Joergensen et al. 1995). We concur that soil microbial amino sugars track the fate of organic materials in soils.

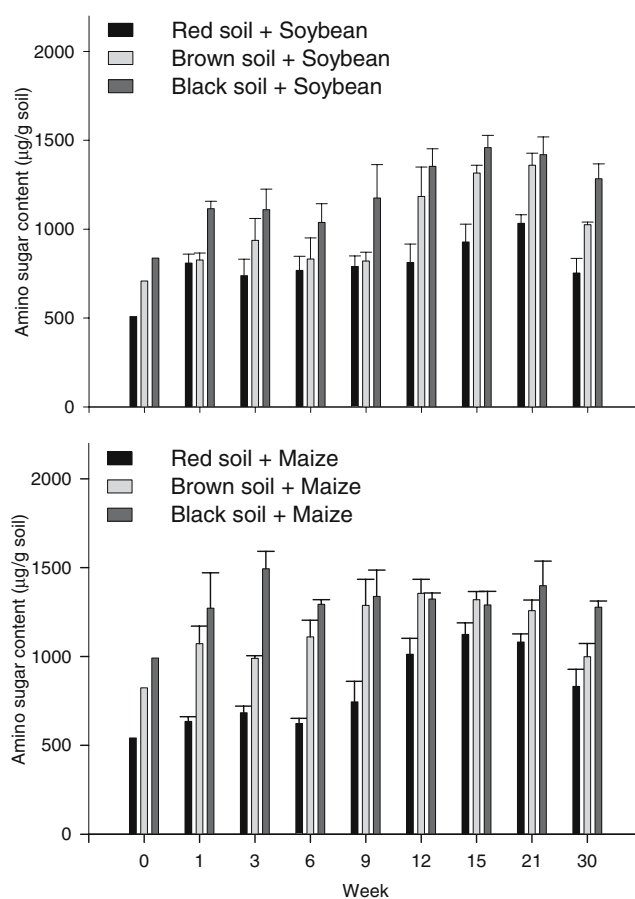
### Amino sugar content

Amino sugars have been previously used to identify the origins of different microbial residues (Sowden and Ivarson 1974; Parsons 1981; Glaser et al. 2004), and are relatively stable in soils due to formation of heterogeneous polymers,

which make them resistant to microbial metabolism (Bondietti et al. 1972). We hypothesized that changes in soil amino sugar content would occur when soil nutrient conditions were altered.

We quantified amino sugars based on soil weight to monitor amino sugar changes independently of changes in C, N, or soil type. Regardless of soil and plant amendment type, we found that the total soil amino sugar concentration initially increased but later decreased over the course of incubation (Fig. 2). As might be expected, amino sugars in soil incubations were in a state of concurrent production and degradation, with the total amino sugar content at any point in time defined by the relative rates of production and degradation.

In our study, total amino sugar content increased over approximately the first 15 weeks of the incubation in soybean-leaf-amended soils, and subsequently decreased. Total amino sugar content of soil amended with maize stalk peaked at an earlier time than it did for soybean-leaf-amended soil (Fig. 2). Differences in the magnitudes and rates of amino sugar accumulation and loss were attributed



**Fig. 2** Amino sugar content over time in soils amended with plant materials (soybean leaf or maize stalk). Error bars represent the standard deviation of three replicates

to differences in the properties of the two added organic materials. We propose that the rates of amino sugar production and degradation depended on microbial accessibility to C and N in the plant amendments. Soybean leaves had a C/N ratio far in excess of any soil microorganism, and soils amended with these leaves demonstrated a greater overall C loss during incubation. These soybean-leaf-amended soils with greater overall microbial substrate utilization also sustained net amino sugar production for a longer time period. In contrast, the net gain in amino sugars was overcome by degradation at an earlier time in soils amended with maize stalk. The decline in amino sugar content at later time supports the hypothesis of Schlegel (1992) that soil microorganisms preferentially decompose residues of their own cell walls when available nutrients and energy are limiting.

Amino sugar content of each of the three soils was different at each sampling time within a particular treatment group (soybean leaf or maize stalk) decreasing in the following order: black soil > brown soil > red soil (Fig. 2). Each amended soil exhibited unique variations in its amino sugar content over time. The time required for amino sugar content to approach its maximum value in maize-stalk-amended soils generally increased in the order: black soil < brown soil < red soil. This order also may have occurred in the soybean-leaf-amended soils, although the data were not clear (Fig. 2). Initial organic matter content of the soils significantly decreased in the order: black soil > brown soil > red soil (Table 1). Our data suggest that soils higher in organic C may be able to maintain relatively higher levels of amino sugars, and that organic C is a controlling factor in the temporal dynamics of amino sugars.

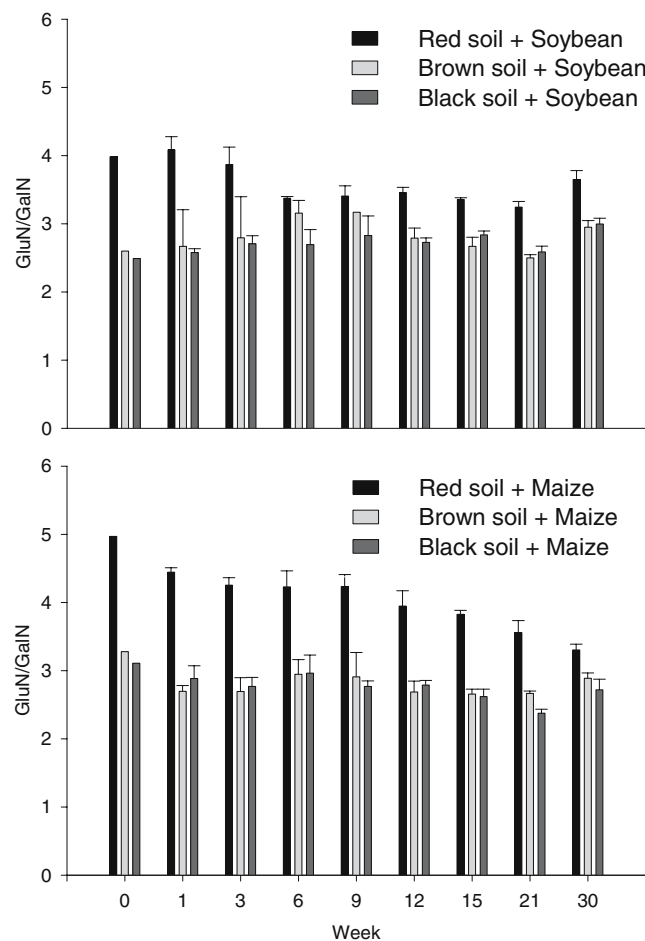
Exceptions to the reported trends in soil amino sugar content occurred at weeks 12 and 15 of the incubation with maize stalk, where the total amino sugar content of black soil appeared to be slightly less than that of brown soil, although the difference was not statistically significant. We rationalized these observations by noting that the rates of amino sugar degradation exceeded rates of amino sugar synthesis at different time points for different soils. Hence, in the case of black soil at 12 and 15 weeks, the rate of amino sugar degradation was relatively greater than the rate of amino sugar production, while the rate of amino sugar production still relatively dominated for the brown soil. After the transition from synthesis to degradation, the soil amino sugar content returned to the state: black soil > brown soil > red soil, and remained that way throughout the remainder of the incubation.

#### Amino sugar patterns and distributions

The ratio of GluN to GalN has been successfully used to track the relative contributions of fungi and bacteria to

SOM turnover and accumulation (Kögel and Bochter 1985; Zhang et al. 1998; Amelung et al. 1999; Solomon et al. 2001). The ratio of GluN to MurA has been used to track the fate of bacteria-derived amino sugars in temperate soils (Chantigny et al. 1997; Zhang et al. 1998; Solomon et al. 2001). In our study, we selected these commonly referenced ratios (GluN/GalN and GluN/MurA) to investigate how soil amino sugar patterns respond to added plant materials.

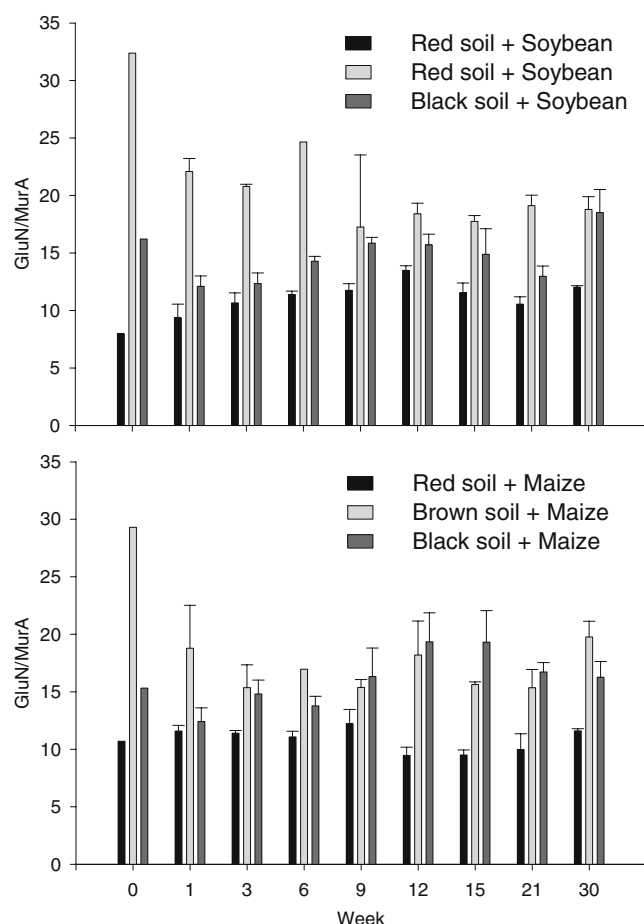
The ratio of GluN to GalN (Fig. 3) was significantly greater in red soil compared to brown soil and black soil, while no significant difference was found between brown soil and black soil. We hypothesize that the greater GluN/GalN ratio observed in red soil resulted from differences in microbial community composition at the time of sampling. Turrión et al. (2002) found pH to be the primary variable determining the relative representation of fungi and bacteria in soil. As red soil had the lowest pH among the three soils investigated (Table 1), and as low pH favors dominance of fungi over bacteria, the larger GluN/GalN ratio, which is characteristic of fungus-rich soils, was a reasonable observation. The higher GluN/GalN ratio further permitted



**Fig. 3** GluN/GalN ratios over time in soils amended with plant materials (soybean leaf or maize stalk). Error bars represent the standard deviation of three replicates

us to infer that there was a greater contribution by fungi to SOM cycling in red soil relative to brown or black soil. The GluN/GaN ratio significantly decreased as substrate decomposition proceeded in maize-stalk-amended red soil, but the ratio failed to show any regular temporal variations in brown or black soils, or any of our soils amended with soybean leaves. It is unclear whether the differences observed between the GluN/GaN trends in soils amended with maize stalk and those amended with soybean leaves were due entirely to substrate characteristics. It is also uncertain whether the shift from GaN to GluN reflected only differences in relative accumulation of bacterial residues to fungal residues in soils, or whether the shift also reflected the changes in the composition of living bacterial and fungal biomass. Impact of substrate on living microbial community composition is not completely understood and warrants further research.

The ratio of GluN to MurA (Fig. 4) in soils varied over time, and the patterns of variation differed considerably from those exhibited by the GluN to GaN ratio. Such an observation is not paradoxical, but rather supports the



**Fig. 4** GluN/MurA ratios over time in soils amended with plant materials (soybean leaf or maize stalk). Error bars represent the standard deviation of three replicates

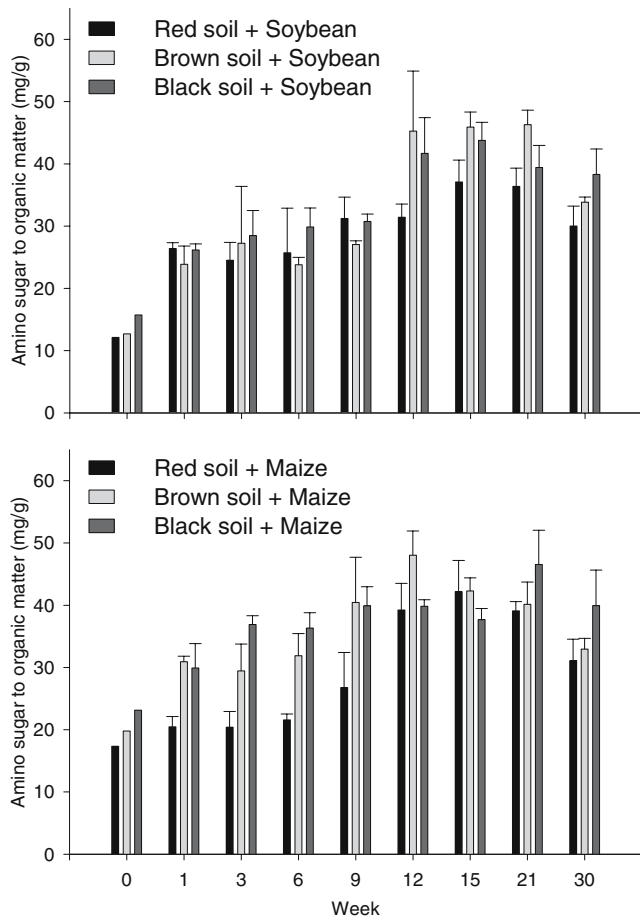
previous hypothesis that amino sugar compounds have unique turnover characteristics (Parsons 1982; Amelung 2001). Zhang et al. (1998) found that GluN/MurA ratios among four different soil particle-size fractions differed from corresponding ratios of GluN/GaN. In our study, the contrasting trends of the GluN/GaN ratio and GluN/MurA ratio show that the dynamics of GaN in soils are different from those of MurA. This observation further suggests that the ratios of GluN/GaN and GluN/MurA can provide distinct information when used to evaluate the relative fungal and bacterial contributions to the soil C and N pool. The use of the GluN/MurA ratio when describing younger soils (due to the relatively short residence time of MurA), and the GluN/GaN ratio when describing older soils is recommended (Zhang, personal communication). Before elucidating the mechanism of accumulation and turnover of GaN and MurA in soils, we recommend using both the GluN/GaN and GluN/MurA ratios as complementary markers to track the fate of the microbial residues.

#### Amino sugar to organic matter proportion

We used the proportion of amino sugars to SOM to describe the relative accumulation of amino sugars in SOM. During decomposition of soybean leaf or maize stalk, the proportion of amino sugars to SOM initially increased, reaching a maximum between 12 and 21 weeks (Fig. 5). The proportion subsequently decreased, but did not return to its initial value within the 30-week incubation.

Parabolic regression models were fitted to describe the relationship between the amino sugar proportion to SOM and the incubation time in each amended soil ( $R^2 > 0.78$ ,  $P < 0.01$ , data not shown, Liang 2003). To evaluate the effect of different plant materials on the amino sugar to SOM proportion, we pooled all replicates of the three soils according to amendment type (soybean leaf or maize stalk) (Fig. 6). Amino sugar to SOM proportion increased over approximately the first 19 weeks of incubation. This observation suggested a slower mineralization and/or faster synthesis of amino sugars relative to other organic constituents of SOM during the early stages of plant-derived organic material decomposition (i.e., amino sugars are more recalcitrant and have greater C sequestration capacity compared with other organic compounds at this stage). We observed a decrease in the amino sugar to SOM proportion at later stages of the incubation, probably as a consequence of increasing limitation of available nutrients.

Amino sugar accumulation was influenced by the type of plant material added to soil. Soils amended with maize stalk accumulated more amino sugars than soils amended with soybean leaves, especially in the first stage of incubation (Fig. 6). From the models, the maximum amino sugar to SOM proportion was reached at approximately 19 weeks in



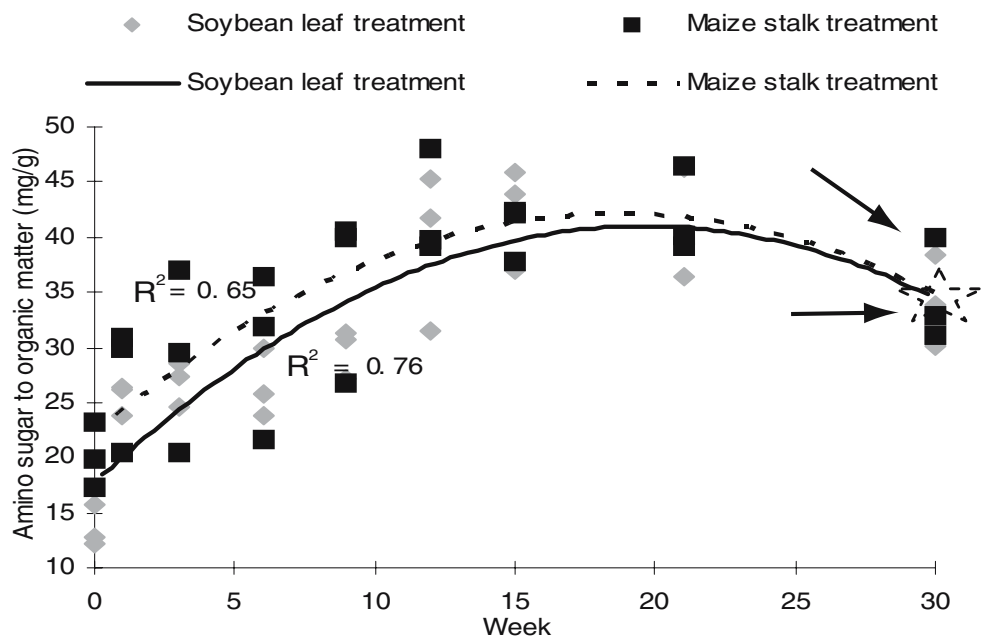
**Fig. 5** Amino sugar to organic matter proportions over time in soils amended with plant materials (soybean leaf or maize stalk). Error bars represent the standard deviation of three replicates

soil amended with maize stalk, and at approximately 20 weeks in soil amended with soybean leaves. We hypothesize this trend resulted from differences in nutritional composition of the amendments. Soils amended with soybean leaves, which have a higher C/N ratio, demonstrated a longer period of amino sugar accumulation.

The regression curves describing temporal changes in the amino sugar to SOM proportion of the two amendment groups appeared to converge (Fig. 6). The apparent convergence suggests that SOM is capable of maintaining a generally stable baseline level of amino sugars. Variation in the amino sugar to SOM proportions in real soils likely results from differences in soil matrix and microbial community characteristics. Provided sufficient time after a disturbance (e.g., a nutrient input) to the soil, we expect the amino sugar to SOM proportions will return to their initial levels.

Based on these observations, we propose to differentiate soil amino sugars into two pools: the Stable Pool (SP) and Transition Pool (TP). The SP consists of the steady state of amino sugar content in a soil (an intrinsic soil trait), which does not vary appreciably in response to changing conditions, while the TP does conditionally vary over time. We interpret the TP as a theoretical value representing the total possible amount of amino sugars attainable in soil regardless of the amount of amino sugars initially present, while many descriptions of the TP consider only the measurable labile fraction. In our interpretation, the SP and TP of amino sugars coexist in soils at steady state without external disturbance, and the capacity of the SP substantially exceeds that of the TP. The magnitude of the TP depends

**Fig. 6** Regression models describing changes in amino sugar to organic matter proportions over time in soil amended with soybean leaf or maize stalk in microcosms



on nutrient and organic C availability. Addition of plant materials rapidly augments the size of the TP, which subsequently diminishes toward the SP as substrates are decomposed. We argue that the TP consists of readily bioavailable amino sugars and hypothesize that its magnitude will approach zero as all labile components in a soil are exhausted. Our data and interpretation suggest that changes in amino sugars are mainly restricted in the TP, which is a component of the total available N transition pool in the soil.

## Conclusion

Our investigation showed that nutrient amount and composition of organic amendments influence the microbial accumulation of amino sugars in soils. Fungi and bacteria produce Kingdom-specific amino sugars, which contribute varying fractions of the total amino sugar content of a soil. The net synthesis of amino sugars in soils amended with plant materials can be easily supplanted by net degradation of amino sugars in soils of high organic content. Addition of plant materials can accelerate the accumulation of amino sugars in soils, and organic material with a higher C/N ratio appears to sustain the net amino sugar production period for a longer time. Response of the amino sugar to organic matter proportion to a perturbation suggests two kinds of amino sugar pools in soils: the SP and TP. Further research is needed to substantiate the existence and interpretation of these two pools.

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