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Soil-based cycling and differential uptake of amino acids by three species of strawberry (*Fragaria* spp.) plants

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ABSTRACT

Evidence is growing that amino acids can be an important source of plant N in nutrient limited natural ecosystems, but relatively little is known about the effect of agricultural management on soil amino acid pools and turnover. Organic management in particular relies on slow-release organic inputs as fertilizer, which could result in greater pools of soil amino acids available for plant uptake. Moreover, we know little about potential differences in amino acid uptake ability within plant families and whether this ability may have been lost during domestication. In order to determine the relative effects of soil type and management on amino acid turnover, we measured the effect of fine- versus coarse-textured soil and organic versus conventional management on free amino acids and proteolytic activity in the field. Secondly, we conducted greenhouse experiments to determine the ability of domestic and wild strawberry to utilize amino acid-N. Fine-textured and organically managed soils contained significantly higher total C and N than coarse-textured and conventionally managed soils. There were no significant differences in free amino acids or protease activity in relation to texture or management. Amino acid turnover was calculated at 0.7–1.5 h. Turnover time was significantly greater in fine-textured soils. Turnover time as a result of substrate additions was significantly shorter in coarse-textured soils; in fine-texturedsoils turnover time was shorter under conventional management. This suggests less competition for amino acids in soils with greater C, N and/or cation exchange capacity (CEC), such as fine-textured and organically managed soils. Two wild species of strawberry, *Fragaria virginiana* and *Fragaria chiloensis*, took up significantly more ^{14}C labeled glycine than the domesticated species, *Fragaria fragaria*. More research is needed to determine whether strawberry cultivars could be selected or bred for their ability to capture amino acid-N, thus improving N-use efficiency in farming systems relying on the breakdown of organic matter as a N source.

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1. Introduction

The question of whether plants can utilize organic nitrogen was asked as early as 1935 (Virtanen and Linkola, 1946). Methodology at the time was not sufficiently developed to determine whether all organic molecules were first mineralized before nutrient uptake. Recent research, however, has shown that many plants do have transporters for the uptake of organic forms of nitrogen, particularly amino acids (Soldal and Nissen, 1978; Jones and Darrah, 1994). In addition, plant uptake of organic nitrogen can be quite important to total plant production in nutrient limited systems such as the arctic tundra (Lipson and Näsholm, 2001). The significance of these findings to agriculture is controversial since agriculture uses great inputs of inorganic N and contains only small pools of free amino acids in the soil solution (Owen and Jones, 2001; Jones et al., 2005a).

Since organic and low-input agriculture rely primarily on green manures and/or composts and animal manures to meet crop N demands, amino acid-N may be present in greater supply in these systems. There is currently little published research on available pools and amino acid cycling in these systems. Relying on N mineralization from organic inputs can limit plant uptake and growth, especially at times of peak crop demand or in cool or dry soil conditions where mineralization is limited. Even small contributions of organic N to total N uptake at critical periods could improve yields in these systems. Moreover, crop varieties developed under high soluble N conditions could have inadvertently selected against the ability to use organic N. Murphy et al. (2007)

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showed that wheat cultivars selected under organic management perform better in organic systems, and cultivars selected under conventional management perform better in conventional systems. Selecting varieties with the ability to utilize a significant portion of their N as amino acid-N could be important when developing crops suited to organic and low-input systems.

The goal of this research was to compare amino acid pools and turnover in organic and conventionally managed strawberry fields and to determine amino acid uptake ability in two wild species and a domestic variety of strawberry. We tested the following hypotheses: (1) fine-textured and organically managed soils have higher concentrations of amino acids present in the soil solution than coarse-textured and conventionally managed soils; (2) amino acid turnover is slower in fine-textured and organically managed soils; and (3) wild species of strawberry take up more organic N than domestic varieties.

2. Materials and methods

2.1. Soil sampling and analyses

Soil was sampled in April 2005 at 0–10 cm from eight paired organic and conventional strawberry fields in the area of Watsonville, CA. Paired fields were carefully selected for the same soil type, strawberry variety, and all other environmental conditions except management, according to the method described by Reganold (1988). Surface soil texture of each field pair was either loamy sand or sandy loam (referred to as coarse-textured) or silty clay loam (referred to as fine-textured). Each sample consisted of 10–15 random subsamples, thoroughly homogenized. Soils were shipped on ice by overnight mail and analysis proceeded immediately on soils stored at 4 °C until completion 15 days later.

The following tests used methods by Gavlak et al. (2003): soil texture (method S14.10); nitrate-N (method S3.30); and ammonium-N (method S3.50). Additional soil parameters were analyzed as follows: total C and N were measured by combustion using a Leco CNS 2000. Protease enzyme activities were measured in 1 g dry weight soil using casein as protein substrate for potential protease activity and no added substrate for native protease activity (Ladd and Butler, 1972). Samples were measured on a Perkin Elmer Lambda 2 UV/VIS spectrometer at 700 nm with tyrosine standards. Amino acids were extracted from 1 g dry weight soil in a 1:5 w/v ratio with either water or a weak organic acid solution of 0.1 M malic acid and 0.1 M acetic acid. Samples were shaken for 30 min, centrifuged, filtered through 0.2 μm nitrocellulose paper and frozen until amino acid quantification with a Hitachi F-3010 fluorometer using the OPAME procedure with mercapto-propionate (Jones et al., 2002). Amino acid turnover was calculated by dividing the pool of free amino acids in the soil (as extracted in water) by the flux (native protease activity) of amino acids (Schlesinger, 1997; Berthrong and Finzi, 2006). Turnover as a result of substrate addition was determined by dividing the pool by the potential flux (potential protease activity). Potential nitrification was measured as described by Schmidt and Belser (1994) using 10 g moist weight soil. Nitrate-N after 10 days incubation was measured on a Latchett QuickCHem FIA+8000 series autoanalyzer, using the NH_4Cl_2 and salicylate methods. All laboratory measurements were carried out in triplicate per field and averaged for statistical analysis.

2.2. Amino acid uptake

Coarse-textured soils sampled from both organic and conventionally managed fields described above were pooled and utilized for greenhouse experiments. Bulk density and water holding capacity of the soil were measured by filling 50 mL plastic test tubes (11.5 × 3.0 tapering to 0.5 cm) with 78 g dry soil and adding water slowly until water dripped out (20.75 mL); total dry weight divided by 50 mL is bulk density and weight of water held divided by weight of dry soil is water holding capacity. Three strawberry species *Fragaria chiloensis*, *Fragaria virginiana*, and *Fragaria fragaria* (cultivar: Tribute) were used in this study. The two wild species, *Fragaria chiloensis* and *F. virginiana*, were obtained from Plants of the Wild (Tekoa, WA) and the domestic species, *F. fragaria*, was obtained from the WSU Organic Farm. Strawberry plants were maintained in the greenhouse until ample runners were produced. Runners were selected from each of the mother plants and rooted in tubes in a humidity chamber in a greenhouse under natural light. Plants were watered as needed with a 100 μg L^{-1} solution of Peter's 20-20-20 NPK Fertilizer (3.94% N as NH_4^+, 6.05% N as NO_3^-, 10.01% N as urea) plus 2 μg L^{-1} STEM trace elements + Fe (Scotts-Sierra Horticultural Products Co, Marysville, OH). Plants were used in two laboratory experiments at approximately 3 weeks as described below.

2.2.1. Experiment 1

Using intact plants in growth tubes, the surface of the tubes was sealed with melted paraffin wax and 3 mL ^{14}C labeled glycine solution injected through the wax in the following dilutions: 33.3, 16.5, 10.0 and 3.0 mM, which equaled 5.0, 2.5, 1.5, and 0.5 mM in soil solution or 18.0, 9.0, 5.4, and 1.6 μg glycine-N g^{-1} soil. Three milliliters of H_2O was injected into control tubes. The holes were then plugged with more wax and tubes placed in an open fume hood under grow lights (25 μmol m^{-2} s^{-1}) at room temperature, in a completely randomized design with five replicates. After 24 h, shoots were removed into individual test tubes and dried at 60 °C. Roots were removed from the soil, washed twice in 0.02 mM $CaCl_2$ solution using a brush to remove soil particles, and finally sprayed with fresh 0.02 mM $CaCl_2$. Roots were placed in individual test tubes and dried as above. Dried samples were weighed before combustion in a Biological Oxidizer OX700 and ^{14}C measured using a Perkin Elmer liquid scintillation analyzer Tri-Carb 2900 TR. Background ^{14}C levels present in the controls were subtracted from treatment values and uptake of glycine calculated as μg glycine g^{-1} of root or shoot material.

2.2.2. Experiment 2

Tubes containing growing plants were sealed as above and injected with 3 mL ^{14}C labeled 10 mM glycine, 5 mM ^{15}N labeled $(NH_4)_2(SO)_2$ or 10 mM ^{15}N labeled KNO_3 with seven replicates per treatment. Each treatment contained equimolar amounts of all three constituents with one constituent labeled in each treatment. Final soil concentrations of glycine, $(NH_4)_2(SO)_2$ and KNO_3 equaled 1.5, 0.75 and 1.5 mM, respectively, or 5.4 μg N g^{-1} soil. Control plants received 3 mL H_2O only. After 24 h, the experiment was terminated and samples processed as above. After drying, samples were placed inside tin foil capsules and total N and ^{15}N determined on a Thermo Finnigan Delta Plus Advantage mass spectrometer.

2.3. Statistical analysis

Differences and similarities in soil parameters between treatment and soil type were tested using a split-plot incomplete block experimental design with whole plot as soil type and subplot as management. Experiment 1 was analyzed using the test for heterogeneity of slopes (Little et al., 1993). Experiment 2 was analyzed as a completely randomized design (CRD) with a two-way treatment structure (treatment and species). Shoot and root data were analyzed separately. All statistics were analyzed using the SAS system for Windows version 9.1 ANOVA and LSmeans (SAS Institute, Cary, NC). Data were checked for model assumptions and transformed as necessary using the natural log. Data for amino acid uptake did not meet model assumptions so that a non-parametric ranked ANOVA was used for data analysis. When data were

Table 1
Means ($n = 8$) for soil (0–10 cm depth) analyses

Soil property	Coarse-textured soil	Fine-textured soil	Organic soil	Conventional soil
Total carbon (g kg^{-1})	7.18	14.8***	12.8*	9.19
Total nitrogen (g kg^{-1})	0.64	1.25**	1.01**	0.79
C:N ratio	11.6	11.8	11.4	11.9
Nitrate (mg kg^{-1})	24.3	26.0	30.1	20.2
Ammonium (mg kg^{-1})	1.33	2.17	1.27	2.23
Protease potential (μg amino acid-N g^{-1} soil h^{-1})	5.74*	2.93	4.92	3.75
Protease native (μg amino acid-N g^{-1} soil h^{-1})	1.32**	0.567	0.940	0.948
Free amino acids water extracted (μg amino acid-N g^{-1} soil)	0.543	0.683	0.687	0.538
Free amino acids weak acid extracted (μg amino acid-N g^{-1} soil)	0.624	0.686	0.746	0.564
Amino acid turnover time (h)	0.711	1.45*	1.35	0.818
Total mineralizable nitrogen (μg N g^{-1} soil)	1.34	0.945	1.13	1.15
Sand (g 100 g^{-1})	71.1****	18.9	45.3	44.7
Clay (g 100 g^{-1})	5.87	28.8***	17.4	17.3
Silt (g 100 g^{-1})	23.0	52.3**	37.3	38.0
Cation exchange capacity (cmol (+) kg^{-1})	7.35	27.4***	18.4	16.4

Means are significant at *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, and ****$P < 0.0001$.

transformed, LSmeans and standard errors are reported in original units. P values are significant at <0.05 unless otherwise stated. Pearson correlation coefficients were conducted using the SAS system for Windows version 9.1 ANOVA (SAS Institute, Cary, NC).

3. Results

3.1. Amino acid turnover

Fine-textured soils contained significantly greater total C and N and supported significantly greater native and potential protease activity than coarse-textured soils (Tables 1 and 2). There were no significant differences in C:N ratio, NO_3^-, NH_4^+ or total mineralizable N. Organically managed soils contained significantly higher total C and N than conventionally managed soils, but there were no significant differences in C:N ratio, NO_3^-, NH_4^+, free amino acids, protease activity or total mineralizable N. Amino acid turnover ranged from 0.7 to 1.5 h across treatments and soil textural groups; turnover time was significantly greater in fine-textured soils than in coarse-textured soils. Turnover time in the conventional soils was 39% shorter, although this difference was not significant. Amino acid turnover time was correlated with total N ($r = 0.56$, $P < 0.05$), CEC ($r = 0.50$, $P < 0.05$) and weakly correlated with total C ($r = 0.49$, $P = 0.055$).

Potential turnover time with substrate was shorter in coarse-textured soils. Within fine-textured soils, conventionally managed soils had shorter potential turnover times than organically managed soils.

3.2. Plant amino acid uptake

3.2.1. Experiment 1

Fragaria virginiana, *F. chiloensis* and *F. fragaria* all took up ^{14}C labeled glycine within 24 h when grown in non-sterile soil (Fig. 1). Total uptake into roots and transport into shoots increased with greater available concentrations of amino acid for the two wild relatives *F. virginiana* and *F. chiloensis*. The species had significantly different levels of glycine in both roots ($P < 0.001$) and shoots ($P < 0.0001$); however, there was no significant difference in uptake or transport proportion (slopes) among the species.

Table 2
LSmeans ($n = 8$) showing the interaction between soil type and treatment for potential amino acid turnover time (h) at 0–10 cm depth

Interaction effects	Organic soil	Conventional soil
Coarse-textured soil	0.400	0.460
Fine-textured soil	1.17*,***	0.741**

Means are significant at *$P < 0.05$ within soil type and between treatments; **$P < 0.05$ within treatment and between soil type; ***$P < 0.001$ within treatment and between soil type.

3.2.2. Experiment 2

Both wild species took up significantly more glycine-N and NH_4^+-N than the domestic *F. fragaria* (Fig. 2). *F. virginiana* took up significantly less NO_3^--N than either *F. chiloensis* or *F. fragaria*. *F. chiloensis* and *F. fragaria* both took up similar amounts of N as NO_3^- and NH_4^+, while *F. virginiana* took up significantly less NO_3^--N than NH_4^+-N. Both *F. chiloensis* and *F. fragaria* took up significantly more NO_3^--N and NH_4^+-N than glycine-N, while *F. virginiana* took up

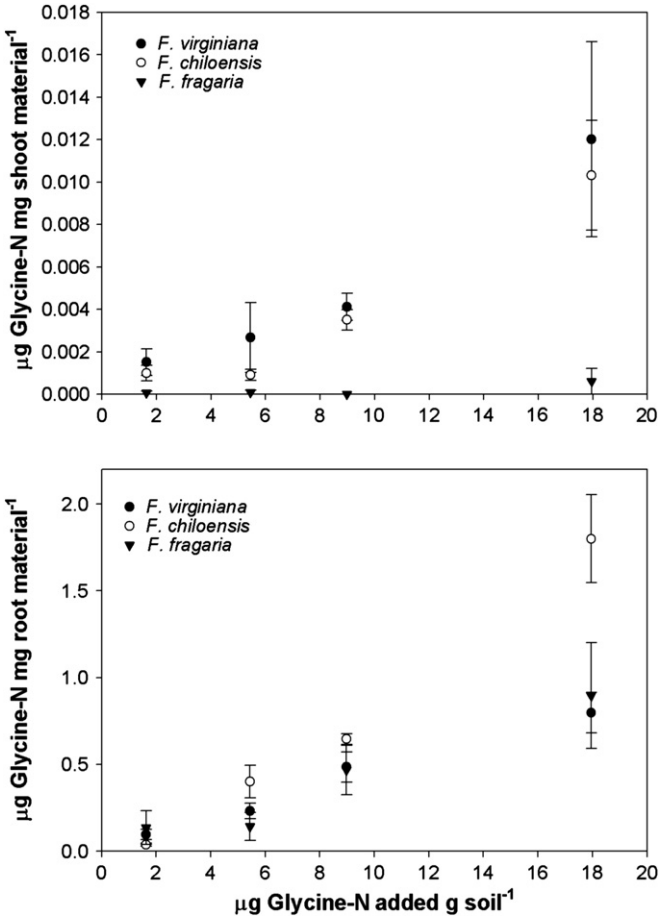

Fig. 1. Glycine concentration in roots and shoots of three strawberry species after 24 h in soil with ^{14}C-glycine at a range of concentrations.

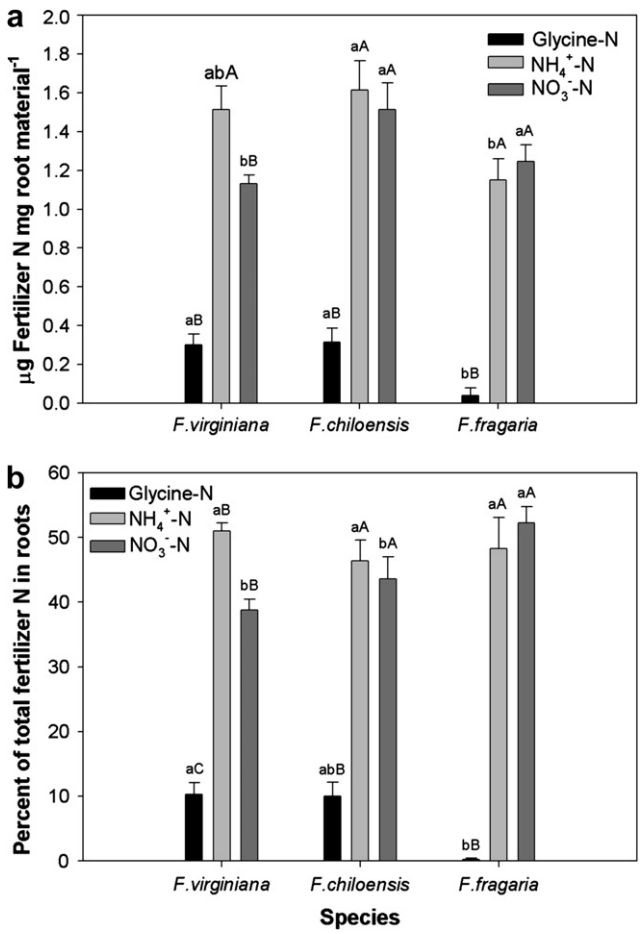

Fig. 2. Glycine, ammonium and nitrate-N uptake by three strawberry species (a) and glycine, ammonium and nitrate-N uptake as percentage of total fertilizer N uptake (b). Significant differences are designated by different letters: lower case for between species differences and upper case for within species differences.

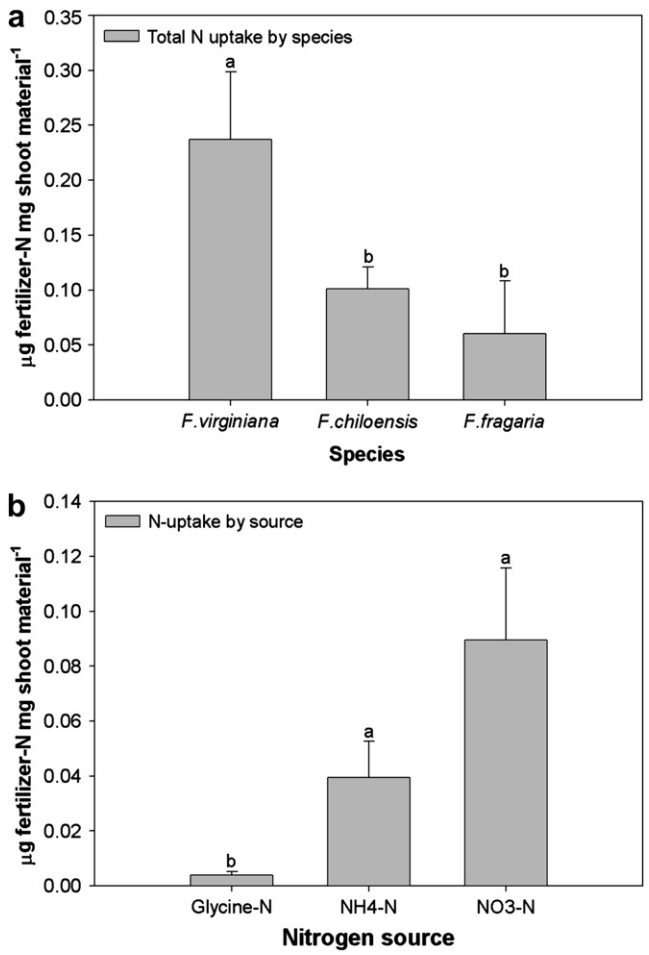

Fig. 3. Fertilizer N translocation to shoots over 24 h by three strawberry species (a) and relative translocation of glycine, ammonium and nitrate-N to shoots by three strawberry species (b) over 24 h. Significant differences are designated by different letters.

similar levels of N as glycine and NO_3^- (Fig. 2). In *F. virginiana* the large non-significant difference between NH_4^+-N and glycine-N uptake is attributed to the fact that the statistics were calculated on ranked means while raw data and associated standard errors are presented in the graph.

Glycine-N constituted 10% of total fertilizer N uptake in 24 h in both *F. chiloensis* and *F. virginiana*, but only 0.2% of N in *F. fragaria* roots (Fig. 2). These differences were significant between *F. virginiana* and *F. fragaria* but not ($P = 0.056$) between *F. chiloensis* and *F. fragaria*. This again is attributed to the non-normality of the data which had to be ranked, shifting the ranked means on which the statistics were run away from the raw means presented in the graph. Transport to shoots was affected by treatment by species interactions (Fig. 3). Significantly more labeled glycine was detected in the shoots of the wild species compared to the domestic species (Fig. 3), whereas significantly more NO_3^--N and NH_4^+-N than glycine was translocated to shoots of all species (Fig. 3). Total plant uptake of labeled glycine-N, NH_4^+-N and NO_3^--N in 24 h was 1, 8 and 6% of the total available amount, respectively.

4. Discussion

4.1. Amino acid turnover

While a growing body of literature has focused on the amino acid uptake ability of plants, less research has measured the dynamics of amino acid cycling in soils (Kielland et al., 2007), particularly agricultural soils. Contrary to Scheller and Raupp (2005), we found no significant differences in soil amino acid pools as a result of organic management, despite significantly higher total C and N in organically managed soils. Use of a stronger HCl based extractant by these authors could explain this discrepancy. We used water extractions and a weak acetic/malic acid solution to simulate plant produced acids in the rhizosphere (Curl and Truelove, 1986).

The estimated time of amino acid turnover in this study was within the range reported in a number of recent studies (Jones, 1999; Jones and Hodge, 1999; Jones et al., 2005a). The greater turnover time, or slower rate of turnover, in fine-textured soils, suggests less competition for amino acids in soils with higher C and N content and/or cation exchange capacity (from higher C and clay contents). Differences between management type in potential turnover time were dependent on soil type. Potential turnover time was significantly less in conventionally managed fine-textured soils only, while there was no difference between managements on coarse-textured soils. Jones (1999) and Jones et al. (2005b) showed no difference in amino acid turnover due to management history and concluded that soil type and microbial activity were the major drivers of amino acid availability; however, they did not include long-term organically managed soils with greater organic C and N contents in their study. While we also found soil type exerting a stronger influence on amino acid dynamics, our data suggest that the practice of adding large amounts of organic matter to the soil, as in organic agriculture, may also influence amino acid turnover times in fine-textured soils.

Our findings of slower turnover times in fine-textured soils and a similar trend in organically managed soils are contrary to much of the literature, where turnover has been shown to be higher in systems containing larger amounts of organic matter and a higher microbial biomass (Jones, 1999; Berthrong and Finzi, 2006; Kielland et al., 2007). These studies, however, were conducted in natural ecosystems. In contrast our system was highly disturbed in terms of intensive tillage and mounding of the soil, use of plastic mulch, and, in the case of the conventional soils, methyl bromide fumigation. Unlike many natural soils, our soils were also highly substrate limited as demonstrated by the response to added casein.

Jones et al. (2004, 2005b) found evidence that amino acid turnover may be slower in N limited soils. Although our data do not strongly support this hypothesis, organically managed soils are frequently N limited as opposed to conventionally managed soils. While we showed higher total N in fine-textured and organically managed soils, N mineralization over 10 days was similar indicating these soils might have undergone initial N immobilization or that the organic N present was recalcitrant. In addition, many authors have shown soil amino acid pools to be strongly controlled by CEC (Lipson and Näsholm, 2001). Both fine-textured soils and soils amended with organic matter show higher CEC. It is a strong possibility that immobilization of amino acids onto soil exchange sites would reduce their availability to microorganisms, thus slowing turnover under these conditions.

An assumption implicit in calculating amino acid turnover based on measurements of protease activity is that the substrate used adequately represents the proteins present in the soil. Some soil proteins may in fact break down more quickly or more slowly than added casein. However, we would expect relative rates of casein breakdown between soil type and treatments to be similar. We would therefore expect the relative differences to hold true for real soil conditions even if absolute rates differed in the field. Future research is needed to compare amino acid turnover using protease activity with amino acid measured with labeled tracers in order to gain insight into how this method relates to turnover measured directly under field conditions.

More research is warranted to confirm that greater amino acid turnover times occur in organically managed soils and whether this is associated with higher total C, N and/or CEC. If confirmed, greater amino acid turnover times in organically managed soils could indicate less microbial competition and improved plant availability of amino acid-N. This could be of benefit to organic farmers provided efficient crop cultivars in terms of amino acid-N acquisition are grown. More research is also needed to determine the role of available C and N in amino acid turnover. Although research on soil amino acid turnover is still limited, it is now acknowledged that protease activity is the limiting step in the production of amino acids in soil (Lipson and Näsholm, 2001; Kielland et al., 2007). However, the limiting constraints on protease activity – whether it is limited by protein availability in soil (Lipson et al., 1999), stimulated by nitrogen deficiency (Smith et al., 1989; Weintraub and Schimel, 2005), inhibited by N deficiency (Jones et al., 2004, 2005b) or controlled by soil pH (Kielland et al., 2007) – remain unclear.

Fine-textured and organically managed soils had significantly higher total C and N, coarse-textured soils had greater potential protease activity, but there were no differences in soil pH, C:N ratio or mineralizable N. This suggests that protease activity in these soils was limited by substrate and not affected by pH, mineral nitrogen or the C:N ratio of the soil. A different potential turnover time in organically and conventionally managed fine-textured soils after substrate addition also supports this conclusion. Amino acid turnover time was significantly shorter as a result of substrate addition in conventionally managed fine-textured soils than in organically managed fine-textured soils. Hence, conventionally managed fine-textured soils may have been more substrate limited than organically managed fine-textured soils.

4.2. Plant amino acid uptake

Given the potential for different pool sizes and turnover times of amino acids in different soils and management systems, the ability of crop plants to take up amino acid-N from the soil in significant amounts needs to be determined. Jones et al. (2005c) showed maize had the ability to capture increasing amounts of amino acid-N with increasing soil concentrations and our work has found similar results for wheat (unpublished data). Our results with strawberry show that the cultivar Tribute only captured a small portion of N in amino acid form. Our results show a large difference in the ability of Tribute and two wild strawberry relatives to take up amino acid-N. Although more research is needed to confirm this in a larger number of wild and domestic strawberry cultivars, these results support the hypothesis that domesticating strawberry may have inadvertently selected against the ability to efficiently utilize organic N. We are unaware of any other publications that have measured amino acid uptake by strawberry or that have specifically addressed the effects of domestication on organic N-use ability. While the pool dilution of added amino acids by native soil nutrients could not be calculated in this study, qualitative comparisons are considered useful (Jones et al., 2005a). Few studies have measured amino acid-N uptake concurrently with NH_4^+-N and NO_3^--N. Our result showing that amino acid-N uptake constituted 10% of total fertilizer N uptake in wild strawberry is comparable to the 10–18% of total N uptake measured in *Artemisia*, *Acomastylis* and *Carex* spp. in a subalpine meadow (Miller et al., 2007).

More research is needed in order to determine the variability in amino acid-N uptake among domestic strawberry cultivars. It is likely that there may be considerable variation in N-use efficiency between strawberry cultivars (Brent Black, personal communication). Bull et al. (2005) showed that high yielding strawberry cultivars grown under organic management were not the same cultivars typically grown in conventional production. Moreover, they found a highly significant correlation between yield and tissue N. Whether there is a correlation between N-use efficiency and organic N uptake in strawberry is not known. Should this turn out to be the case, selecting or breeding strawberries for organic N uptake could be warranted in order to provide cultivars especially adapted to organically managed conditions.

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