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Soil microbial community structure and diversity in a turfgrass chronosequence: Land-use change versus turfgrass management

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Abstract

A diverse soil microbial community is an important measure of sustainable land use. Turfgrasses are usually managed as a monostand, which may result in reduced soil microbial diversity. However, there is little information on the structure and diversity of soil microorganisms in managed turfgrass systems. We examined the soil microbial community in a turfgrass chronosequence (i.e., 1, 6, 23 and 95 years), established from native pines, to address (1) the degree to which microbial diversity is achieved and maintained in turfgrass soils and (2) the relative importance of turfgrass management versus land-use change (i.e., native pines to turfgrass) in structuring the soil microbial community. Soil microbial communities were fingerprinted using phospholipid fatty acid (PLFA) composition, and also by the pattern of sole C source utilization (i.e., community-level physiological profiles, CLPP). The relative diversities of soil microbial communities as a function of land use and turfgrass ages were compared using the Shannon index. Multivariate analysis was used to detail variations in soil microbial communities. Despite the differences in land use and turfgrass age, microbial biodiversity was generally similar for the various soils, with the exception that diversity was lower in soils taken from 5 to 15 cm depth of the two youngest turfgrass systems. This reduction was correlated with low soil C, and suggests that soil organic matter (OM) is a primary determinant of microbial community diversity. Both CLPP- and PLFA-based principal component analyses (PCA) revealed distinct groupings of soil microbial communities based on land use but not on turfgrass age. There was a preferential use of phenolic compounds and carboxylic acids by the microbial community in native pine soils, whereas carbohydrates were the preferred C source for microbial communities in turfgrass soils. This difference in catabolic function was mirrored by a compositional change of phospholipid fatty acids. Cluster analysis of community structure indicated that microbial communities in older turfgrass systems (23 and 95 years old) diverged from younger systems (1 and 6 years old), implying some effect of management on composition and structure of the soil microbial community. Our study concludes that a diverse soil microbial community was achieved and maintained in turfgrass systems, and that shifts in soil microbial community structure were attributed primarily to the change of land use rather than the length of turfgrass management.

Keywords: Microbial community; Phospholipid fatty acids (PLFA); Community-level physiological profiles (CLPP); Land-use change; Pines; Turfgrass

1. Introduction

Turfgrasses, including golf courses, parks, and home lawns, cover 14% of the cropland in the USA and provide recreational and environmental benefits (Beard and Green, 1994; Qian and Follett, 2002). However, there is a widespread concern that the environmental

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sustainability of turfgrass systems is limited due to intensive use of fertilizers, pesticides, and irrigation. Soil microbial community structure is a sensitive indicator of sustainable land use, but one that has not been evaluated in turfgrass systems. Because most turfgrasses are grown as a monostand, and receive considerable chemical inputs, it is conceivable that soil microbial diversity would be reduced compared to native ecosystems or polystands.

Managed ecosystems may have less diverse microbial communities compared to their natural counterparts (Torsvik et al., 2002). In cultivated soils, the decline in soil microbial diversity is probably related to reductions in soil organic C (Degens et al., 2000). Unlike most other crops, turfgrass systems are not harvested or cultivated, at least in the traditional sense. The leaf canopy grows continuously, and mowed clippings are usually left on site to decompose, contributing to soil OM. Depending on the age of the turf and the environment, soil OM can reach relatively high concentrations under turfgrasses (i.e., >20 g C kg^{-1} soil) (Shi et al., 2006).

Management practices may alter the composition and structure of soil microbial communities. This has been documented in agricultural soils and managed grasslands by examining either whole soil microbial communities or specific functional groups, such as ammonia oxidizers (Ka et al., 1995; Lundquist et al., 1999; Webster et al., 2002; Clegg et al., 2003). Donnison et al. (2000) reported that intense management created a shift in soil microbial community composition and structure, highlighting their sensitivity to change.

Land-use changes often alter plant species and associated soil properties, which can affect the soil microbial community composition and structure (Nüsslein and Tiedje, 1999). Plants are an important determinant of soil microbial communities (Grayston et al., 1998, 2001; Nüsslein and Tiedje, 1999; O'Donnell et al., 2001). However, management may have a greater effect than plant species on soil microbial community structure. For example, Buckley and Schmidt (2001) found that soil tillage and chemical use, compared to plant species, was the primary factor affecting soil microbial community composition and structure. Bossio et al. (1998) reported that soil type was predominant in structuring soil microbial community compared to factors such as seasonal change, specific farming operation, management system, and spatial variation. Similarly, Girvan et al. (2003) singled out soil type as the dominant factor for changing soil microbial community structure in arable soils. Turfgrass establishment at a new site involves considerable disturbance to the existing ecosystem, and subsequent management results in accretion of soil organic C and N. One might thus postulate that the soil microbial community composition and structure would respond to both the land-use change and the duration of subsequent turfgrass management. It is unknown which factor is the greater determinant of microbial communities in turfgrass soils.

We chose as the study site a chronosequence of turfgrass systems (four golf courses) from the Sandhills region of central North Carolina. All sites were constructed in defined areas cleared from native pine forests. Pine trees were left standing between the fairways, such that each golf course consisted of islands of managed grassland surrounded by non-managed buffers of native trees. The four sites were in very close proximity, with nearly identical soils, turfgrass species, and climate conditions. Thus, we could ascribe differences between sites as being primarily due either to the land change from pines to turf, or to the age of the turfgrass system.

Our previous work (Shi et al., 2006) showed that microbial metabolic efficiency increased with turfgrass system age. We hypothesized this increase was associated with a change in soil microbial community structure and/or diversity. In the present study, we determined community structure of soil microbial communities using PLFA and CLPP along a chronosequence of managed turfgrass systems. Our objectives were to (1) evaluate the establishment and maintenance of a diverse soil microbial community in long-term managed turfgrass systems and (2) assess the relative importance of turfgrass management versus land-use change in structuring soil microbial communities.

2. Materials and methods

2.1. Site description and soil sampling

Four golf courses were selected as study sites. Each was in or near the Pinehurst Resort and Country Club, located in the Sandhills region of North Carolina. The courses were established in 1907, 1979, 1996, and 2001 and were 95, 23, 6, and 1 years old, respectively when soil samples were taken. They were in close proximity and had similar or identical soils (sand or loamy sand). Each golf course was permanently planted to hybrid bermudagrass (*Cynodon dactylon* × *transvaalensis*), a warm-season perennial. They were overseeded in the fall with perennial ryegrass (*Lolium perenne* L.) to provide a temporary green canopy during the period of bermudagrass dormancy. The surrounding vegetation

was primarily native longleaf pines (*Pinus palustris* Miller). Turfgrass sites received split applications of N averaging approximately 150 kg N ha^{-1} y^{-1}, except that the oldest course likely received lower amounts of N per year during the first half of the 20th century. Inorganic and synthetic organic sources have been the most common N fertilizers during the past 50 years. Turfgrass sites were also fertilized with phosphorus (P) and potassium (K), and limed to maintain soil pH of ~6.5. Additional standard golf course management included mowing, irrigation, and chemical pest control. By contrast, the adjacent pines were essentially unmanaged, i.e., no fertilization, pesticide use, irrigation, or harvest. Detailed site description is given in our previous work (Shi et al., 2006).

Soils were sampled from six individual fairways selected at random within each golf course in December 2002. Four cores (5 cm diameter × 15 cm length) were taken from each fairway. Soil cores were obtained in an identical manner from the native pine "buffers" to assess the variability between sites independent of the golf course development, and as a comparison for the highly managed turfgrass system. The 24 cores were assembled into four replications; consisting of one core from each of six fairways per golf course. Intact soil cores were placed on ice and transported to the lab. The cores were then sectioned into 0–5 and 5–15 cm depths. Soil from each section was sieved (<4 mm). After removing visible plant litter and roots, a part of soil was immediately freeze-dried for PLFA analysis, and the rest was stored at 4 °C for later analysis of chemical and microbiological properties (i.e., ~1 month after sampling). Selected soil chemical and microbiological properties are given in Table 1 (see Shi et al., 2006 for detailed analyses).

2.2. Community-level physiological profiles (CLPP)

Sole C source utilization tests were performed as previously described by Yao et al. (2000). Briefly, fresh soil (10 g) was added to 100 ml of distilled water in a 250 ml flask and shaken on a wrist action shaker at 250 rpm for 10 min. Ten-fold serial dilutions were made and the 10^{-3} dilution was used to inoculate Biolog ECO plates. Plates were incubated at 25 °C for 7 days, color development was measured as absorbance daily using an automated plate reader at 590 nm, and the data were collected using Microlog 4.01 software (Biolog Inc., Hayward, CA, USA). Average well color development (AWCD) over time was used to select comparable time points to avoid confounding effects of inoculum density differences between treatments in the multivariate analysis (Garland, 1996; Campbell et al., 1997).

2.3. Phospholipid fatty acid analysis (PLFA)

Lipid extraction and PLFA were performed using the method of White et al. (1979). Briefly, 5.0 g soil was extracted with a chloroform methanol–phosphate buffer mixture (1:2:0.8, v/v/v), and the phospholipids (PLs) were separated from other lipids on a silicic acid column. Phospholipid-phosphate (PL-P) was quantified colorimetrically following persulfate digestion (White et al., 1979). A significant correlation was found between PL-P and soil microbial biomass C ($r^2 = 0.65$, $P < 0.05$), indicating that the PLs extraction was consistent among soil samples. PLs were subjected to a mild-alkali methanolysis and the resulting fatty acid methyl esters were separated using a Hewlett Packard

Table 1
Soil chemical and microbiological properties at 0-5 and 5–15 cm soil depths of turfgrass systems and adjacent native pines

	Soil C (mg C g^{-1} soil)	Soil (C:N)	pH	Biomass C (μg C g^{-1} soil)	Biomass (C:N)
0–5 cm soil depth					
Native pine	26.2 c	28.9 a	4.7 c	217 c	7.0 a
1-Year turf	9.5 d	15.2 b	6.4 ab	181 c	4.5 c
6-Year turf	30.4 bc	13.4 bc	6.4 a	564 b	5.6 b
23-Year turf	38.4 b	12.6 bc	6.4 a	663 b	5.9 b
95-Year turf	72.5 a	10.4 c	6.1 b	1126 a	5.2 bc
5–15 cm soil depth					
Native pine	9.5 b	26.7 a	5.0 d	68 b	6.1 a
1-Year turf	2.3 c	11.3 bc	5.6 c	26 c	5.4 a
6-Year turf	2.8 c	9.2 c	6.3 a	28 c	5.3 a
23-Year turf	8.2 b	18.1 b	6.2 a	53 b	5.9 a
95-Year turf	13.3 a	12.3 bc	5.9 b	110 a	5.1 a

Values followed by different letters within each column of 0–5 or 5–15 cm soil depths are significantly different (multiple comparisons of Bonferroni *t*-test, $P < 0.05$).

5890 Gas Chromatograph. The fatty acids were identified by quantitative and qualitative standards of bacterial methyl ester mixes (Supelco, CA, USA) and expressed as nmol g^{-1} soil (Shi et al., 2002).

2.4. Data analysis

Microbial community diversity was calculated using the Shannon index: $H = -\sum_{i=1}^{n} p_i \ln p_i$, where n is the number of species and p_i is the measure of ith species proportional to the total measure of all species (Zak et al., 1994). In the case of Biolog data, species represents individual substrates and p_i is the measure of color change of ith substrate relative to the sum of the color changes of all substrates. As a result, the maximum attainable diversity would be 3.43 when soil microbial community responds equally to the 31 substrates used in the Biolog Eco plate. In the case of PLFA data, species denotes the identified fatty acids and thus p_i is the concentration of ith individual fatty acid relative to the concentration of all fatty acids. Up to 37 fatty acids were identified in our samples, and thus maximum PLFA diversity would be 3.61 if these fatty acids were equally present in the soil microbial community. ANOVA of a split-plot design with restricted randomization on sites was used to determine significant differences among land uses, ages of turfgrass systems and soil depths; intact soil cores corresponding to individual sites (i.e., native pine, or 1, 6, 23, and 95 years old turfgrass systems) being the whole plot, soil depth being the split-plot, and four replications being nested within the individual sites. Separation of means was performed with Bonferroni multiple t-test. When comparing turfgrasses with native pines, we performed ANOVA of a split-plot design with individual sites (i.e., four pairs of turfgrass system and its adjacent native pines) being the whole plot, and soil depth being the split plot.

Species composition is considered to be more important than species number in determining soil ecosystem function (Jones and Bradford, 2001). Biolog and PLFA data sets were, therefore, subjected to comprehensive assessments using principal components analysis (PCA) using CANOCO software (Microcomputer Power, Inc., Ithaca, NY). For the Biolog data set, the proportional color changes of all individual substrates were used for the PCA. For the PLFA data set, the mole fractions of 19 individual fatty acids were used for the PCA because they occurred in all the soil samples and their relative abundance comprised about 90% of the total concentration or peak area of identified fatty acids. The entire PLFA data set was also analyzed with PCA, and results were similar to those performed with the subset of 19 fatty acids. The values of first two principal components were subjected to ANOVA with Bonferroni multiple t-test to determine if the dissimilarity of soil microbial communities was statistically significant.

The effects of turfgrass age on the change in soil microbial communities could not be discerned with PCA of the whole data sets. Thus, soil samples from turfgrass systems and native pine were subjected to separate cluster analysis by the unweighted pair-group method of arithmetic mean (Girvan et al., 2003). We used the means of three (PLFA) or four (CLPP) replicates for the cluster analysis and expressed the results as dendrograms so that differences of soil microbial communities could be more easily ascertained.

3. Results

3.1. Soil microbial community diversity

Based on the Shannon diversity index calculated from the CLPP data set, there was no significant change in population diversity due to land use (pines versus turf), turfgrass age, or soil depth (Table 2). Similar results were found for the PLFA data set, with the exception that diversity was significantly lower at the 5–15 cm depth for the two youngest turfgrass systems. Independent of land use, turfgrass age or soil depth, soil microbial diversity was quite broad at ~90% of the

Table 2
Shannon index calculated from the substrate use pattern (Biolog) and fatty acid methyl-ester composition (PLFA) of soil microbial community

Soils	Diversity index from Biolog	Diversity index from PLFA
0–5 cm soil depth		
Native pine	3.13 a	2.72 a
1-Year turf	3.25 a	2.56 a
6-Year turf	3.20 a	2.63 a
23-Year turf	3.25 a	2.65 a
95-Year turf	3.31 a	2.67 a
5–15 cm soil depth		
Native pine	3.15 a	2.66 a
1-Year turf	3.15 a	2.26 b
6-Year turf	3.23 a	2.37 b
23-Year turf	3.24 a	2.65 a
95-Year turf	3.22 a	2.68 a

Mean values within the same column followed by different letters are significantly different (multiple comparisons of Bonferroni t-test, $P < 0.05$).

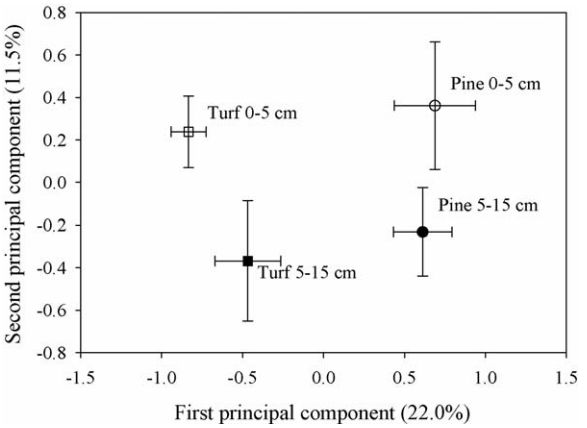

Fig. 1. CLPP-based principal components analysis showing the separation of soil microbial communities in different ages of turfgrass systems and adjacent native pines. The loading scores along the first and second principal components were the average over the cluster of microbial communities inhabiting native pines/turfgrass systems at 0–5 and 5–15 cm soil depths. The first two components explained 33.5% of the variation in the data set.

CLPP-based maximum diversity. Microbial diversity based on PLFA data was slightly lower at ∼70% of the maximum diversity.

3.2. Soil microbial community in response to land-use change

Four major assemblages of microbial communities were recognized from the PCA of CLPP and PLFA data sets (Figs. 1 and 2). CLPP-based PCA showed that soil

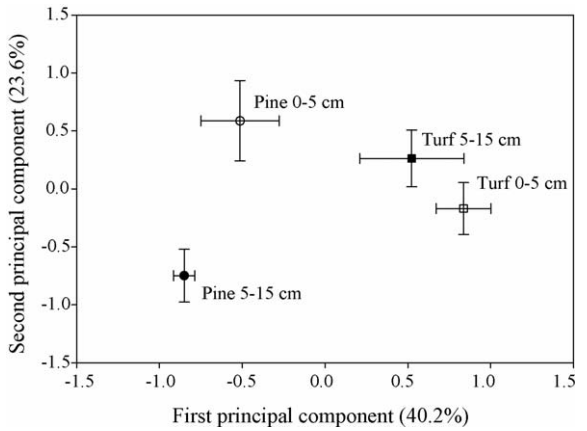

Fig. 2. PFLA-based principal component analysis showing the separation of soil microbial communities in different ages of turfgrass systems and adjacent native pines. The loading scores along the first and second principal components were the average over the cluster of microbial communities in native pines/turfgrass systems at 0–5 and 5–15 cm soil depths. The first two components explained 63.8% of the variation in the data set.

microbes populating turfgrass soils differed from those in native pines along the first principal component ($P < 0.05$), which accounted for ∼22% of the variation (Fig. 1). Microbial communities also differed as a function of soil depth, which explained ∼10% of the change. It should be noted that soil pH, especially under the native pines, was fairly acidic (Table 1), and that the bacterial extract was neutral. It is unlikely, however, that this pH difference affected our results. In a similar study with acidic soils, Yao et al. (2000) reported that changing the pH of soil bacterial extracts from neutral to acidic pH did not affect the separation patterns of CLPP-based microbial communities.

PLFA-based PCA corroborated the results of CLPP-based PCA (Fig. 2). The microbial communities in turfgrass and pine soils were significantly separated along the first principal component, accounting for ∼40% of the variation ($P < 0.05$). Differences between soil depths were observed in the second principal component, explaining ∼20% of the variation; this difference was more pronounced in native pines than in turfgrass soils.

Microbial communities from turfgrass and pine soils differed in their preferred C substrates (Table 3). The 31 compounds from the Biolog ECO plates were categorized based on their contribution to the separation of soil microbial communities along the first principal component. The compounds with positive loading scores within their respective substrate class were tallied under the pine forests, while the compounds with negative loading scores were tallied under the turfgrass systems (Table 3). In general, carbohydrates were preferred by turfgrass microbial communities, whereas carboxylic acids, amino acids, and the two phenolic compounds were preferred by native pine microbial communities. Differences in soil microbial community composition between native pines and turfgrass systems were also illustrated by the PLFA-based PCA. The fatty acids a15:0, 16:1, 16:0, 18:1 and cy17:0 were positively correlated with the soil microbial communities in turfgrass systems, while the fatty acids cy19:0 and i16:0 were positively correlated with the soil microbial communities in native pines. Fatty acid 18:2, an indicator of fungal biomass, was slightly correlated with the soil microbial communities in native pine soils.

3.3. Soil microbial community in response to soil management

Land-use change had a large and significant effect on microbial community (Figs. 1 and 2), which may

Table 3
Biolog ECO plate substrates in differentiating soil microbial communities of turfgrass systems from those of native pines by the first principal component

Substrate	Substrate class	Substrate loading score
Loading scores		
γ-Hydroxybutyric acid	Carboxylic acids	−0.722
D-Xylose	Carbohydrates	−0.563
α-D-Lactose	Carbohydrates	−0.545
Glucose-1-phosphate	Phosphate compounds	−0.530
Phenylethylamine	Amides	−0.526
4-Hydroxy benzoic acid	Phenolic acids	0.523
Tween 40	Polymeric compounds	0.525
L-Asparagine	Amino acids	0.527
D,L-α-Glycerol phosphate	Phosphate compounds	0.603
D-Galacturonic acid	Carboxylic acids	0.701

Substrate classes	Turf soils	Native pines
Overall substrate contribution		
Carbohydrates	5	2
Carboxylic acids	3	5
Phenolic acids	0	2
Amino acids	2	4
Polymeric compounds	2	2
Phosphate compounds	1	1
Amides	1	1

For loading scores of the 10 most influential individual substrates, substrates having negative values are associated with turfgrass systems whereas those with positive values are associated with native pines. For substrate class contribution to the community separation, data are the number of substrates that have either positive values for native pines or negative values for turfgrass systems in each substrate class.

have obscured any possible effects of management (turfgrass age). To examine management effects, we compared the relative changes in diversity in turfgrass systems across the chronosequence to the relative changes in the pine system, as a control. We assumed that any changes observed in the pine chronosequence were due to soil heterogeneity, and that turfgrass management effects would be visible as a difference between the two systems. CLPP and PLFA data for both systems were subjected to cluster analysis, and the results were compared. Based on the CLPP results, there were no clear differences between the native pines and the turfgrass systems (Fig. 3). By contrast, PLFA-based cluster analysis showed differences between turfgrass systems and pines (Fig. 4). For example, note the clustering of the two oldest turfgrass sites and their separation from the two youngest sites.

4. Discussion

4.1. Soil microbial community diversity

Surface soils are physically, chemically and structurally heterogeneous and may provide numerous micro-environments for microbial survival and growth. These micro-environments spatially separate microbes that may be competitors or antagonists. Consequently, microbes capitalize on micro-environments and evolve into diverse communities (Ranjard and Richaume, 2001). Zhou et al. (2002) assessed phylogenetic diversity of soil microorganisms using samples varying in organic C content. They suggested that spatial isolation in surface soils limited the competitive interaction of microbes and therefore surface soils could support diverse populations at relatively low soil C levels. Microbial community diversity of ∼90% of CLPP- or 70% of PLFA-based maxima indicates that turfgrasses are similar to other ecosystems in supporting diverse microbial communities regardless of land-use change or management practices.

Soil organic matter may be a prime determinant of soil heterogeneity and thus the diversification of soil microbial community (Degens et al., 2000). However, turfgrass systems may be somewhat different since the relationship between microbial community diversity and soil organic matter content appears to be discontinuous rather than linear. Lower diversity was observed only in young turf soils having organic C less than 3 g C kg^{-1} (5–15 cm samples). Above this value, soils had nearly constant PLFA-based Shannon indices, despite organic C ranging from 8 to 72 g C kg^{-1} (Tables 1 and 2).

It is not surprising that the CLPP-based Shannon index was somewhat higher than the PLFA-based index, since the two methods measure different aspects of soil microbial community. CLPP measures metabolic capabilities and is an indicator of functional diversity. Functional redundancy is very common in microbial community systems and a loss of some species may not affect the overall function of soil microbial community (Setälä and Mclean, 2004). Although some microbes probably were lost in changing land use from native pines to turfgrass (i.e., reduction of PLFA-based Shannon index), the community function was apparently not influenced (i.e., no change in CLPP-based Shannon index).

Turfgrass age also had little effect on population diversity, despite relatively long-term applications of agricultural chemicals. It is possible that any potential negative impact of long-term management was offset by

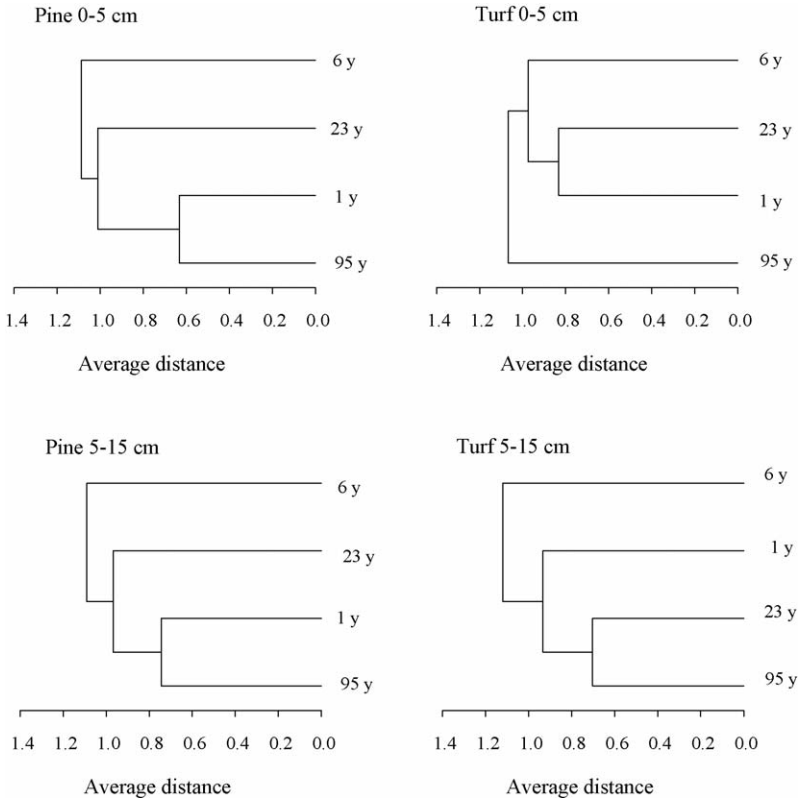

Fig. 3. CLPP-based cluster analysis showing the similarity of soil microbial communities in different ages of turfgrass systems and adjacent native pines. Cluster analysis was conducted by unweighted pair-group method using arithmetic average. The scale shows the distance between clusters.

the increase in soil C content, acting as microbial substrate and as a buffer for applied chemicals. Since both CLPP and PLFA methods provide a relatively coarse measure of community composition and structure (Bossio et al., 1998), it is also possible that changes were simply not detectable.

4.2. Microbial community structure and land-use change

Soil microbial communities were significantly separated on the basis of land use but not by age of the turfgrass system (Figs. 1 and 2), indicating that land-use change was paramount in structuring the soil microbial community. This response to land-use change was not related to soil organic matter content or microbial population size, but was correlated with the change in soil C:N, microbial biomass C:N, and soil pH (Table 1).

Significant shifts in microbial community composition occurred within 1 year of changing land use from pines to turf. This finding is at odds with those reported for a land-use change from cultivation to an unmanaged ecosystem (Buckley and Schmidt, 2001; Steenwerth et al., 2002). Those authors stated that it might take decades for the soil microbial community to recover from the long-term effects of cultivation. This disparity is not surprising, since the establishment of golf course turf usually involves considerable disruption of the soil, including cultivation, compaction, and liming to adjust pH. Our results are consistent with those of Nüsslein and Tiedje (1999), who studied the response of soil bacteria to a change from forest to pasture. They concluded that shifts in microbial community structure resulted directly from the change in soil C resource and soil pH.

It is well known that soil organic matter quality differs between forests and grasslands. For example, the ratio of fulvic acid to humic acid is generally higher in grasslands than in forests (Stevenson, 1982). Saviozzi et al. (2001) observed that water soluble carbohydrates were three times higher, and phenolic compounds were two times higher in grassland than in forest soils. Martens et al. (2003) showed that carbohydrates were slightly higher in pasture than in forest soils, while phenolic compounds were significantly higher in forest

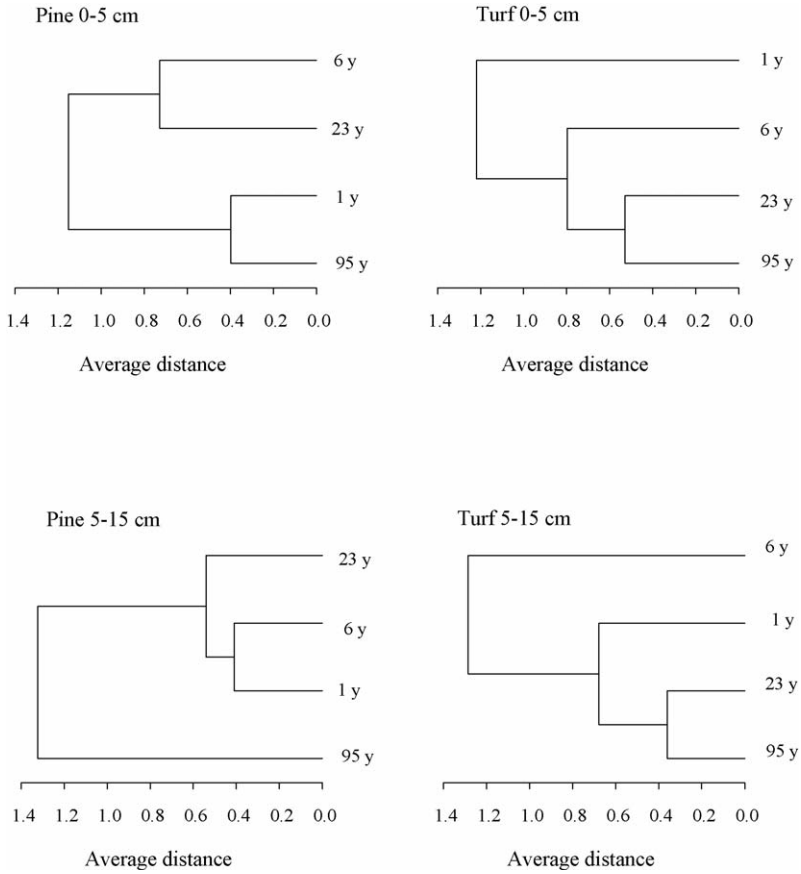

Fig. 4. PLFA-based cluster analysis showing the similarity of soil microbial communities in different ages of turfgrass systems and adjacent native pines. Cluster analysis was conducted by unweighted pair-group method using arithmetic average. The scale shows the distance between clusters.

than in the pasture (Martens et al., 2003). Our CLPP-based PCA suggests that the change in soil microbial community structure was related to an altered composition of soil organic C (Table 3). We had expected that newly established turfgrass systems would be fairly similar to native pines in terms of soil organic matter composition, since the soil would presumably still be dominated by organic matter accumulated before the land-use change. However, CLPP-based PCA showed that regardless of their age, turfgrass soil microbial communities grouped together and differed from those of native pines (Fig. 1). This may indicate that fresh C derived from turfgrass clippings, root exudates and debris might be the predominant C resource for soil microbes, as opposed to older residual, and more recalcitrant organic matter from the pine forest.

Certain components of PLFA appear to be tightly linked with specific soil environments. For example, cyclopropyl fatty acids are associated with highly acidic, low C soils, whereas the monounsaturated fatty acids are considered to be indicators of higher substrate C availability (Zelles et al., 1992; Bååth et al., 1995; Bossio and Scow, 1998). In the present study, several fatty acids corresponded to land-use change. Specifically, cyclopropyl 19:0 decreased, whereas the monounsaturated fatty acids (i.e., 16:1 and 18:1) increased in turfgrass, compared to pine soil. This was likely related to pH adjustment and altered soil C resources (Table 1). Further, the relative abundance of fungi marker 18:2 slightly decreased in turfgrass soils, probably in response to the lower soil C:N. A reduced fungi population in turfgrass soils is also suggested by significantly lower microbial biomass C:N, compared to that in pine soils (Table 1).

4.3. Microbial community structure and soil management

Many studies have documented that soil microbial community composition and structure respond to management practices such as fertilization, pesticide use and irrigation (Ka et al., 1995; Schimel et al., 1999;

Donnison et al., 2000; Clegg et al., 2003; Fierer et al., 2003). For example, application of inorganic N at 218 kg N ha^{-1} in a silage corn field with crimson clover/ryegrass as winter cover crop enhanced the relative abundance of Gram-positive bacteria (Peacock et al., 2001). Some microbes are more resistant than others to environmental change, such as osmotic shock (Mellefont et al., 2003) or saturation (Haverson et al., 2000). We were unable to distinguish any effects of management on community structure when analyzing the entire data set (turfgrass and native pines; Figs. 1 and 2). Nevertheless, when data from turfgrass systems were analyzed separately, there were clear effects of age (Fig. 4), indicating that long-term turfgrass management impacted community composition and structure. It is possible that management effects were obscured in our initial analysis by the strong influence of land-use change. Several studies have reported that management practices were secondary to other factors, such as soil type and cultivation, in determining soil microbial community structure (Bossio et al., 1998; Buckley and Schmidt, 2001; Girvan et al., 2003), and our results are consistent with these reports.

4.4. Microbial community structure and microbial catabolic efficiency

While a significant correlation ($r^2 = 0.38$, $P < 0.05$) of the first principal components of PLFA versus CLPP suggests that changes in microbial catabolic functions were causally related to changes in microbial community composition and structure, it must be cautioned that CLPP may not represent in situ microbial functions (Konopka et al., 1998).

In our previous study (Shi et al., 2006), we observed that two indicators of catabolic efficiency (qCO_2, CO_2 per microbial biomass and qN, mineralized N per microbial biomass) declined with turfgrass age. We hypothesized the decline was controlled, at least partly, by concomitant changes in the composition and structure of the soil microbial community. The present study shows that microbial community composition and structure do change with turfgrass age, albeit only moderately (Fig. 4). In all likelihood, there are probably numerous factors influencing qCO_2 and qN. Consequently, the decline in qCO_2 and qN with turfgrass age might be a response to parallel changes in soil physicochemical properties.

In summary, managed turfgrass systems and adjacent native pine can be distinguished at the level of microbial community composition. Both ecosystems were characterized by a very diverse microbial community. Microbial community composition was greatly affected by land-use change, and to a lesser extent by long-term management. It is possible that community compositional change contributed to increased soil microbial metabolic efficiency in older turfgrass systems.

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