

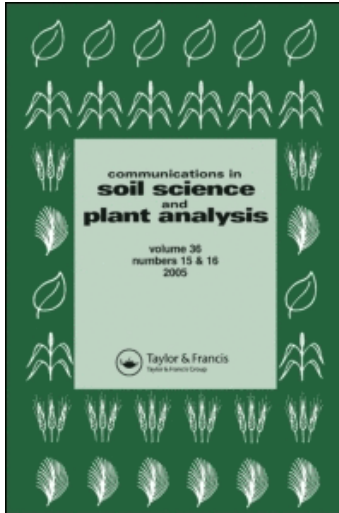
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Communications in Soil Science and Plant Analysis

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t713597241>

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To cite this Article Ye, Rongzhong , Wright, Alan L. , Inglett, Kanika , Wang, Yu , Ogram, Andy V. and Reddy, K. R.(2009) 'Land-Use Effects on Soil Nutrient Cycling and Microbial Community Dynamics in the Everglades Agricultural Area, Florida', Communications in Soil Science and Plant Analysis, 40: 17, 2725 — 2742

To link to this Article: DOI: 10.1080/00103620903173772

URL: <http://dx.doi.org/10.1080/00103620903173772>

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Land-Use Effects on Soil Nutrient Cycling and Microbial Community Dynamics in the Everglades Agricultural Area, Florida

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Abstract: Soil subsidence has become a critical problem since the onset of drainage of the organic soils in the Everglades Agricultural Area (EAA), which may impair current land uses in the future. The objectives of this study were to characterize soil microbial community-level physiology profiles, extracellular enzymatic activities, microbial biomass, and nutrient pools for four land uses: sugarcane, turfgrass, pasture, and forest. Long-term cultivation and management significantly altered the distribution and cycling of nutrients and microbial community composition and activity in the EAA, especially for sugarcane and turf fields. The least-managed fields under pasture had the lowest microbial biomass and phosphorus (P) levels. Turf and forest had more microbial metabolic diversity than pasture or the most intensively managed sugarcane fields. Land-use changes from sugarcane cropping to turf increased microbial activity and organic-matter decomposition rates, indicating that changes from agricultural to urban land uses may further contribute to soil subsidence.

Keywords: Everglades, land use, microbial community composition, nutrient cycling

Received 28 November 2007, Accepted 9 July 2008

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INTRODUCTION

Soil supports diverse microbial communities that play important roles in ecosystem-level processes such as decomposition of organic matter and nutrient cycling (Wright and Reddy 2001a). In natural systems, soil microbial community composition and activity are related to the efficiency of nutrient cycling and ecosystem function (Yao et al. 2000). However, the richness, abundance, and activity of the microbial community is vulnerable to influence by soil physical and chemical properties such as pH, moisture, organic-matter content, and nutrient availability. Alterations in the physical and chemical nature of the soil may lead to shifts in microbial community composition and changes in microbial function. Agricultural practices such as fertilization and tillage influence soil chemical properties and nutrient dynamics throughout the soil profile (Gesch et al., 2007; Wright, Dou, and Hons 2007). Therefore, changes in land uses with different intensity or history of agricultural practices consequently results in distinctive changes in microbial community composition and function (Grayston et al., 2004). Land-use changes can also disrupt carbon (C) and nitrogen (N) dynamics and organic-matter storage in soils across a range of habitats (Garcia-Oliva, Lancho, and Montano 2006; Monkiedje et al. 2006), which are commonly viewed as major factors causing shifts in microbial community composition (Schimel and Bennett 2004; Cookson et al. 2007).

The Everglades Agricultural Area (EAA) is located south of Lake Okeechobee and north of the water conservation areas (WCAs) in south Florida. It consists of an area of approximately 283,300 ha that was artificially drained in the early 1900s for agricultural production (Chen et al. 2006). Currently, the land use is primarily sugarcane with a smaller portion dedicated to vegetables. The soils in the EAA are primarily histosols with organic-matter content as high as 80–90% (Snyder et al. 1978). Because of the drainage and establishment of the EAA, soil subsidence has become a critical problem, which results from the oxidation of organic matter (Gesch et al. 2007). Along with subsidence, excessive N and phosphorus (P) are released from organic-matter mineralization, which alters nutrient cycling and soil processes (Morris and Gilbert 2005). The current long-term estimate of soil subsidence is approximately 1.5 cm yr^{-1} (Morris and Gilbert 2005). At this rate of loss, soils will become too shallow for agricultural use and sugarcane production in the future (Anderson and Flaig 1995; Morris and Gilbert 2005). Acknowledging the fact that the subsidence clouds the future of agriculture in EAA, strategies have been implemented to increase sustainability of agriculture (Grigg, Zinder, and Millar 2002; Morris et al. 2004). However, land-use changes in the EAA are considered

inevitable in the near future, likely on the order of decades (Anderson and Rosendahl 1998; Snyder 2005).

An emerging interest is to convert current land uses back to prior uses as prairies. Under flooded conditions, degradation of organic matter and the subsidence rate can be reduced or eliminated (Grigg, Zinder, and Miller 2002). Snyder (2005) further proposed the possible land uses in the EAA over the next 50 years, which included growing pasture grasses and planting cypress trees in areas with shallow organic soils. Additionally, in consideration of the continuous growing population and urbanization, more agricultural lands are expected to change to home development sites with turfgrass coverage (Anderson and Rosendahl 1998). Obviously, many land-use options can be explored to serve as alternatives to traditional agriculture. However, far less is known about the influence of land-use change on EAA ecosystems with regard to nutrient cycling and microbial community dynamics. The objectives of the present study were to determine and characterize the impacts of land use on the soil microbial community composition and activity and to investigate the effects of land use on nutrient cycling.

MATERIALS AND METHODS

Site Description

The study sites are located in the northern EAA at the Everglades Research and Education Center near Belle Glade, Fl. The long-term average annual rainfall is 133 cm, and temperature is 24 °C. All soils are Dania muck (euic, hyperthermic, shallow Lithic Medisaprists) with a depth to the bedrock of approximately 45 cm. These organic soils developed under seasonal flooding and low nutrient status and supported vegetation adapted to these conditions, primarily sawgrass (*Cladium jamaicense* Crantz). Because of conversion to agricultural use by drainage, the dominant vegetation shifted to annual crops of vegetable and sugarcane (*Saccharum* sp.) in the early 1900s. Four land uses were selected for this study to mirror possible land uses in the future: soils under forest for 19 years, fields under sugarcane production for approximately 50 years, turfgrass lawns for 60 years, and fields under perennial pasture for approximately 100 years. Four field sites were randomly sampled for each land use. The forest soils were previously cropped to sugarcane but planted to bald cypress (*Taxodium distichum*) and pond cypress (*Taxodium ascendens*) in 1988. These fields did not receive any fertilization after land-use change but were extensively tilled prior to seedling establishment, and no further management has been applied. The sugarcane fields were managed for vegetable production

from the early 1900s to the 1950s, but mainly for sugarcane since the 1950s. Fertilization was applied at a rate of $40 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ (Gilbert and Rice 2006) prior to planting. Sugarcane is planted from August through January and harvested from October through April. Tillage operations included several disking (to 15 cm deep) after crop harvest, subsoil chiseling (to 30 cm deep) to improve drainage, and frequent in-season tine cultivations (to 4 cm deep) for weed control (Morris et al. 2004). The turf fields were vegetated by St. Augustinegrass [*Stenotaphrum secundatum* (Walt) Kuntze] turf since the mid-1940s. The pasture field was primarily occupied by paragrass [*Panicum purpurascens* (L.) Raddi] and bermudagrass [*Cynodon dactylon* (L.) Pers]. Turf and pasture fields were periodically mowed with residues returned to soil but received no fertilization and tillage since establishment.

Soil Sampling and Physical-Chemical Analysis

Surface soil (0–15 cm) samples were collected from four replicate fields of each land use in March 2007. The soils were homogenized after the removal of large plant particles and stored at $4 \text{ }^{\circ}\text{C}$ until use. Moisture content was measured as the mass loss after drying at $70 \text{ }^{\circ}\text{C}$ for 5 days. Soil organic-matter content was estimated by the loss-on-ignition method after ashing at $550 \text{ }^{\circ}\text{C}$ for 4 h (Anderson 1976). Total organic C was then calculated from the organic content by using a factor of 0.51 (Anderson 1976). Total C, total N, and total P were determined using the oven-dried ($70 \text{ }^{\circ}\text{C}$) and ground soil. Total C and N were measured with a Carlo-Erba NA 1500 CNS analyzer (Haak-Buchler Instruments, Saddlebrook, N.J.), while total P was evaluated after ashing (Bremner 1996) using the ascorbic acid–molybdenum blue method (Kuo 1996) with an AQ2+ discrete analyzer (Seal Analytical Inc., Mequon, Wisc.).

Microbial Biomass

Microbial biomass C (MBC), N (MBN), and P (MBP) were measured by the fumigation–extraction method (White and Reddy 2001). The amount of potassium sulfate (K_2SO_4)–extracted C was determined with a total organic C analyzer, TOC-5050A (Shimadzu, Norcross, Ga.). The MBC was calculated from the difference in extractable C between fumigated and unfumigated samples using a conversion factor of 0.37. After digestion, the K_2SO_4 extracts were measured for total Kjeldahl N using an AQ2+ discrete analyzer (Seal Analytical Inc., Mequon, Wisc.). The MBN was calculated from the difference in total Kjeldahl N between fumigated and unfumigated samples using $K_{\text{EC}} = 0.54$. The total P

content of the sodium bicarbonate (NaHCO_3) extracts used for MBP analysis was measured for P as previously described (Kuo 1996). The MBP was determined as the difference in total P of NaHCO_3 extracts from fumigated and unfumigated samples. Labile inorganic P (NaHCO_3 -Pi) was measured for unfumigated soil extracts and analyzed for P as previously described (Kuo 1996).

Potentially Mineralizable N and P

Potentially mineralizable N (PMN) was determined according to methods of White and Reddy (2000) based on a 10-day incubation followed by extraction with 2 M potassium chloride (KCl). Extracts were analyzed for ammonium (NH_4)-N (White and Reddy 2000). Potentially mineralizable P (PMP) was measured using the method of Corstanje et al. (2007) with slight modifications. Dry soil (0.5 g) was placed in 30-mL serum bottles and mixed with 5 mL of water. The bottles were then capped and incubated in the dark at 40 °C for 10 days. At 10 days, 20 mL of 1 M HCl was injected, and soil was shaken for 3 h. Extracts were filtered through 0.45- μm membrane filters. Another set of equivalent weight samples, without incubation, were directly extracted with 25 mL of 1 M HCl, and extracts were analyzed for total P. The PMP was determined as the difference in total P of extracts between incubated and nonincubated soil.

Enzyme Activity Assay

Approximately 1 g moist soil was placed in polypropylene centrifuge tubes, mixed with 30 ml of water, and shaken for 25 min. Homogenized samples were further diluted five times for enzyme assays. Enzyme assays were conducted in three or four replicates with controls to offset nonenzymatic production. For cellobiohydrolase assay, the substrate used was 2 mM p-nitrophenol-cellobioside (Acros Organics, Geel, Belgium). A 0.75-mL aliquot of the diluted samples and 0.75 mL of substrates were mixed in 2-mL microcentrifuge tubes and incubated at 20 °C for 20 h with gentle shaking. At the end of the incubation, the mixtures were centrifuged at 10,000 rpm for 1 min, and 0.75 mL supernatants were transferred to new tubes, followed by the addition of 0.075 mL of 1 N NaOH to stop the reaction and develop the color. The mixtures were then analyzed for absorbance with a UV-160 spectrophotometer (Shimadzu, Norcross, Ga.) at 420 nm. The enzymatic activity was expressed as mg p-nitrophenol released per g dried soil per h. Leucine aminopeptidase assay was conducted in 96-well microtiter plates (Prenger

and Reddy 2004). Two hundred μL of samples were incubated with 50 μL substrates and 5 mM L-leucine 7-amino-4-methylcoumarin (Biosynth, Naperville, Ill.) at 20 °C for 8 h. The fluorescence readings were collected at 1-h intervals using a fluorescence plate reader, Bio-TEK FL600 (Bio-TEK Instruments Inc., Winooski, Vt.), at a setting of 365 nm excitation and 450 nm emission. Enzyme activity was determined by calculating the mean fluorescent reading changes over time with a standard curve and expressed as mg 7-amino-4-methylcoumarin released per g dried soil per h. Alkaline phosphatase and sulfatase assays were conducted according to the methods of Wright and Reddy (2001a).

Community-Level Physiological Profile by BIOLOG Assay

Community-level physiological profiles (CLPPs) were determined by direct incubation of fresh soil extracts in Biolog Eco-plates (31 substrates) (Biolog Inc., Hayward, Calif.). Approximately 1 g moist soil samples were mixed with 20 mL of water and gently shaken for 20 min. The homogenized samples were then diluted 400 times, and soil particles were allowed to settle for 15 min at 4 °C. One hundred fifty μL of the supernatants were subsequently dispensed into each well of Eco-plates and incubated at 20 °C for 7 days. Optical densities were measured every 6 or 12 h using Bio-Tek FL600 (Bio-Tek Instruments Inc., Winooski, Vt.) at 590 nm. Absorbance values of each well with C sources were blanked against control wells before analysis. Negative values were considered as 0. Community metabolic diversity (CMD) was calculated by summing up the numbers of positive responses in each plate. Positive responses were defined as any absorbance values greater than 0.25 (Garland 1997). Average well color development (AWCD) was determined as described by Garland (1996, 1997). To overcome possible interference by inoculum density on color development, absorbance values for various C sources were standardized by dividing the blanked value of each well by the AWCD of the plate and were subsequently used for principal component analysis.

Statistical Analysis

Significant differences among land uses for all the variables were determined by one-way analysis of variance (ANOVA) and Tukey's test at $\alpha = 0.05$. Multivariate analysis on the Biolog profiles was carried out by principal component analysis (Preston-Mafham, Boddy, and Randerson 2002; Campbell et al. 2003). All computations were conducted on computing software JMP V4 (SAS Institute Inc., N.C.).

RESULTS

Soil Physical and Chemical Properties

Soil organic-matter content was greatest in pasture soil and decreased in the order of forest, sugarcane, and turf soil, respectively (Table 1). Total C and N were also greatest in pasture, averaging 461 g C kg⁻¹ and 32 g N kg⁻¹, respectively. However, in contrast to total C and N, total P was lowest in pasture, averaging 0.78 g P kg⁻¹. Extractable C was significantly greater in sugarcane (2.34 g C kg⁻¹) than other land uses (Table 1). However, no difference in extractable C was found among forest, turf, and pasture soil. Extractable ammonium (NH₄)-N in forest and sugarcane soils was less than turf and pasture soils (Table 1). Labile inorganic P was more in sugarcane soil (96 mg P kg⁻¹) than forest (43 mg P kg⁻¹) and pasture (17 mg P kg⁻¹). The most inorganic P was found in turf soil (173 mg P kg⁻¹); however, it was not statistically different from other land uses. Potentially mineralizable N was four times less in sugarcane (2.66 mg N kg⁻¹ d⁻¹) than other land uses (Table 2). Potentially mineralizable P varied widely in the turf soil, averaging 33.1 mg P kg⁻¹ d⁻¹, which was about eight times more than other land uses (Table 2), but the difference was not significant.

Microbial Biomass

Soil MBC, ranging from 9.3 to 13.5 g C kg⁻¹, was less in pasture than forest and sugarcane (Table 2). The MBC to organic matter ratio in the

Table 1. Properties of forest, sugarcane, turf, and pasture soils (0–15 cm)

Parameter	Forest	Sugarcane	Turf	Pasture
Moisture (%)	49 a	54 a	46 ab	37 b
LOI (%)	83 ab	81 a	57 a	85 b
Total C (g kg ⁻¹)	449 a	445 a	319 a	461 b
Total N (g kg ⁻¹)	30 a	29 a	21 ab	32 b
Total P (g kg ⁻¹)	1.25 a	0.98 b	2.71 ab	0.78 c
TOC (g kg ⁻¹)	424 ab	411 a	293 a	433 b
DOC (g kg ⁻¹)	1.13 a	2.34 b	1.14 a	1.14 a
DON (mg kg ⁻¹)	141 a	197 b	148 ab	132 a
NH ₄ -N (mg kg ⁻¹)	12 a	10 a	21 b	42 c
LIP (mg kg ⁻¹)	43 a	96 b	173 abc	17 c
TLP (mg kg ⁻¹)	122 a	165 b	236 ab	97 a

Notes. LOI, loss on ignition; TOC, total organic C; DOC, dissolved organic C; DON, dissolved organic N; NH₄-N, extractable NH₄⁺; LIP, labile inorganic P (NaHCO₃-extractable P); and TLP, total labile P. Different letters following numbers indicate significant differences among land uses (p < 0.05).

Table 2. Microbial biomass, enzymatic activities, potentially mineralizable N (PMN), and potentially mineralizable P (PMP) of forest, sugarcane, turf and pasture soils (0–15 cm)

Parameter	Forest	Sugarcane	Turf	Pasture
MBC (g kg ⁻¹)	12.7 a	13.5 a	13.3 ab	9.3 b
MBN (g kg ⁻¹)	0.24 a	0.16 a	0.32 ab	0.12 b
MBP (mg kg ⁻¹)	52 a	48 a	99 a	41 a
MBC/OM (mg kg ⁻¹)	15183 a	16857 a	23374 b	10918 c
PMN (mg kg ⁻¹ d ⁻¹)	10.14 a	2.66 b	10.42 a	12.79 a
PMP (mg kg ⁻¹ d ⁻¹)	4.75 a	4.18 a	33.10 a	3.92 a
CBHase (mg g ⁻¹ h ⁻¹)	140 a	51 b	191 c	271 abc
LAPase (mg g ⁻¹ h ⁻¹)	1.42 a	1.96 a	3.64 a	2.58 a
APase (mg g ⁻¹ h ⁻¹)	0.70 a	0.94 a	1.29 ab	1.21 b
Sulfatase (mg g ⁻¹ h ⁻¹)	0.32 ab	0.24 a	0.44 ab	0.42 b

Notes. MBC, microbial biomass C; MBN, microbial biomass N; MBP, microbial biomass P; OM, organic-matter content; CBHase, cellobiohydrolase; LAPase, leucine aminopeptidase; and APase, alkaline phosphatase. Different letters following numbers indicate significant differences among land uses ($p < 0.05$).

turf soil (23,374 mg kg⁻¹) was two times greater than in pasture soil, which was also more than in the forest (15183 mg kg⁻¹) and sugarcane (16857 mg kg⁻¹) soils. As well, the MBC to organic matter ratio was less in pasture than forest and sugarcane. Additionally, MBN was lowest in pasture soil (0.12 g N kg⁻¹) and greatest in turf soil (0.32 g N kg⁻¹). Soil MBP was not significantly different among land uses.

Extracellular Enzyme Activity

Cellobiohydrolase activity was highly varied in pasture soil, averaging 271 mg g⁻¹ h⁻¹, which was not significantly different from other land uses (Table 2). However, activities in forest, sugarcane, and turf soils varied considerably, averaging 140, 51, and 191 mg g⁻¹ h⁻¹, respectively. Pasture soil had higher alkaline phosphatase (1.21 mg g⁻¹ h⁻¹) than forest (0.70 mg g⁻¹ h⁻¹) and sugarcane (0.94 mg g⁻¹ h⁻¹). Sulfatase activities were greater in pasture soil (0.42 mg g⁻¹ h⁻¹) than sugarcane soil (0.24 mg g⁻¹ h⁻¹) but were not different from turf soil (0.44 mg g⁻¹ h⁻¹) and forest soil (0.32 mg g⁻¹ h⁻¹).

Microbial Community Composition and Function

We used the CMD and AWCD to describe the average numbers of substrates potentially utilized and respiration rates from the C sources by

microbial communities. Both CMD (Figure 1) and AWCD (data not shown) followed a sigmoidal curve over time. On day 1, no color development was observed; nevertheless on day 3.25 both CMD and AWCD of forest and turf reached their midpoint. Because the actual rates of color development changed with time, the comparison among land uses in relative rates was made in the interval of day 1 to day 3.25. The CMD of the microbial communities was greater in forest and turf than sugarcane and pasture (Figure 1). On day 3.25, more than 55% of the wells were positive in plates inoculated with turf or forest soil, yet only 15% of wells were positive in plates from sugarcane soils and 6% of wells from pasture soils (Figure 1). The rates of color development (AWCD) followed the same pattern with CMD, being greatest in turf and forest and less for sugarcane and pasture (data not shown). Principal component analysis on the utilization patterns of all of the 31 substrates on day 3.25 revealed clear differentiation among land uses in the composition of active members of the soil microbial community (Figure 2). In particular, ordination axis 1 demonstrated obvious separation between turf and either the pasture or sugarcane. Furthermore, ordination axis 1 separated the soil microbial community in forest from that of pasture. No apparent separations were observed on axis 2. However, microbial community composition in forest soils was distinct from sugarcane soils on ordination axis 3.

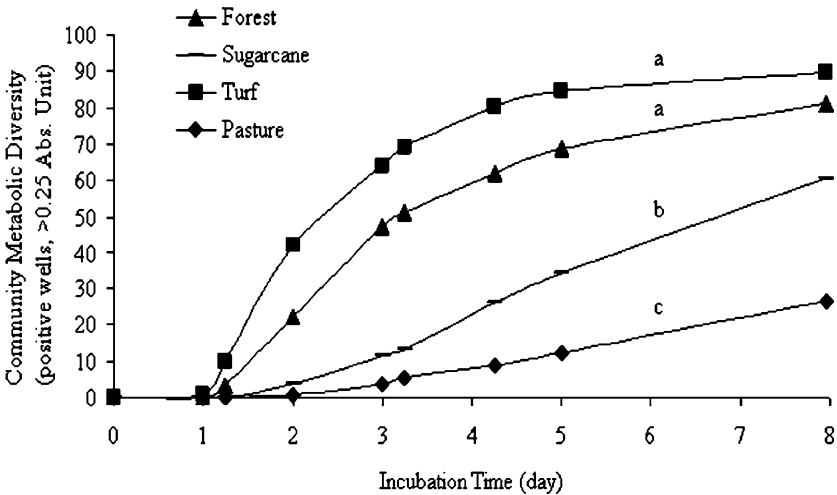


Figure 1. Microbial community metabolic diversities of forest, sugarcane, turf, and pasture soils. Different letters indicate significant differences between land uses ($p < 0.05$).

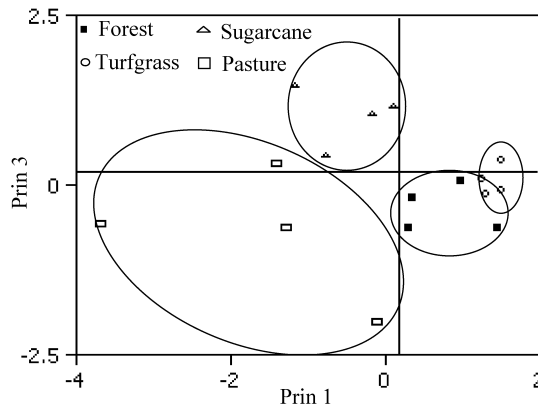


Figure 2. Principal component analysis of community-level physiological profiles from forest, sugarcane, turf, and pasture soils.

DISCUSSION

Nutrient Distribution and Cycling

To investigate land-use effects on nutrient distribution and cycling, samples from the 0- to 15-cm depth were utilized because surface soils are most susceptible to changes in chemical and physical properties (Garcia-Oliva, Lanco, and Montano 2006). Long-term cultivation and fertilization in the EAA greatly altered nutrient distribution and increased the organic-matter turnover rates (Table 1). Pasture soils had more organic-matter content than other land uses and were the only land use never subjected to tillage, whereas various tillage practices were often applied to sugarcane fields to maintain drainage and for weed control (Morris et al. 2004). It has been reported that tillage practices alter the belowground ecosystem and expose subsurface organic matter to the aerobic environment, which increases organic-matter decomposition rates and may lead to soil subsidence (Reicosky and Lindstrom 1993; Gesch et al. 2007). Thus, tillage operations in sugarcane likely contributed to its lower organic-matter content than other land uses. Lohila et al. (2003) proposed that tillage-induced soil C loss was likely greater for histosols than mineral soils. Because the dominant soil of EAA is histosols and the subsidence problem is considered a result of aerobic oxidation of organic C (Shih, Glaz, and Barnes 1998), it is reasonable to postulate that frequent tillage may worsen the subsidence problems in EAA (Gesch et al. 2007).

Labile inorganic P is a readily available fraction of P that remains soluble until either absorbed or precipitated to iron (Fe), aluminum (Al), calcium (Ca), and magnesium (Mg) (Anderson et al. 1994). Therefore, it is mobile with drainage, runoff, or shallow groundwater. Sugarcane soil had about six times more labile inorganic P than pasture and two times more than forest because of its intensive fertilization history. However, we did not find any significant difference in labile organic P and PMP among soils of those land uses. In addition, labile inorganic P of the sugarcane soil accounted for 10% of its total P stock, which was more than other land uses, especially pasture (2%). In contrast, pasture soil had 10% of its total P as labile organic P, which was significantly greater than other land uses. Thus, intensive fertilization and management increased soil P retention in inorganic forms rather than organic, and conversely, land uses with minimal cultivation had a greater P sequestration in organic fractions (Graham et al. 2005). Furthermore, practices under sugarcane cropping releases more dissolved inorganic P to drainage water than both pasture and forest, which poses a greater threat to the downstream ecosystems. The Florida Everglades is highly sensitive to small increases in P concentrations (Noe, Childers, and Jones 2001). Phosphorus in the drainage water from the EAA is considered to be the key contributor to the eutrophication of Lake Okeechobee and the Everglades (Childers et al. 2003). Our results support the idea that reduced management practices and P fertilization intensity potentially decrease the P content in the EAA drainage water (Izuno et al. 1991); thus land uses that minimize soil disturbance decrease potential for eutrophication of downgradient aquatic systems.

The C/N/P ratios of forest, sugarcane, turf, and pasture soil were 939:54:1, 1178:67:1, 399:23:1, and 1528:93:1, respectively, suggesting that the pasture soil was the most P-limited land use, followed by the sugarcane and forest. There were no obvious differences in C/N ratios among land uses. However, the difference in both the C/P and N/P ratios were significant, indicating that agricultural practices greatly influenced the P sequestration in the soil. Alkaline phosphatase activity plays an important role in the P-limited ecosystem with respect to the regeneration of P from organic forms (Wright and Reddy 2001a). Hence, it was not surprising to find that the pasture soil had the most alkaline phosphatase activity, followed by the sugarcane and forest soils. No significant correlation between alkaline phosphatase activity and soil P parameters implied that other environmental factors likely contributed to this phenomenon.

Microbial Community Dynamics

Microbial communities are in close contact with soil microenvironments and therefore are easily subjected to change following alteration of soil

properties (Corstanje et al. 2007). Hence, changes in land use may cause a shift in the composition of active fractions of microbial communities, which can be explained by the changes to indices of microbial activity such as respiratory capacities and extracellular enzymatic activities (Wright and Reddy 2001b; Corstanje et al. 2007).

Significant correlations between MBC and either organic matter or dissolved organic C have been frequently observed (Yao et al. 2000; Cookson et al. 2007). However, in the present study, we did not find any such correlation. The MBC to organic matter ratio is thought to be indicative of the organic-matter quality and availability (Monkiedje et al. 2006). Our results showed that the ratio was greatest in turf and lowest in pasture (Table 2), which probably suggested that turf had the most chemical diversity in organic-matter sources and efficiency of C utilization and that conversely the pasture soil had the least. This statement was further supported by the findings that MBC to organic-matter ratio was significantly correlated with AWCD ($R^2 = 0.81$) and CMD ($R^2 = 0.65$). Pasture has less overall plant coverage than turf, forest, and sugarcane (Shih et al. 1982); thus it is reasonable to expect less chemical diversity of organic-matter sources. Analysis of PMN to MBN ratio also revealed that pasture soil had a significantly greater ratio than other land uses, indicating that its microbial communities had the least efficiency in utilizing N resources. Regarding the fact that pasture soil had less MBC and N, it was possible that pasture had the least abundance of microbial populations, which may explain its low efficiency in C and N utilization. No statistical difference was found in PMP to total P ratio and to MBP ratio, suggesting less effects of land use on the overall potential P turnover rates and utilization efficiency. In consideration of its lower abundance of microbial populations and poorer efficiency of C and N utilization, pasture soil may experience lower rates of organic-matter degradation, which was also evidenced by its greater organic-matter content (Table 1). Shih et al. (1982) reported that oxidation rates were faster in pasture than sugarcane and forest because of its higher soil temperature, mainly resulting from less vegetative cover and greater exposed area. Pasture fields were periodically mowed with residues returned back to soil, and soil was periodically covered with layers of plant residues, which provided inputs of organic matter and prevented the temperature increases. Thus, results of temperature effects on soil oxidation may be confounded by differences in sampling time and sites. Interestingly, we found significant correlations between MBC to organic-matter ratio and total P ($R^2 = 0.70$), labile inorganic P ($R^2 = 0.72$), total labile P ($R^2 = 0.73$), and MBP ($R^2 = 0.58$), implying that P plays a critical role in determining the efficiency of C utilization and degradation of organic matter by soil microorganisms. It is well known that nutrient availability, such as P, greatly influences soil

microbial activity and function (Wright and Reddy 2001a, 2001b; Corstanje et al. 2007). As demonstrated previously, pasture soil was the most P-limited system, followed by the sugarcane and forest soils. Probably, P deficiency deeply confined the microbial population, limited microbial activity, subsequently inhibited efficiency of C utilization, and reduced oxidation rates of organic matter for pasture soil.

Extracellular enzymes are excreted by the microorganisms to the soil for sequestering nutrients. The activities of those enzymes are critical for the degradation of soil organic matter and plant detritus (Wright and Reddy 2001a) and regulated by the availability of the substrates and other environmental factors (White and Reddy 1999; Corstanje et al. 2007). To characterize the effects of land uses on microbial activity, we conducted the enzymatic assays of cellobiohydrolase in the C cycle, leucine aminopeptidase in the N cycle, alkaline phosphatase in the P cycle, and arylsulfatase in the S cycle. Most of the enzymes were sensitive to the changes in land use, except leucine aminopeptidase, indicating possible differences in the composition of active fractions of soil microbial populations and biochemical processes among different land uses (Monkiedje et al. 2006). Application of land management and plant coverage greatly affected the distribution and availability of substrates and the quantity and quality of organic-matter sources, which primarily contributed to differences in enzyme activities. Significantly negative correlations were found between the leucine aminopeptidase activities and moisture content ($R^2 = -0.55$), LOI ($R^2 = -0.80$), labile organic P ($R^2 = -0.70$), and MBC ($R^2 = -0.58$), respectively. It was possible that leucine aminopeptidase was sensitive to factors other than the quality and quantity of organic-matter sources.

Sole C-source utilization patterns are commonly used to evaluate changes in microbial community composition and functional diversity and have been successfully applied to ranges of soil habitats undergoing changes in land use (Garland 1996; Campbell et al. 2003). Biolog Eco-plates were employed to investigate the utilization patterns of 31 different substrates by soil microbes. Our results indicated clearly that the microbial community composition and functional diversity differed across land uses. The CMD was greatest in turf and forest soils and least in pasture soil (Figure 1). Because the difference in the CMD profile reflects the variation in substrate diversity and availability (Grayston et al. 2004), the C sources in turf and forest soils appeared more divisive than those of the sugarcane and pasture fields, which further confirmed our aforementioned statements on the results of MBC to organic-matter ratios. Average well color development describes the average respiration of the C sources by the microbial community (Garland 1997). Results demonstrated that microbial communities of turf and forest soils were more functionally adapted to use those C resources than sugarcane and

pasture, which was consistent with our previous postulation that turf had the greatest efficiency of C utilization and pasture the lowest. Results also indicated that microbial communities of turf and forest had more capacities to acclimatize to alterations in land use (Preston-Mafham, Boddy, and Randerson 2002). Principal component analysis on the color development profiles revealed no similarity in the microbial community composition between any two of those four land uses, except that of the forest and turf (Figure 2). It has been proposed recently that both dissolved organic C and dissolved organic N indeed greatly regulate the composition of the active fractions of the soil microbial community (Schimel and Bennett 2004; Cookson et al. 2007). In the present study, we did not find any such effect. On the contrary, we found remarkable correlations between AWCD and total P ($R^2 = 0.70$), labile inorganic P ($R^2 = 0.64$), total labile P ($R^2 = 0.62$), soil C to P ratio ($R^2 = -0.92$), and soil N to P ratio ($R^2 = -0.92$). Therefore, concentrations of labile inorganic P in soil profiles play a critical role in regulating microbial community composition. Moreover, labile inorganic P is of importance in determining the C-utilization efficiency and organic-matter decomposition by microbes, which was evidenced by the fact that it was highly negatively correlated with organic-matter content (Table 3). Apparently, good agreement between results of MBC to organic-matter ratio and Biolog profile analysis firmly supported the statement that long-term intensive P fertilization in EAA might stimulate microbial communities with greater efficiency of C utilization, which in turn will enhance the organic-matter decomposition rates and consequently result in increasing soil subsidence and nutrient regeneration.

Table 3. Significant correlations of soil and microbial properties at $p < 0.05$, $n = 16$

	OM	Total P	LIP	MBC/OM	MBC	MBN	MBP	CMD
Total P	-0.61							
LIP	-0.67	0.92						
MBC/ OM	-0.72	0.70	0.72					
MBC	NS	NS	NS	0.48				
MBN	NS	NS	NS	NS	0.76			
MBP	NS	0.56	NS	0.58	0.62	0.62		
CMD	-0.57	0.56	NS	0.65	NS	NS	NS	
AWCD	-0.78	0.70	0.64	0.81	NS	NS	NS	0.88

Notes. OM, organic-matter content; LIP, labile inorganic P; MBC/OM, microbial biomass C to organic-matter content ratio; MBC, microbial biomass C; MBN, microbial biomass N; MBP, microbial biomass P; CMD, community metabolic diversity; AWCD, average well color development; and NS, not significant at $p < 0.05$.

Indicators of Land-Use Changes

Indicators have been widely recommended to specify early effects of land-use change or nutrient enrichment (Corstanje et al. 2007; Monkiedje et al. 2006). Soil organic matter is one of the key indicators for its role as nutrient source and impact on soil physical structure. Organic-matter content of soils in the EAA approximates 80–90%. Hence, alteration of the organic-matter content in the short term is probably not sensitive enough to indicate changes in land use. Instead, our results show that MBC to organic-matter ratio was highly distinct across land uses, which indicates substrate availability to soil microorganisms, and can be used as an indicator of prospective alterations in organic-matter status along with land-use changes in the EAA. Soil enzyme activities are generally the most sensitive indicators of changes of belowground microbial communities (Sicardi, Garcia-Prechac, and Frioni 2004). In our study, cellobiohydrolase activity exhibited the most variation among land uses, suggesting that this enzyme can be considered as a sensitive indicator of land use changes.

CONCLUSIONS

Long-term cultivation and fertilization in the EAA greatly altered soil nutrient distribution and increased organic-matter decomposition rates. Sugarcane cropping sequestered more P in inorganic fractions and may pose threats to the downstream Everglades ecosystems. Uncultivated pasture soils retained more P in organic fractions. Pasture soil was the most P-limited system and thus had the lowest efficiency of C and N utilization. Soil microbial community structure and metabolic diversity significantly changed after variable long-term land management. Turf and forest soils had the most diversity of C sources and utilization rates of C resources, whereas the pasture soil had the least. Soils of forest and turf were close to each other in terms of microbial community composition but were significantly different from sugarcane or pasture. Labile inorganic P played important roles in regulating organic-matter decomposition and microbial community composition and function. Our results also support the notion that changes in microbial activity represent a shift in microbial community composition. Microbial biomass C to organic-matter ratio and cellobiohydrolase activity were sensitive indicators of alterations in land uses. Turf soils potentially had a faster rate of soil subsidence and pasture soils had the slowest. Land-use change from sugarcane cropping to turf grass in EAA is likely to enhance soil subsidence. Nonetheless, land-use change from sugarcane cropping to pasture tends to slow down the oxidation rates of organic matter and subsequently may minimize soil subsidence.

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