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Carbon fluxes, nitrogen cycling, and soil microbial communities in adjacent urban, native and agricultural ecosystems

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Abstract

Urban ecosystems are expanding globally, and assessing the ecological consequences of urbanization is critical to understanding the biology of local and global change related to land use. We measured carbon (C) fluxes, nitrogen (N) cycling, and soil microbial community structure in a replicated ($n = 3$) field experiment comparing urban lawns to corn, wheat–fallow, and unmanaged shortgrass steppe ecosystems in northern Colorado. The urban and corn sites were irrigated and fertilized. Wheat and shortgrass steppe sites were not fertilized or irrigated. Aboveground net primary productivity (ANPP) in urban ecosystems ($383 \pm 11\,C\,m^{-2}\,yr^{-1}$) was four to five times greater than wheat or shortgrass steppe but significantly less than corn ($537 \pm 44\,C\,m^{-2}\,yr^{-1}$). Soil respiration ($2777 \pm 273\,g\,C\,m^{-2}\,yr^{-1}$) and total belowground C allocation ($2602 \pm 269\,g\,C\,m^{-2}\,yr^{-1}$) in urban ecosystems were both 2.5 to five times greater than any other land-use type. We estimate that for a large ($1578\,km^2$) portion of Larimer County, Colorado, urban lawns occupying 6.4% of the land area account for up to 30% of regional ANPP and 24% of regional soil respiration from land-use types that we sampled. The rate of N cycling from urban lawn mower clippings to the soil surface was comparable with the rate of N export in harvested corn (both ~ 12–$15\,g\,N\,m^{-2}\,yr^{-1}$). A one-time measurement of microbial community structure via phospholipid fatty acid analysis suggested that land-use type had a large impact on microbial biomass and a small impact on the relative abundance of broad taxonomic groups of microorganisms. Our data are consistent with several other studies suggesting that urbanization of arid and semiarid ecosystems leads to enhanced C cycling rates that alter regional C budgets.

Keywords: Colorado, land-use change, primary productivity, soil respiration, urban ecosystems, urbanization

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Introduction

It is now widely accepted that land-use change can dramatically alter ecosystem function. Particularly well documented are changes in nutrient cycles, soil structure, and carbon (C) sequestration that occur when native ecosystems are converted to agricultural use (Matson *et al*., 1987; Burke *et al*., 1995; Houghton *et al*., 1995; Paustian *et al*., 1995; Hughes *et al*., 1999). Tropical deforestation and temperate cultivation have been extensively studied because they are thought to affect the global C cycle. A third type of land-use change, urbanization, is also prevalent globally (UN (United Nations), 1987, 2001; Dwyer *et al*., 2000), but has received little attention from global change biologists. Urbanization is defined by the demographic dynamic of increasing percentages of the global population living in cities and by the concurrent land-use dynamic of conversion of unmanaged or agricultural land to urban commercial, industrial, recreational, and residential uses.

While the trend of urbanization is global, the impact is not evenly distributed. Changes in land cover and

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use are concentrated near existing expanding towns, cities, and metropolitan regions (Dwyer *et al*., 2000; UN (United Nations), 2001). Thus, most ecological research on urbanization to date contrasts urban and nonurban ecosystems at the scale of the town, city, or region. These ecological case studies suggest that urbanization causes dramatic changes in ecosystem structure and function. Forests near New York City have different soil invertebrate and fungal densities (Pouyat *et al*., 1994), soil chemistry (Pouyat *et al*., 1995), soil trace gas fluxes (Goldman *et al*., 1995), and tree ozone impacts (Gregg *et al*., 2003), than forests in rural areas. The urban ecosystems, industry, and vehicles of Phoenix, Arizona generate high nitrogen (N) gas emissions to the atmosphere resulting in greater N deposition to the urban and near urban deserts (Baker *et al*., 2001; Fenn *et al*., 2003). The urban ecosystems of Phoenix also have different soil inorganic N pools (Zhu *et al*., submitted), mycorrhizal species (Cousins *et al*., 2003), plant species (Hope *et al*., 2003), and spider population dynamics (Shochat *et al*., 2004) than nonurban ecosystems.

A few studies suggest that expanding urban land area (and not just the expansion of urban industry) may be linked to regional N and C cycles. Urban lawns occupying 6.4% of the land area in northern Colorado accounted for up to 30% of the soil N_2O emissions from that region (Kaye *et al*., 2004). Urban land-use types occupying $\sim$ 25% of the greater Phoenix, Arizona area account for $\sim$ 20% of soil respiration from that region (Koerner & Klopatek, 2002). Satellite-derived estimates of vegetative activity or simulated net primary productivity (NPP) suggest that urbanization may increase NPP in arid areas and decrease NPP in mesic regions (Imhoff *et al*., 2000; Milesi *et al*., 2003). While these studies highlight the potential importance of urbanization as a component of regional change, current knowledge of urban ecosystem ecology and feedbacks between urbanization and other components of global change lags far behind our knowledge of unmanaged and agricultural ecosystems. More local and regional scale case studies are needed to elucidate consistent patterns among urban ecosystems that will enable future analyses of the global impacts of urbanization.

The main purpose of this study was to advance our understanding of urban ecosystems as components of global change by comparing C pools and fluxes in urban lawns with simultaneous measurements in nearby irrigated agriculture (corn), dryland agriculture (wheat), and grasslands (native shortgrass steppe) in northern Colorado. We measured soil C storage, aboveground net primary productivity (ANPP), soil respiration, and belowground C allocation and estimated the contribution of urban land to regional C budgets. We compared sites that had been in their current land use for at least 60 years to identify the long-term effects of urbanization on ecosystem structure and function. In this semiarid region, we expected land-use types with high water and fertilizer inputs (lawns and corn) to have the highest ANPP. Cultivation is known to decrease soil C storage so we expected uncultivated ecosystems (lawns and shortgrass steppe) to have the highest soil C storage. With both high C inputs (NPP) and large soil organic matter pools, we expected urban ecosystems to have the highest soil respiration rates. Finally, we expected that land-use induced variability in C fluxes would lead to and be linked to variability in both ecosystem N cycling and soil microbial community structure. Thus, we compared annual N cycling in aboveground plant tissues and soil microbial community structure among land-use types.

Materials and methods

Study sites and experimental design

Fort Collins, CO was settled on the western edge of the Great Plains (latitude: 40.6N, longitude: 105.1W) in the late 1800s. Upon settlement, the native shortgrass steppe of the region was grazed by domestic livestock and cultivated for dryland crops (e.g. wheat) (Lauenroth *et al*., 1999). Intensive water development in the early 1900s enabled cultivation of irrigated crops (first beets and later corn) near rivers and canals. The population and aerial extent of the city remained small ($<$15 000 people) until the late 1950s. Currently, Fort Collins anchors the northern end of one of the fastest growing metropolitan regions in the US (US Census, 2000). Within 20 km of Fort Collins, we sampled native shortgrass steppe, dryland wheat–fallow, irrigated corn, and well-maintained urban lawns. These land-use types cover $>$75% of the area in the grassland region of Larimer County, CO (for a map of the distribution of land-use patches in this region see Kaye *et al*., 2004). We sampled Aridic Argiustolls and Ustollic Haplargids (USDA, 1999) with loamy to fine surface texture because these soils cover $>$50% of the region. We also controlled for elevation (1493–1620 m) and land-use history; all sites had been in their current land use since at least 1938, the year of the earliest aerial photograph. We gained permission to sample four to 10 sites that met these criteria and randomly selected three sites per land-use type (a stratified random sampling design).

The native vegetation of the region is shortgrass steppe grassland, with mean annual air temperature 8.9 °C and precipitation 38.5 cm yr^{-1} (100 year record at

Colorado State University, Campus Weather Station, Fort Collins, CO, USA), and wet atmospheric inorganic N deposition 0.25 g N m^{-2} yr^{-1} (National Atmospheric Deposition Program, http://nadp.sws.uiuc.edu/). Precipitation during the calendar year 2001 (our main sampling year) was 32 cm. To our knowledge (based on aerial photos, ethnography, range characteristics, and soil profiles), none of the native grassland sites we sampled were ever plowed, irrigated, or fertilized, but all were grazed in the past. The native grassland sites are dominated by *Bouteloua gracilis* (HBK) Lag. ex Steud., *Agropyron smithii* Rybd., and *Buchloe dactyloides* (Nutt.) Engelm., but exotic species (e.g. *Bromus tectorum*) were also present.

The dryland wheat cropping system in this region is a winter wheat–summer fallow rotation (during any given year each field is half wheat and half fallow). We sampled wheat and fallow areas simultaneously and present the mean value here. Wheat fields were planted in October and harvested in June, but received no irrigation or fertilization. The cornfields were continuous corn systems without legume or wheat rotations. They received 127 ± 13 cm irrigation from June to August, and were fertilized with 15 ± 2 g N m^{-2} before being planted in May. One field was fertilized in November and two were fertilized in April. As is typical in this region, the corn was harvested for silage in September or October.

The urban ecosystems are lawns dominated by Kentucky bluegrass (*Poa pratensis* L.) and bordered by trees (mostly *Ulmus*, *Populus*, and *Fraxinus* spp.). One site was institutional, one site was a rented residential home, and the third site was a residential home occupied by the owners. Management (e.g. mowing, irrigation, and fertilization) during our experiment was consistent with past management at the sites. Sprinkler irrigation monitored with rain gauges from May to October totaled 54 ± 4 cm yr^{-1} (mean $\pm$ one standard error). N fertilization in June and October totaled 11 ± 1 g N m^{-2} (two applications of 5.5 g N m^{-2} each based on Colorado State University Extension Service Gardening Series Fact Sheet 7.202; http://www.ext.colostate.edu/pubs/garden/07202.pdf). We mowed all urban sites 0.5 to two times/week from April to October with a mulching mower. Lawn clippings were not bagged, they were left on site to mimic lawn management practices in the region.

Basic soil characteristics

In June 2001, we collected five soil cores (5 cm diameter, 30 cm depth) from each site, divided the cores into 0–15 and 15–30 cm sections, weighed each core sample, composited core samples from the same site and depth, and subsampled composited soil for the following analyses. On oven dried (105 °C to constant mass) and sieved (2 mm) subsamples, we measured soil texture using a 40 s hydrometer reading for percent clay and sieving (53 μm) for percent sand. On oven dried, sieved (2 mm), and ground subsamples, soil total C and N content were determined by dry combustion (LECO-1000, LECO Corporation, St Joseph, MI, USA), inorganic C content was determined by pressure calcimeter (Wagner *et al.*, 1998), and organic C content was determined by difference. Bulk density was determined from the mean rock free (2 mm sieve), oven dry mass of the cores and the core volume. We determined soil pH on the supernatant of a 1 : 1 mixture (10 g air dry soil to 10 mL solution) of either deionized H_2O or 0.01 M $CaCl_2$ after shaking and allowing the suspension to settle for 30 min.

We estimated potential C mineralization and net N mineralization on four fresh soil samples (20 g each) from the same June 2001 soil collection using 30 day laboratory incubations. The first subsample was used to determine gravimetric water content by oven drying (105 °C) to constant mass. The second subsample was immediately extracted (100 mL of 2 M KCl). The remaining two subsamples were placed in plastic specimen cups and brought to field capacity soil moisture, then the specimen cups were sealed in an airtight 2 L glass jar with 20 mL of deionized water to maintain humidity and prevent soil drying. Before the jars were sealed, they were fanned with ambient air to provide a uniform background CO_2 concentration. After 2 weeks, we used a syringe to mix and sample the headspace gas through septa in the jar lids, and determined the concentration of CO_2 in a 2 mL headspace sample using an infrared gas analyzer (LI-COR-6252, LI-COR Bioscience, Lincoln, NE, USA). Three sealed jars without soil were used as blanks to correct for ambient CO_2. Atmospheric pressure, air temperature, the volume of the jars, the volume of gas sampled, and oven dry soil mass were used to convert headspace concentration to μg C g $soil^{-1}$. We repeated this CO_2 sampling protocol for the second 2 weeks of the incubation and calculated potential C mineralization as total C released over 30 days. Following the final headspace gas sampling, we removed the two incubated specimen cups and extracted them separately for inorganic N. Ammonium and nitrate plus nitrite concentrations were determined on initial and final KCl extracts using flow injection colorimetry and the soil water volume, KCl volume, and the dry mass of the extracted soil converted results to μg N g $soil^{-1}$. We calculated potential net N mineralization as the mean inorganic N concentration of incubated subsamples minus the inorganic N concentration of the initial extract.

Field flux measurements

We estimated soil respiration by measuring the accumulation of CO_2 in a static soil cover (1.5 L) every 4 s for 1 min using a PP Systems (Haverhill, MA, USA) EGM-1 infrared gas analyzer equipped with a chamber baffle that prevented high fan speeds from creating erroneously high CO_2 flux values. We could not use permanent chamber bases (because management practices would destroy them), so at each measurement point we inserted the gas chamber into the soil and then removed the chamber and waited 15 min before the chamber was reinserted in the same location to record CO_2 fluxes. Green foliage was clipped in the area of the CO_2 chamber prior to the first chamber insertion. At all sites, daily flux measurements were estimated from the mean of six samples collected approximately twice per month during the growing season once per month during the winter, with additional samples preceding and following fertilization and irrigation events. All gas samples were taken between 09:00 and 13:00 hours because previous diel chamber measurements (Arvin Mosier, USDA ARS, personal communication) suggested that this time was representative of the average flux value for the day in our research area. We tested this assumption in June and August by repeatedly sampling sites over a 24 h period (four samples from a given site over 24 h) and found that in all land-use types and both sampling dates, the midmorning measurement was an excellent predictor of mean soil respiration over 24 h (midday $= 0.007 + 0.95 \times 24$ h-mean; $r^2 = 0.98$). It was impractical to sample all 12 sites on a single morning. Values presented here as a mean flux rate on a specific day were actually collected on 3 different days within 5 days of each other. On each of the 3 days, one site from each land-use type was sampled. We calculated the annual soil CO_2 flux for the period January 1, 2001 to December 31, 2001 (the one sampling date from 2000 was not used for interpolation), using linear interpolation between measurement dates unless a measurement preceded or followed a climatic or management event known to have a large effect on gas fluxes (e.g. snowmelt, fertilization, irrigation), in which case, the interpolation was truncated based on the timing of the event.

ANPP and plant N uptake (urban and agricultural sites only) were determined using a variety of clipping, litterfall collection, and allometric methods appropriate for the different ecosystem types (Sala *et al.*, 2000), followed by drying (70 °C), grinding, and dry combustion analysis of C and N concentrations in plant tissues. While traditional ecosystem studies typically compare NPP among systems using a constant methodology, our experimental design required a more complex approach that tailored NPP methods to each land-use type. We used established clipping methodology for native and agricultural NPP measurements and a combination of clipping, litterfall collection and allometry to estimate urban NPP. This approach enabled us to obtain the best estimate for each land-use type under real-world management conditions. The ANPP of each shortgrass steppe site was determined from the mean of six small circular plots (0.25 m^2). Herbaceous biomass within each plot was clipped and biomass from previous years was identified by color and brittleness and removed. In corn and wheat ecosystems, ANPP was estimated by clipping three plots (1 m $\times$ 4 m) at each site immediately prior to harvesting. Following the commercial harvest, we measured the mass of stubble left on the site to be ploughed into soil in the following spring. Weeds were negligible in the corn ecosystems, but in the fallow portion of the wheat fields, weed ANPP was estimated by clipping prior to weed management practices (e.g., mechanical ripping and herbicide). The ANPP of urban grass clippings was estimated using a bagging mower. On each mowing date, we collected clippings captured in the mower bag in one mower pass (53 cm wide) that spanned the entire length of the longest dimension of the lawn. We found that passing over this strip of lawn twice collected more than 99% of the clippings. Dry clipping mass was divided by the sampled area (mower width times lawn length; always >13 m^2), to estimate clipping productivity. Because lawns were mowed on different days and with variable frequency throughout the season, productivity is presented here as a monthly rate. N cycling in grass clippings was estimated by compositing samples within a site each month prior to analysis for N concentration and multiplying by monthly productivity. The live biomass of grass below the mower (stubble; grass below 5.24 cm) was estimated in six plots (0.25 m $\times$ 0.25 m) per lawn at the end of the growing season (October) and ANPP of this C pool was calculated as the product of measured biomass and turnover rate (Dahlman & Kucera, 1965). We did not directly measure turnover, so we used the mean of three published estimates of Kentucky bluegrass stubble turnover rate (0.48, 0.625, and 0.5 $year^{-1}$ from Falk, 1976, 1980; Jo & McPhearson, 1995, respectively), all of which calculated turnover as the annual increment of stubble mass divided by maximum stubble biomass.

The ANPP and N cycling in urban litter fall from trees and shrubs were estimated by raking 10 plots (1 m^2 per plot) in each yard at intervals of 2–7 days in the autumn. The ANPP of urban tree biomass increment was estimated by taking two short increment cores 180° apart from a subset of trees in each yard.

Immediately after taking the cores, bark thickness was measured and then cores were mounted and surfaced, and annual radial growth from 1992 to 2001 was recorded to the nearest 0.001 mm with an incremental measuring stage. Annual radial growth increments were averaged per tree, doubled, and subtracted from the measured 2001 DBH to calculate DBH values for 1992–2001. We assumed that bark thickness did not change significantly from 1992 to 2001. Some homeowners did not allow us to core some smaller trees, so we developed a regression between 2001 DBH and 2001 growth increment ($r^2 = 0.60$; $P < 0.001$) using trees from other residential lots and public parks. The productivity of uncored trees accounted for 11–29% of total tree productivity at a given site. DBH values were converted to tree biomass using an allometric equation derived from 24 urban hardwood trees ranging from 25 to 99 cm DBH (*Ulmus*, *Fraxinus*, and *Acer* spp.; Jo & McPhearson, 1995):

$$\ln \text{biomass} = -3.5618 + 2.6645 \ln \text{DBH};\ r^2 = 0.95, \quad (1)$$

where biomass (kg) is total aboveground mass of wood, bark, and foliage. Annual productivity was estimated by subtracting biomass at the end of the 2001 growing season from biomass at the end of the 2000 growing season. Because new increments in foliage were already accounted for in our autumn raking sample, using the equation of Jo & McPhearson (1995) overestimates total tree ANPP. Equations relating urban tree DBH to foliar biomass alone only exist for smaller (11–53 cm) hardwoods (Nowak, 1996). Applying this equation to trees in our study suggested that we overestimated total aboveground tree biomass by 4–5%. There were no major pruning events at our sites during the study, and using urban trees to generate Eqn (1) accounts for the long-term effects of pruning on ANPP.

Total belowground C allocation (TBCA) was calculated based on Raich & Nadelhoffer (1989) as: soil respiration − ANPP that enters the soil + Δ (soil C storage). The ANPP that enters the soil is clipping plus below mower stubble productivity in urban ecosystems, unharvested stubble in agricultural systems, and total ANPP in shortgrass steppe. We assumed that annual changes in soil C were negligible because all of the sites that we sampled had been in their current land use since at least 1938 and previous research in nearby turfgrass (Qian & Follett, 2002) and agricultural (Burke *et al*., 1995) ecosystems suggests that soil C pool sizes are near steady state within 50 years of initial urban or agricultural land use.

To determine the role of urban lawns in the regional C budget, we used our previously published estimates of the fraction of urban ecosystems that are lawn, and the regional coverage of all land-use types in the eastern portion of Larimer County (Colorado, USA) (Kaye *et al*., 2004). Land-use types that we sampled cover 77% of the land area in this 1578 km^2 region with water (5%) and hay pasture (12%) accounting for most of area in land-use types that we did not sample. We weighted mean values for ANPP and soil respiration by their proportional land cover to determine the relative contribution of each land-use type to the regional fluxes of C. We interpret (Kaye *et al*., 2004) these estimates of regional C flux as an upper bound for the contribution of urban land to regional fluxes because: (1) we assumed that land not occupied by pavement and buildings is lawns (invalid for gravel driveways and vacant lots), (2) poorly managed lawns would have smaller irrigation and fertilizer inputs than our plots, and (3) newer housing developments may have less lawn per unit area than the older neighbourhoods that we sampled. However, it is also worth noting that our calculated total urban land area is an underestimate because of rapid urban expansion between the time of the land cover classification (early 1990s) and our analysis.

Microbial community structure

We assessed microbial community structure using phospholipid fatty acid (PLFA) analysis (Vestal & White, 1989). PLFA analysis allows quantification of the viable microbial biomass and the taxonomic group composition at the time of sampling based on the total amount of phospholipids extracted and the chemical make-up of the constituent fatty acids (Vestal & White, 1989). Soils were collected in June 2001 at the same time samples were taken for basic soil characterization, placed on dry ice immediately following sampling in the field, and stored in a −70 °C freezer until processed. Frozen samples were allowed to thaw for 15–30 min. Each sample/core was homogenized, and then ~ 20 g of field moist soil was extracted in a single phase, phosphate buffered $CHCl_3$–CH_3OH solution to remove PLFAs (Bligh & Dyer, 1959). We separated PLFAs by silicic acid chromatography and derivitized the PLFAs in an alkaline system to form fatty acid methyl esters (FAMEs) (White *et al*., 1979). We separated and quantified FAMEs on a Hewlett Packard 5890 Series 2 gas chromatograph (equipped with a 50 m long, 0.33 μm thick, and 0.2 mm i.d. column) linked to a Hewlett Packard 5971A mass spectrometer detector (Agilent Technologies, Palo Alto, CA, USA). Column temperature was held at 70 °C for the first 0.5 min of the analysis and was then increased to 110 °C (at 20 °C min^{-1}) and then to 120 °C (at 10 °C min^{-1}). The injector and detector were maintained at 240 °C and 280 °C, respectively. Individual FAME spectra were

identified using an existing FAME library (D. C. White, unpublished data, 1999).

FAMEs are described by standard nomenclature (IUPAC-IUB, 1977) (A : BωC), where 'A' indicates the total number of C atoms, 'B' the number of unsaturated bonds, and 'ωC' indicates the number of C atoms between the aliphatic end of the molecule and the first unsaturated bond. *Cis* and *trans* isomers are indicated by the suffixes 'c' and 't', respectively. Other notations are 'Me' for methyl groups, 'cy' for cyclopropyl groups, and the prefixes 'i' and 'a' for *iso* and *anteiso* methyl branching, respectively.

Statistics

Prior to statistical analyses, we averaged wheat and fallow data because our emphasis was on urban ecosystems and how they compare with the surrounding agricultural and grassland landscape rather than details about variability within the agricultural landscapes. Ecosystem C fluxes and total quantity of PLFA extracted were analyzed with a one-way analysis of variance (ANOVA) testing for the effect of land use. We transformed data as needed to fit the normality assumptions, and we used least-significant difference means separation tests to interpret the significant main effect of land use.

The microbial community structure data included 19 FAMEs that were consistently found in all of the samples; these represent a wide array of microbial taxonomic groups (additional FAMEs identified but excluded from the principal components analysis (PCA) occurred in low amounts, $<1.0\%$ mole in all cases). Many of these FAMEs are autocorrelated, so we extracted the most important variability in the data set using PCA on those 19 FAMEs. We log transformed the mole fraction of each FAME used in the PCA to achieve normal distributions. Once we acquired the first (PC1) and second (PC2) principal component scores for each sample, we ran ANOVAs to determine whether PC1 and PC2 scores differed among land-use types. To further evaluate the change in microbial community structure, the mole fractions of each of the FAMEs used in the PCA were analyzed via ANOVA for significant 'land-use' main effects.

Results

Basic soil characteristics

Urban lawns contained $4758 \pm 272\,\mathrm{g\,organic\,C\,m^{-2}}$ (mean and one standard error) and $465 \pm 34\,\mathrm{g\,N\,m^{-2}}$ in surface soils (0–15 cm), which is 65% more C and N than shortgrass steppe soils and 100% more than agricultural soils (Table 1). In deeper soils (15–30 cm), there were no differences in organic C and total N among land-use types. In surface soils, the organic C : total N ratio was greater in urban and shortgrass steppe soils (~ 10) than in agricultural soils (~ 8–9) and in deeper soils, urban soils (~ 10) had a wider C : N ratio than all other land-use types (~ 7–9). Inorganic C content, soil texture (with the exception of low % sand in deeper wheat soils), and soil pH (with the exception of low pH in $CaCl_2$ from corn surface soils) generally did not differ among land-use types at either depth. Bulk density in surface (but not deeper) soils was higher in urban and agricultural ecosystems than in shortgrass steppe.

Field C and N fluxes

The C and N fluxes from mown grass clippings to the soil surface increased rapidly from April ($\sim 9.5\,\mathrm{g\,C\,m^{-2}\,month^{-1}}$ and $0.75\,\mathrm{g\,N\,m^{-2}\,month^{-1}}$) to maxima in May ($\sim 43\,\mathrm{g\,C\,m^{-2}\,month^{-1}}$ and $3.2\,\mathrm{g\,N\,m^{-2}\,month^{-1}}$) and then declined steadily (Fig. 1). Seasonal variations in N cycling in mown grass were driven mainly by biomass changes as the N concentration (from 3% to 4% N by mass) and C : N ratio (from 10 to 14) of grass clippings varied much less than productivity (Fig. 1). The annual rate of N cycling in grass cut by the mower ($11.3 \pm 0.5\,\mathrm{g\,N\,m^{-2}\,yr^{-1}}$) was comparable with corn harvesting ($15.2 \pm 1.4\,\mathrm{g\,N\,m^{-2}\,yr^{-1}}$) and five to 10 times greater than urban tree litter fall removal or wheat harvesting (both $<2\,\mathrm{g\,N\,m^{-2}\,yr^{-1}}$; Table 2). The annual C flux in grass cut by the mower ($133 \pm 4\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$; cut grass was $42.1 \pm 0.3\%$ C throughout the growing season) was comparable with tree wood productivity ($159 \pm 15\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ assuming wood is 48% C), and greater than below-mower stubble productivity ($42 \pm 5\,\mathrm{C\,m^{-2}\,yr^{-1}}$ assuming stubble is 42.1% C), or tree and shrub litter fall ($49 \pm 3\,\mathrm{C\,m^{-2}\,yr^{-1}}$ with measured C concentration $42.2 \pm 0.6\%$ C). At the ecosystem level (Fig. 2), total aboveground urban productivity ($383 \pm 11\,\mathrm{C\,m^{-2}\,yr^{-1}}$) was four to five times greater than wheat or shortgrass steppe productivity but significantly less than corn productivity ($537 \pm 44\,\mathrm{C\,m^{-2}\,yr^{-1}}$).

Urban soil respiration increased rapidly as soils warmed in the spring, and high rates ($>0.5\,\mathrm{g\,C\,m^{-2}\,h^{-1}}$) were sustained from April until soils cooled in October (Fig. 3). In all other land-use types, spring warming produced short-lived maximum CO_2 fluxes $<0.3\,\mathrm{g\,C\,m^{-2}\,h^{-1}}$, followed by a rapid decline correlated with seasonal soil drying (Kaye *et al.*, 2004). Corn ecosystems reached a second peak in soil CO_2 flux in July after the onset of irrigation and rapid plant growth. Sustained, high soil CO_2 fluxes in the urban lawns

Table 1 Selected soil characteristics at the study sites

Soil characteristic	Depth (cm)	Land use			
		Urban	Wheat	Corn	Native
Organic carbon ($g\,m^{-2}$)	0–15	4758 (272)^{c}	1847 (418)^{ab}	1662 (373)^{a}	2852 (287)^{b}
	15–30	2184 (626)^{a}	1662 (133)^{a}	1857 (753)^{a}	1925 (203)^{a}
Inorganic carbon ($g\,m^{-2}$)	0–15	126 (64)^{a}	720 (394)^{a}	77 (68)^{a}	19 (12)^{a}
	15–30	199 (158)^{a}	1372 (823)^{a}	71 (64)^{a}	1214 (32)^{a}
Total nitrogen ($g\,m^{-2}$)	0–15	465 (34)^{b}	233 (18)^{a}	189 (51)^{a}	282 (28)^{a}
	15–30	212 (67)^{a}	236 (21)^{a}	212 (88)^{a}	225 (12)^{a}
Organic C : Total N	0–15	10.3 (0.6)^{b}	7.8 (1.3)^{a}	9.0 (0.6)^{a}	10.1 (0.0)^{ab}
	15–30	10.5 (0.4)^{c}	7.1 (0.5)^{a}	8.9 (0.2)^{b}	8.5 (0.5)^{b}
Sand (%, by weight)	0–15	58 (8)^{a}	29 (6)^{a}	59 (10)^{a}	39 (11)^{a}
	15–30	59 (9)^{b}	24 (6)^{a}	58 (11)^{b}	52 (4)^{b}
Clay (%, by weight)	0–15	21 (5)^{a}	42 (4)^{a}	23 (8)^{a}	39 (8)^{a}
	15–30	24 (5)^{a}	45 (5)^{a}	25 (8)^{a}	29 (3)^{a}
Bulk density ($g\,cm^{-3}$)	0–15	1.19 (0.02)^{b}	1.27 (0.03)^{b}	1.25 (0.02)^{b}	1.10 (0.03)^{a}
	15–30	1.33 (0.08)^{a}	1.43 (0.03)^{a}	1.40 (0.01)^{a}	1.23 (0.04)^{a}
pH in H_2O	0–15	7.7 (0.1)^{a}	7.9 (0.1)^{a}	7.6 (0.2)^{a}	7.7 (0.1)^{a}
	15–30	7.9 (0.2)^{a}	8.0 (0.0)^{a}	7.6 (0.3)^{a}	8.1 (0.0)^{a}
pH in $CaCl_2$	0–15	6.9 (0.2)^{b}	7.1 (0.1)^{b}	6.5 (0.1)^{a}	7.0 (0.1)^{b}
	15–30	7.1 (0.4)^{a}	7.3 (0.2)^{a}	6.7 (0.2)^{a}	6.8 (0.1)^{a}
C_{min} ($\mu g\,C\,g\,soil^{-1}\,day^{-1}$)*	0–15	31.6 (10.3)^{a}	9.7 (3.5)^{a}	15.7 (8.7)^{a}	20.5 (7.3)^{a}
N_{min} ($\mu g\,N\,g\,soil^{-1}\,day^{-1}$)*	0–15	1.76 (0.86)^{b}	0.14 (0.05)^{a}	0.29 (0.09)^{a}	0.04 (0.02)^{a}

Values are means ($n = 3$) with one standard error in parentheses. Different lowercase letters within a row denote statistical differences among land-use types ($P < 0.05$).
*Potential carbon (C) and net nitrogen (N) mineralization during 30-day laboratory incubations.

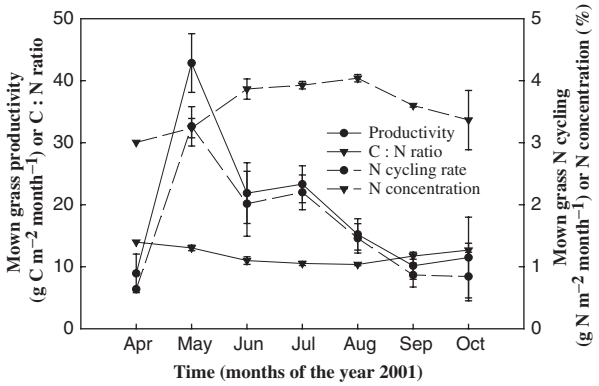

Fig. 1 Seasonal dynamics in the productivity (expressed as carbon (C)), C : N ratio, nitrogen (N) concentration, and N cycling rate of mown grass clippings in urban lawns. Points are means ($n = 3$) and one standard error.

appear to result from persistently elevated soil moisture, rather than an urban heat island; summer soil temperatures were lowest in urban ecosystems (Kaye *et al*., 2004). Mean annual soil respiration from urban ecosystems was $2777 \pm 273\,g\,C\,m^{-2}\,yr^{-1}$, which is three to five times greater than the other land-use types in this study (Fig. 2). TBCA in urban ecosystems ($2602 \pm 269\,g\,C\,m^{-2}\,yr^{-1}$) was also three to five times greater than other land-use types (Fig. 2).

Table 2 Mean (and one standard error; $n = 3$) plant tissue nitrogen (N) concentrations (% of dry mass) and managed N fluxes in urban and agricultural ecosystems

Management type	N concentration (% N)	N flux ($g\,N\,m^{-2}\,yr^{-1}$)
Urban grass mowing	3.0–4.0*	11.3 (0.5)
Urban tree and shrub litter fall	0.99 (0.04)	1.1 (0.1)
Corn harvest	1.2 (0.0)	15.2 (1.4)
Wheat harvest	0.9 (0.1)	1.8 (0.4)

*Range is from seasonal variation, see Fig. 1.

Scaling annual fluxes to the region (Table 3), we found that urban lawns that covered 6.4% of the region accounted for up to 30% of regional ANPP and 23% of regional soil respiration from land-use types that we sampled. Corn was also a major contributor to regional ANPP (49%) and shortgrass steppe was the other major regional source of soil respiration (55%).

Soil microbial community structure and function

The quantity of extractable PLFAs per gram of soil (a good index of total viable microbial biomass at the time

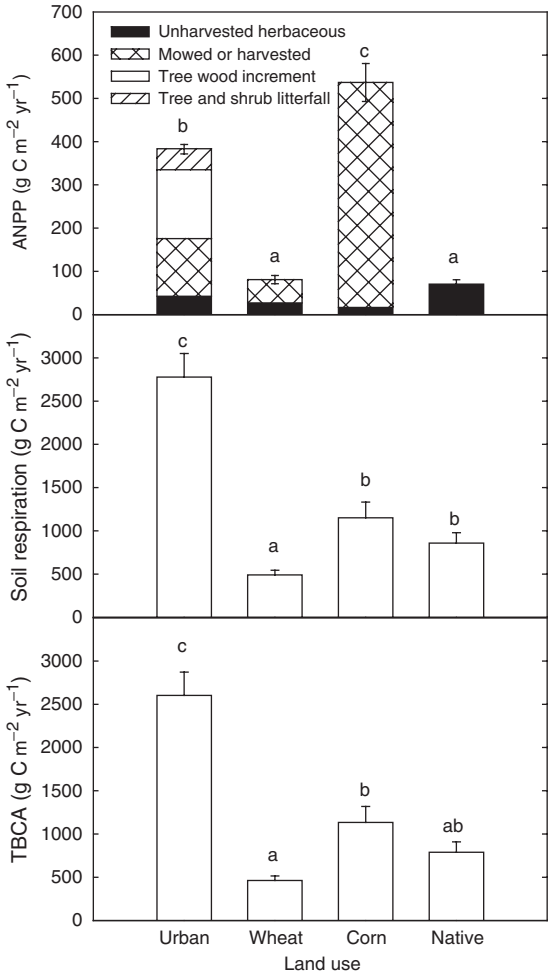

Fig. 2 Aboveground net primary productivity (ANPP), soil respiration, and total belowground carbon (C) allocation (TBCA) in urban, agricultural, and native shortgrass steppe ecosystems. Bars are means ($n = 3$) and one standard error and land uses differ significantly ($\alpha = 0.05$) when bars have different lowercase letters. Unharvested herbaceous biomass refers to stubble below lawn mowers in urban ecosystems, stubble left behind after commercial agricultural harvesting, or all ANPP in the shortgrass steppe.

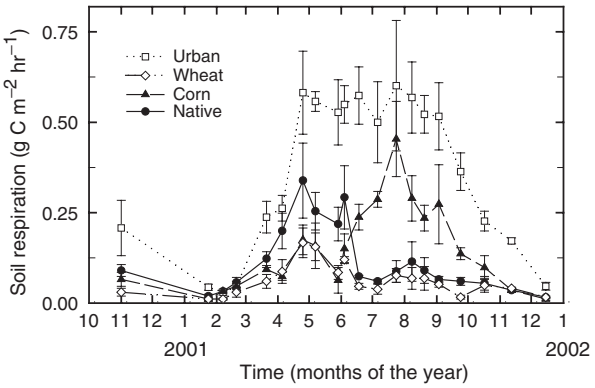

Fig. 3 Seasonal variation in soil respiration among urban, agricultural, and native grassland ecosystems. Points are mean ($n = 3$) plus or minus one standard error.

of sampling; Vestal & White, 1989) was twice as great in urban ecosystems as in any other land-use type (Table 4). Both fungal and bacterial biomass were highest in urban ecosystems (Table 4). Total soil N and field soil respiration at the time soils were collected explained 77% of the variability in total PLFA [log(total PLFA) = 9.231 + 0.002 × (total N) + 0.246 × log(soil respiration); $P < 0.01$].

Significant 'land use' main effects occurred in only six of the 19 FAME markers included in the PCA, including all Gram-negative markers, one other bacterial marker, and one fungal marker (Fig. 4). Within these six FAMEs, no consistent trends with regard to land use were identified. The first two principal components in the ordination analysis explained 45.4% of the variability in the FAME data, but showed little systematic variation in microbial community composition across land-use types (Fig. 5). Neither PC1 nor PC2 axis scores were significantly related to the main effect 'land use.' FAMEs with large positive (>0.3) weights were i17:0, a17:0, 17:0, and 10Me18:0 for PC1 and i14:0, 14:0, and cy17:0 for PC2. Large negatively (<−0.3) weighted FAMEs included 16:1w7c,t and 18:1w9t for PC1 and 18:1w9c,t for PC2.

Despite greater microbial biomass and total organic C in urban surface soils in the field, potentially mineralizable C in the laboratory did not differ among land-use types. Potentially mineralizable N was greater in urban ecosystems than in other land-use types (Table 1).

Discussion

Comparing urban ecosystem C and N fluxes to other ecosystems

Regional and global C studies often omit urban areas or assume that urban lands have similar C fluxes to other land-use types (Baron *et al*., 1997; Running *et al*., 2000). Our data show that neither of these approaches is appropriate for understanding regional C fluxes in semiarid environments; urban ecosystems accounted for large portions of regional ANPP and soil respiration despite the fact that lawns covered only 6.4% of the area (Table 3). Similar results have been measured for soil respiration in Arizona (Koerner & Klopatek, 2002) and simulated for ANPP in the southeastern US (Milesi *et al*., 2003).

Several factors distinguished urban C fluxes from other ecosystems that we sampled. Urban ANPP

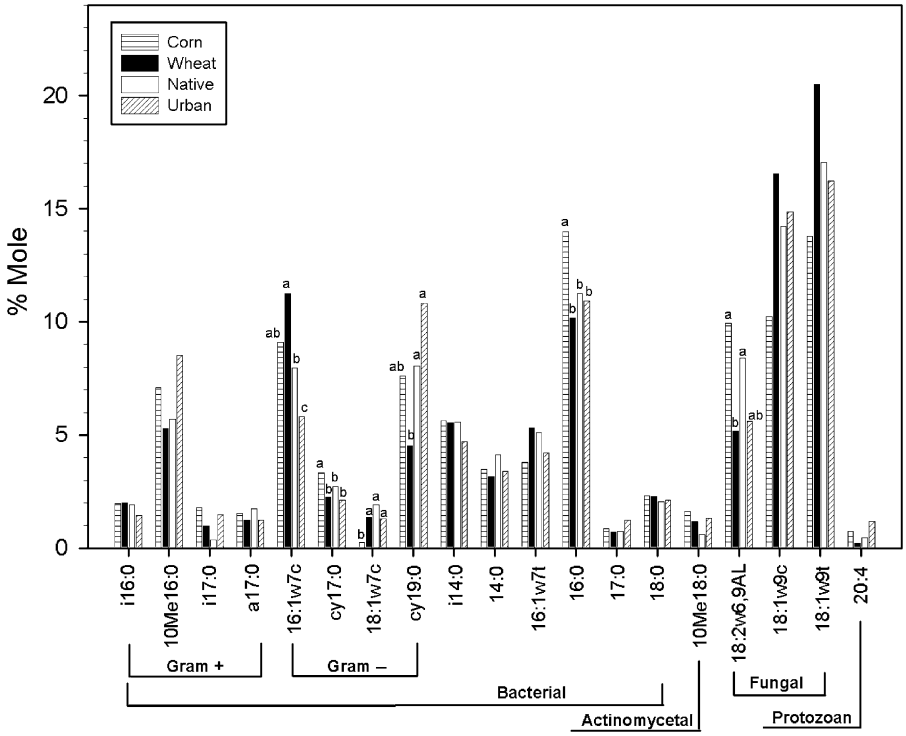

Fig. 4 Relative abundance (% mole fraction) of 19 fatty acid methyl esters included in the principal component analysis for the four land-use types and their placement into the microbial taxonomic groups (bacteria, actinomycetal, fungal, and protozoan). Bars are the mean of $n = 3$ sites per land-use type. Different letters represent significant differences between land-use types ($P < 0.05$).

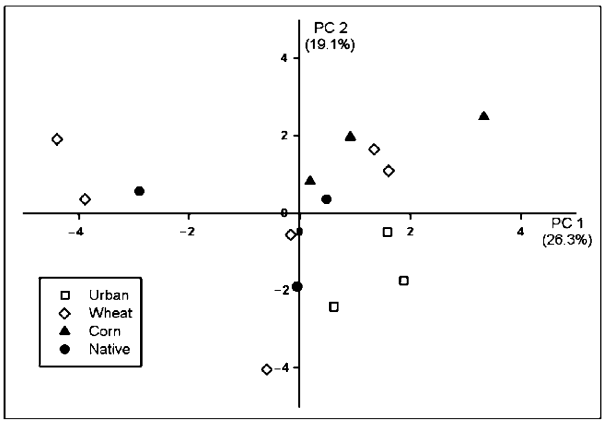

Fig. 5 Ordination of the fatty acid methyl ester dataset from four land-use types (principal component axes 1 and 2 – PC1 and PC2; $n = 6$ for wheat because of fallow and wheat treatments being run separately). ANOVAs testing the main effect of 'land use' on PC1 and PC2 scores were not statistically significant. Positive scores on both axes were driven by bacterial fatty acid methyl ester (FAME) markers, while negative scores reflect dominance of fungal FAMEs within a sample.

Table 3 The contribution of different land-use types to regional aboveground net primary productivity (ANPP) and soil respiration

		% from sampled area	
Land use	Land area (% of region)*	ANPP	Soil respiration
Urban impervious	3.8	0	0
Urban lawns	6.4	29.6	22.6
Corn	12.6	49.0	18.3
Wheat–fallow	7.6	2.5	4.7
Shortgrass steppe	50.2	18.9	54.5
Total sampled area	76.8	100	100

The 'region' refers to the entire eastern portion of Larimer County, CO and 'sampled area' refers to the area within that region that is occupied by the land-use types that we sampled. Impervious urban surfaces were not measured, they were assumed to be zero. These estimates represent and upper bound for the contribution of urban lands to regional ANPP and soil respiration (Kaye *et al.*, 2004)
*From Kaye *et al.* (2004).

included approximately equal contributions from woody and herbaceous components, while all other local ecosystems were dominated by herbaceous ANPP (Fig. 2). Urban herbaceous ANPP showed high spring productivity typical of C3 grasses, but unlike other C3 grasses in the region (e.g. wheat and some shortgrass

steppe species), lawns remained productive in late June and July whereas C4 plants are the most active herbaceous species in nonurban systems at this time of year (e.g. corn and dominant shortgrass steppe species). The seasonality of soil respiration in urban ecosystems was not correlated with natural precipitation patterns; high fluxes occurred when soils were warm (Fig. 3). Urban ecosystems allocate far more C belowground (Fig. 3) and have greater surface soil C storage (Table 1) than native or agricultural ecosystems in this region. Urban lawns in New England, Baltimore and Arizona, USA also have greater soil C storage than nonurban land-use types (Pouyat *et al*., 2002; Zhu *et al*., submitted).

Our measured ANPP and soil respiration rates (Fig. 2) are similar to previous estimates from shortgrass steppe (Milchunas & Lauenroth, 1992; McCulley *et al*., in press), irrigated corn (Brye *et al*., 2002), and dryland wheat (Buyanovsky & Wagner, 1995; Lauenroth *et al*., 2000). We know of only one other estimate of total ANPP from urban landscapes (Jo & McPherson, 1995), but we could not extract a value for ANPP from their estimated total C flux (including mulch import, mower fuel, etc.). Our estimate of ANPP for mown grass in urban lawns (Fig. 2) is within the range of previous studies (77–197 $g C m^{-2} yr^{-1}$; Herte *et al*., 1971; Madison, 1971; Jo & McPherson, 1995; Qian *et al*., 2003). The productivity of grass beneath the mower (Fig. 2) may be the most uncertain number in our ANPP calculation (based on published turnover rates and one field measurement of standing biomass), but it falls within the range of published values (25–75 $g C m^{-2} yr^{-1}$; Falk, 1976; Jo & McPherson, 1995; Qian *et al*., 2003). The only other published estimate of urban shrub and tree litter fall (75–150 $g C m^{-2} yr^{-1}$; Jo & McPherson, 1995) is somewhat higher than our estimate (Fig. 2). Our ANPP value did not include productivity from shrub wood increment and nongrass herbaceous production, but literature values suggest that these components contribute $<10\%$ of urban ANPP (Herte *et al*., 1971; Jo & McPherson, 1995).

The only other published estimates of soil respiration from urban lawns are from Phoenix, AZ (Koerner & Klopatek, 2002; Green & Oleksyszyn, 2002) where the range of daily flux rates was similar to ours, and annual rates ($\sim 2000 g C m^{-2} yr^{-1}$) were near the low end of the variance in our estimates (Fig. 2). These data suggest that soil respiration from urban lawns is greater than in most natural ecosystems (Raich & Potter, 1996) and comparable with wet tropical forests and pastures (Townsend *et al*., 1995).

Two of the variables that we measured, ANPP and soil C storage, have been measured across climate variability gradients and simulated in various global climate change scenarios for this region. Measured shortgrass steppe ANPP varied from 23 to 69 $g C m^{-2} yr^{-1}$ (assuming biomass was 42% C) during years with mean annual precipitation ranging from 100 to 600 mm (Lauenroth & Sala, 1992). Burke *et al*. (1991) simulated changes in soil C storage in shortgrass steppe following 50 years of warming (5 °C) and small changes in precipitation ($<5 cm yr^{-1}$) and found that soil C storage decreased by 100–150 $g C m^{-2}$. Paustian *et al*. (1996) simulated changes in wheat–fallow systems (in eastern Colorado) and found that changes in the amount and distribution of precipitation could change both ANPP and surface soil C storage by up to 20 $g C m^{-2}$. Warming in conjunction with changes in precipitation caused soil C losses of 100–200 $g C m^{-2}$ (Paustian *et al*., 1996). Thus, changes in shortgrass steppe or wheat–fallow ANPP and soil C storage resulting from interannual climate variability or predicted climate change are much smaller differences in ANPP ($\sim 300 g C m^{-2} yr^{-1}$) and soil C storage ($>1000 g C m^{-2}$) between these land-use types and urban lawns. For corn, simulated effects of climate warming on ANPP (+2% to –12% change; Baron *et al*., 1997) are similar to the difference in ANPP between corn and urban ecosystems.

These results suggest that urbanization of certain land-use types (shortgrass steppe and wheat–fallow) may have a larger impact on ANPP and C storage than climate change. However, it is important to note that all of our sites had been in their current land use for >60 years. Our comparison among ecosystems represents the long-term effects of urbanization without elucidating important dynamics at times scales <60 years. For example, a chronosequence near our sites showed that turfgrass soils >50 years old are near steady state with respect to soil C (Qian & Follett, 2002). Thus, despite the high-current annual TBCA observed in our study, current differences in soil C must have resulted from rapid accumulation during the first several decades of turf establishment. Future research that includes a chronosequence of urban lawns, and multiyear measurements of lawn responses to interannual climate variability are still needed to develop a complete understanding of urban C dynamics.

While urban and agricultural ecosystems both have large inorganic N inputs, we predicted that differences in management practices would lead to large differences in N cycling, including N export among these systems. As expected (Burke *et al*., 2002), fertilized and irrigated corn ecosystems had large N exports in harvested biomass while unfertilized dryland wheat ecosystems had small N exports (Table 2). Urban leaf raking represents a major C export from the system ($\sim 20\%$ of ANPP), but removes only a small amount of

N. In contrast, N cycling in urban lawn clippings (Table 2) was similar to fertilizer N inputs ($11\,g\,N\,m^{-2}\,yr^{-1}$). Mown grass clippings are not typically removed from lawns in this region (Colorado State University Extension Service Gardening Series Fact Sheet 7.202; http://www.ext.colostate.edu/pubs/garden/07202.pdf), so mowing represents a large human-induced internal N flux that does not occur in fertilized corn fields. Our results support the simulations of Qian *et al*. (2003) suggesting that clipping removal could have a large impact on the N budget of lawns in Colorado.

Comparing the urban soil microbial community to other ecosystems

Because plant C fuels the metabolism of many soil microorganisms, we anticipated that altered C fluxes coupled with N fertilizer (which provides a substrate for microbial growth and an energy source for nitrifying bacteria) and irrigation (which creates a periodic anaerobic microbial environment) would cause urban microbial community structure to differ from native or agricultural microbial communities. We collected soils for the microbial community analysis in June when we expected the greatest differences in microbial communities because of high potential inorganic N cycling (Table 1) and soil moisture (Kaye *et al*., 2004) in urban systems. These differences in soils clearly affected the biomass of microorganisms; total, fungal, and bacterial biomass were twice as great in urban ecosystems as nonurban ecosystems (Table 4). The link between microbial biomass and ecosystem C and N dynamics was also assessed via multiple regression; a model including soil total N and soil respiration explained 77% of the variance in total PLFA.

In contrast to microbial biomass, the relative abundance of broad microbial taxonomic groups were surprisingly similar among the land-use types (Figs 4 and 5). Out of 19 FAME markers, land-use effects on relative abundance were restricted mainly to Gram-negative bacterial markers (Fig. 4). Land-use effects were not systematic even within a taxonomic group of markers. For example, within Gram-negative bacterial markers, urban lawns had high relative abundances of two FAMEs (18 : 1w7c and cy19 : 0), but had the lowest abundances of the other FAMEs within the taxonomic group (16 : 1w7c and cy17 : 0; Fig. 4).

Our results at a coarse taxonomic grouping may not reflect changes in the abundance of genera or species. Future studies could increase both taxonomic and temporal resolution to determine whether our one-time estimates of community structure via FAME markers are effective at describing variability in microbial communities among land-use types. If our data are representative, they suggest that dramatic changes in ecosystem function because of land use are not linked to comparably dramatic changes in the soil microbial community. This conclusion is contrary to ecological theory that hypothesizes a tight link between microbial diversity and ecosystem function (Finlay *et al*., 1997).

Table 4 Mean (and one standard error; $n = 3$) bacterial, fungal, and total viable microbial biomass from surface (0–15 cm) soils of different land-use types

	μmol PLFA $g\,soil^{-1}$			
	Urban	Wheat	Corn	Native
Bacterial	34.6 (7.5)[a]	11.1 (0.7)[b]	16.1 (3.7)[b]	16.4 (0.4)[b]
Fungal	28.2 (5.8)[a]	7.8 (1.3)[b]	10.9 (1.0)[b]	13.7 (1.5)[b]
Total microbial	76.4 (14.7)[a]	21.5 (1.7)[b]	32.4 (3.7)[b]	34.4 (2.2)[b]

Different lowercase letters within a row denote statistical differences among land-use types ($P < 0.01$).
PLFA, phospholipid fatty acid.

Conclusion

We found that urban ecosystems had dramatically altered ANPP and soil respiration rates compared with native grasslands and agricultural ecosystems. Differences in both seasonality and annual magnitude of the C fluxes were observed, with the most striking being consistently high soil respiration rates and belowground C allocation in urban systems. Differences in the C cycle among land-use types had a large effect on N cycling and soil microbial biomass and a smaller effect on the composition of the soil microbial community. Our data are consistent with several other studies (Imhoff *et al*., 2000; Koerner & Klopatek, 2002) in suggesting that urbanization of arid and semiarid ecosystems (the most prominent type of urbanization globally; UN (United Nations), 2001) leads to enhanced C cycling rates that are large enough to alter regional C budgets. In several cases, we found that differences in C storage and cycling among land-use types were larger than changes predicted by climate change.

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