

Influence of Irrigated Agriculture on Soil Carbon and Microbial Community Structure

JAMES A. ENTRY*

USDA Agricultural Research Service
Northwest Irrigation and Soils Research Laboratory
Kimberly, Idaho 83341, USA

JEFFRY J. FUHRMANN

Department of Plant and Soil Sciences
University of Delaware
Newark, Delaware 19717-1303, USA

R. E. SOJKA

USDA Agricultural Research Service
Northwest Irrigation and Soils Research Laboratory
Kimberly, Idaho 83341, USA

GLEN E. SHEWMAKER

University of Idaho
Research and Extension Center
Twin Falls, Idaho 83303-1827, USA

ABSTRACT / Increasing the amount of carbon (C) in soils is one method to reduce the concentration of carbon dioxide (CO₂) in the atmosphere. We measured organic C stored in southern Idaho soils having long-term cropping histories that supported native sagebrush vegetation (NSB), irrigated moldboard plowed crops (IMP), irrigated conservation-chisel-tilled crops (ICT), and irrigated pasture systems (IP). The CO₂ emit-

ted as a result of fertilizer production, farm operations, and CO₂ lost via dissolved carbonate in irrigation water, over a 30-year period, was estimated and used to calculate net C fixation. Organic C in ecosystems decreased in the order IP>ICT>IMP>NSB. In February 2001, active fungal, bacterial, and microbial biomass was greater in IP soils than all other soils. Active fungal, bacterial, and microbial biomass was least in ICT soils at the 15–30-cm depth than all other soils. In August 2001, active bacterial biomass was greater in IMP soils than IP, ICT, and NSB soils. Active fungal biomass was greater in IP soils than all other soils. Whole-soil fatty acid profiles differed among management regimes and sampling dates and, to a lesser extent, with soil depth. FAME profiles from the NSB soils were distinct from the agricultural treatments and contained greater amounts of total fatty acids than the other treatments. The IMP and ICT soils yielded fatty acid profiles that were similar to each other, although those at the 15–30-cm depth were distinct from all other treatment-depth combinations. The IP FAME profiles suggest that arbuscular mycorrhizal fungi are more common in these soils than soils from the other treatments. Differences in carbon substrate utilization patterns (BIOLOG) among treatments were more variable and less pronounced than FAME results. In general, irrigated arid soils can both increase C storage while increasing microbial biomass and changing microbial diversity.

Land-use changes can impact the amount of carbon (C) stored in the soil by altering C inputs and losses. In forest, grassland, and wetland ecosystems, conversion of native vegetation to agricultural cropping has resulted in substantial C transfer to the atmosphere as a result of loss of climax vegetation to the lower equilibrium C concentration in soil (Lal and others 1999; Wang and others 1999; Cambardella and Elliot 1992; Johnson 1992). In arid and semiarid environments, plant survival and growth is limited by available water, and irrigation is required to increase plant production to the point where crops become economically viable. Irriga-

tion also increases C input to soils via increased litter and root production (Tribe 1994).

Many farm management practices, including conservation tillage and erosion control, have reduced the amount of CO₂ emitted to the atmosphere in both Canada and the United States (West and Marland 2001; Janzen and others 1997; Paustian and others 1997; Rasmussen and Collins 1991). Intensively managed crop or pasture lands have the potential for C gain through the use of improved grazing regimes, improved fertilization practices, and irrigation management (Bruce and others 1999; Follett 2001).

Soil microbial diversity is important because it is often regarded as an important index of soil ecosystem health (Perry 1994; Tilman 1996). Soil micro-organisms are present in soil ecosystems and are important for several ecosystem functions. Soil micro-organisms provide for organic matter degradation and the mineralization of essential plant nutrients. Soil micro-organ-

KEY WORDS: Microbial biomass; Biolog, Fatty acid methyl esters; Arbuscular mycorrhizae

Published online March 23, 2004.

*Author to whom correspondence should be addressed, *email:* jentry@kimberly.ars.pn.usbr.gov

isms have much shorter life spans than higher plants and therefore can react more quickly to changes in ecosystem management (e.g., fire or harvesting) than plants. We hypothesized that increasing plant growth on arid and semiarid lands by conversion to irrigated agriculture increases C storage in soils. Increasing soil C and soil moisture have been shown to increase microbial biomass (Entry and others 1986, 1996; Donnelly and others 1990). Having previously shown that land converted from irrigated moldboard plowed regimes to irrigated conservation tillage or irrigated pasture can increase C sequestration (Entry and others 2002), we hypothesized that irrigated agriculture would increase soil microbial biomass and community structure.

Materials and Methods

Site Descriptions

The study area is located on the Snake River Plain, between 42°30'00" and 43°30'00" N and 114°20'00" and 116°30'00" W. The sites occur across an elevational gradient ranging from 860 to 1300 m. The area is classified as a temperate semidesert ecosystem (Bailey 1998). The climate is typified by cool, moist winters and hot, dry summers with annual precipitation ranging from 175 to 305 mm, two-thirds of which occurs during October through March (Collett 1982). Average annual temperature ranges from 9°C to 10°C. Soils are typically well-drained loams and silt loams derived from loess deposits overlying basalt. Vegetation throughout the general area was historically dominated by basin big sagebrush (*Artemisia tridentata* var. *tridentata* Nutt.), Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis* Nutt.), and perennial bunch grasses, including Sandberg bluegrass (*Poa secunda* J. Presl), bottlebrush squirreltail (*Elymus elymoides* Raf. Swezy.), bluebunch wheatgrass (*Pseudoroegneria spicata* Pursh. A. Love), and Thurber's needlegrass [*Achnatherum thurberianum* (Piper) Barkworth].

Native Vegetation Sagebrush Sites

Native sagebrush sites were vegetated with native steppe vegetation and a low composition of exotic annual grasses. Sites were chosen for this study based on a history of no livestock grazing (BLM, Bruneau Resource Area, unpublished data). All study sites had 5–10% slopes and were on areas that supported basin big sagebrush or Wyoming big sagebrush communities. Soils were classified as fine, montmorillonitic, mesic Xerollic Haplargid on the Brown's Creek site, coarse-loamy, mixed nonacid, mesic Xeric Torriorthents on the Simco site, and loamy, mixed, mesic lithic Xerollic Camborthids on the Kuna Butte site (Collett 1982).

Irrigated Pasture Sites

Three irrigated pastures were selected that were formerly crop land and converted to and maintained as irrigated pasture (IP) for the past 30 years. The Buhl site was vegetated with Kentucky bluegrass (*Poa pratensis* L.) and orchardgrass (*Dactylis glomerata* L.) on a Rakane–Blacknest soil complex of fine-loamy, mixed, mesic Xerollic Durargids. The Gooding site was vegetated with smooth brome (*Bromus inermis* Leyss.) and orchardgrass on a Paulville–Idow soil complex of fine-loamy, mixed, mesic Xerollic Haplargids. The Kimberly site was vegetated with smooth brome–orchardgrass pasture on a Portneuf soil, coarse-silty, mixed, superactive, mesic Durinodic Xeric Haplocalcid soil. Grazing rates on these pastures were 10–12 animal unit months/year.

Irrigated Conservation Tillage Sites

Three sites with fields rotating among alfalfa, wheat, potato, and beans that were managed with irrigated conservation (chisel) tillage for 8 years were sampled. All sites were located on fields managed by USDA Agricultural Research Service's Northwest Irrigation and Soils Research Laboratory or the University of Idaho, Research and Extension Center. Soil on all sites was classified as coarse-silty, mixed, superactive, mesic Durinodic Xeric Haplocalcids, with 10–21% clay and 60–75% silt, and organic matter of $\sigma \sim 13$ g/kg. The soil has a pH of 7.6–8.0. Slope on these sites ranges from 1.0% to 3.0%.

Irrigated Moldboard Tillage Sites

Three sites with fields rotating among alfalfa, wheat, potato, and beans that were managed with irrigation and moldboard plowing were sampled. All sites were located on fields managed by USDA Agricultural Research Service's Northwest Irrigation and Soils Research Laboratory or the University of Idaho, Research and Extension Center. Soil on all sites had soil characteristics matching the irrigated conservation-chisel-tilled (ICT) sites.

Experimental Design

The experiment was arranged in a completely randomized design (Kirk 1982). Soil samples were taken from (1) sites supporting native sagebrush vegetation (NSB) located near agricultural land in Southern Idaho (each site supported a basin big sage and a Wyoming big sage vegetation type), (2) sites that were formerly crop land and converted to and maintained as IP for the past 30 years, (3) sites that were irrigated crop land and have been managed with conservation tillage

(ICT) for the past 8 years, and (4) irrigated agricultural crop lands in moldboard plowing systems (IMP) that were each growing (a) alfalfa, (b) wheat, (c) potato, and (d) beans. Three sites were sampled for each vegetative treatment. The NSB sites were sampled at 0–5, 5–15, and 15–30 cm due to distinct differences in root density. The ICT sites were sampled at 0–15 and 15–30 cm because soil was chiseled to 15 cm due to distinct differences in root density during the growing season. The IMP sites were sampled at 0–30 cm due to the frequent plowing that these sites received prior to the growing season which resulted in little difference in rooting density among depths during the growing season. The IP sites were sampled at 0–30 cm because there was little difference in rooting density among depths during the growing season.

Sampling Procedures

We sampled the top 30 cm of soil each season to determine if the amount of C in the soil would be affected by vegetation and irrigation. Sampling locations were randomly chosen at each site or field. Separate 2.0-cm-diameter cores were taken and partitioned into 0–5-cm, 5–15-cm, and 15–30-cm depths. Roots greater than 1.0 cm in diameter were measured separately. We sampled soil organic C with 4 treatments (NSB, IMP, ICT, and IP) using 7 soil depths of NSB (0–5, 5–15, 15–30 cm), ICT (0–15- and 15–30- cm), IMP (0–30- cm), and IP (10–30 cm) \times 3 sites for each treatment (replications) \times 10 soil cores at each site for a total of 210 samples. Active bacterial biomass, active fungal biomass, and whole-soil fatty acid methyl esters carbon substrate utilization were sampled with 4 treatments (NSB, IMP, ICT, and IP) incorporating 7 soil depths of NSB (0–5, 5–15, and 15–30 cm), ICT (0–15 and 15–30 cm), IMP (0–30 cm) and IP (0–30 cm) \times 3 sites for each treatment (replications) \times 3 cores taken within each treatment \times 3 sampling times at each site \times 3 sampling times for a total of 189 samples. Treatments were sampled on May 23, 2000, February 15, 2001, and August 10, 2001. Carbon in aboveground vegetation was estimated by measuring the amount of material in 10 separate 1.0-m² areas in each site or field (Entry and Emmingham 1998). In February and August 2001, samples analyzed for active bacterial and fungal biomass, microbial diversity with fatty acid methyl esters and carbon substrate utilization (BIOLOG) patterns were collected and stored in watertight plastic bags and prepared for microbial testing within 24 h to minimize the effects of storage on microbial activity (West and others 1986).

Carbon in Soil, Plants, and Litter

The concentration of organic C in each sample of mineral soil and aboveground vegetation was determined by the Walkley–Black procedure (Nelson and Sommers 1996). The amount of C per hectare of the 0–30 cm of soil was calculated assuming 0.44 g C/g organic matter with correction for soil bulk density. Bulk density was measured by dividing the volume of the sample by the oven dry weight after drying at 105°C for 48 h (Blake and Hartage 1982). Aboveground vegetation was collected and separated into sage, grass, forbs, herbs, and litter. Aboveground material was dried at 80°C for 48 h, weighed, and ground to pass a 1-mm opening. The amount of C in the aboveground material was assumed to contain 0.44 g C/g organic matter on an ash-free basis (Nelson and Sommers 1996).

Active Bacterial and Fungal Biomass

Active and total bacteria and fungi numbers and biomass in each soil depth was determined for each treatment using methods described by Ingham and Klein (1984). Active fungi were estimated by placing a 1.0-g soil sample in 9 mL of a phosphate buffer (pH 6.0) and shaking the mixture at σ -120 rpm for 5 min. A 1-mL aliquot was removed and stained with 1 mL of a 20 fg/mL fluorescein diacetate (FDA) solution in a 0.2 M phosphate buffer for 3 min. One milliliter of 1.5% agar in a 0.1 M phosphate buffer (pH 9.5) was added to the FDA suspension. The sample was mixed and an aliquot placed on a microscope slide containing a cavity of known volume (Ingham and Klein 1984). Immediately after preparation, slides were examined for FDA-stained hyphal length by epifluorescent microscopy. Total fungal biomass was estimated by measuring the length and diameter of hyphae with phase-contrast microscopy. Three slides were evaluated from each sample and 10 fields per slide were evaluated with phase-contrast microscopy for total hyphal length, and 3 transects were evaluated for FDA-stained (active) hyphal length at 160 \times total magnification.

Iodonitrotetrazolium (INT) stain was used for counting active bacteria (Stadmatiadis and others 1990). An initial soil suspension of 1 mL soil to 9 mL water was diluted to a final dilution in a 0.2-mg soil in 4 mL buffer. The suspension was incubated with 4 mL of filtered INT buffer for 60 min in the dark at 20°C. Total bacteria per milliliter of water were estimated from the mean number of bacteria (fluorescent and nonfluorescent bacteria), their average diameter, and length per field. Three slides were evaluated for each sample and 10 fields per slide were evaluated using

epifluorescent oil-immersion microscopy to determine the numbers and size of fluorescent and total bacteria (Lodge and Ingham 1991).

Bacterial biomass was computed from the numbers of active and total bacteria, and active and total fungal biomass were determined from hyphal length. Bacterial biomass was computed from the number of soil bacteria per gram of soil by assuming that the bacterial spheres were 1 μm in diameter (Jenkinson and Ladd 1981). Active and total fungal biomass were computed by assuming average hyphal diameter to be 1 μm in diameter and then multiplying by the length of observed hyphae (Jenkinson and Ladd 1981). A carbon-to-volume conversion factor of 120 $\mu\text{g C}/\text{mm}^3$ was used for both bacteria and fungi, assuming 1.1 g/cm^3 wet density, 20% dry matter content, and a 0.41 carbon content in the bacterium or fungus (Jenkinson and Ladd 1981).

Fatty Acid Methyl Ester Analysis

Fatty acids were extracted from soil in hexane and transmethylated under mildly alkaline conditions as described elsewhere (Olexa and others 2000). The resulting fatty acid methyl esters (FAMES) were analyzed with a HP 5890 gas-liquid chromatograph (Hewlett Packard, Rolling Meadows, Illinois, USA) equipped with a HP Ultra 2 capillary column (cross-linked phenyl methyl siloxane, 0.2 mm \times 25 m) and a flame ionization detector. The standard EUKARY chromatographic program and peak naming table (MIDI, Microbial ID, Newark, Delaware, USA) were used to identify FAMES by their retention times. Mixed FAME standards were obtained from MIDI to adjust and monitor the calibration of the system. Longer-chain fatty acids (> 20 carbons) and those having average peak areas < 500 (which was used as the minimum threshold for acceptable peak recognition) were eliminated from the statistical analyses. The former are generally associated with higher plants and animals (Kennedy 1994), whereas eliminating the latter helped minimize the influence of intermittent small peaks on the analyses. The peak areas from the remaining FAMES were summed for a given sample and used to calculate the percent contribution of each FAME to the total peak area (Olexa and others 2000). Peaks identified by MIDI as "summed features" (groups of known fatty acids that are not resolved due to similar retention times) and recognized "unknowns" were treated identically to unambiguously named FAMES

Carbon Utilization Analysis

Gram-negative (GN) BIOLOG microtiter plates (BIOLOG, Inc., Hayward, California), each contain-

ing 95 individual carbon substrates plus a negative control, were used to determine the nutritional versatility of microbial communities from the various soil treatments. An initial 10^{-1} soil dilution was prepared by suspending 10 g of soil in 95 mL of sterile distilled water. Serial dilutions were carried out to the 10^{-3} dilution. Each well of a GN BIOLOG plate was inoculated with 150 μL of the 10^{-3} dilution for a given soil sample. Plates were incubated at 28°C, and absorbance at 590 nm was measured at 72 h using a microplate reader (Bio-Tek Instruments, Winooski, Vermont, USA). The value obtained for the negative control well of each plate was subtracted from the values for the remaining 95 wells. The adjusted absorbances were analyzed by principal components analysis (PCA) as described for the FAME analysis, except that the average well color development (AWCD) (Garland, 1996) was included as a covariable (Fang and others 2001).

Statistical Analysis

Carbon data were subjected to a one-way vegetation-type analysis of variance (ANOVA) for a completely randomized design (Snedecor and Cochran 1980; Kirk 1982). Residuals were normally distributed with constant variance. Statistical Analysis Software programs (SAS Institute Inc. 1996) were used to conduct the ANOVA. Significance of treatment means were determined at $P < 0.05$ with the least square means test.

The data matrix for each FAME sampling was examined by PCA based on a correlation matrix using CANOCO software (Microcomputer Power, Ithaca, New York, USA). Distances among sample FAMES for a given date of sampling were determined using Euclidean scaling of the PCA axis, whereas correlation biplot scaling was used to determine relationships among the individual samples, FAME data, and treatment variables (land management and sampling depth) (ter Braak and Smilauer 1998).

Results

Soil Carbon

Statistical comparisons in the ANOVA showed that soil bulk density and soil organic C in site and vegetation interactions are not significant at $P \leq 0.05$. Therefore, results are discussed with respect to vegetation differences (Snedecor and Cochran 1980; Kirk 1982). Bulk density was higher in IP, ICT, and IMP soils than in NSB soils. Bulk density was lower in the NSB 0–5-cm soil depth than the 5–15- and 15–30-cm depths and all other soils (Table 1). Soil organic C was higher in the

Table 1. Bulk density and Walkley–Black carbon (WBC) in soils growing native sagebrush, irrigated moldboard plowed cropland, irrigated conservation tilled cropland and irrigated pastures in southern Idaho

Treatment	Soil depth (cm)	Bulk density (mg/m ³)	WBC (g C/kg soil)
Native sagebrush	0–5	0.97 b	127 a
	5–15	1.28 ab	47 c
	15–30	1.34 a	54 c
Irrigated moldboard plow crop	0–30	1.28 ab	78 b
Irrigated conservation tilled crop	0–15	1.38 a	89 b
	15–30	1.38 a	69 bc
Irrigated pasture	0–30	1.33 a	85 b

Note: In each column, values followed by the same letter are not significantly different as determined by the least square means test ($P \leq 0.05$), $n = 30$.

Table 2. Active bacterial biomass, active fungal biomass, active microbial biomass (all in mg C/g) and DNA in native sagebrush and irrigated agricultural soils

Treatment	Winter			Summer		
	Bacterial biomass	Fungal biomass	Microbial biomass	Bacterial biomass	Fungal biomass	Microbial biomass
Native sagebrush, 0–5-cm depth	4.0c	5.2b	9.2b	6.7b	6.1b	12.9b
Native sagebrush, 5–15-cm depth	1.1c	0.8c	1.9d	6.1b	4.1bc	10.3b
Native Sagebrush, 15–30-cm depth	3.4c	3.7b	7.1c	4.8b	2.8c	7.7c
Irrigated moldboard plow, 0–30-cm depth	7.8b	3.9b	11.2b	12.0a	5.0b	17.0a
Irrigated conservation tillage, 0–15-cm depth	1.4c	1.0c	2.4d	7.9b	6.5b	14.5ab
Irrigated conservation tillage, 15–30-cm depth	0.2d	0.6c	3.0d	5.6b	3.5c	9.2bc
Irrigated pasture, 0–30-cm depth	10.5a	9.5a	20.0a	7.9b	9.6a	17.4a

Note: In each column, values followed by the same letter are not significantly different as determined by the least square means test ($P \leq 0.05$; $n = 9$).

NSB 0–5-cm soil depth than the 5–15- and 15–30-cm depths and all other soils.

Active Bacterial and Fungal Biomass

In winter, active fungal, bacterial, and microbial biomass were greater in IP soils than all other soils (Table 2). Active fungal, bacterial, and microbial biomass were least in ICT soils at the 15–30-cm depth than all other soils. In summer, active fungal biomass was greater in IMP soils. In summer, active bacterial, fungal, and microbial biomass correlated with soil C in positive curvilinear relationships ($r^2 = 0.76, 0.99, \text{ and } 0.70$, respectively). In winter, active bacterial, fungal and microbial biomass correlated with soil C as in positive curvilinear relationships ($r^2 = 0.93, 0.80, \text{ and } 0.76$, respectively).

Fatty Acid Methyl Esters

Whole-soil fatty acid profiles differed among the management regimes and sampling dates and, to a lesser extent, with soil depth (Table 1, Figures 1, 2, 3). Fatty acids extracted from the NSB soils were generally distinct from those for the other treatments, particu-

larly for the 0–5-cm-depth range. Soil from the IMP and ICT tillage treatments yielded fatty acid profiles that were generally similar to each other, although the 15–30-cm depth for the ICT soils at the February 2001 sampling was distinct from all other treatment-depth combinations (Figure 2). For the May 2001 sampling time and possibly for February 2001, the IP soil appeared to produce relatively unique fatty acid profiles (Figures 2 and 3). The NSB soils contained, for at least two of the three sampling times, significantly ($P \leq 0.05$) greater relative amounts of the fatty acids $i15 : 1 G$ $16 : 0$, $i16 : 1 G$, $17 : 1 \omega 8c$, $18 : 0 2OH$, $18 : 1 \omega 9c$, $18 : 1 \omega 9c a$, $19 : 1 \omega 7c/\omega 9t$, $20 : 0$, $20 : 4 \omega 6c$, $20 : 5 \omega 3c$, C18 N al, and C20 N al, and significantly lesser amounts of $i14 : 0$, $a15 : 0$, $i15 : 0$, $16 : 1 \omega 5c$, $a17 : 0$, $i17 : 0$, $18 : 1 \omega 7c/\omega 9t$, and $19 : 0 cy c11-12$ (Table 1) than did the remaining treatments. The latter generally exhibited the opposite trends for these fatty acids. Exceptions to this occurred for the IP soil, which typically yielded uniquely greater amounts of $i14 : 0$, $15 : 0$, $16 : 1 \omega 5c$, $18 : 3 \omega 6c$, $20 : 1 \omega 9c$, and lesser amounts of $18 : 1 \omega 9c$ and $18 : 2 \omega 6c$ compared with the remaining treatments.

Figure 1. PCA plot of FAME results from the August 2000 sampling. Fatty acid methyl esters are described using standard nomenclature. Numbering of carbons begins at the aliphatic end of the fatty acid molecule. The number of double bonds within the molecule is given after the colon. Cis and trans conformations are designated using suffixes *c* and *t*, respectively. Other notations are *al* for alcohol, *OH* for hydroxy, and *cy* for cyclopropane ring, the prefixes *i* and *a* are for iso- and anteiso-branched fatty acids, and ? is for uncertain structural features. (Treatments: conservation tillage, 0–15 cm; conservation tillage, 15–30 cm; conventional tillage, 0–30 cm; irrigated pasture, 0–30 cm; native sagebrush, 0–5 cm; native sagebrush, 5–15 cm; native sagebrush, 15–30 cm.)

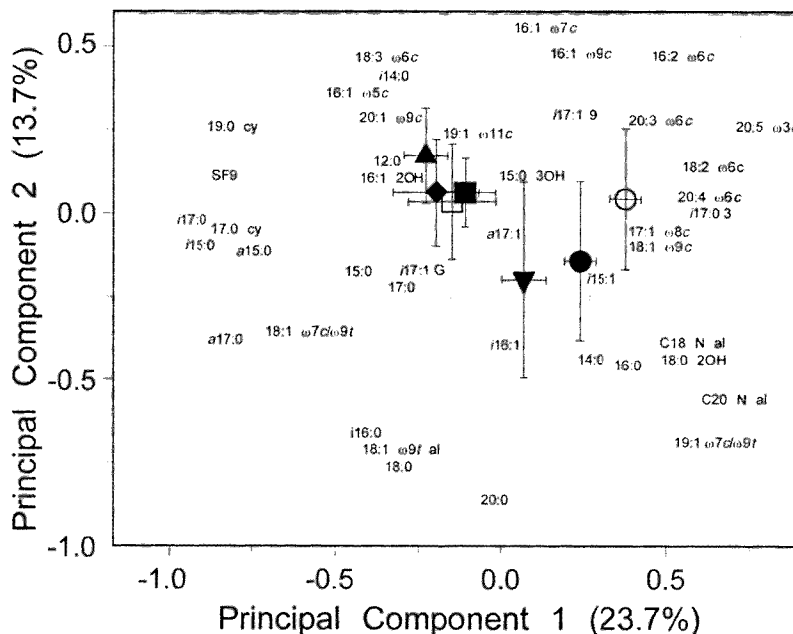
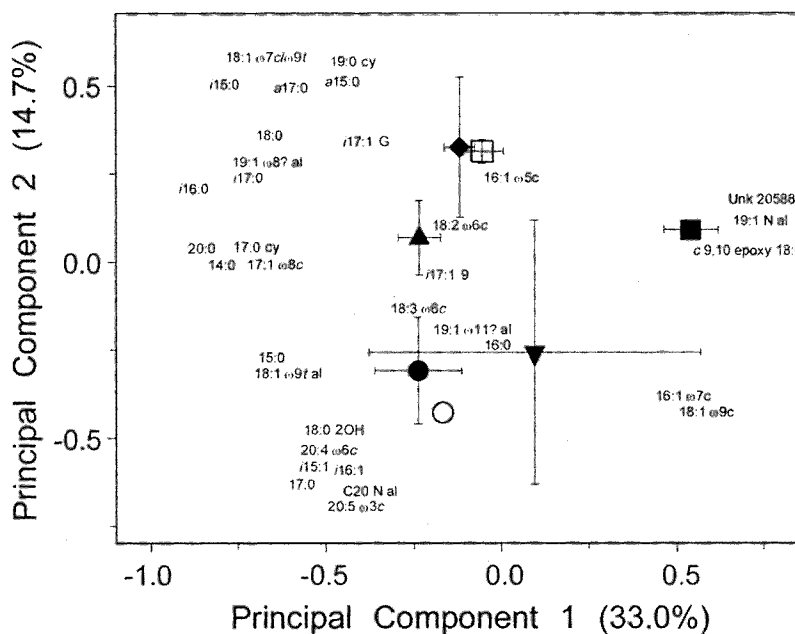


Figure 2. PCA plot of FAME results from the February 2001 sampling. See Figure 1 for explanation of symbols and FAME designations.



BIOLOG Results

Differences in substrate utilization patterns among the treatments were generally more variable, both within and among sampling times, and less pronounced than those observed for the FAME results (results not shown). In general, the ICT and NSB treatments exhibited the greatest degree of separation observed among the various treatments, regardless of time

of sampling. This separation was most apparent at the February 2001 sampling, for which there was a uniformly inverse relationship among these management regimes. For all three samplings, the covariate (AWCD) accounted for a large percentage of the total variation detected by PCA (48.0–61.5%). By comparison, principal components 1 and 2 accounted for 37.4%, 24.3%, and 24.1% of the variability remaining after fitting the

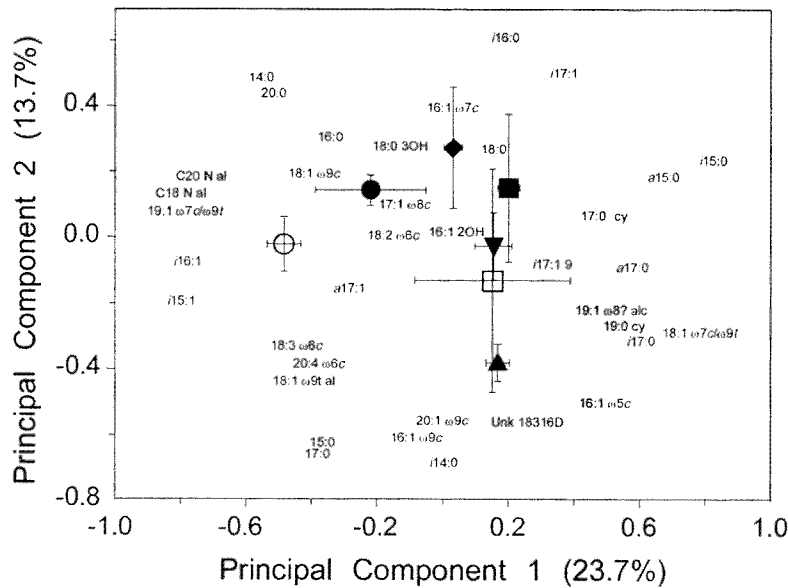


Figure 3. PCA plot of FAME results from the May 2001 sampling. See Figure 1 for explanation of symbols and FAME designations.

covariable for the August 2000, February 2001, and May 2001 sampling time, respectively.

Discussion

Soil Carbon

When data are averaged within the top 30 cm of soil, our data shows that when NSB sites are converted to ICT or IP soil organic C increases. If crops were produced via high-output irrigated agriculture, while less productive rain-fed agricultural land was returned to temperate forest or native grassland, there may be substantial reductions in atmospheric CO₂. Irrigated agricultural land typically produces twice the crop yield of rain-fed agricultural land. If irrigated agriculture were expanded 10%, each hectare of new irrigated land could produce the same crop yield as 2 ha of rain-fed land (Bucks and others 1990; Tribe 1994; Howell 2000). Policy-makers and agricultural research infrastructure should recognize the enormous potential benefit of land and water management strategies, policies, and incentives that could expand arid-zone irrigated agriculture as a means of efficient food and fiber production along with substantial C sequestration potential. We recognize that such an expansion would have to be accompanied by renewed efforts in water development. Although water resource development has been occurring at a modest pace worldwide since 1990, Howell (2000) indicated the potential for an increased extent of irrigation via efficiency improvements and wastewater use. Recognition of these potential C benefits should provide an incentive to fund

research and pursue management strategies that are possible without sacrificing production and which could increase restoration of native ecosystems, reduce erosion, and improve water quality through appropriate targeting of the strategy.

Irrigated agricultural systems cannot accrue C indefinitely. Soil organic C concentration reflects net production in terrestrial ecosystems (Jobbagy and Jackson 2000; Schimel and others 2000; Schlesinger 1990). When grasslands or forests are converted to agriculture, their soil organic C concentration declines by 20–30% (Schlesinger 1990; Mann 1986; Detwiler 1986). The loss is greatest during the first few years, but, eventually, a lower concentration of C is reached that is in equilibrium with the lower plant production and input of plant detritus to the soil and increased organic matter decomposition rates (Houghton and others 1999; Paus-tian and others 1997; Davidson and Akerman 1993). However, when native sagebrush ecosystems are converted to agriculture, irrigation is necessary for crop growth and soil C increases ~20% (Entry and others 2002). With improved management, irrigated agricultural systems can potentially remove substantial amounts of C from the atmosphere for the next 30–50 years. The potential C sequestered on site by conversion of native vegetation to irrigated agriculture is above the steady-state equilibrium of native vegetation (Entry and others 2002). This is in contrast to rain-fed agricultural systems, where managers are currently measuring modest C gains to attain below-baseline C concentrations by implementing reduced or no-tillage practices and which actually have their greatest poten-

tial for C sequestration via return to native grassland or arboreal ecosystems because of the additional C sequestration in permanent grass or forest ecosystems.

Active Bacterial and Fungal Biomass

We found that active bacteria and fungal biomass were strongly related to soil organic C concentrations. Active bacteria and fungal biomass also increased with increasing soil moisture and temperature and were positively correlated with these variables (Hunt and Fogel 1983; Entry and others 1986, 1990, 1996). Increasing soil C appears to increase active bacterial and fungal biomass during the summer when irrigation water is applied and crop plants are actively growing and during the winter when IP, ICT, and IMP are not supporting actively growing vegetation. Active bacterial and fungal biomass did not consistently differ among irrigated agricultural treatments.

FAME Analysis of Soil Microbial Communities

Consistent trends in FAME profiles were observed among the four land management systems. Because certain fatty acids have been shown to be markers for rather broad groupings of soil micro-organisms (Cavigelli and others 1995), determining the relative abundances of these marker fatty acids permits inferences to be made regarding general differences in microbial community structure among soils.

Branched (iso and anteiso) fatty acids, considered markers for Gram-positive bacteria, including actinomycetes, exhibited strong and consistent differences among treatments. In particular, the saturated branched FAMEs (*i*14 : 0, *a*15 : 0, *i*15 : 0, *a*17 : 0, *i*17 : 0) showed strongly negative correlations with the NSB samples; *i*16 : 0 was an exception to this. The remaining treatments, especially the ICT and IMP soils, exhibited positive correlations with these same fatty acids. Conversely, nonsaturated or otherwise modified branched fatty acids (*i*15 : 1 G, *i*16 : 1 G, *i*17 : 0 3, *a*17 : 1 9, *i*17 : 1 G, *i*17 : 1 ω 9c), sometimes also considered to be indicative of Gram-positive bacteria, generally yielded the opposite trends among the land management treatments compared to the saturated unmodified branched fatty acids. Reasons for this inverse relationship are unclear, but it suggests that saturated and nonsaturated branched fatty acids are not necessarily equivalent indicators for Gram-positive bacteria.

Fatty acids that are considered markers for Gram-negative bacteria and which were detected in this study include hydroxy (15 : 0 3OH, 16 : 1 2OH, and 18 : 0 2OH) and cyclic fatty acids (17 : 0c and 19 : 0 cy c11–12). Also detected was 18 : 1 ω 7c/ ω 9t, which has

been shown to be associated with Gram-negative bacteria isolated from soil (Schutter and Fuhrmann 2001). The hydroxy fatty acids exhibited trends opposite of the branched saturated fatty acids (indicative of Gram-positive bacteria), a pattern one might reasonably expect to occur, with the NSB soils yielding a relatively greater concentration of the former. Conversely, 18 : 1 ω 7c/ ω 9t and the cyclic FAMEs were present in higher relative amounts in the ICT, IMP, and IP soils than in the NSB soil.

Reasons for the observed trends in Gram-positive (i.e., branched saturated fatty acids) and Gram-negative markers are not immediately apparent. Given that the common Gram-positive genus *Bacillus* produces endospores resistant to environmental stresses, including desiccation, one might expect these organisms to be relatively more common in the nonirrigated treatment (NSB), a pattern not observed in this study. However, it is conceivable that the frequent wetting–drying cycles associated with the irrigated treatments may have provided environmental conditions selective for *Bacillus* and related organisms. It is also possible that populations of spore-forming bacteria were stable or increased by the NSB treatment but that reductions in the amounts of fatty acids from other less environmentally resistant Gram-positive bacteria dominated the NSB FAME profiles.

Fatty acids detected in this study that have been identified as possible markers for fungi are 16 : 1 ω 5c, 18 : 2 ω 6c, and 18 : 3 ω 6c. The latter two fatty acids, considered general indicators for the presence of fungi, did not exhibit trends among the treatment combinations, especially for the IP soil, for which they exhibited opposing and generally significant correlations at all sampling dates. It is not known if this resulted from the two FAMEs tracking two distinct fungal populations or from one or both of the FAMEs being inappropriate markers for fungi present in the soils studied. The remaining fatty acid 16 : 1 ω 5c has been suggested as a possible marker for arbuscular mycorrhizal (AM) fungi (Olsson 1999; Drijber and Duran 2000). It is tempting to speculate that the greater relative amounts of this FAME in the IP soil reflects the minimal amount of soil disturbance and accompanying reduced disruption of fungal mycelia, represented by this treatment when compared to the ICT and IMP treatments. These tilled soils may also have received greater amounts of phosphorus-containing fertilizers, thereby reducing the resident plants' dependence on mycorrhizal-mediated uptake of this nutrient, compared with the IP regime. Reasons for the relatively low relative amounts of 16 : 1 ω 5c detected in the NSB soil may reflect any of several limiting conditions, including comparatively low plant

densities, low mycorrhizal dependence of the resident species, and reduced plant vigor due to limited water availability or other environmental factors.

The remaining marker FAMES detected among the various treatments are 20 : 3 ω 6c and 20 : 4 ω 6c, both of which are considered to indicate the presence of protozoa. With one exception, the presence of 20 : 3 ω 6c and 20 : 4 ω 6c were positive for the IP and NSB treatments and negative for the ICT and IMP treatments. It is possible that the nature of the soil and rhizosphere environments, or the stability thereof, represented by the former regimes may encourage the development of protozoa populations possessing these FAMES. However, the mechanisms providing this speculated selective pressure are unknown.

It is perhaps noteworthy that additional FAMES were detected in this study that, although of uncertain usefulness taxonomically, yielded consistent and generally significant correlations among the land management regimes. These fatty acids are 17 : 1 ω 8c, 19 : 1 ω 7c/ ω 9, 20 : 5 ω 3c, C18 N al, and C20 N al. It is suggested that monitoring "nonmarker" fatty acids such as these may be useful, particularly if they exhibit similarly significant and consistent trends as part of other studies. This may be especially true given that current knowledge of marker FAMES are based on the analysis of isolated organisms, which are generally acknowledged as being representative of only a small percentage of the microorganisms present in soils.

BIOLOG Analysis of Soil Microbial Communities

Although considerable differences in relative substrate utilization were observed among the land management treatments, these were generally highly variable within and among the three sampling times in accordance with other reports (Haack and others 1995). Also in agreement with the results of others (Palojarvi and others 1997), determination of substrate utilization produced less distinct separation of microbial populations compared with fatty-acid-based analyses, and it has been suggested that this may result from functional redundancy among microorganisms exhibiting distinct FAME profiles (Buyer and Drinkwater 1997). Inclusion of AWCD (Garland 1996) as a covariable in the PCA helped reduce the effect of large differences in this variable among treatments (results not shown). The most consistent differences among the treatment-sampling combinations occurred between the ICT and NSB management regimes, an observation that agrees generally with the results of the FAME analyses.

Conclusions

We found that as soil organic C increased, the total amount of fatty acids produced and soil microbial biomass increased and soil fatty acid profiles changed when native sagebrush soils were converted to agriculture. It is generally assumed that agricultural management systems, such as conservation tillage, can increase soil organic C and microbial community structure; however, agricultural operations do not increase biodiversity or species richness of vascular plants, animals, or insects (Klejin and others 2001). We also found that conservation tillage increases soil organic C and microbial diversity compared to conventional tillage. However, conversion of native sagebrush to irrigated agriculture, regardless of reduced tillage, does not increase microbial diversity in this semiarid environment. Agricultural operations cannot simply rely on tillage operations to increase biodiversity of agricultural ecosystems. The primary concern of farmers is necessarily to secure an income. As a result, conservation of natural resources is important to them but must be balanced with economic concerns (Klejin and others 2001). Conversion of forest, grassland, or wetland ecosystems to rain-fed agriculture can decrease soil organic C from 5.0 to 63 kg C/m⁻² (Houghton and others 1999; Amthor and Huston 1998; Schlesinger 1977). Irrigated agricultural systems that maintain economic sustainability while both increasing soil C and soil microbial diversity and increasing biodiversity of the entire agroecosystem need to be devised.

References

- Atlas, R. M. 1984. Diversity of microbial communities. *Advances in Microbial Ecology* 7:1-47.
- Amthor, J. S., and M. A. Huston. 1998. Terrestrial ecosystem responses to global change: A research strategy. Report No. ORNL/TM-1998/27. Oak Ridge National Laboratory. 157 pp.
- Bailey, R. G. 1998. Ecoregions of North America. US Department of Agriculture, Forest Service. US Government Printing Office, Washington, DC.
- Blake, G. R., and K. H. Hartage. 1982. Bulk density. Pages 363-375. in A. L. Page, R. H. Miller, and D. R. Keeney. Eds, Methods of soil analysis. Part 2. Chemical and microbiological properties. American Society of Agronomy, Madison, Wisconsin.
- Bruce, J. P., M. Frome, E. Haites, H. Janzen, R. Lal, and K. Paustian. 1999. Carbon sequestration in soils. *Journal of Soil Water Conservation* 59:382-389.
- Bucks, D. A., T. W. Sammis, and G. L. Dickey. 1990. Irrigation for arid areas. Pages 449-548. in G. J. Hoffman, T. A. Howell, and K. H. Solomon. Eds, Management of farm irrigation Systems. American Society of Agricultural Engineers, St. Joseph, Missouri.

- Buyer, J. S., and L. E. Drinkwater. 1997. Comparison of substrate utilization assay and fatty acid analysis of soil microbial communities. *Journal of Microbiological Methods* 30:3–11.
- Cambardella, C. A., and E. T. Elliott. 1992. Particulate soil organic matter changes across a grassland cultivation sequence. *Soil Science Society of America Journal* 56:777–783.
- Cavigelli, M. A., G. P. Robertson, and M. J. Klug. 1995. Fatty acid methyl ester (FAME) profiles as measures of soil microbial community structure. *Plant and Soil* 170:99–113.
- Collett, R. A. 1982. Soil Survey of Ada County area. US Department of Agriculture, Natural Resources Conservation Service. US Government Printing Office, Washington, DC 182.
- Davidson, E. A., and I. L. Akerman. 1993. Changes to soil carbon inventories following cultivation of previously untilled soils. *Biogeochemistry* 20:161–164.
- Detwiler, R. P. 1986. Land use change and the global carbon cycle. *Biogeochemistry* 2:67–93.
- Donnelly, P. K., J. A. Entry, D. L. Crawford, and K. Cromack, Jr. 1990. The effect of soil temperature, moisture and acidity on lignin and cellulose decomposition. *Microbial Ecology* 20:289–295.
- Drijber, R. A., J. W. Doran, A. M. Parjhurst, and D. J. Lyon. 2000. Changes in soil microbial community structure with tillage under long-term wheat-fallow management. *Soil Biology and Biochemistry* 32:1419–1430.
- Entry, J. A., and W. H. Emmingham. 1998. Influence of forest age on forms of carbon in Douglas-fir soils in the Oregon Coast Range. *Canadian Journal of Forest Research* 28:390–395.
- Entry, J. A., R. E. Sojka, and G. Shewemaker. 2002. Management of irrigated agriculture to increase carbon storage in soils. *Soil Science Society of America Journal* 66:1957–1964.
- Entry, J. A., D. W. Reeves, C. B. Backman, and R. L. Raper. 1996. Influence of wheel traffic and tillage on microbial biomass, residue decomposition and extractable nutrients in a Coastal Plain Soil. *Plant and Soil* 180:129–137.
- Entry, J. A., C. L. Rose, and K. Cromack, Jr. 1990. Litter decomposition and nutrient release in ectomycorrhizal mat soils of a Douglas-fir ecosystem. *Soil Biology and Biochemistry* 22:285–290.
- Entry, J. A., N. M. Stark, and H. Loewenstein. 1986. The effect of timber harvesting on soil microbial biomass in the organic horizon of the northern Rocky Mountain forest soil. *Canadian Journal of Forest Research* 6:1076–1081.
- Fang, C., M. Radosevich, and J. J. Fuhrmann. 2001. Characterization of rhizosphere microbial community structure in five similar grass species using FAME and BIOLOG analyses. *Soil Biology and Biochemistry* 33:679–682.
- Follett, R. F. 2001. Soil management concepts and carbon sequestration in cropland soils. *Soil Tillage and Research* 61:77–92.
- Garland, J. L. 1996. Patterns of potential C source utilization by rhizosphere communities. *Soil Biology and Biochemistry* 28:223–230.
- Haack, S. K., H. Garchow, M. J. Klug, and L. J. Forney. 1995. Analysis of factors affecting the accuracy, reproducibility, and interpretation of microbial community carbon source utilization patterns. *Applied and Environmental Microbiology* 61:1458–1468.
- Houghton, R. A., J. L. Hackler, and K. T. Lawrence. 1999. The U.S. carbon budget: contributions from land use change. *Science* 285:574–578.
- Howell, T. A. 2000. Irrigation's role in enhancing water use efficiency. Pages 67–80. in R. G. Evans, B. L. Benham, and T. P. Trooien. Eds, National Irrigation Symposium. American Society of Engineers, St. Joseph, Michigan.
- Hunt, G. A., and R. Fogel. 1983. Fungal hyphal dynamics in a western Oregon Douglas-fir stand. *Soil Biology and Biochemistry* 15:641–649.
- Ingham, E. R., and D. A. Klein. 1984. Soil fungi relationships between hyphal activity and staining with fluorescein diacetate. *Soil Biology and Biochemistry* 16:273–278.
- Janzen, H. H., C. A. Campbell, E. G. Gregorich, and B. H. Ellert. 1997. Soil carbon dynamics in Canadian ecosystems. Pages 57–80. in R. Lal, J. Kimble, E. Levine, and B. A. Stewart. Eds, Soils and global change. CRC Press, Boca Raton, Florida.
- Jenkinson, D. S., and J. M. Ladd. 1981. Microbial biomass in soil: Measurement and turnover. Pages 415–471. in E. A. Paul, and J. N. Ladd. Eds, Soil Biochemistry Vol. 5. Marcel Dekker, New York.
- Jobbagy, E. G., and R. B. Jackson. 2000. The vertical distribution of organic carbon and its relation to climate and vegetation. *Ecological Applications* 10:423–436.
- Johnson, D. W. 1992. Effects of forest management on soil carbon storage. *Water, Air, and Soil Pollution* 64:83–120.
- Kennedy, A. C. 1994. Carbon utilization and fatty acid profiles for characterization of bacteria. Pages 543–556. in R. W. Weaver Eds, Methods of soil analysis. Part 2. Microbiological and Biochemical Properties. Soil Science Society of America, Madison, Wisconsin.
- Kirk, R. E. 1982. Experimental design: Procedures for the behavioral sciences. 2nd ed. Brooks/Cole Publishing, Monterey, California 911.
- Kleijn, D. F., R. Berendse, R. Smit, and N. Gillissen. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature* 413:723–725.
- Lal, R., R. F. Follett, J. Kimble, and C. V. Cole. 1999. Managing U.S. cropland to sequester carbon in soil. *Journal of Soil Water Conservation* 59:374–381.
- Lodge, D. J., and E. R. Ingham. 1991. A comparison of agar film techniques for estimating fungal biovolumes in litter and soil. *Agriculture, Ecosystems and Environment* 5:31–37.
- Mann, L. K. 1986. Changes in carbon storage after cultivation. *Soil Science* 142:279–288.
- Nelson, D. W., and L. E. Sommers. 1996. Total carbon, organic carbon and organic matter. Pages 961–1010. in J. M. Bigham Eds, Methods of soil analysis. Part 3. Chemical and microbiological properties. ASA, CSSA, SAAJ, Madison, Wisconsin.
- Olexa, T. J., T. J. Gentry, P. G. Hartel, D. C. Wolfe, J. J. Fuhrmann, and C. M. Reynolds. 2000. Mycorrhizal colonization and microbial community structure in the rhizo-

- sphere of annual ryegrass grown in pyrene-amended soils. *International Journal of Phytoremediation* 2:213–231.
- Olsson, P. A. 1999. Signature fatty acids provide tools for determination of the distribution and interactions of mycorrhizal fungi in soil. *FEMS Microbiology Ecology* 29:303–310.
- Palojärvi, A., S. Sharma, A. Rangger, M. van Lützow, and H. Insam. 1997. Comparison of biology and phospholipid fatty acid patterns to detect changes in microbial community. Pages 37–48. in H. Insam, and A. Rangger. Eds, *Microbial communities: Functional versus structural approaches*. Springer-Verlag, New York.
- Paustian, K., O. Anderon, H. Janzen, R. Lal, P. Smith, G. Tian, H. Tiessen, P. van Noordwijk, and P. Woomer. 1997. Agricultural soil as a C sink to offset CO₂ emissions. *Soil Use and Management* 13:230–244.
- Perry, D. A. 1994. *Forest ecosystems*. John Hopkins University Press, Baltimore, Maryland 649.
- Pimm, S. L. 1991. *The balance of nature? Ecological issues in the conservation of species and communities*. University of Chicago Press, Chicago, Illinois 454.
- Rasmussen, P. E., and H. P. Collins. 1991. Long-term impacts of tillage, fertilizer and crop residue on soil organic matter in temperate semi-arid regions. *Advances in Agronomy* 45:93–134.
- SAS Institute Inc. 1996. *SAS user's guide: Statistics—Version 6.03 Edition*. Statistical Analysis System (SAS) Institute Inc., Cary, North Carolina, 584 pp.
- Schimel, D., J. Melillo, H. Tian, A. D. McGuire, D. Kicklighter, T. Kittel, N. Rosenbloom, S. Running, P. Thornton, O. Ojima, W. Parton, R. Kelly, M. Sykes, R. Neilson, and B. Rizzo. 2000. Contribution of increasing CO₂ and climate to carbon storage by ecosystems in the United States. *Science* 287:2004–2006.
- Schlesinger, W. M. 1977. Carbon balance in terrestrial detritus. *Annual Review in Ecology* 8:51–81.
- Schlesinger, W. M. 1990. Evidence from chronosequence studies for a low carbon-storage potential of soils. *Nature* 348:232–234.
- Schutter, M. E., and J. J. Fuhrmann. 2001. Soil microbial community responses to fly ash amendment as revealed by analyses of whole soils and bacterial isolates. *Soil Biology and Biochemistry* 33:947–1958.
- Snedecor, W. G., and W. G. Cochran. 1980. *Statistical methods*. 7th ed. Iowa State University Press, Ames, Iowa 354.
- Stadmatiadis, S., J. W. Doran, and E. R. Ingham. 1990. Use of staining inhibitors to separate fungal and bacterial activity in soil. *Soil Biology and Biochemistry* 22:81–88.
- ter Braak, C., and J. J. Smilauer. 1998. *CANOCO reference manual and user's guide to CANOCO for windows: Software for canonical community ordination*. Microcomputer Power, Ithaca, New York.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77:350–363.
- Tilman, D., and J. A. Downing. 1994. Biodiversity and sustainability in grasslands. *Nature* 367:363–365.
- Tribe, D. 1994. *Feeding and greening the world: The role of agricultural research*. CAB International, Wallingford, United Kingdom 274.
- Wang, Y., R. Amundson, and S. Trumbore. 1999. The impact of land use change on C turnover in soils. *Global Biogeochemical Cycles* 13:47–57.
- West, T. O., and G. Marland. 2001. A synthesis of carbon sequestration, carbon emissions, and net carbon flux in agriculture: Comparing tillage practices in the United States. *Agriculture, Ecosystems and Environment* 91:217–232.
- West, A. W., D. J. Ross, and J. C. Cowling. 1986. Changes in microbial C, N, P, and ATP contents, numbers and respiration on storage of soil. *Soil Biology and Biochemistry* 18:141–148.