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Evolution of CO₂ and soil carbon dynamics in biologically managed, row-crop agroecosystems

E.A. Paul^{a,*}, D. Harris^b, H.P. Collins^c, U. Schulthess^a, G.P. Robertson^d

^a Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824, USA

^b Stable Isotope Facility, University of California at Davis, Davis, CA 95616, USA

^c 7535 Mesplay Avenue SE, Lacey, WA 98503, USA

^d W.K. Kellogg Biological Station, Hickory Corners, MI 49060, USA

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Abstract

Field CO₂ production was related to soil carbon pools and fluxes determined by laboratory incubation of soils from agroecosystems designed to test the possibility of substituting biological for chemical inputs. Treatments included: conventional and organic-based row crops, woody and herbaceous perennial crops and historically tilled and never tilled successional fields. The CO₂ efflux in corn and soybeans was affected by crop residues from previous years and growing season temperatures but not soil moisture. Overwinter cover crops and perennials such as alfalfa and poplar, resulted in fairly uniform fluxes of approximately 20 kg CO₂-C ha⁻¹ day⁻¹ throughout the non-frozen period. Highest fluxes occurred in alfalfa, historically tilled successional and never tilled, grassland successional treatments, although, highest aboveground productivity occurred in the corn and poplar. Summed, field CO₂ fluxes were similar to residue-C inputs. Measurement of CO₂ mineralized in extended incubations in the laboratory made it possible to use soil enzyme activity to determine the size and dynamics of soil C pools. The residue of acid hydrolysis defined the size of the resistant pool C_r. Carbon dating determined its mean residence time (MRT). Curve analyses of CO₂ evolution plotted on a per unit time basis gave the active (C_a) and slow (C_s) pool sizes and decomposition rate constants *k_a* and *k_s*. Temperature correction factors provided field MRTs. The active pool of this coarse textured soil represents 2% of the soil C with a MRT of 30–66 days. The slow pool represents 40–45% of the SOC with field MRTs of 9–13 years. The poplar soil has the greatest MRT for both the active and slow pools. The system approach to land use sustainability (SALUS) model, which predicts CO₂ evolution from decomposition in the field as part of a plant growth – soil process model, was tested using the decomposition parameters determined by incubation and ¹⁴C dating. The model satisfactorily predicted the intra and inter year differences in field CO₂ but over predicted fluxes from residues in the fall. It does not yet adequately consider a lag period during which the residues lose their hydrophobicity, are comminuted and colonized. © 1999 Elsevier Science B.V.

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1. Introduction

The evolution of CO₂ under field conditions represents respiration by plant roots and soil biota and is a

sensitive indicator of abiotic controls, crop residue decomposition, soil organic carbon (SOC) turnover and ecosystem disturbance. Other CO₂ producing reactions such as anaerobic respiration, methane formation and carbonic acid reactions only slightly affect the relationship between CO₂ flux and aerobic

*Corresponding author. Tel.: +517 355 0262; fax: +517 355 0270.

respiration. There is generally a good agreement between dynamic, infrared gas analysis or static chambers with a CO₂ absorbent (Zibilske, 1994) and eddy flux methodology (Rochette et al., 1997). In some cases, static chamber systems show more CO₂ flux than the dynamic systems at low rates of evolution; the converse is true at high evolution rates (Jensen et al., 1996).

Soil management in sustainable agriculture is aimed at developing economically sound, environmentally safe cropping systems that substitute biological management for chemical inputs. It involves differing tillage and crop rotations with different inputs and qualities of residues. Sustainable agronomic systems usually are associated with significant pools of SOC. These include both rapid and slow release pools (Paul et al., 1995), whose size and turnover are utilized in describing SOC dynamics. The size and turnover rates of these pools have in the past been difficult to measure. The active (C_a) and slow (C_s) fractions now can be ascertained by analyzing the rates of CO₂ released during SOC decomposition under extended laboratory conditions (Nicolardot et al., 1994; Collins et al., 1998). The residue of acid hydrolysis has been shown to indicate the size of the resistant pool (C_r). Carbon dating measures its mean residence time (MRT) (Trumbore, 1993; Paul et al., 1997a).

Comparison of field CO₂ evolution rates with CO₂ rates determined in the laboratory allows one to better model field data and interrelate knowledge on SOC dynamics with the field decomposition rates under differing management. The evolution of CO₂, in extended laboratory incubations, indicates substrate availability because the microbes and their enzymes effectively characterize the availability of SOC pools. Substrate availability is a function of the amount present, its quality (Kern and Johnson, 1993), its location (Holland and Coleman, 1986) and the degree of physical protection within soil (Aiken et al., 1991; Carter and Stewart, 1996). These characteristics can best be determined under constant conditions in the laboratory. Field CO₂ evolution rates are dependent on root respiration, moisture and temperature controls of plant residue decomposition and mixing of both above and beneath ground substrates. They also reflect microbial biomass (Horwath et al., 1996), and diversity (Klug person. comm.), plant changes (Huberty

et al., 1998), and the effect of the soil water content on CO₂ transfer rates; in situ fluxes of CO₂ are too complex for the determination of SOC pool sizes.

We conducted field CO₂ evolution measurements and extended laboratory incubation of soils from a long-term agroecosystem study aimed at developing economically sound and environmentally safe cropping systems that substitute biological management for agricultural chemicals. The laboratory incubations supplement other measurements such as carbon dating and ¹³C/¹²C analyses used to determine SOC dynamics on these soils (Collins et al., 1998). The use of such related measurements on long-term plots with known histories of climate, plant residue inputs, and biotic diversity allows better concept development relating soil characteristics (Sollins et al., 1996) to ecosystem functioning. It also facilitates the testing of models (Paustian et al., 1992; Parton and Rasmussen, 1994), and extrapolation of both the models and concepts to other sites (Paul et al., 1997b) involved in climate change and sustainable agriculture research (Robertson and Paul, 1998).

2. Materials and methods

2.1. Site characteristics

This study was conducted at the W.K. Kellogg Biological Station (KBS) Long Term Ecological Research (LTER) site for agricultural ecology located in southwest Michigan. Climate is characterized by cool moist winters and warm humid summers. Precipitation averages 920 mm year evenly distributed throughout the year. Surface soil temperatures are usually less than 5°C from December through March. They exceed 10°C by 15 April (Fig. 1). The KBS site is located on a pitted outwash plain-moraine complex. Upland soils are Alfisols that developed under oak-hickory (*Quercus-Carya*) forests with minor areas of elm-ash (*Ulmus-Fraxinus*) and beech-maple (*Fagus-Acer*) (Kuchler, 1964). Current vegetation is a mixture of forest, successional and agricultural species (Burbank and Pregitzer, 1992). The principal soil types are Kalamazoo (Fine-loamy, mixed, mesic), and Oshtemo (Coarse-loamy, mixed, mesic), Typic Hapludalfs that vary mainly in the thickness of the argillic (Bt) horizon (Whiteside, 1982; Crum et al., 1988).

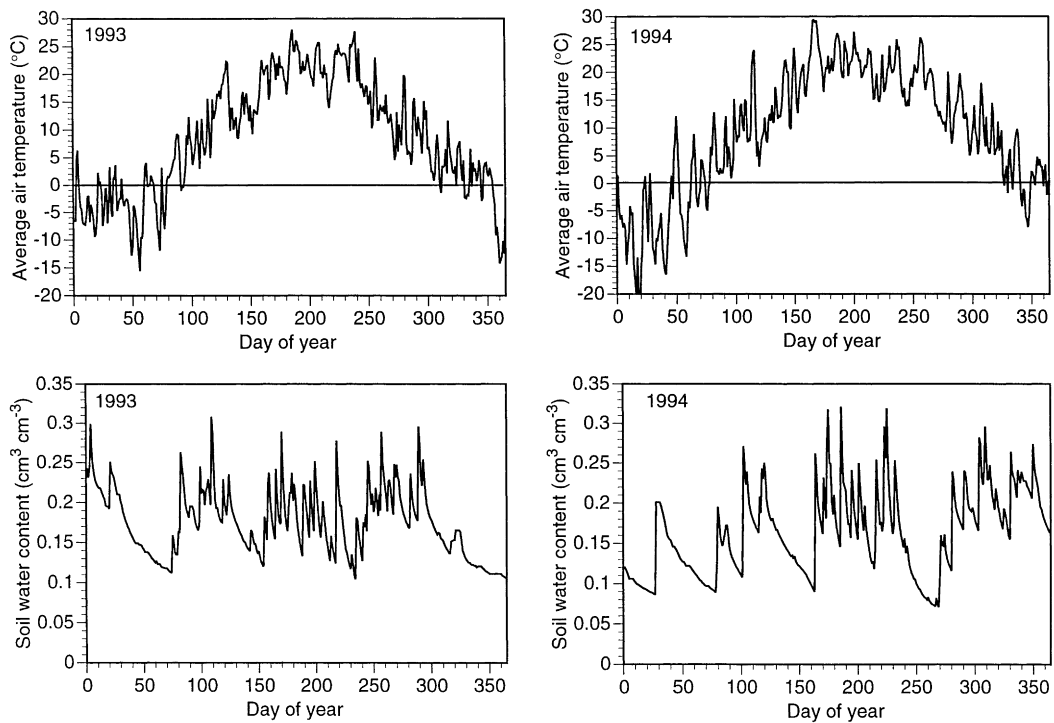


Fig. 1. Measured air temperature and modelled soil water contents during the period of field measurement.

Four annual crop and three perennial treatments were established in 1989 on a 42 ha cultivated field, that had been in a corn/soybean (*Zea mays* L./*Glycine max* L.) rotation under moldboard plow tillage for >50 years. Treatments consisted of: (1) a moldboard plowed (conventional) corn/soybean rotation (CT), (2) no-tillage (NT) corn/soybeans, (3) a corn/soybean / wheat rotation that included legume cover crops and low chemical inputs (LI), and (4) a treatment similar to (3) but with zero-chemical inputs (ZI). Management of the LI and ZI incorporated mechanical weed control and inputs of leguminous residue to offset lower or no inorganic fertilizer and pesticides (Robertson et al., 1998).

The three perennial treatments consist of hybrid poplar (*Populus euramericana* cv Eugenei), alfalfa (*Medicago sativa* L.) and a historically tilled successional community (HTS) allowed to establish in 1989 on the previously tilled site. A never-tilled successional (NTS) plot located 200 m south of the main site on the same soil series comprises the eighth treatment. Old-growth trees were harvested from this site around

1956; mowing since then, has maintained a herbaceous community.

2.2. Field measurements

Plant biomass was measured by clipping corn, soybeans, wheat, alfalfa, legume, and weed spp. and by allometric measurements of the poplars. The field-crop-residue returned to the soil was calculated by subtracting the grain yield from the total above-ground plant biomass. Alfalfa was harvested in late May, early July, mid-August, and mid-October in 1993. It was killed by herbicide and replanted in spring 1994. Total soil C and N were measured on a Carlo Erba CHN analyzer. Soil moisture was determined gravimetrically during CO₂ sampling. A weather station recorded air and soil temperature, windspeed and direction, solar radiation, and wet deposition of atmospheric N inputs. There were more temperature fluctuations in 1994 than in 1993; and more extensive dry periods accompanied the temperature fluctuations. Rainfall generally exceeds potential

evapotranspiration (PET from the middle of September through late April (Crum et al., 1988).

Field fluxes of CO₂ from soil were determined by measuring time-series changes in CO₂ concentrations in static chambers. A two-piece chamber composed of a high impact white polystyrene lid and an aluminum base, with a total headspace of 16.7 l and covering 0.075 m⁻², was inserted 2.5 cm into mineral soil. At 0, 45, 90, and 135 min, 10 ml headspace air samples were collected and stored, over-pressurized, in 3 ml serum bottles. Carbon dioxide concentration was measured by injecting 1 ml of the sample into a helium or N₂ carrier gas flowing through a calibrated infrared gas analyzer (Beckman Model 865). Linear regression of CO₂ concentration vs. elapsed sampling time provided CO₂ flux estimates for individual chambers. Analysis of the CO₂ fluxes included regression analysis using CO₂ efflux as the dependent variable and independent variables such as soil and air temperature and gravimetric soil moisture. Responses to temperature were also tested using the Arrhenius equation.

Laboratory incubations were conducted on composite samples of soil sieved to 4 mm and adjusted to 50% of water holding capacity. The soils were incubated in 1 l canning jars at 25°C in the dark. Carbon dioxide was trapped in NaOH (2 ml, 2 M) in a 20 ml vial. The CO₂ traps were replaced initially at 10-days intervals and later after longer periods. Control jars contained no soil. The average rate of CO₂ evolution for each interval was measured by titration of residual NaOH to pH 7.0 with 0.3 M HCL, after the addition 2 ml of 2 M SrCl₂ (Harris et al., 1997).

We determined pool sizes and dynamics by a combination of techniques. The analyses are based on the use of a model with three pools, which decompose according to first-order kinetics with the equation

$$C_{\min} = C_a e^{-k_a t} + C_s e^{-k_s t} + C_r e^{-k_r t}$$

where; C_a, k_a=active pool; C_s, k_s=slow pool; C_r, k_r=resistant pool. Acid hydrolysis, consisting of refluxing soil in 6 M HCL, determined the size of the non-hydrolyzable, resistant pool (C_r). Carbon dating determined its MRT (Paul et al., 1997a). We determined the size and turnover rates of the C_a and C_s pools by non-linear regression of the rate of change of CO₂ evolution with time. Three parameters, C_a, k_a and k_s were estimated using the non-linear regression routine

(PROC NLIN) of SAS. The C_s pool was defined as the residual (C_s = C_t - C_a - C_r).

MRT is the reciprocal of the decomposition rate constant in first-order reactions. The MRT derived from laboratory incubation at 25°C was scaled to average field temperature (9°C) by assuming a Q₁₀ of 2(2^{(25-9)/10} = 3).

We used the system approach to land use sustainability (SALUS) model (Schulthess and Ritchie, 1996) to simulate the daily CO₂-C evolution from SOC and crop residues. The model runs on a daily time-step. It simulates a water balance, SOC, N dynamics, a heat balance, plant growth and plant development. The SOC dynamics are simulated with procedures adapted from the CENTURY-model (Parton et al., 1988; Paustian et al., 1992). The model does not predict root respiration from plants. Data from the incubation study (Tables 5 and 6) were used to initialize the soil C pools. The model was calibrated to predict a similar amount of biomass production as measured in the field.

3. Results

3.1. Soil CO₂-C efflux rates

The 4–5 years of treatment imposed at this site prior to the time of sampling had not yet resulted in significant differences in SOC (Table 1). The efflux of CO₂-C in 1993 (Fig. 2) and 1994 (Fig. 3) was seasonally dependent in the cultivated crop (CT) with no ground cover. Efflux rates were more temporally uniform in the no-till (NT) site and even more so in the low input (LI) and zero input (ZI) that incorporated a legume ground cover. Killing and reseeded of the alfalfa in 1994 resulted in more seasonally uniform evolution of CO₂ that year. The uniformity in CO₂ evolution throughout the growing season was even more evident in the poplar, HTS and in the NTS.

The CO₂ flux was not significantly correlated with soil moisture. Better correlations were obtained with air temperature than with modeled soil temperatures (data not shown). Linear regression models between air temperature and evolved CO₂-C for the agronomic sites (Table 2) explained 55–80% of the variance except for the NT treatment in 1994 that had an R²

Table 1
Soil carbon and nitrogen of cultivated and never-tilled successional fields

Treatment	Depth increment (cm)	Organic C (kg m ⁻²)	SE ^b	Total N (kg m ⁻²)	SE
Conventional till ^a	0–25	2.4	0.01	0.30	0.01
	25–50	1.5	0.15	0.27	0.02
	50–100	0.1	0.01	0.08	0.001
Never-till succession	0–25	4.5	0.23	0.46	0.02
	25–50	1.7	0.13	0.31	0.02
	50–100	0.1	0.01	0.08	0.01

^a Other treatments were not significantly different from the conventional till and are not shown.

^b SE: standard error, $n=6$.

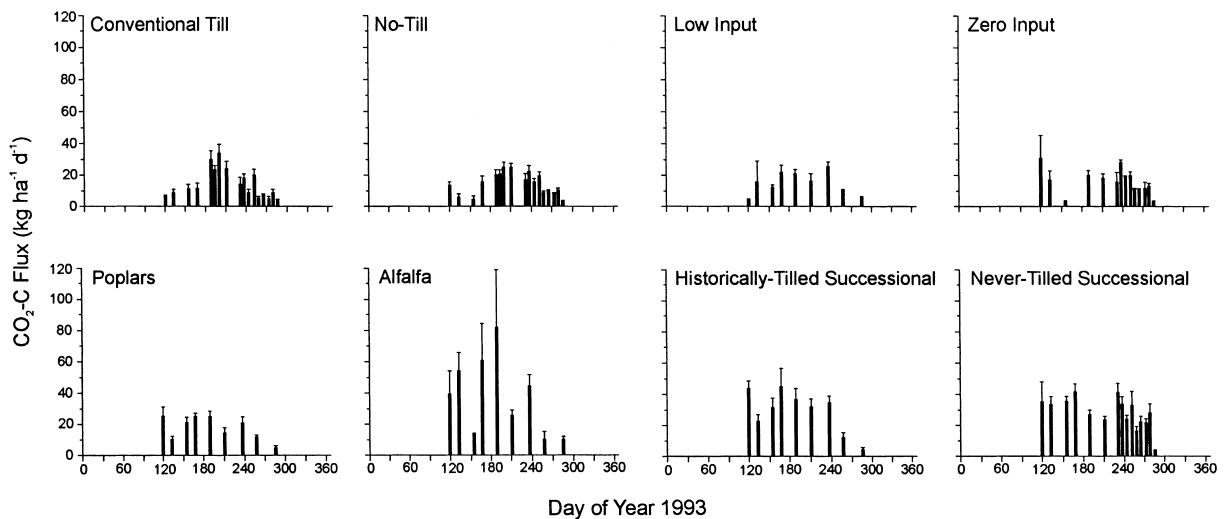


Fig. 2. Field CO₂ fluxes in 1993.

Table 2
Relationship between air temperature and field CO₂ fluxes (kg ha⁻¹d⁻¹) of the annually cropped treatments

Treatment ^a	1993				1994			
	x coefficient	Intercept	R^2	SE	x coefficient	Intercept	R^2	SE
CT	1.07	-3.6	0.55	6.6	3.0	-22	0.80	8.3
NT	0.91	-0.6	0.66	4.5	0.98	3.1	0.36	7.6
LI	0.85	0.5	0.80	3.4	0.96	0.8	0.30 ^b	6.5
ZI	0.67	5.1	0.57	4.2	2.6	-20	0.7	8.9

^a CT – Conventional tillage; NT – No-tillage; LI – Low input; ZI – Zero input.

^b Two outliers removed from regression analysis. SE: standard error of the estimate.

of 0.36. This was a reflection of the low CO₂ estimated for that site in that year. There was no relation ($R^2 < 0.2$ data not shown) between temperature and CO₂ efflux in the perennial, non-disturbed treatments (HTS, NTS,

poplar and alfalfa). The use of an Arrhenius equation to test the temperature CO₂ interactions, did not provide a more meaningful interpretation than the regressions and is not further discussed.

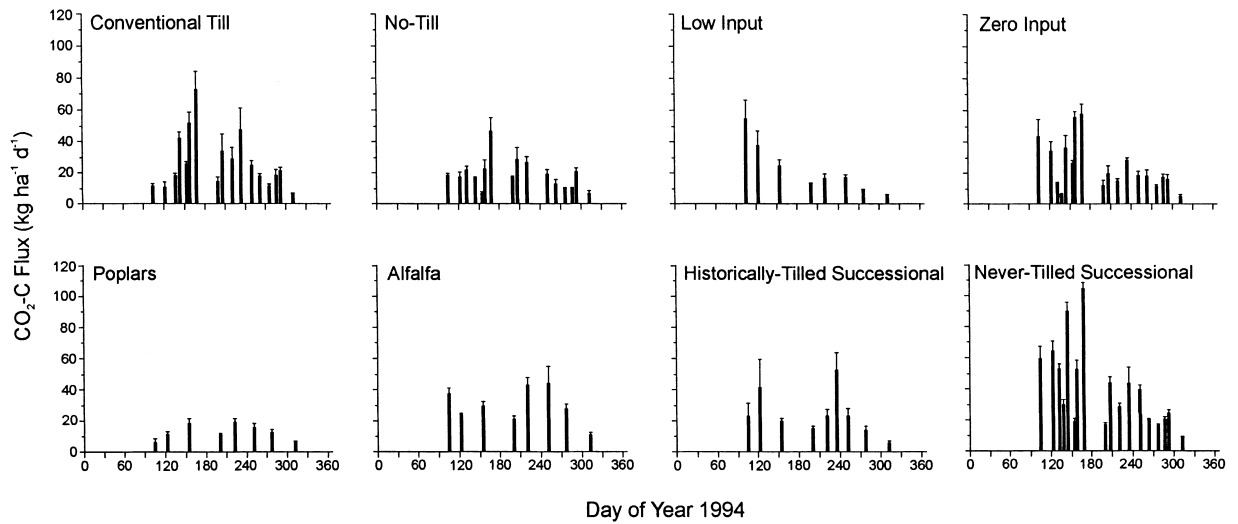
Fig. 3. Field CO₂ fluxes in 1994.

Table 3
Carbon inputs from the annually cropped agronomic treatments during 1993 and 1994

Treatment ^a	Crop residue C ^b (Mg C ha ⁻¹)	Crop root C ^c	Non crop-C ^d	Total C input
Corn residues 1993				
CT	3.5 (0.20)	1.9	0.22	5.6
NT	3.5 (0.28)	1.9	0.89	6.3
LI	2.9 (0.24)	1.5	1.17	5.6
ZI	2.1 (0.20)	1.1	1.56	4.8
Soybean residues 1994				
CT	1.8 (0.60)	0.85	0.30	2.9
NT	1.5 (0.08)	0.72	0.36	2.6
LI	1.6 (0.14)	0.73	0.95	3.2
ZI	1.3 (0.08)	0.60	0.95	2.8

^a CT – Conventional tillage; NT – No-tillage; LI – Low input; ZI – Zero input.

^b Crop residue × 0.4 = Crop residue C.

^c Crop residue C × 0.53 = Root-C for corn; Crop residue C × 0.47 = Root-C for soybeans.

^d Non-crop biomass × 0.4 = Aboveground non-crop-C; Aboveground non-crop-C + (Aboveground non-crop-C × 0.5) = Non-crop C. (Willson et al., 1997).

3.2. Carbon inputs and annual CO₂ evolution

Inputs of aboveground residue were measured at peak standing crop and at predetermined time intervals for the non-crop biomass. The C inputs from corn (Table 3) were twice those from soybeans. Both organic treatments, LI and ZI, had lower crop yields; the over-winter cover crop did not raise the C inputs to equal those of conventional treatments. The contribution of root C to the corn crop (Table 3) was deter-

mined on an adjacent plot using extensive root coring and ¹³C analyses (Willson et al., 1997). Our estimate of 53% of non-grain C being underground is slightly higher than the value of 47% developed in Missouri by Buyanovsky and Wagner (1997). Soybean roots were not measured on our site; we used the 47% value determined by Buyanovsky and Wagner (1997).

Non-crop biomass included weeds and the cover crop, where present. Beneath ground, non-crop C was estimated as 50% of the total aboveground C. This is

Table 4
Carbon balance of inputs and outputs for the cropped treatments in 1993 and 1994

Treatment ^a	Corn (1993) (Mg C ha ⁻¹)	Soybeans (1994)	Total-C	CO ₂ evolved	CO ₂ -total C/total C (%)
CT	5.6	2.9	8.5	9.0	6
NT	6.3	2.6	8.9	7.9	-11
LI	5.6	3.2	8.8	9.6	9
ZI	4.8	2.8	7.6	9.1	20

^a CT – Conventional tillage; NT – No-tillage; LI – Low input; ZI – Zero input.

substantially higher than the ratio of root C to total aboveground C (including grain) of 0.24, we measured for corn. Total C inputs (Table 3) reflect the lower yields of the zero input (ZI) plots and the lower inputs under soybeans.

The CO₂ evolved annually on the agronomic sites (Table 4) was calculated by integrating the daily values over the measurement period. The CO₂ evolution, during non-growing periods, when measurements were not made, was estimated using the regression constants developed for temperature and daily rates of CO₂ evolution. The less-disturbed sites had fairly constant CO₂ flux over the growing season and did not give significant regressions for the daily evolution rates. Therefore, annual flux rates were not calculated. There was a delay in CO₂ evolution relative to crop growth and residue inputs. The 1993 CO₂ data, when the field was planted to corn, represent the corn root respiration plus the decomposition of the soybean residues from the previous year. The CO₂ evolved in 1994, composed of soybean root respiration and the decomposition of the corn residue from the previous year, was 26% higher than in 1993. Comparison of C inputs with CO₂ evolution (Table 4) shows a slight positive balance for CO₂-C evolution values except for the NT site which was shown earlier (Table 2) to have low evolution rates and a poor regression between temperature and CO₂ evolution.

3.3. Carbon mineralization in the laboratory

Laboratory incubation utilizes the degradative enzymes of the soil biota to provide an analytical estimate of the soil C pools and fluxes. These can be related to field CO₂ evolution and plant-C inputs in determining the role of biological inputs in sustainable systems. Cumulative CO₂ evolution curves for the 0–25 cm layer for each of the eight treatments were

similar in 1993 and 1994 and were combined. The data for the various cultivated treatments and alfalfa were not statistically different and only the curves for the CT, poplar, HTS, and NTS are shown (Fig. 4, upper). Carbon dioxide evolution, expressed on a soil weight basis, showed the NTS site to have the highest evolution with the release from 350 days of laboratory incubation being equivalent to 1600 µg C g⁻¹ soil. The historically NTS is still not different in total measurable SOC, but after 4–5 years of succession is showing an accumulation of active C as determined by incubation. Expressing the data on the basis of the C in the soil (Fig. 4, lower) shows the HTS site evolves C at the same rate as the NTS treatment with 14% of its SOC being released in the 350 days incubation. The active fraction is small; 80% of the CO₂ released came from the slow pool.

The size of the old resistant pool (C_r), determined as that fraction not solubilized by acid hydrolysis, contains 56% of the SOC in the disturbed sites with a MRT of 1435 years (Table 5). The native successional site (NTS) site, originally in deciduous forest, but clear cut in 1956 and managed as a mowed grassland had 53% of its C in the C_r pool with a mean residence time of 170 years (Table 5). Replotting the data from the CT, poplar and two successional treatments on the

Table 5
Dynamics of the resistant carbon (C_r) of the 0–25 cm layer

Treatment ^a	Total-C (µg g ⁻¹)	Resistant C	
		(%)	MRT (yr)
CT	8758	56	1435
POP	9040	nd ^b	nd
HTS	9000	nd	nd
NTS	14560	53	170

^a CT – Conventional tillage; HTS – Historically tilled successional; NTS – Never tilled successional.

^b nd: nd should be identical to CT.

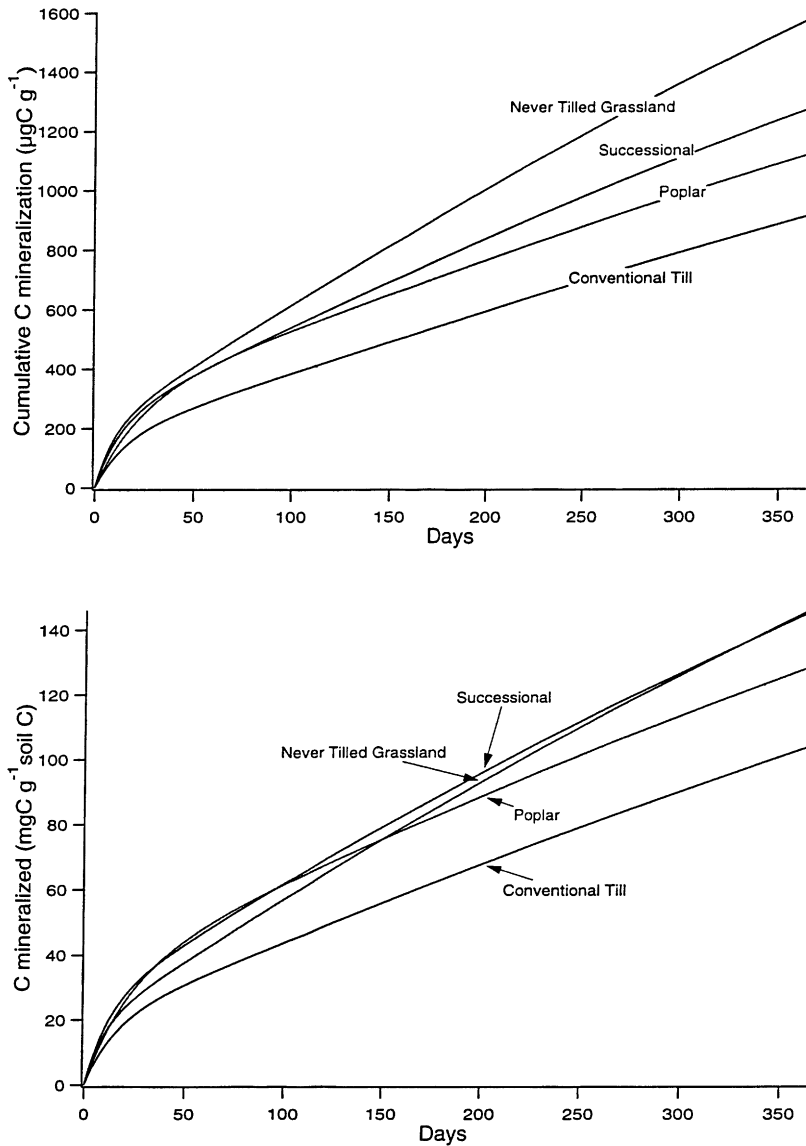


Fig. 4. CO₂ evolution during extended laboratory incubation of the 0–25 cm soil layer. Upper=µg CO₂-C g⁻¹ soil, Lower=mg CO₂-C g⁻¹ soil C.

basis of CO₂ evolution per unit time (Fig. 5) provides more statistically valid parameters (Hess and Schmidt, 1995) that allow one to calculate the pool sizes and decomposition rate constants of the active and slow pools.

Curve fitting and statistical analyses showed high regression coefficients for the output of the three pool analysis for the surface soils (Fig. 5). The active C

pool (C_a), comprising 1.8% of the SOC in the CT site, had a field MRT of 45 days. The C_a pool in the soil under poplar reflects the slower, more consistent, initial CO₂ evolution rates and represents 3.5% of the SOC with a 66 days MRT. The NTS site had both the smallest C_a pool and lowest MRT (Table 6). The active pool is most closely related to recent inputs with residence times of less than a year. Little of the old,

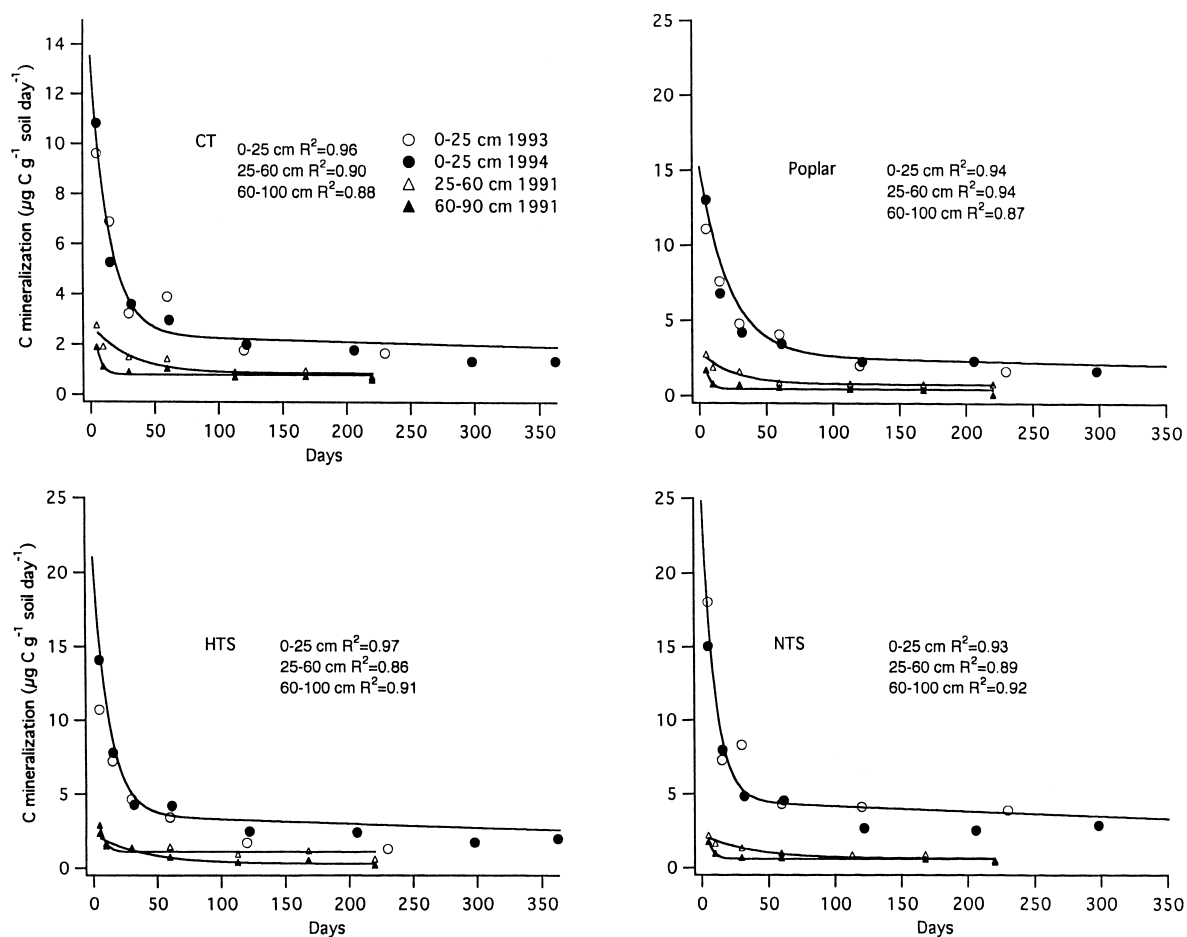


Fig. 5. CO₂ evolution during long term laboratory incubation, plotted on a discrete time basis.

Table 6

Decomposition kinetics of the active and slow C pools of the surface horizons as determined by extended incubation

Treatment ^a	Active C			Slow C		
	% of Total C	Lab MRT ^b	Field MRT ^c	% of total C	Lab MRT	Field MRT
	(%)	days		(%)	yr	
CT	1.85 (0.26)	15 (2.8)	45	42.1	4.4 (0.56)	13.2
POP	3.32 (0.32)	22 (5.1)	66	40.8	3.7 (0.79)	11.1
HTS	2.45 (0.29)	12 (2.1)	36	41.6	3.9 (0.39)	8.7
NTS	1.78 (0.29)	10 (2.8)	30	45.2	3.1 (0.63)	9.3

^a CT – Conventional tillage; POP – Poplar; HTS – Historically tilled successional; NTS – Never-tilled successional.

^b Values in parentheses are asymptotic standard errors.

^c Calculated on a basis of a laboratory temperature of 25°C versus a mean annual field temperature of 9°C.

resistant C is evolved in a 350 days incubation. Long, asymptotic, low level of CO₂ evolution (Fig. 5) is indicative of the slow pool. This in the surface layer

constitutes a daily emission of 0.02–0.045% of the SOC with the slow pool comprising 40–46% of the SOC in the different treatments. The field MRT's of

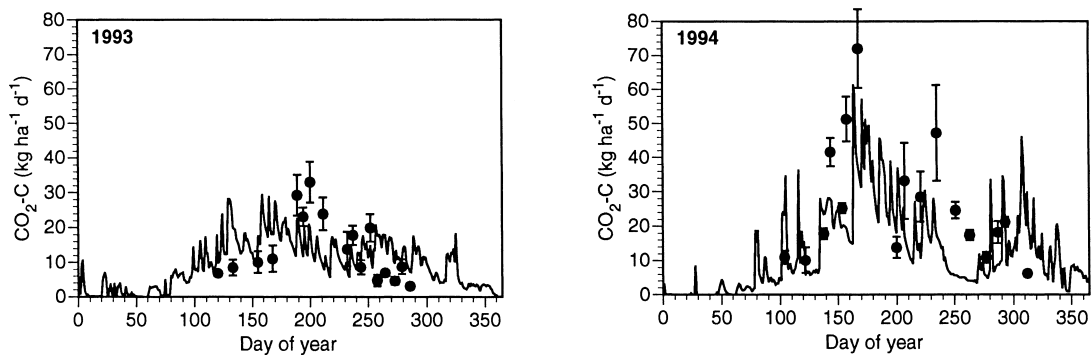


Fig. 6. Simulated CO_2 fluxes for the conventional till plots in 1993 and 1994.

this pool were 9 years in the two successional plots, 11 years in the poplar and 13 years in the conventionally tilled site (Table 6). The CO_2 evolution rates from the lower horizons were low when expressed per unit weight of soil (Fig. 5); these become substantial when expressed on a unit C basis (data not shown).

Fig. 6 shows the simulated CO_2 -C flux from the conventional tillage treatments for 1993 and 1994. Predicted daily CO_2 -C fluxes were in good agreement with measured data during the periods when no living crop was in the field; there was a tendency to over predict CO_2 -C evolution from plant residues in the fall. The model used the analytically determined pool sizes and fluxes for the three soil depths in its simulation. The decomposition rates of the subsurface samples were lowered by 20% to take into account the observations that subsurface burial of materials such as, cellulose results in lower decomposition rates than those at the surface (Coleman et al., 1980). It also considers our observation that subsurface SOC is old but not necessarily resistant to decomposition in the laboratory (Paul et al., 1998). Nine percent of the CO_2 was predicted to evolve from the surface residue, 70% from the 0 to 25 cm depth and 21% from lower depths.

4. Discussion

The biological-input treatments (LI and ZI) established in 1989 had by 1993 not shown an equivalence in yield and residue inputs to the normally used chemical treatments (CT and NT). They did not differ in SOC levels from the CT and NT. Other plots have

required a period of 5–7 years for conversion from chemical to biological-organic inputs (Peters et al., 1997). The field CO_2 evolution patterns of the LI and ZI plots reflect the greater diversity of plant C input and extended period of root respiration, in that the CO_2 evolution is more uniform throughout the year than in the CT and NT plots.

The annual rates of CO_2 evolution reflect high inputs in the NTS plots, where the annual production of 5 Mg C ha^{-1} is not removed. The historically tilled successional treatment showed nearly as much field CO_2 evolution and has accumulated active C, as shown by the laboratory incubations. Its aboveground production was only 3.6 Mg C ha^{-1} . The possibility of extensive rhizosphere associations in such regenerating systems needs to be explored. The alfalfa plots evolved $8.4 \text{ Mg CO}_2\text{-C ha}^{-1}$ while producing $10.9 \text{ Mg C ha}^{-1}$ of aboveground biomass, most of which was removed as hay by harvest. This crop therefore, not only has high sustainable productivity but also shows a high potential for beneath ground fluxes and C storage. This can be attributed to its extensive roots and to the mycorrhiza and rhizobia that each require transported photosynthate (Paul and Clark, 1996). The poplar plantations have a ground cover of perennial grasses representing an input of $2.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. Annual woody production was 9.4 Mg C and leaf fall 6.5 Mg . The low rates of CO_2 evolution are noteworthy; the soil is only slowly building up its SOC pools with most production going to aboveground C storage. Poplars have been shown to result in SOC losses during the first 4–6 years growth but growth in plantations for 6–12 years resulted in sequestration of significant SOC (Hansen, 1993).

The difference between the values for total CO₂ efflux and plant residue C inputs in a steady-state system should be root respiration. Our calculations for beneath ground production reflect peak standing crops and are higher than most literature values. We have shown that the plant CO₂ flux is derived primarily from the previous years residue as well as from the large slow pool with MRT's of 10 years. The difference technique therefore is not applicable to root respiration calculations; and tracer techniques will have to be utilized.

Expression of the CO₂ evolved during the laboratory incubations on a unit C basis showed the HTS treatment, initiated in 1989, to have as great a proportion of its C available for biological mineralization as the older NTS treatment. The sharp change in the laboratory evolution rates that occurs between 50 and 70 days demarcates the active and slow pools. The slow pool with more than 40% of the C and a turnover rate under these conditions of 9–13 years in the field is central to soil fertility and ecosystem sustainability. Tracer N experiments in these soils confirm the large size and relatively slow turnover of the slow pool. While, 40% of fertilizer ¹⁵N was left in the SOM after growth of a fertilized crop, growth of a subsequent crop removed only 5–10% of the ¹⁵N. Later crops removed 1–2% of the stored soil N each year (Harris et al., 1994).

The information on pool sizes and mean residence times can best be related to field measurements, by modeling the CO₂ evolution in the field on the basis of field abiotic conditions and known plant residue inputs into our long term plots. Incorporation of the analytically derived SOC pool sizes and flux rates into the SALUS-model predicted trends in CO₂-C evolution within a year quite well. The model, which is basically the Century SOM model integrated with a plant growth model under predicted CO₂-C evolution during the summer months; it does not simulate root respiration. The tendency of SALUS to over predict CO₂-C evolution in the fall is attributable to the fact that it does not consider a lag period until the residues are colonized and comminuted. In accordance with observed data, the model predicted a higher CO₂-C evolution for 1994 as compared to 1993. The higher rates in 1994 were attributable to residues from the previous corn crop. In 1993, the previous crop was soybean. The SALUS-Century model has a complex

series of interpool fluxes. These are oversimplified when the pool sizes and decomposition rates for the three soil pools are based only on the laboratory derived data. The model when run for 2 years with our pool and flux rate data showed a slight accumulation of crop residues and an equivalent drop in the C_s.

4.1. *Implications for sustainability and global C storage*

Sustainable agriculture and the storage of C in global change scenarios must rely on soil pools that can accumulate C and other nutrients within reasonable time periods. The 56% of the C in the agronomic treatments that has a MRT of 1435 years does not participate in short term changes but stabilizes structure, supplies exchange complexes and other adsorption sites. The active pool is of the same general size as the microbial biomass in these plots. It is not comprised exclusively of this source as it is the entry point of residues into the soil; long term incubations decrease the active pool more rapidly than the biomass-C. It is the active and slow pools that must be managed in substituting biological management for chemical inputs. The active pool must be managed such that the nutrient release from the SOM is synchronized temporally with the needs of a growing crop. This ensures that N released during decomposition will be utilized by the crop and not lost to the environment, as can happen when N is mineralized during non-crop periods such as the late fall and early spring. The accumulation of SOC is essential for the possibility of enhanced transfer of atmospheric CO₂ to terrestrial pools in global change scenarios. This is happening in the slow pool of our HTS plots and to a lesser extent in the poplar. The HTS plots however, do not produce an income from the land and thus are viable only with alternate management strategies involving government agencies or prior to development of the land for alternate usage.

Combination of field and laboratory studies have made possible an interpretation of the field CO₂ evolution rates relative to SOC changes in different cropping systems. The systems with more organic inputs produced CO₂ more evenly throughout the year than the conventional fertilized systems. There was enough variability in field CO₂ rates that specific calculations of root contributions could not be made

but the extended seasonal evolution should be attributable to roots rather than microbial activity. This extended activity reflects plant activity that should reduce losses of nutrients such as nitrate during the winter months.

Laboratory measurement of SOC mineralization is a sensitive indicator of SOC changes long before they can be measured in the field. The HTS plots are showing major SOC accumulations in the active and slow fractions. The poplar plots have the most distinctive laboratory evolution patterns with differing pool sizes and fluxes. These should eventually lead to a buildup of SOC although, this was not apparent at the time of sampling. The ability to realistically model the field evolution of CO₂ based on SOC pool sizes and fluxes, determined by acid hydrolysis and C dating, together with extended incubation demonstrates that we have the techniques necessary for the analytical determination of the SOC components involved in SOC dynamics. Knowledge of these pools and fluxes can be utilized for better decision making in sustainable agriculture and global change calculations.

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References

- Aiken, R.M., Jawson, J.D., Grahammer, K., Polymenopoulos, A.D., 1991. Positional, spatially correlated and random components of variability in carbon dioxide efflux. *Environmental monitoring. J. Environ. Qual.* 20, 301–308.
- Burbank, D.H., Pregitzer, K.S. et al., 1992. Vegetation of the W.K. Kellogg Biological Station. Michigan State University, Agricultural Experiment Station Research Report 510.
- Buyanovsky, G.A., Wagner, G.H., 1997. Crop residue input into soil organic matter on Sanborn field. In: Paul, E.A., Paustian, K., Elliott, E.T., Cole, C.V. (Eds.), *Soil Organic Matter in Temperate Agroecosystem*. CRC Press, Boca Raton, FL, pp. 73–83.
- Carter, M.R., Stewart, B.A. (Eds.), 1996. *Structure and Organic Matter Storage in Agricultural Soils*. CRC Press, Boca Raton, FL.
- Collins, H.P., Paul, E.A., Blevins, R.L., Bundy, L.G., Christenson, D.R., Dick, W.A., Huggins, D.R., Lyon, D.J., Peters, S.E., Turco, R.F., 1998. Carbon pools and dynamics in Corn Belt agroecosystems. *Soil Sci. Soc. Am. J.*, in press.
- Coleman, D.C., Breymeyer, A.I., Dash, M.C., Dommergues, Y., Hunt, H.W., Paul, E.A., Sasson, A., Schaefer, R., Ulova, B., Zlotin, R.I., 1980. Decomposer subsystem. In: Breymeyer, A.I., van Dyne, G.M. (Eds.), *Grasslands System Analysis and Man*. Cambridge University Press, Cambridge, UK.
- Crum, J.R., Robertson, G.P., Nurnberger, F., 1988. Long-term climate trends and agricultural productivity in southwest Michigan. In: Greenalnd, D., Swift Jr., L.W. (Eds.), *Climate Variability and Ecosystem Response*. Proc. Long-term Ecological Research Workshop. Boulder, CO, 65, 53–58.
- Hansen, E.A., 1993. Soil carbon sequestration beneath hybrid poplar plantations in the North Central United States. *Biomass and Bioenergy* 5, 431–436.
- Harris, G.H., Hesterman, O.B., Paul, E.A., Peters, S.E., Janke, R.R., 1994. Fate of legume and fertilizer ¹⁵N in a long-term cropping systems experiment. *Agronomy J.* 86, 910–915.
- Harris, D., Porter, L.K., Paul, E.A., 1997. Continuous flow isotope ratio mass spectrometry of ¹³CO₂ trapped as strontium carbonate. *Comm. Plant and Soil Anal.* 28, 747–757.
- Hess, T.F., Schmidt, S.K., 1995. Improved procedure for obtaining statistically valid parameter estimates from soil respiration data. *Soil Biol. Biochem.* 27, 1–7.
- Holland, E.A., Coleman, D.C., 1986. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. *Ecology* 68, 425–433.
- Horwath, W.R., Paul, E.A., Harris, D., Norton, J., Jagger, L., Horton, K.A., 1996. Defining a realistic control for the chloroform-fumigation incubation method using microscopic counting and ¹⁴C-substrates. *Can. J. Soil Sci.* 96, 459 – 467.
- Huberty, L.E., Gross, K.L., Miller, C.J., 1998. Effects of nitrogen addition on successional dynamics and diversity in Michigan old-fields. *J. Ecol.*, submitted.
- Jensen, L.S., Mueller, T., Tate, K.R., Ross, D.J., Magid, J., Nielsen, N.E., 1996. Soil surface CO₂ flux as an index of soil respiration in situ: a comparison of two chamber methods. *Soil Biol. Biochem.* 28, 1297–1306.
- Kern, J.S., Johnson, M.G., 1993. Conservation tillage impacts on national soil and atmospheric carbon levels. *Soil Sci. Soc. Am. J.* 57, 200–210.
- Kuchler, A.W., 1964. Potential natural vegetation of the conterminous United States. *Am. Geo. Soc. Spec. Pub.* 36, New York.
- Nicolardot, B., Molina, J.A.E., Allard, M.R., 1994. C and N fluxes between pools of soil organic matter: model calibration with long-term incubation data. *Soil Biol. Biochem.* 26, 235–243.
- Parton, W.J., Rasmussen, P.E., 1994. Long-term effects of crop management in wheat-fallow: II. CENTURY model simulations. *Soil Sci. Soc. Am. J.* 58, 530–536.

- Parton, W.J., Stewart, W.B., Cole, C.V., 1988. Dynamics of C, N, P and S in grassland soil. A model *Biogeochemistry* 5, pp. 109–131.
- Paul, E.A., Collins, H.P., Haile-Mariam, S., 1998. Analytical determination of soil C dynamics. 16 Int. Congr. Soil Sci., Montpellier, France, Trans.
- Paul, E.A., Follett, R.F., Leavitt, S.W., Halvorson, A., Peterson, G.A., Lyon, D.J., 1997a. Radio carbon dating for determination of soil organic matter pool sizes and fluxes. *Soil Sci. Soc. Am. J.* 61, 1058–1067.
- Paul, E.A., Paustian, K.L., Elliott, E.T., Cole, C.V. (Eds.), 1997b. *Soil Organic Matter in Temperate Agroecosystems: Long-term Experiments in North America*. CRC Press, Boca Raton, FL, pp. 414 plus disk.
- Paul, E.A., Clark, F.E., 1996. *Soil Microbiology and Biochemistry*, 2nd ed. Academic Press, San Diego, CA., pp. 340.
- Paul, E.A., Horwath, W.R., Harris, D., Follett, R., Leavitt, S.W., Kimball, B.A., Pregitzer, K., 1995. Establishing the pool sizes and fluxes in CO₂ emissions from soil organic matter turnover. In: Lal, R., Kimble, J., Levine, E., Stewart, B. (Eds.), *Advances in Soil Science of Soils and Global Change*. CRC Press, Boca Raton, FL, pp. 297–305.
- Paustian, K., Parton, W.J., Perrson, J., 1992. Modeling soil organic matter in organic amended and N-fertilized long-term plots. *Soil Sci. Soc. Am. J.* 56, 476–488.
- Peters, S.E., Wander, M.M., Saporito, L.S., Harris, G.H., Friedman, D.B., 1997. Management impacts on SOM and related soil properties in a long-term farming systems trial in Pennsylvania. In: Paul, E.A., Paustian, K., Elliott, E.T., Cole, C.V. (Eds.), *Soil Organic Matter in Temperate Agroecosystems*. CRC Press, Boca Raton, FL, pp. 183–196.
- Robertson, G.P., Paul, E.A., 1998. Ecological research in agricultural ecosystems: contributions to ecosystem science and to the management of agronomic resources. In: Groffman, P.M., Pace, M.L. (Eds.), *Successes, Limitations and Frontiers in Ecosystem Science*. Cary Conference VII, Springer, NY, in press.
- Robertson, G.P., Collins, H.P., Gage, S.H., Gross, K.L., Halstead, S.H., Harwood, R.H., Klingensmith, K.M., Klug, M.J., Paul, E.A., 1998. Long-term research in agricultural ecology: objectives and establishment of a site in the US Midwest. *Agric. Ecosyst. and Environ.*, in press.
- Rochette, P., Ellert, B., Gregorovich, E.G., Desjardins, R.L., Pattey, E., Lessard, R., Johnson, B.G., 1997. Description of a dynamic closed respiration chamber for measuring soil respiration and its comparison with other techniques. *Can. J. Soil Sci.* 77, 195–203.
- Schulthess, U., Ritchie, J., 1996. Simulation of tillage and crop residue dynamics with the SALUS-model. 26th Annual Crop Simulation Workshop. Fort Collins, 9–11 April, pp. 24–25.
- Sollins, P., Homann, P., Caldwell, B.A., 1996. Stabilization and destabilization of soil organic matter: mechanism and controls. *Geoderma* 74, 65–105.
- Trumbore, S.E., 1993. Comparison of carbon dynamics in tropical and temperate soils using carbon dating. *Global Biogeochem. Cycles* 7, 275–290.
- Whiteside, E.P., 1982. *Soil survey of the Kellogg Biological Station*. Research Report XX. W.K. Kellogg Biological Station Library, Hickory Corners, MI.
- Willson, T.C., Paul, E.A., Harwood, R.R., Smucker, A.J.M., Parker, E.M., Harris, D., 1997. Analysis of below ground productivity and soil respiration. *Agric. Abstract*, 218.
- Zibilske, L.M., 1994. Carbon mineralization. *Methods of Soil Analyses 2. Microbiological and Biochemical Properties*. SSSA Book Series No.5, pp. 836–864.