WILEY

Comparative Analyses of Carbon Dynamics in Native and Cultivated Ecosystems
Author(s): G. A. Buyanovsky, C. L. Kucera and G. H. Wagner
Source: *Ecology*, Vol. 68, No. 6 (Dec., 1987), pp. 2023-2031
Published by: Wiley
Stable URL: http://www.jstor.org/stable/1939893
Accessed: 03-01-2017 20:51 UTC

REFERENCES

Linked references are available on JSTOR for this article:
http://www.jstor.org/stable/1939893?seq=1&cid=pdf-reference#references_tab_contents
You may need to log in to JSTOR to access the linked references.

COMPARATIVE ANALYSES OF CARBON DYNAMICS IN NATIVE AND CULTIVATED ECOSYSTEMS[1]

G. A. Buyanovsky
Department of Agronomy,

C. L. Kucera
Division of Biological Sciences,

AND

G. H. Wagner
Department of Agronomy, University of Missouri, Columbia, Missouri 65211 USA

Abstract. Plant productivity, litter decomposition rates, and soil organic matter accumulation for winter wheat and for unbroken tallgrass prairie in Central Missouri were analyzed and compared. As measured in this 3-yr study, annual production of dry matter above- and belowground for the cultivated system averaged slightly higher than that for the natural vegetation burned every 3–4 yr. Prairie was characterized by greater year-to-year fluctuation of productivity, which in some years exceeded productivity of the cultivated system. More litter and structural biomass older than 1 yr occurred in the prairie, reflecting the perennial nature of the root system. Principal pathways of carbon transfer in both ecosystems were modeled, and mean residence time in major storage compartments estimated. Combined CO_2 losses from above- and belowground litter decay, expressed as a percentage of total soil respiration, were twice as great under wheat as for native prairie. A relatively greater fraction of net primary production was available for synthesis of soil organic matter in native prairie. Under equilibrium conditions, decomposition constants for this compartment, however, were similar. Contrasts in community structure and phenology, seasonal dynamics of litter decay, and levels of soil disturbance are suggested influences affecting transfer and storage characteristics.

Key words: carbon flow; decay constant; litter; plant productivity; soil organic matter; soil respiration; tallgrass prairie; winter wheat.

INTRODUCTION

Carbon flow through the ecosystem may be defined as the transfer of plant, animal, and microbial biomass carbon from one trophic level to another. In this process, some of the carbon accumulated by plants is mineralized to CO_2 and returned to the atmosphere, and the rest is incorporated for longer periods into different forms of soil organic matter. For mature soils of temperate zones the amount of carbon added to this pool in any one year is a small fraction of the soil carbon already present (Jenkinson 1965, 1977). The rate of carbon transfer through the system and amounts deposited in the soil profile are functionally related to biological productivity and decomposition potential. In a steady-state system, input of carbon from primary production and output as a result of mineralization are balanced; thus the soil organic carbon content remains at equilibrium levels.

The transition of virgin soils to arable status causes up to a 50% reduction in organic matter content during the first years of cultivation (Lee and Bray 1949, Puhr and Worzella 1952, Haas et al. 1957, Coleman et al.

1984). Following initial sharp decreases, the reduced level of humus is finally stabilized after several decades of agricultural use (Bauer and Black 1981), and the ecosystem usually regains steady-state status.

Although total carbon losses are well documented, it is unclear what part of the carbon cycle is affected by conversion of virgin soils to the cultivated state. Probably because of the "nonnutrient" status of carbon, its flow rate and storage characteristics rarely have been included in agronomic studies, and information on carbon dynamics of cultivated soils is incomplete. Despite recent achievements, quantitative gaps occur in our knowledge of primary production, the turnover rate of crop residues, the relative size of carbon pools, and the mean residence time of carbon at these storage sites in agroecosystems (Coleman et al. 1984, Mitchell 1984).

Detailed comparative analysis of carbon flow and storage characteristics of cultivated systems and their native counterparts can assist in revealing sources of carbon losses after conversion of the prairie. At the University of Missouri, data have been and are being accumulated during the past two decades on major components of the carbon cycle in native prairie and winter wheat stands, situated under similar edaphic

TABLE 1. Characteristics of soils under winter wheat and unbroken prairie (Mexico-Putnam silt loam).

Site	Horizon	Depth (cm)	Organic matter (%)	Bulk density (g/cm^3)	Clay (%)	pH
Winter wheat	Ap	0–13	2.9	1.37	22.2	6.1
	A$_1$	13–20	2.5	1.35	23.5	6.0
	A$_2$	20–28	1.7	1.33	23.7	5.3
	B$_1$	28–36	1.1	1.29	31.1	5.2
	B$_{21}$	36–51	1.2	1.29	53.0	5.1
Native prairie	A$_{11}$	0–5	6.4	0.95	22.3	5.2
	A$_1$	5–25	3.6	1.31	28.1	5.0
	A$_2$	25–35	2.1	1.42	30.4	4.8
	B$_{1,2}$	35–50	0.9	1.35	58.2	4.4

and climatic conditions. Although conducted independently, the objectives of these programs paralleled one another. These studies, aided by use of ^{14}C as a tracer, evaluated both above- and belowground production as sources of organic carbon. Data for native Missouri prairie, though available in different publications of Kucera and his co-workers (Dahlman and Kucera 1965, 1969, Koelling and Kucera 1965a, b, Kucera et al. 1967, Kucera and Dahlman 1968a, b, Kucera and Kirkham 1971, Herman and Kucera 1975, Herman 1977, Zimmerman and Kucera 1977, Callahan and Kucera 1981) have never been generalized, and new, unpublished information recently has been accumulated. Some details on productivity and soil respiration losses of a winter wheat ecosystem have been published recently by Buyanovsky and Wagner (1986, 1987), and Buyanovsky et al. (1986). Results of all these published and unpublished investigations are adapted here to compare and model primary production, litter decomposition rates, turnover time, and storage attributes of the two systems.

STUDY SITES

The two study areas are located in Central Missouri, on the Putnam–Mexico soil series (Table 1). A well-developed claypan derived from fine loess overlies drift materials of Kansas glaciation. Special test plots with winter wheat (*Triticum aestivum* L.) as a monoculture have been maintained for 4 yr at Sanborn Field on the University of Missouri campus, Columbia, where wheat has been grown since 1888. The Tucker Prairie Research Station, with an unbroken soil, was acquired by the University in 1957, and is ≈30 km from the campus. The native plant cover is characterized by several dominant warm season grasses including big bluestem (*Andropogon gerardi* Vitman), little bluestem (*Schizachyrium scoparium* Nash), prairie dropseed (*Sporobolus heterolepis* [A. Gray] A. Gray), and Indian grass (*Sorghastrum nutans* [L.] Nash). These four species in a total flora of more than 235 native plants, constitute ≈75% of the total biomass at the native prairie site. During the study period no large herbivores were pres-

ent, although fire was employed periodically. No fertilizers were used.

Both sites are located in the same climatic region (Scrivner et al. 1972), with ≈973 mm of mean annual precipitation and 790 mm of potential evapotranspiration. Water balance for the normal year is characterized by two major periods: (1) June through August, when evapotranspiration demands are greater than precipitation and plants rely on soil-stored water; and (2) from September to May, when precipitation generally exceeds evapotranspiration. Annual temperature averages 12.5°C, with the mean weekly maximum of 26° occurring in late July–early August, and the minimum of −3° in January. By mid-March, soil temperatures under winter wheat at 10-cm depth generally exceed 10°, and from April through September are usually >20°. Soil layers 50–65 cm deep reach 20° by late June. Native prairie soil temperatures in the surface layer warm more slowly in spring and are generally lower throughout the summer months. Average diurnal temperatures in soil under a litter cover are typically <10° in early spring. Readings reach 20° levels 2–3 wk later than for wheat soils. As air temperatures begin to cool in the fall, readings for the surface soil also lag behind those in the cultivated soil.

METHODS

During a 3-yr experiment on Sanborn Field, wheat was planted between 5 and 15 October at the rate of 90 kg/ha in 20-cm rows, to which commercial mixed fertilizer (N at 50 kg/ha, P at 25 kg/ha, and K at 12.5 kg/ha) was applied. Wheat was harvested at the end of June or beginning of July the next year by cutting the plants close to the soil surface. Heads were collected manually and threshed. All remnants excluding grain were weighed and returned to the soil. To determine root biomass, soil cores 10 cm in diameter to a depth of 50 cm were taken both in the row and between two rows. Cores were divided into 10-cm slices and washed over a 0.5-mm sieve.

Aboveground productivity for the prairie was assessed at approximately monthly intervals through the growing season. Replicated 0.5-m^2 quadrats were clipped 5 cm above ground level. Foliage was separated into current growth and dead materials from previous seasons, oven-dried at 70°C for 24 h, and weighed. Net annual production was estimated as the positive sum of incremental changes in green biomass recorded between successive samplings. By employing frequent clipping, the underestimate commonly associated with such attrition factors as insect herbivory, disease, and normal phenological curing was minimized. For root studies, samples were taken at 3-mo intervals through the year starting in January. Ten core samples, 4.19 cm in diameter, were extracted by mounted hydraulic lift for each sampling period. Cores were divided by morphological horizons, washed and sieved manually, and the roots oven-dried and weighed.

Dry combustion described by Allison (1965) was used to assess carbon content of plant materials in both studies.

Soil respiration under wheat was measured by the alkali absorption method (Anderson 1982). Respiration rates were taken every other week during periods of expected high biological activity, and at other times at monthly intervals. In tallgrass prairie, soil respiration studies were conducted continuously through an 18-mo period employing both infrared analysis and alkali absorption. Alkali absorption was also used in prairie studies to refine earlier estimates for separating active root and heterotrophic respiration in the soil profile.

Carbon-14 labelling of wheat was carried out in early May, when plants were between jointing and flowering stages. According to Karlen and Whitney (1980), this developmental period is characterized by the maximum CO_2 uptake and dry matter accumulation. A homogeneous plot 3×2.4 m was divided into four subplots, three of which were labelled. Subplots intended for labelling were sealed by a clear plastic canopy into which $^{14}CO_2$ was released during morning hours, to avoid heat damage. Plants were exposed to $^{14}CO_2$ during a 2-h period, after which the canopy was removed. A total of 11 MBq of activity per 1 m^2 was released in three applications over a 2-wk period. The concentration of CO_2 under the tent was maintained at $\approx 400 \pm 200$ $\mu L/L$.

The labelling scheme was designed to allow subsequent partitioning of root and straw carbon transferred to soil organic matter, and evolved during decomposition. To distinguish between root and straw origin, aboveground biomass from the unlabelled plot immediately after harvest was exchanged with a plot with labelled plants. This provided information on the decomposition dynamics of labelled roots in the presence of unlabelled straw, and vice versa. Radioactivity associated with carbon released in soil respiration was measured in precipitated $^{14}BaCO_3$ after titration (Anderson 1982). Scintillation counting used Aquasol-2 solution and a Packard Tri-Carb counter.

Labelling experiments at the prairie using clear plastic enclosures were carried out in the early morning hours of late summer when temperatures in the enclosure were lower than earlier in the season. In these experiments 5.59 MBq/m^2 of activity was released into each of 10 plots, each 6.63 m^2 in area. Five of the plots had been clipped 6 wk prior to labelling to provide regenerated growth. Herbage, roots, and soil organic matter were periodically sampled and analyzed for residual activity in the postlabelling period, which extended into the following growing season.

The labelling and subsequent data collection for the two systems were carried out in different years. The reported results, however, are those representing trends over several years, justifying comparison between the two systems and minimizing any effects of annual variation in temperature and precipitation on carbon allocations.

Supporting work on carbon flow in the prairie was also conducted in a controlled environmental chamber. In this experiment labelled roots were deposited in simulated profiles using soils from native horizons to quantify CO_2 losses from decomposition and radiocarbon appearing in soil organic matter over selected periods of time.

On the basis of these results a simplified model for carbon balance applicable to both ecosystems was developed. In the model the following pathways of plant carbon accumulated in above- and belowground biomass in a given year were considered:

1) mineralization to CO_2
2) transfer to above- and belowground litter
3) transfer to humus pool.

Compartments of carbon accumulation were designated as follows: plant biomass, litter, and soil organic matter. For this initial model of carbon balance, neither investigation separated the humus pool into microbial, labile, and resistant fractions. Additional studies are needed to stratify the total humus pool.

Mineralization losses summarized in total soil respiration (C_{sr}) are composed of root respiration (C_{rr}) and the mineralization of litter (C_l) and humus (C_h):

$$C_{sr} = C_{rr} + C_l + C_h \qquad (1)$$

$$\text{or } C_{sr} - C_{rr} = C_l + C_h. \qquad (2)$$

Assuming a balanced budget for both ecosystems, the total soil respiration without its active root respiration component is an estimate of total net production on an annual basis (C_{TNP}):

$$C_{TNP} = C_{sr} - C_{rr}. \qquad (3)$$

Root respiration on an annual basis was approximated using the last equation. In the prairie, root respiration also was verified by measuring total soil respiration in relation to varying root biomass. By extrapolating the resulting regression trend to zero biomass, it was possible to separate total soil respiration into two components, carbon loss attributed to active root metabolism, and that associated with heterotrophic breakdown of belowground litter and soil organic matter. Although heterotrophic respiration may not be constant for differing quantities of root biomass, and the estimates of heterotrophic respiration in an active root environment may be minimal, these calculations provided additional information to be compared with estimates of ^{14}C transferred from roots to the soil humus compartment.

RESULTS AND DISCUSSION

Total net productivity values for wheat and prairie averaged 14% more for the former, 1111 $\pm$ 59 g/m^2

TABLE 2. Plant production and biomass accumulation (g/m²) in winter wheat and tallgrass prairie ecosystems.

	Winter wheat		Tallgrass prairie	
Plant material	Range	Mean ± SD	Range	Mean ± SD
Net primary production				
Aboveground	563–616	590 ± 26	409–570	479 ± 65
Belowground*	477–562	521 ± 42	463–511	495 ± 28
Total	1040–1178	1111 ± 59	872–1081	974 ± 60
Past years' residue				
Aboveground	212–230	220 ± 8	325–474	414 ± 54
Belowground*	162–182	173 ± 10	1285–1418	1374 ± 76
Total	374–412	393 ± 16	1610–1892	1788 ± 151
Total biomass	1414–1590	1504 ± 80	2482–2973	2762 ± 168

* Belowground values based on 50-cm profile.

and 974 ± 60 g/m², respectively. Variations in year-to-year yields of prairie herbage, however, were greater and ranged up to three times those in wheat (Table 2). It should be noted that these comparisons considered data from the prairie based on fire schedules averaging one burn in 3 or 4 yr, the time required for 75–90% surface litter equilibrium.

Herbage production invariably was greater on plots burned annually where litter accumulation was less, and sometimes exceeded $1.0 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. Under these conditions, viewed to be a less realistic fire regime for tallgrass prairie, forage yields would exceed mean values for wheat under present cultural treatments.

Total dry matter at any given time during the year, however, is significantly greater in prairie for both surface litter and old roots (Table 2). Maximum biomass accumulation in the prairie profile which includes perennial roots of varying ages averaged 1374 ± 76 g/m². Approximately 75% of the total root system consists of intact roots >1 yr old. A significant portion of this perennial system is concentrated in the upper profile. Approximately 60% of the roots in the A_1 horizon (0–25 cm) occur in the upper 5-cm layer, which is characterized by high humus content (6.4%). For the 50-cm profile, ≈90% of the prairie root system is in the A_1 horizon.

Wheat roots were concentrated primarily in the upper 20 cm of soil where 90% of the total biomass was recovered, 75% in the upper 10 cm. Straw : roots ratio for wheat varied within very narrow limits (1.13 ±

0.09); the mean yield for roots was 521 ± 42 g/m². Based on ¹⁴C deposition in the soil, however, total production of root carbon including exudations and sloughed material ranged 40–50% greater than the yields obtained by washing over a sieve at the time of plant maturity. The larger estimate is in close agreement with values of Barber and Martin (1976) and Sauerbeck and Johnen (1977), and was used in carbon balance calculations and development of the present model.

Estimates of net root production in prairie were considered minimum values, since exudates and solubles would not be accounted for in the washing process. It was shown, however, that exudation and sloughing in perennial grasses are 2–3 times less than in wheat (Milchunas et al. 1985), which would tend to decrease the magnitude of error.

Carbon equivalents of above- and belowground dry matter values for the two systems are presented in Table 3. While wheat produced more fixed carbon annually than prairie (543 vs. 450 g/m²), total litter accumulation in the latter was almost five times as great (759 vs. 155 g/m²). The relatively smaller litter accumulation under wheat implicates a faster rate of decomposition in the soil. The accelerated rate is reflected also in lower soil organic matter accumulation. Soil under wheat, compared to that in prairie, has ≈35–40% less total carbon in the 50-cm profile, indicating that less litter carbon persists in the system as a basis for building soil organic matter.

The oxidizing activity of soil organisms and active

TABLE 3. Carbon equivalents (g/m²) of net primary production (NPP) and maximum litter residues (LR) in winter wheat and native prairie stands.

	Winter wheat				Tallgrass prairie			
Compartment	NPP	LR	Total	LR (% of total)	NPP	LR	Total	LR (% of total)
Aboveground	253	90	343	26	215	193	408	47
Belowground*	290	65	355	18	235	566	801	71
Total	543	155	698	22	450	759	1209	63
Soil organic matter	6500–7000				10 500–11 000			

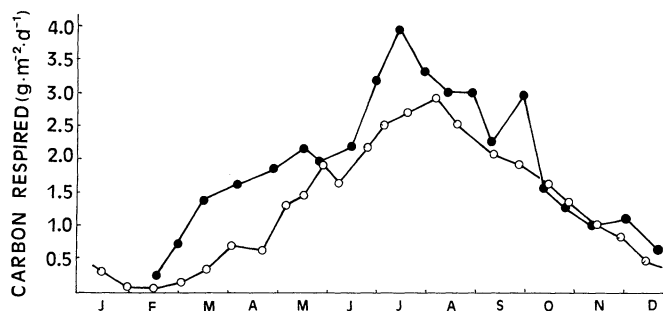* Belowground values based on 50-cm profile.

FIG. 1.   Seasonal trends in total soil respiration for winter wheat (●) and tallgrass prairie (○).

root metabolism are significant sources of carbon loss from the soil. These processes and their relative rates strongly influence the seasonal dynamics of carbon dioxide evolution from the soil and the distribution of residual carbon in an ecosystem. Seasonal trends in CO_2, in general, were similar in both ecosystems, with maximum evolution occurring in July and August when air and soil temperatures were highest (Fig. 1). During these 2 mo, approximately 35–40% of the annual carbon in the respective systems was released. However, seasonal patterns show different rates for the two systems at any given time. An earlier, steeper peak characterizes the cultivated system, compared to the more gradual rise for prairie vegetation dominated by warm season grasses. In the former, following winter dormancy, active root respiration is an important source of seasonal increases in CO_2 evolution occurring from March through May. This is succeeded by a brief period when plants are maturing and the curve remains mostly static. In the postharvest period there is a sharp increase in CO_2 evolution, reaching maximal values as the root system in toto dies and becomes immediately available to soil decomposers. Heterotrophic respiration thus is the single most important source of CO_2 until a new crop is established. A secondary rise in the respiration curve for wheat is attributed to improving soil moisture conditions in the fall, as a stimulus for increased decomposer activity.

The multispecies prairie community dominated by slower growing perennials and extended phenological activity in the aggregate expresses a less punctuated CO_2 curve. Here, the respective roles of autotrophs and heterotrophs run concurrently for most of the year and are distinguished with more difficulty. Root and decomposer respiration was separated on the basis of linear relationships between root biomass and total soil respiration extrapolated to zero biomass.

From 25 to 30% of total soil respiration under prairie was attributed to root systems, and the balance to heterotrophic activity (Table 4). Values for other native grasslands ranged from ≈15% for broom-sedge in an old field (Coleman 1973) to 19% in Canadian mixed-grass prairie (Warembourg and Paul 1973). Less root contribution to total soil respiration in these sites is

possibly related to lower root biomass. For Missouri tallgrass prairie, with characteristically larger biomass values, the greater percentage allocation to root respiration is not unreasonable.

Percentage allocation of root metabolism to total respiration in winter wheat on an annual basis was estimated as the difference between carbon input from wheat residues and output measured as total soil respiration for the years following labelling. On an annual basis, root respiration contributed 12–15% of the total carbon evolved as CO_2, which was approximately one-half of the share of root respiration for prairie (Table 4). This difference may be attributed to several factors, including the considerably greater root biomass under prairie, annual vs. perennial habits of root systems, and the distinctive seasonal dynamics of wheat-roots respiration, which show intense activity during the short period from April to May and cessation at the time of full maturity.

The shorter life cycle of wheat and one-time input of large amounts of residues make heterotrophic processes the principal source of carbon respired during a year. The percentages for both above- and belowground decay processes are approximately twice those for undisturbed prairie (Table 4). A comparison of percentages of total soil respiration attributed to decay of stable organic matter in the respective systems shows wheat with a value about one-third of that for prairie. These contrasts would suggest basic differences in the soil biota, particularly microbial populations of the respective systems. Results obtained by the fumi-

TABLE 4.   Comparison of major sources of CO_2 as percent of total respiration.

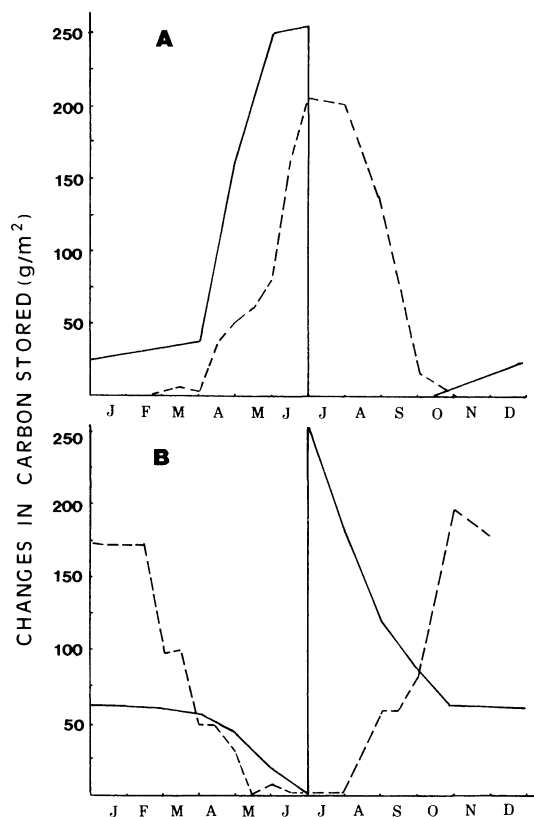| Source	Winter wheat	Native prairie
	% of total respiration	
Litter decay		
Aboveground	35–40	15–20
Belowground	40–45	20–25
Root respiration	12–15	25–30
Soil organic matter decay	10–12	30–35

FIG. 2. Seasonal changes in carbon stored in different compartments of winter wheat (———) and tallgrass prairie (-----). (A) Green biomass. (B) Aboveground litter.

gation–respiration technique showed that the microbial biomass of grassland soils is usually at least double that of cultivated ones (Jenkinson and Powlson 1976, Lynch and Panting 1980, Lynch 1984). Schimel et al. (1985) also suggests a change in microbial species composition after cultivation, based on the fact that microbial biomass has a narrower C:N ratio in cultivated sites.

Seasonality and amplitude of change on an annual basis for carbon stored in green biomass and in surface litter are compared in Fig. 2. A distinctive feature is growth response distinguishing a cool-season monoculture from a community dominated by warm-season species. Following the cold season with less than 50 g/m² of accumulated growth, wheat assumes a sigmoid pattern of growth, increasing most rapidly between jointing and flowering (Fig. 2A). Peak root production also occurs earlier by ≈2 mo compared to prairie. During this early period, from March through May, the wheat system accumulates 200–300 g/m² of carbon belowground and 200–250 g/m² aboveground. While growth is rapid at this time, changes in litter (Fig. 2B) are relatively small, since most of the residue was decomposed in the postharvest period of the preceding summer. Litter decomposition would be accelerated when large supplies of residues become available in

conjunction with higher soil temperatures throughout the summer.

Prairie litter remaining relatively intact through winter undergoes rapid depletion during the early spring season, stabilizing for a time as decomposition is generally balanced by fresh inputs of the current year. The principal increase in litter occurs in late summer as growth rates in green biomass decline and amounts of dead residues increase. A peak in litter production is reached in late fall, when decay potentials have diminished as well, thus delaying the breakdown process until the following year.

A greater synchrony of plant and microbial activity in the native prairie compared to winter wheat has several implications. In the native prairie, plants and microorganisms reach a peak of development in midsummer. This condition may increase competition for nutrients, especially nitrogen and water, and effectively decrease the decomposition potential of the system, contribute to litter accumulation, and consequently slow growth, particularly of the grasses. In winter wheat, accumulation of carbon and its mineralization are separated in time, facilitating decomposer activities after growth of the annual crop is terminated.

Carbon flow models were constructed from the foregoing data for an average year (Fig. 3A, B). Compartment accumulation and flow rate provide an overview of annual carbon transfer characteristics and the final product as soil organic matter. The relatively larger share of total heterotrophic consumption of wheat-litter components compared to prairie litter serves to explain significant differences in soil organic matter accumulation. In the cultivated system ≈80% of the total starting carbon (433/543 $g \cdot m^{-2} \cdot yr^{-1}$) is terminated at the litter level; the balance is transformed subsequently into soil organic matter. In the prairie the apportionment is more nearly equal, with only 56% of total carbon fixed in photosynthesis (254/450 $g \cdot m^{-2} \cdot yr^{-1}$) being respired in the litter stages. It is recognized that carbon budget results depend on the assumption of a steady state. Any failure in this assumption, however, would not be sufficient to invalidate the major contrasts demonstrated between the two systems.

Assuming equilibrium or near-equilibrium conditions for carbon accumulation in the soil profile, the determination of annual turnover rate appears valid. As a relative value it is a comparative index of decom-

TABLE 5. Comparison of annual decay constants, k, and half-life, $T_{1/2}$, for winter wheat and native prairie.

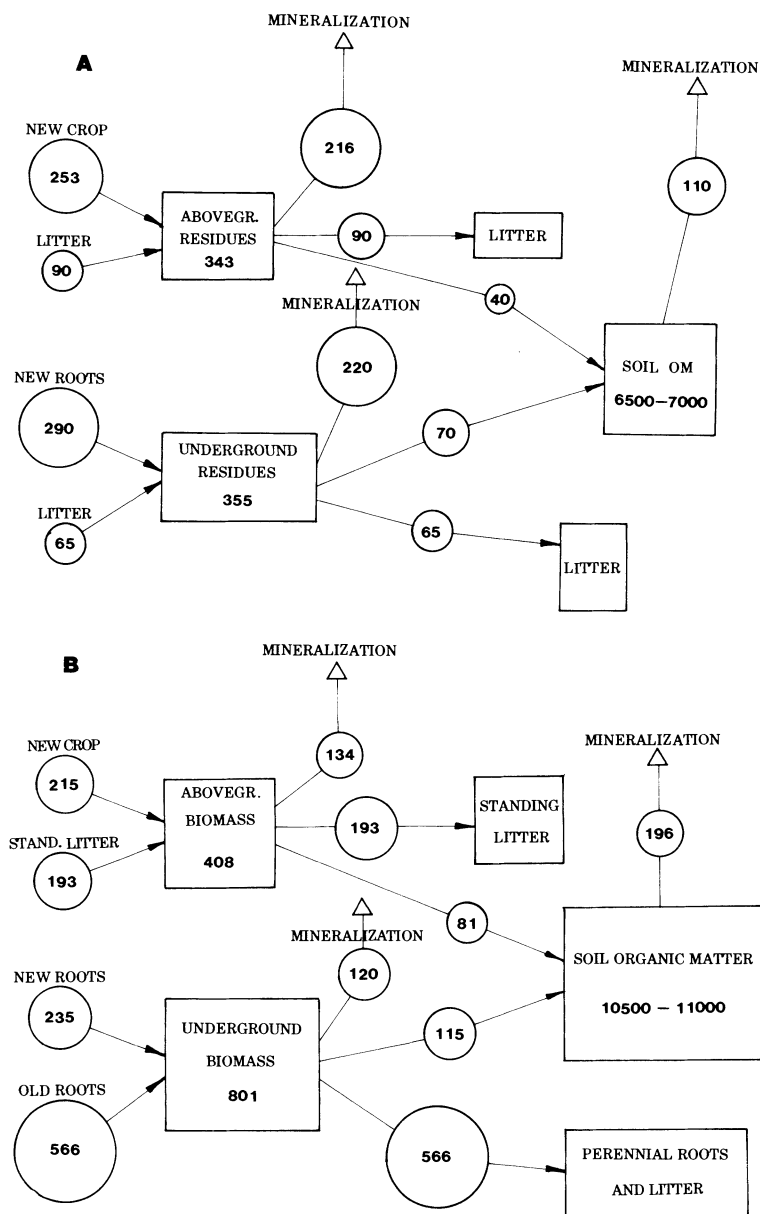| Compartment	Winter wheat		Native prairie	
	k	$T_{1/2}$	k	$T_{1/2}$
Aboveground biomass	0.74	0.9	0.53	1.3
Belowground biomass	0.82	0.9	0.29	2.4
Soil organic matter	0.016	43.3	0.018	38.5

FIG. 3. Carbon flow models for average year for winter wheat (A) and tallgrass prairie (B). Rectangles = carbon storage compartments with figures showing maximum accumulation in g/m². Circles with arrows = carbon pathways with figures showing amounts of carbon transferred during annual cycle, g/m².

position rates between different ecosystems (Jenny et al. 1949, Olson 1963, and others). Despite the implicit limitations of an exponential model expressed by a single decay constant (k), the constant and half-life values should provide additional comparison of the decomposition dynamics characterizing these contrasting systems.

The greatest differences in decay constant and half-life values occur in the biomass material, particularly belowground (Table 5). These differences in breakdown rates suggest several factors requiring more detailed analyses in the future to establish causal rela-

tionships. Presumably, enhanced oxidative effects from tillage disturbance and higher soil temperatures, especially in the postharvest period, are important in the wheat ecosystem. The water regime of soils under winter wheat, with no transpiration losses during summer when moisture stress is normally greatest, would appear to favor faster decay of residues, views reported also by Shields and Paul (1973), Wildung et al. (1975), and Jenkinson (1977). Another factor may be an increased surface–volume ratio for wheat litter resulting from the harvesting and incorporation processes. Tillage and incorporation of litter in the surface soil en-

hanced decomposition rates in grassland studies (Nyhan 1975, Ross et al. 1978, Lussenhop 1981). Breaking up the litter thatch with a roto-mower at the Missouri prairie site accelerated in situ disappearance compared to intact litter plots (Zimmerman and Kucera 1977).

There is a general consensus that environmental factors, including cultivation, can modify the rate at which either native soil organic matter or plant residues are transformed (Alexander 1977). Conventional management was shown to cause losses of organic matter, whereas no-till practice, which tends to mimic natural conditions, increases organic carbon content (Moschler et al. 1972, Fleige and Baeumer 1974). Changes in aeration, water content, and microbial population and activity are cited factors (Barber and Standell 1977, Doran 1980a, b, Doran and Power 1983, Linn and Doran 1984). In these studies no suggestions are given as to what part of the carbon cycle is most affected by these changes in physical and biological factors: the soil organic matter fraction, or carbon introduced into the soil from fresh residues. Our data show that cultivation under winter wheat results in greater availability of freshly introduced carbon for decomposing organisms at the season of year when the decay potential is highest. The amount of carbon allocated annually to the soil organic matter pool in the prairie was 43% of combined above- and belowground increments, as compared to 20% for winter wheat. However, if we relate these allocations to maximum biomass values generated by each system, which includes current crop plus residues (Fig. 3) the percentages are similar, 15% (110/698 g/m²) for winter wheat and 16% (196/1209 g/m²) for the native prairie. Moreover, decay constant (k) values and half-life, $T_{1/2}$, for soil organic matter are similar for both ecosystems, despite the difference in size of the respective pools. While the transient sources of soil organic matter are strongly influenced in terms of decay rate by ecosystem differences such as level of disturbance, aeration, and temperature and moisture, stable organic matter at equilibrium, once achieved, appears to be less affected. It is assumed, however, that the actual level reached by carbon equilibrium in the soil is under the control of the relative intensity of these factors in each system.

LITERATURE CITED

Alexander, M. 1977. Introduction to soil microbiology. Second edition. John Wiley and Sons, New York, New York, USA.

Allison, L. E. 1965. Organic carbon. In C. A. Black, editor. Methods of soil analysis, Part 2. Agronomy 9:1367–1378.

Anderson, J. 1982. Soil respiration. In A. L. Page et al., editors. Methods of soil analysis, Part 2. Second edition. Agronomy 9:831–871.

Barber, D. A., and J. K. Martin. 1976. The release of organic substances by cereal roots into soil. New Phytologist 76: 69–80.

Barber, D. A., and C. J. Standell. 1977. Preliminary observations on the effects of direct drilling on the microbial activity of soil. Pages 58–60 in Agricultural Research Council 1976 Annual Report, Letcombe Laboratory, Wantage, England.

Bauer, A., and A. L. Black. 1981. Soil carbon, nitrogen, and bulk density comparisons in two cropland tillage systems after 25 years and in virgin grassland. Soil Science Society of American Journal 45:1166–1170.

Buyanovsky, G. A., and G. H. Wagner. 1986. Post-harvest residues in cropland. Plant and Soil 93:57–65.

Buyanovsky, G. A., and G. H. Wagner. 1987. Pathways of carbon transfer in a winter wheat ecosystem. Soil Biology and Fertility, in press.

Buyanovsky, G. A., G. H. Wagner, and C. J. Gantzer. 1986. Soil respiration in a winter wheat ecosystem. Soil Science Society of America Journal 50:338–344.

Callahan, J., and C. L. Kucera. 1981. Magnesium flux and storage relationships in tallgrass prairie. American Midland Naturalist 106:345–351.

Coleman, D. C. 1973. Soil carbon balance in a successional grassland. Oikos 24:195–199.

Coleman, D. C., C. V. Cole, and E. T. Elliot. 1984. Decomposition, organic matter turnover, and nutrient dynamics in agroecosystems. Pages 83–104 in R. Lowrance et al., editors. Agricultural ecosystems: unifying concepts. John Wiley and Sons, New York, New York, USA.

Dahlman, R. C., and C. L. Kucera. 1965. Root productivity and turnover in native prairie. Ecology 46:84–89.

Dahlman, R. C., and C. L. Kucera. 1969. Carbon-14 cycling in the root and soil components of a prairie ecosystem. Pages 652–660 in Proceedings of the Second Symposium on Radioecology, Ann Arbor, Michigan, 15–17 May 1967. Publication Number 272, Radiation Ecology Section, Health Physics Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

Doran, J. W. 1980a. Microbial changes associated with residue management with reduced tillage. Soil Science Society of America Journal 44:518–524.

———. 1980b. Soil microbial and biochemical changes associated with reduced tillage. Soil Science Society of America Journal 44:765–771.

Doran, J. W., and J. F. Power. 1983. The effects of tillage on the nitrogen cycle in corn and wheat production. Pages 441–455 in R. Lowrance, R. Todd, L. Asmussen, and R. Leonard, editors. Nutrient cycling in agricultural ecosystems. University of Georgia College of Agriculture Special Publication Number 23. Athens, GA.

Fleige, H., and K. Baeumer. 1974. Effect of zero-tillage on organic carbon and total nitrogen content. Agro-Ecosystems 1:19–29.

Haas, J. H., C. F. Evans, and E. F. Miles. 1957. Nitrogen and carbon changes in Great Plains soils as influenced by cropping and soil treatments. United States Technical Bulletin Number 1164, United States Department of Agriculture, Washington, D.C., USA.

Herman, R. P. 1977. Root contribution to 'total soil respiration' in a tallgrass prairie. American Midland Naturalist 98:227–232.

Herman, R. P., and C. L. Kucera. 1975. Vegetation management and microbial function in a tallgrass prairie. Iowa State Journal of Research 50:255–260.

Jenkinson, D. S. 1965. Studies on the decomposition of plant material in soil. I. Losses of carbon from ¹⁴C labelled

ryegrass incubated with soil in the field. Journal of Soil Science 16:104–115.

———. 1977. Studies on the decomposition of plant material in soil. V. The effects of plant cover and soil type on the loss of carbon from ^{14}C labelled ryegrass decomposing under field conditions. Journal of Soil Science 28:424–434.

Jenkinson, D. S., and D. S. Powlson. 1976. The effect of biocidal treatments on metabolism in soil. V. A method for measuring soil biomass. Soil Biology and Biochemistry 8:209–213.

Jenny, H., S. P. Geasel, and F. T. Bingham. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Science 68:419–432.

Karlen, C. L., and D. A. Whitney. 1980. Dry matter accumulation, mineral concentrations, and nutrient distribution in winter wheat. Agronomy Journal 72:281–286.

Koelling, M. R., and C. L. Kucera. 1965a. Productivity and turnover relationships in native tallgrass prairie. Iowa State College Journal of Science 39:387–392.

Koelling, M. R., and C. L. Kucera. 1965b. Dry matter losses and mineral leaching in bluestem standing crop and litter. Ecology 46:529–532.

Kucera, C. L., and R. C. Dahlman. 1968a. A method for incorporating high activity carbon-14 in prairie grasses for turnover studies. Iowa State Journal of Science 43:13–17.

Kucera, C. L., and R. C. Dahlman. 1968b. Root-rhizome relationships in fire-treated stands of big bluestem, Andropogon gerardi Vitman. American Midland Naturalist 80:268–271.

Kucera, C. L., R. C. Dahlman, and M. R. Koelling. 1967. Total net productivity and turnover on an energy basis for tallgrass prairie. Ecology 48:536–541.

Kucera, C. L., and D. R. Kirkham. 1971. Soil respiration studies in tallgrass prairie. Ecology 52:912–915.

Lee, C. K., and R. H. Bray. 1949. Organic carbon and nitrogen contents of soils as influenced by management. Soil Science 68:203–212.

Linn, D. M., and J. W. Doran. 1984. Aerobic and anaerobic microbial populations in no-till and plowed soils. Soil Science Society of America Journal 48:794–799.

Lussenhop, J. 1981. Microbial and microarthropod detrital processing in a prairie soil. Ecology 62:964–972.

Lynch, J. M. 1984. Interactions between biological processes, cultivation and soil structure. Plant and Soil 76:307–318.

Lynch, J. M., and L. M. Panting. 1980. Cultivation and the soil biomass. Soil Biology and Biochemistry 12:29–33.

Milchunas, D. G., T. H. Lauenroth, J. S. Singh, C. V. Cole, and H. W. Hunt. 1985. Root turnover and production by ^{14}C dilution:implications of carbon partitioning in plants. Plant and Soil 88:353–365.

Mitchell, R. 1984. The ecological basis for comparative primary production. Pages 13–54 in R. Lowrance et al., editors. Agricultural ecosystems. Unifying concepts. John Wiley and Sons, New York, New York, USA.

Moschler, W. W., G. M. Shear, D. C. Martens, G. D. Jones, and R. R. Wilmouth. 1972. Comparative yields and fertilizer efficiency of no-tillage and conventionally tilled corn. Agronomy Journal 64:229–231.

Nyhan, J. W. 1975. Decomposition of carbon-14 labelled plant materials in a grassland soil under field conditions. Proceedings of the Soil Science Society of America 39:643–648.

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322–331.

Puhr, L. J., and W. W. Worzella. 1952. Fertility maintenance and management of South Dakota soils. South Dakota Agricultural Experiment Station Circular 92.

Ross, D. J., L. F. Molloy, B. H. Bridger, and A. Cairns. 1978. Studies on a climosequence of soils in tussock grasslands. Decomposition of cellulose on the soil surface and in the topsoil. New Zealand Journal of Science 21:459–465.

Sauerbeck, D. R., and B. G. Johnen. 1977. Root formation and decomposition during plant growth. Soil organic matter studies. International Atomic Energy Agency, Vienna, Austria.

Schimel, D. S., D. C. Coleman, and K. A. Norton. 1985. Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. Geoderma 36:201–214.

Scrivner, C. L., J. D. McQuigg, and D. R. Brees. 1972. Climatic areas and soil resources. Pages 20–23 in Research in agronomy. Department of Agronomy, University of Missouri–Columbia, Miscellaneous Publications 72-5.

Shields, E. A., and E. A. Paul. 1973. Decomposition of ^{14}C labelled plant material under field conditions. Canadian Journal of Soil Science 53:297–306.

Warembourg, F. R., and E. A. Paul. 1973. The use of $^{14}CO_2$ canopy techniques for measuring carbon transfer through the plant-soil system. Plant and Soil 38:331–345.

Wildung, R. E., T. R. Garland, and R. L. Buschbom. 1975. The interdependent effects of soil temperature and water content on soil respiration rate and plant root decomposition in arid grassland soils. Soil Biology and Biochemistry 7:373–378.

Zimmerman, U. D., and C. L. Kucera. 1977. Effects of composition changes on productivity and biomass relationships in tallgrass prairie. American Midland Naturalist 97:465–469.