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SECONDARY PRODUCTIVITY BELOW GROUND IN PAWNEE GRASSLAND, 1971

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ABSTRACT

Carbon cycling below ground at Pawnee was studied by monitoring carbon dioxide evolution from soil and by measuring carbon losses from litter materials buried in the soil. In unirrigated grassland during the late April to the early September portion of the growing season in 1971, CO_2 evolution ranged from a low of 1.03 $g/m^2/day$ to a high of 13.38 g. In general, the data indicated that major spurts of microbial activity follow any major precipitation or irrigation event occurring during the warm season and that this activity is located principally in the uppermost portion (0 to 5 cm depth) of the soil profile. With soil drying, respiratory activity in the upper profile dropped to a negligible level. During 1971 the soil drying was sufficiently severe that the daily output of respiratory CO_2 was arising almost wholly from that portion of the soil profile deeper than 20 cm.

Carbon losses from buried litters at Pawnee in 1971 occurred principally during the interval mid-April to mid-June; they became negligible during the time of the severe midsummer drought. Carbon losses from four plant materials and two collections of cow manure given soil burial in the laboratory were measured; the loss differences encountered were sufficiently striking to suggest that more data are needed concerning the susceptibility to decomposition of the entire range of litter materials found in grassland.

INTRODUCTION

In a discussion of herbage dynamics in North American grasslands, Sims and Singh (1971) have reported the belowground biomass for ungrazed and grazed grassland at the Pawnee Site in northeastern Colorado as 1635 and 1568 g/m^2, respectively. These values, accounting for 93.4 and 94.6% of the total plant biomass on the site in 1969, emphasize the potential for belowground secondary productivity in a grassland ecosystem.

No really satisfactory data are as yet available concerning belowground secondary productivity. Sims and Singh (1971) calculated root turnover values based on ratios between annual increments in the average total belowground biomass present according to the method of Dahlman and Kucera (1965). The belowground decomposition rates of plant material in ungrazed and grazed grassland were estimated as 2.69 and 2.82 $g/m^2/day$, respectively, during the growing season. Such estimates are valuable approximations, but they nevertheless may reflect procedural and interpretative errors (Sims and Singh, 1971; Head, 1970, Newbould, 1968; Samtsevich, 1965; Ovington, Heitkamp, and Lawrence, 1963).

Other workers (Dahlman, 1968; Kucera and Kirkham, 1971; Coleman, 1972; Macfadyen, 1970; Witcamp and Frank, 1969; Domsch, 1962) have undertaken secondary productivity estimates by measuring the respiratory output of carbon dioxide from the soil. Although such measurements, especially if they involve in situ herbage that has been given labelling with $^{14}CO_2$, are easier in accomplishment and less subjective in interpretation than are herbage biomass measurements based on root-washing

techniques, they too have several shortcomings. Foremost is the difficulty of differentiating between the respiratory carbon dioxide arising from root tissues and that arising from the root-associated soil biota. There is continual transfer of organic root secretions and of exfoliated cellular material to this biota, and just as the resulting decomposer activity precludes quantitation of the transferred organics as a part of the annual increment in root biomass, so too does it preclude assignment of the respired carbon to root and microbial sources within the field soil system. In addition to the contemporary plant and microbial respiratory output, some of the carbon dioxide evolved from the soil may be of earlier respiratory origin and which, after some interval of storage in the soil, may flux to the atmosphere under appropriate conditions, such as barometric changes or soil drying. Evolved carbon dioxide can also be of carbonate origin with its release therefrom due to microbially produced organic or mineral acids. A further complication in making respiratory measurements is the fact that microbial activity in soil can either intensify or disappear with alarming rapidity in response to environmental changes.

Many soil microbiologists are now using litter-bag techniques of one kind or another. Litter exposures are by no means new; they have long been used in studies in invertebrate zoology. The variations currently in use by soil microbiologists are almost as numerous as are the work locations involved. Cellulose (filter paper, cotton fibers, or cloth) or plant litters are commonly used. Their exposure on or in soil commonly involve nylon-net or nylon-cloth confinements or else attachments to glass plates or other devices. Litter burial techniques are proving

to be informative to the investigator involved, and they commonly yield data more useful than that obtained by plate counts. The many and often minor variations in burial techniques, however, make it difficult to compare loss data secured by workers at different locations. With cellulose, variations in the amount of material being used or in the geometry of its exposure can markedly alter the rate of its decomposition. This stems from the fact that the cellulolytic microorganisms must obtain their supplies of essential mineral nutrients from the soil. One can easily demonstrate the importance of nutrient supply on rate of cellulose decomposition either by doubling or tripling the amount of cellulose given burial or else by using a standard amount of cellulose in duplicate sites, one of which is given fertilizer nitrogen. In the former case there is marked reduction and in the latter marked acceleration of the rate of cellulose loss. Such factors as quantity of material or geometry of exposure are less critical with natural litters that usually contain sufficient nitrogen, phosphorus, and other nutrients for the decomposer microorganisms.

In the current study, specific objectives were to get a first approximation of the soil respiratory output, to correlate this output to ambient meteorological and plant growth conditions, and to explore possibilities for compartmentalizing evolved carbon dioxide according to site of origin. Concurrently with the respiratory work some litter-bag decomposition studies involving filter paper cellulose, grass hay, and cow manure were undertaken to determine not only the extent to which such studies might show agreement with the carbon dioxide studies but also the extent to which such materials differ in susceptibility to decomposition when given standardized burials.

PROCEDURES

Three sites on the Pawnee Site were used for measurements of soil respiration. Sites 1 and 2 were on ungrazed pasture in the $S\frac{1}{2}S\frac{1}{2}SW\frac{1}{4}$ of Section 21. Site 1 was in the westerly end of this location and received only the seasonal rainfall. Site 2 was located easterly to Site 1 and in an area in which sprinkler irrigation water could be applied. Site 3 was located in the $S\frac{1}{2}SE\frac{1}{4}$ of Section 15; it was on unirrigated grassland subject to summer grazing at the medium-intensity stocking level. Litter burials were made only at Site 3 and in a portion of the site just southerly to the area used for soil respiration measurements.

To measure field soil respiration, aluminum cylinders (10 cm in diameter) were sunk 10 cm into the ground leaving another 9 cm of cylinder extending above the soil surface. The bottom ends of the cylinders were at no time capped in any way. The top ends were uncovered except during the intervals in which carbon dioxide was being trapped. During such intervals a container of 0.6 M NaOH was placed on the soil surface inside the cylinder, and the top of the cylinder was covered with an air-tight plastic lid. The capped cylinders were also shielded with aluminum foil to minimize any heat-trapping effect. Field collections of carbon dioxide were usually made overnight and usually for durations of 20 to 22 hr. Empty cylinders, with a volume equivalent to that aboveground in the experimental cylinders, were capped at both ends and routinely used as controls. In addition to the 10-cm diameter cylinders, some 20-cm diameter steel cylinders were

used in Site 1 in studies in which successive 5-cm horizons of the soil profile were removed during the course of respiratory measurements. Four successive horizon removals were made at daily intervals during the 4 days that the excavation study was in progress.

In an attempt to compartmentalize the source of the respiratory carbon dioxide being evolved from intact soil cores in the field, soil cores were brought into the laboratory and handled as follows: Firstly, the entire core together with a container of 0.6 M NaOH was placed inside a 2-liter screw-capped plastic jar and incubated for 24 hr. The core was then removed and separated into the component fractions of crowns, roots, and soil, and the respiratory output of CO_2 from each of these fractions was measured during the ensuing 24 hr. Following incubation, weights of the fractions were determined prior to and following oven-drying.

Field litter burials and retrievals were handled according to the technique previously described by Clark (1970). Cellulose filter paper, grass hay, and cow manure burials were made on April 12, May 3, May 24, June 14, and July 6 in 1971, and retrievals were made on May 3, May 24, June 14, July 6, and July 27. At each date of burial a sufficient number of replicates was buried to permit retrievals in triplicate on each of the sampling dates subsequent to that burial date.

Laboratory burials involved the following materials: top growths of summer blue grama, winter blue grama, summer bluestem, and summer *Oxytropis*, and summer-dropped and winter-dropped cow manure. Sufficient nylon-bagged replicates were used to permit multiple removals of each material following 3, 6, 10, 17, and 28 days of soil burial.

SOIL RESPIRATION MEASUREMENTS

Field Measurements Using 10-cm Diameter Enclosures at the Pawnee Site

Respiration measurements in the field were initiated on April 28 and continued until September 8. Dates on which measurements were taken and the rates of CO_2 evolution encountered are shown in Table 1.

The highest rate encountered in the early growing season was 5.77 g CO_2/m^2/day on April 28-29 at Site 1. From this value the rate consistently declined during subsequent sampling intervals and reached a low value of 1.02 g/m^2/day on August 18. The April-August growing season was characterized by abnormally low rainfall and extremely low midsummer soil water content. Immediately following heavy rainfall (about 2.5 cm) on September 7, the rate of CO_2 evolution at Site 1 rose to 13.38 g/m^2/day. The Site 3 values shown in Table 1 generally confirm the seasonal trend encountered at Site 1. Site 2, to which supplemental water was applied during June and July, showed high rates of CO_2 evolution during these months (Table 1).

In an effort to determine the extent to which soil water and temperature account for variability in soil respiration, the accumulated data were used in a stepwise regression program (BMD 38R CSU CCN). Natural log-transformed temperature and soil water had the highest R^2 values, accounting for more of the variability that the other transformed or untransformed variates. Using ln temperature and ln soil water, multiple regression equations were calculated for the irrigated and nonirrigated sites separately and for all sites on all dates (Table 2). The irrigated plots, which had a wide range of soil water values, had a multiple R^2 of .476 for ln soil water and an increase of .007 with the addition of

Table 1. Rates of CO_2 production measured at the Pawnee Site in 1971.

Date of Measurement	Mean Soil Temperature	Percentage Soil Water	$CO_2/m^2/day$
	Site 1.		
28-29 April	--	17.9	5.77
20-21 May	11.1	--	4.83
3-4 June[a/]	21.1	4.5	4.35
4 June[b/]	18.9	4.5	4.13
28-29 June	29.4	--	1.77
7-8 July	26.7	--	1.74
18 August	25.6	1.5	1.03
8 September	--	13.1	13.38
	Site 2.		
28-29 April	--	15.1	4.56
20-21 May	11.1	6.9	3.67
8-9 June	19.4	3.5	2.69
10-11 June[c/]	17.2	16.1	9.66
17-18 June[d/]	22.2	--	9.41
20-21 June	24.4	--	7.57
7-8 July	26.7	--	2.45
20-21 July[e/]	26.7	9.8	14.21
21-22 July[f/]	26.7	8.4	11.33
22-23 July[g/]	23.9	7.4	11.95
24-25 July[h/]	25.6	--	13.09
25-26 July[i/]	24.4	4.7	9.04
18 August	25.6	1.8	1.36
	Site 3.		
28-29 April	--	15.2	3.47
20-21 May	--	6.9	2.64
8-9 June	--	--	2.75
7-8 July	--	--	2.00
1 August	--	--	1.46
18 August	--	1.8	1.31

[a/] Night run of 8 hr.
[b/] Day run of 8 hr.
[c/] Following 5 cm of irrigation on June 10.
[d/] Following 0.5 cm rain on June 14; ca. 3.5 cm irrigation June 15.
[e/] Following 0.13 cm rain June 18 and 2.5 cm irrigation June 19.
[f/] Following 0.38 cm rain on July 21.
[g/] Following 0.08 cm rain on July 22.
[h/] Following 0.33 cm rain on July 24.
[i/] Following 0.33 cm rain on July 25.

Table 2. Multiple regression analysis of CO_2, soil water, and temperature data.

Program	N	ln Soil Water R^2	ln Temperature R^2	Sum
S35AU62[a/]	80	.47604	.00667	.48271
S37AU65[b/]	80	.64327	.06542	.70870
S37AU61[c/]	89	.35083	.32508	.67592
S37AU48[d/]	169	.20614	.50591	.71205

a/ June and July data, irrigated plot, Site 2.

b/ April-August, nonirrigated, excluding September.

c/ April-September, nonirrigated, including September.

d/ All dates and all fields, see a/ and c/.

ln temperature. The unirrigated plots, starting very cool and moist in the spring and then dry for several months, had a multiple R^2 of .643 for ln soil water and an increase of .065 for ln temperature added with the September rain excluded. With this rain included the respective values were .351 and .325. With all data points combined into one multiple regression, multiple R^2 due to ln soil water fell to .206, while that for ln temperature rose to .506.

An analysis of covariance (BMD X82C CSU) was used to test for differences between slopes of the multiple regressions of the respiration responses of irrigated and unirrigated plots. The slopes were significantly different (t test, $P < .01$), indicating that the two treatments should not be considered together.

Obviously, there are factors in addition to soil water and temperature that must be reckoned with when attempting to interpret the respiratory output of field soil. Among the suspect factors is the prior soil water regime. For example, given a favorable soil temperature, the respiratory response to some given and favorable level of soil water can differ markedly depending on whether the soil water regime during the preceding month was consistently at the favorable level or whether it was at the air-dry level.

Field CO_2 Measurements Involving Successive Profile Removals

The field excavation studies involved comparisons of intact and truncated profiles under both moist and dry conditions. Wet profiles were established by application of 10 cm of water 3 days prior to the start of profile excavations. The respiratory data accumulated are summarized in Table 3.

These data indicate that following wetting of field soil during the time of seasonally warm soil temperature, three-fourths of the relatively high daily rate of CO_2 evolution is accounted for by the top of 5 cm of the soil profile. The 5- to 20-cm portion of the profile accounted for roughly an additional 10% of the daily output, leaving only about 15% to be accounted for by the soil at a depth greater than 20 cm. In contrast, most of the CO_2 measured as being evolved from very dry soil can be ascribed to the deeper soil profile. Removal of the top 5 cm of the dry profile or even of the top 10, 15, or 20 cm had only negligible effect, generally of the order of 10%, on the daily rate of CO_2 production.

In both the wet and dry profiles CO_2 output after excavation to 20 cm remained at a relatively constant level during the week immediately following excavation, thus suggesting an ongoing respiratory activity rather than some experimental error associated with the accomplishment of excavation. Finally, although the geometry of the steel cylinder installation minimizes the possibility of CO_2 arising in the upper soil profile outside the cylinder and then diffusing inside via the bottom end, there is no corresponding assurance that the CO_2 entrapped at the 20-cm level represents only strictly vertical upward diffusion from the deeper soil profile.

Table 3. Field soil respiration following profile layer excavations.

Date	Soil Water (%)	A. Profile Depth Removed (g $CO_2/m^2/day$)	B. Unexcavated Control (g $CO_2/m^2/day$)	Ratio A/B
Wet series:				
July 12-13	16.2	5.6 (0-5 cm off)	21.79	.26
July 13-14	10.3	3.46 (0-10 cm off)	16.82	.21
July 14-15	11.5	1.58 (0-15 cm off)	11.61	.14
July 15-16	11.6	1.80 (0-20 cm off)	10.64	.17
Dry series:				
June 22-23	2.0	1.96 (0-5 cm off)	2.24	.87
June 23-24	2.0	1.69 (0-10 cm off)	1.72	.99
June 24-25	3.2	1.35 (0-15 cm off)	1.48	.91
June 25-26	5.1	1.23 (0-20 cm off)	1.34	.91

Contributions of Crowns, Roots, and Soil to the CO_2 Output of Soil Cores Cores in Laboratory Experiments

In an attempt to compartmentalize the total respiratory output of soil into component sources of crowns, roots, and soil, two series of field soil cores taken to a depth of 2.5 cm were used. In the first series collected on August 3, the cores were 10 cm in diameter and they were given 2.5 cm of water as a surface application when brought into the laboratory. In the second series the cores were 5 cm in diameter and were collected September 10, 3 days after 2.5 cm of precipitation. These cores contained 12% soil water when brought into the laboratory and were used without addition of water. For both series the laboratory incubations were conducted at 26.7°C. Respiratory data collected are summarized in Table 4.

No explanation of the discrepancy of 55.6% between the sum of the CO_2 evolved from the compartments and the amount evolved from the intact cores for the September 10 series can be offered. Coleman (1972) has encountered discrepancies of similar magnitude in work conducted elsewhere. Accepting the CO_2 output values as they stand, the precentage contributions of crowns, roots, and soil to the summed total are 60.2, 12.3 and 27.5, respectively, for the August 3 series and 62.8, 7.7, and 29.5, respectively, for the September 10 series. The agreement between the two series is quite good and the ratios appear reasonable for the top 2.5 cm of the profile. However, for the temperature and soil water conditions involved, extrapolation of the yield of CO_2 to a gram per meter squared per day basis gives a value somewhat lower than would be expected by inspection of data in Tables 1 and 2.

Table 4. Contributions of crowns, roots, and soil to the CO_2 output of soil cores.

	Core or Component	Soil Water Content	mg CO_2/g dry wt/day	Mean Weight (g)	Total CO_2 Output (mg)
			August 3 series. N - 4.		
A.	Intact core	16.7	.298	238	70.88
B.	Crowns from A	103.0	4.73	9.09	42.99
C.	Roots from A	68.0	1.38	6.32	8.74
D.	Soil from A	12.0	0.09	222.6	19.67
				(Sum of B, C, D = 71.40)[a/]	
			September 10 series. N - 10.		
A.	Intact core	12.1	.509	43.11	21.94
B.	Crowns from A	29.4	7.27	2.95	21.44
C.	Roots from A	9.5	2.92	0.90	2.62
D.	Soil from A	9.7	0.256	39.40	10.09
				(Sum of B, C, D = 34.14)[b/]	

[a/] The sum of the compartments is 100.7% of the value for the intact core.

[b/] The sum of the compartments is 155.6% of the value for the intact core.

LITTER DECOMPOSITION STUDIES

Decomposition of Litter Materials Given Burial at Pawnee

The extent to which cellulose filter, bluestem hay, and cow manure suffered decomposition during the 1971 season when buried in field soil at the 5- to 7-cm depth is summarized in Table 5.

The rate of cellulose decomposition observed in 1971 was distinctly inferior to that observed in 1970. This no doubt can be attributed to the abnormally dry soil conditions that prevailed during the 1971 summer season. Filter paper cellulose buried on May 24, June 14, or July 6 showed essentially no decomposition at any of the later retrieval dates. Supplemental nitrogen added to the filter papers at the time of burial accelerated their decomposition. Filter papers buried without added nitrogen on April 12 showed 22% decomposition by June 14; those buried with added nitrogen showed 63% decomposition during this same burial interval.

Examination of the cellulose-N data given in Table 5 for the April 12 burial shows continually increasing losses (2.6, 24.3, 63.3, and 68.9 %) for the first four dates of retrieval and a loss value of 56.2% for the July 27 retrieval. Taken at face value, this suggests a gain in filter paper of 12.7% between July 6 and July 27. Statistical treatment (BMD 01V CSU) of the experimental data, however, showed the differences in losses for the June 14, July 6, and July 27 dates to be nonsignificant. A graphic presentation of Tukey's Q test for cellulose-N buried April 12 is shown in Fig. 1.

Table 5. Summary of litter losses encountered at Pawnee in 1971 percentage loss during soil exposure.

Date of Burial and Materials Used	Dates of Retrieval				
	May 3	May 24	June 14	July 6	July 27
April 12:					
Cellulose	3.0	7.7	22.4	24.3	22.1
Cellulose-N[a/]	2.6	24.3	63.3	68.9	56.2
Bluestem hay	16.1	27.9	32.0	31.0	32.3
Cow manure	4.1	13.7	15.1	13.7	20.6
May 3:					
Cellulose		0.7	7.0	11.5	17.5
Cellulose-N		1.0	23.5	46.8	43.4
Bluestem hay		17.9	32.0	27.7	31.8
Cow manure		1.4	8.9	7.5	11.7
May 24:					
Cellulose			5.1	4.7	4.3
Cellulose-N			10.2	16.6	14.9
Bluestem hay			17.6	25.2	25.0
Cow manure			2.0	4.3	4.8
June 14:					
Cellulose				-0.5	1.8
Cellulose-N				-0.4	3.4
Bluestem Hay				9.4	7.6
Cow manure				-6.8	-9.0
July 6:					
Cellulose					2.1
Cellulose-N					1.8
Bluestem hay					0
Cow manure					-12.3

[a/] Filter paper cellulose treated with urea solution prior to burial to give C:N ratio of 10:1.

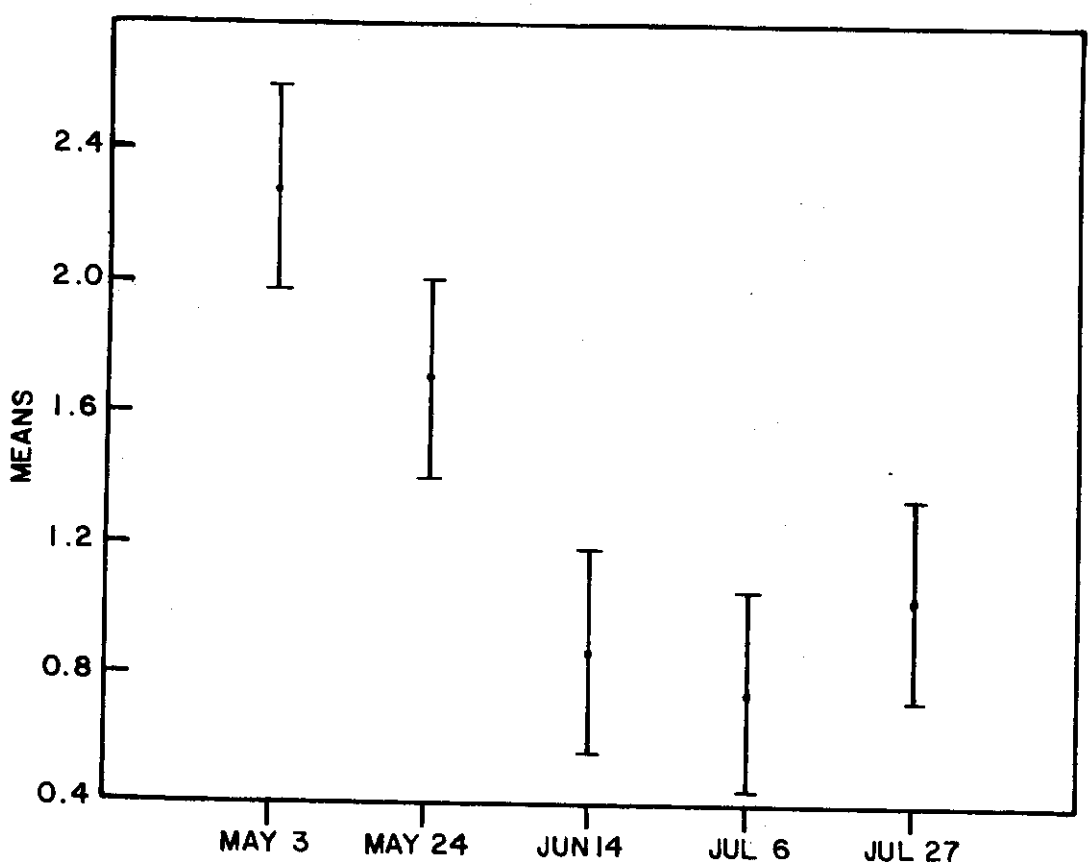

Fig. 1. Graphic presentation of Tukey's Q test for retrievals made from cellulose-N buried on April 12.

$$Q = 4.66 \sqrt{\frac{.620}{3}} = 0.67$$

(Calculated by Marilyn Campion.)

Comparative Decomposition Rates of Selected Litter Materials Given Soil Burial in the Laboratory

The organic matter loss from four plant materials and two collections of cow manure given soil burial for 28 days under standardized conditions (Clark, 1970) is summarized in Table 6 and plotted in Fig. 2.

The data show that the several plant materials differ in their susceptibility to decomposition in the following order: winter-dropped cow manure $\approx$ summer-dropped cow manure < winter blue grama < bluestem hay < summer blue grama < *Oxytropis*. Although the summer and winter collections of blue grama differed in susceptibility to decomposition, no such difference was apparent for the summer and winter collections of cow manure. Although the diet materials ingested by large herbivores may differ quite markedly in their susceptibility to decomposition, apparently what emerges as feces is much more uniform in susceptibility than are the intake materials.

The 1971 data concerning differences of plant materials in susceptibility to decomposition confirm observations made in 1970. Obviously in the writing of equations to describe litter decomposition attention should be given not only to the origin of the plant material but also to the stage or condition of plant growth from which the litter was derived. It would appear desirable to compare the susceptibility to decomposition of as many of the natural litter materials occurring at any given site as is possible. The type of data exemplified in Fig. 2 could be extended to a whole host of plant species, a variety of vertebrate and invertebrate droppings, of animal corpses, and so on.

Table 6. Percentage carbon losses observed for selected litter materials given laboratory burial.

Material Buried[a/]	Days of Burial in Laboratory Soil				
	3	6	10	17	28
Blue grama, winter	19.8	22.7	30.3	38.2	45.7
Blue grama, summer	30.9	37.4	44.2	52.6	59.9
Bluestem, summer	19.0	23.7	32.0	44.3	51.8
Oxytropis, summer	47.8	58.9	68.2	72.8	77.3
Cow manure, summer	8.3	10.9	14.0	19.5	24.2
Cow manure, winter	7.9	12.2	13.0	20.3	27.9

[a/] Fifty replicate burials were made for the first three materials listed, permitting the removal of 10 replicates on each of the five sampling dates and 25 replicate burials of the last three materials, permitting quintuplicate removals on each of five dates.

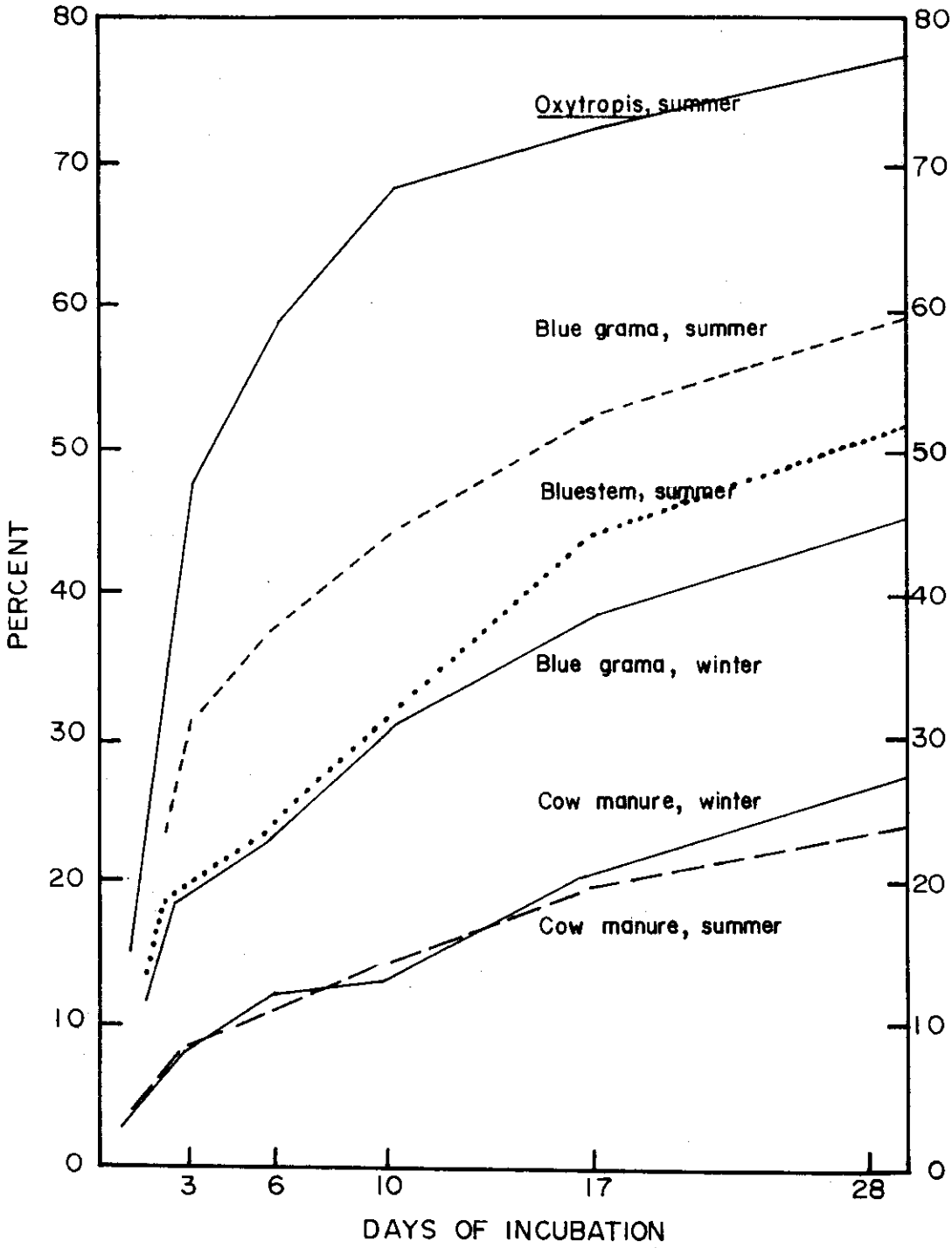

Fig. 2. Percentages of carbon lost from buried litters.

GENERAL REMARKS

As noted in the introduction, Sims and Singh (1971) have estimated the average daily decomposition of belowground plant material in Pawnee grassland as 2.7 g/m^2/day during the growing season. A portion of this organic carbon is converted to microbial tissue in the course of the decay process, and some portion of it remains or accrues as relatively long lasting polycondensate or humic material not recoverable as particulate material. In either case, it does not appear as respiratory carbon simultaneously with the disappearance of the particulate residues. With time, however, the microbial tissue itself will decompose, as will also the soil humates, and it is therefore reasonable to assume that over the longer term and regardless of the number of secondary productivity cycles involved the annual organic carbon input is essentially equal to the respiratory carbon output. Accordingly, the daily CO_2 output to be expected from 2.7 g of input (i.e., belowground decomposing material) should be 5.5 g/m^2 or, for the 152-day growing season at Pawnee, 836 g/m^2.

Assuming linearity between the successive sampling dates involved, the data given in Table 1 for Site 1 for the interval April 28 to September 8 can be summed to show a seasonal CO_2 output of 339 g. Extrapolating the data to September 28, to permit inclusion of the period of relatively favorable soil water during September and also to bring the total interval to approximately 152 days, the calculated CO_2 output becomes only 519 g, distinctly short of the 836 g to be expected from the organic matter input rate given by Sims and Singh (1971).

The discrepancy, however, is not simply one of 300 g, inasmuch as the 539 g of output includes the respiratory output of live roots as well as that of microorganisms. Data given in Table 4 suggest that for the uppermost portion of the soil profile wherein most of the root biomass is known to occur as much as 70% of the total soil respiration is due to the crown and root components therein. This figure, however, must be adjusted downward, partly because not all of the separated root material can be assumed as comprising live root biomass and partly because the soil component of the total root-soil respiration becomes increasingly important at progressively deeper intervals of the soil profile. If in view of these considerations, the root respiration of 70% shown in Table 4 is halved to 35%, then of the 519 g of summed (but not actually measured) CO_2 output, only 337 g can be ascribed to belowground decomposition. This indicates a discrepancy of 500 g (i.e., 337 g vs. 836 g), and it rises several questions.

Were there short bursts of soil respiration that went undetected following intermittent light showers occurring between the dates on which evolved CO_2 was determined? Was the midsummer drought in 1971 of such severity that the belowground root productivity and decay in 1971 was distinctly below normal, making an output value of 836 g entirely unrealistic as a standard to be used in 1971? Is the static absorption procedure employing alkali in an inverted "coffee can" technique an adequate and reliable procedure for measuring field soil respiration? Although the loss of particulate material during the growing season may be of a certain order of magnitude, does that loss translate directly to respiration loss, or stated otherwise, is the

growing season for microorganisms considerably longer than that for plants?

These are challenging questions. More measurements involving field use of the static alkali absorption technique for CO_2 are needed with attention given to the character and quantity of the aboveground vegetation, the soil water and temperature regimes within successive segments of the soil profile, the root biomass in those segments, and the respiratory outputs of truncated soil profiles.

Less promising, particularly until experimental procedures can be further refined, are the compartmental analyses involving transport of soil cores into the laboratory and the continuation of cellulose burials in the field. Priority should be given to problems of secondary productivity involving normally occurring field litters in undisturbed environments. This does not imply that supporting experiments involving artificial placements and measurements of susceptibility to decomposition of natural litters are without merit. Indeed, the type of data shown in Fig. 2 could be extended to a whole host of plant species, a variety of vertebrate and invertebrate droppings, of animal corpses, and so on. The resulting data should be useful in modelling the grassland ecosystem.

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