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INFLUENCE OF ENVIRONMENTAL FACTORS ON THE RESPIRATION RATE OF GRASSLAND SOILS--A MODEL[1/]

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ABSTRACT

In order to accurately predict carbon and energy flow through the terrestrial ecosystem, it is necessary to understand the influence of environmental factors on the soil respiration rate, i.e. the rate of CO_2 evolution from soil. Studies were therefore initiated to determine the influence of soil water, soil temperature and grazing on the rate of CO_2 evolution from soil.

Sampling locations were selected from both grazed and ungrazed grassland sites on the Arid Land Ecology Reserve operated by the U.S. Atomic Energy Commission in south-central Washington. The soil CO_2 evolution rate and surface soil water and temperature were measured at periodic intervals from April 1, 1971 to November 18, 1972.

To provide an estimate of the rate of plant tissue decomposition in soil, shoot and root tissues (Agropyron spicatum) in nylon-mesh bags were buried in the soil at sites employed for soil respiration measurements, and the bags were retrieved at periodic intervals. Tissue weight losses and net changes in organic C and total N were taken as indices of decomposition.

The sensitivity of CO_2 measurements was augmented by improvement of titrimetric methods and by adjustment of the concentration of base utilized for collection of CO_2. The concentration of base was estimated from expected CO_2 evolution rates. The CO_2 evolution rates were predicted from preliminary regression models employing soil water and temperature. With the improved sensitivity, field blanks recorded in 1971 and 1972 became significant. Adjustment of all CO_2 values for the field blanks allowed detection of subtle effects of soil water and temperature on respiration rate.

Using a multiple regression model, it was possible to explain a major portion (approximately 75%) of the variation in soil respiration rate on the basis of changes in soil water and soil temperature. The model was sufficiently versatile to describe marked changes in soil respiration rate resulting from summer rains. Soil water was evidently the limiting factor in the late spring, summer and early fall when soil temperatures were above approximately 15°C; whereas temperature was likely a major factor in the late fall, winter and early spring when soil water content was at a level approximating 50% soil water capacity.

The CO_2 evolution rates on grazed fields were significantly lower (sign test) than ungrazed fields in 1972, perhaps as a result of a decrease in below-ground biomass and root respiration. Grazing effects may be expected to become more pronounced as grazing is continued in subsequent years.

Total decomposition of shoot tissues, measured gravimetrically after burial for periods of 12-15 months, ranged from 30 to 45% of the tissues originally buried. Root tissues decomposed less rapidly exhibiting less than a 13% weight loss over the same period. Grazing did not influence the decomposition rates of shoot or root tissues.

Plant tissue organic C content generally did not change markedly with time, and net C losses therefore approximated those losses measured gravimetrically. The C/N ratios decreased markedly on decomposition, likely as a result of microbial conversion of tissue C to CO_2.

INTRODUCTION

The soil is the principal medium for return of photosynthetic energy to the atmosphere. Soil microorganisms may be represented as receiving reduced forms of C in plant and animal residues and ultimately oxidizing the carbonaceous materials to the lowest energy state of C, i.e. CO_2. The rate of CO_2 evolution from soil is largely a function of the activity of soil microorganisms and plant root respiration but also includes respiration by soil invertebrates (Kononova, 1966). Prediction of C and energy flow through an ecosystem must be predicated upon an understanding of the environmental factors influencing soil respiration rate. Field measurements of soil respiration rate are perhaps the best means of evaluating the integrated influence of these effects.

Previous laboratory and field studies (Katznelson and Stevenson, 1956; Kononova, 1966; Wildung, et al., 1971) have indicated the importance of soil temperature and moisture in influencing the rate of organic matter degradation in soil.

Related studies (Wildung and Schmidt, 1971) were conducted in calendar year 1971 on the Arid Land Ecology Reserve operated by the U. S. Atomic Energy Commission in south-central Washington as a part of an International Biological Program, Grassland Biome effort to determine the influence of grazing on ecological processes. These investigations indicated that whereas seasonal changes in soil water content were significantly correlated with changes in soil CO_2 evolution rate measured at periodic intervals from April to September, changes in soil temperature were not. However, initial predictive models were improved when temperature was included. Temperature effects were not as pronounced

as water effects and detection methods employed were insufficiently sensitive to determine changes in CO_2 evolution rate resulting from small changes in temperature.

The studies further showed that CO_2 evolution rates and litter decomposition on grazed and ungrazed plots were not significantly different in the first year of grazing. It was suggested that grazing effects on soil respiration would become more pronounced as grazing was continued in subsequent years resulting in changes in plant root respiration, soil fertility and soil structure.

In calendar year 1972, the sensitivity of the CO_2 measurements was improved by adjustment, according to expected CO_2 evolution rate, of the concentration of NaOH utilized for collection of CO_2. This reduced the quantity of excess NaOH required and allowed a more sensitive titrimetric determination of trapped CO_2. The expected CO_2 evolution rate was predicted from a preliminary regression model employing temperature and moisture. Measurements of CO_2 evolution using the modified method were extended through 1972 to determine the effect of water, temperature and a second period of grazing on soil respiration rate. Regression models were developed for prediction of soil CO_2 evolution rate utilizing the most influential environmental parameters. For comparative purposes measurements of plant tissue decomposition in soil were also continued. The results of the 1971 and 1972 studies are summarized in this report.

MATERIALS AND METHODS

The grazing studies were conducted on a field plot located at an elevation of approximately 445 m on the northeast-facing slopes of the

Rattlesnake Mountains in south-central Washington. The understory at this elevation is dominated by Bluebunch Wheatgrass (Agropyron spicatum) whereas the principal overstory shrub species is Big Sagebrush (Artemisia tridentata).

The soil at the experimental site, a Ritzville silt loam, developed primarily on aeolian silt parent material and contained 0.66% organic C (Table 1).

The field plot design is illustrated in Figure 1. The field plot (600 X 600 M) consisted of grazed and ungrazed treatments containing two replicates (300 X 300 M). Replicates were subdivided into three strata. To locate sites for analyses, two blocks (15 X 30 M) were randomly selected from each stratum and two plots (1 X 1 M) were randomly selected from each block (12 sample sites per treatment). Grazing (15 head) was alternated at 7 day intervals on replicates 1 and 2 from April 14 to June 10, 1971 and from April 5 to May 16, 1972.

Soil Temperature and Moisture

Soil temperature (10 cm soil depth) was estimated by using a dial-reading, spike stem thermometer inserted into the soil. The thermometer operated on the dual metallic principle. Thermometers were placed inside the CO_2 collection device, inside the shade canopy and outside the shade canopy.

Surface soil (0-8 cm) moisture content was determined gravimetrically after drying (110°C) of samples taken concurrently with measurement of soil respiration rate.

Table 1. Description of the soil (Ritzville silt loam) at the experimental site.

Classification	Vegetative understory	Elevation	pH	Contents[1] of Organic carbon	Sand (> 50μ)	Silt (50 to 2μ)	Clay (< 2μ)	CEC at pH 7.0
		M		%				meq/100g
Andic Aridic Haplustoll	Agropyron	445	6.2	0.66	23.3	64.1	12.6	22.5

[1]Percent organic carbon based on total soil, other values on total minerals.

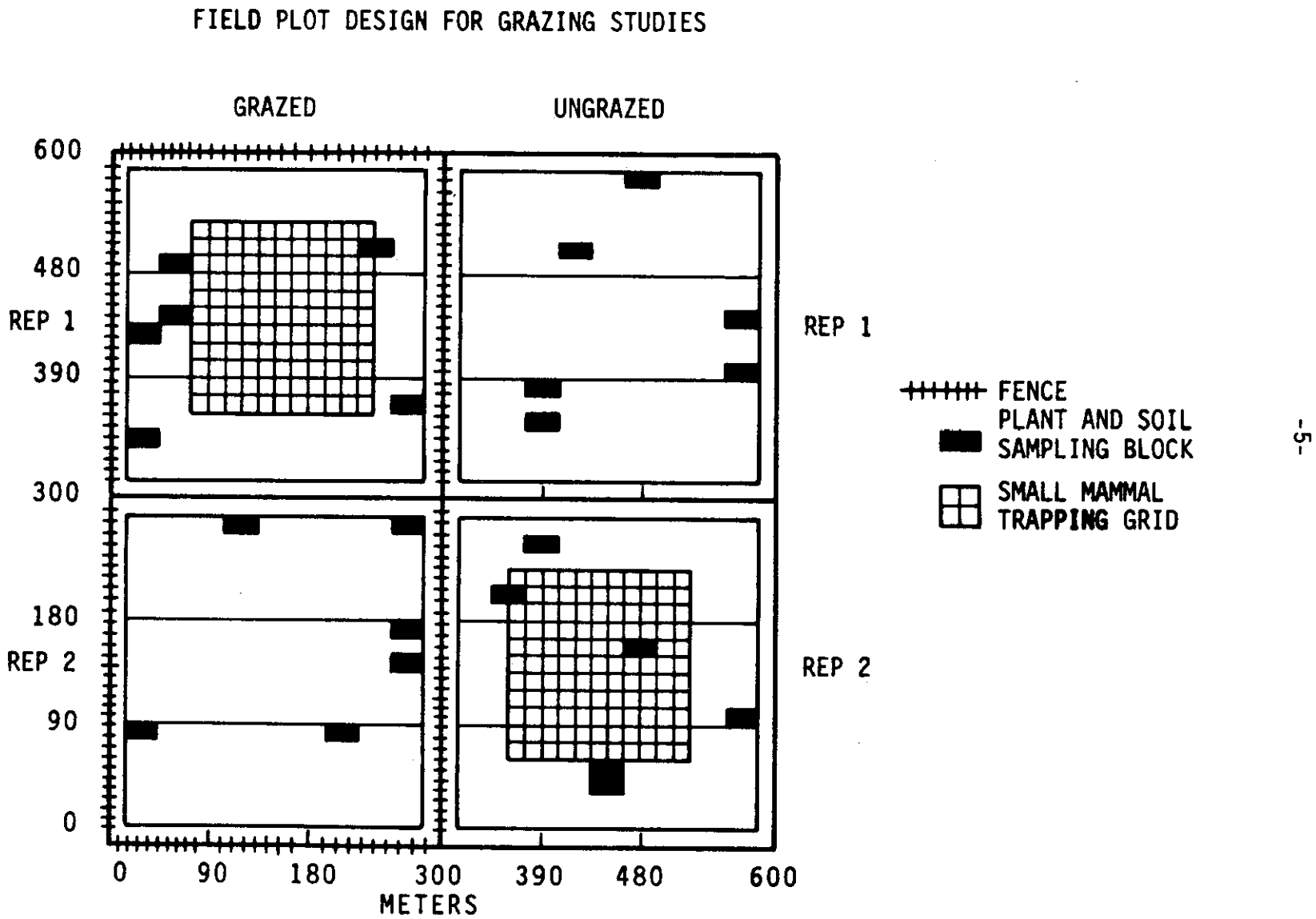

Figure 1. Field plot design for the grazing study

Soil Respiration Rate

The soil CO_2 evolution rate was measured for 24 hour periods (8 a.m. to 8 a.m.) at intervals from April 1, 1971 to November 18, 1972. The measurements were at most frequent intervals throughout the growing season in the spring and early summer.

To collect CO_2 evolved from the soil surface during the 1971 studies, a polypropylene bottle with the bottom removed was inserted into the soil to a depth of 20 cm. The polypropylene became brittle and fractured during the winter, and therefore for the 1972 studies an aluminum pipe (10 cm dia.), driven to the same depth, was utilized (Fig. 2). A vessel containing 0.1 to 1.0 N NaOH (10 ml) was utilized as a CO_2 trap. The bottle containing the CO_2 trap was sealed using a threaded lid containing a moistened "O" ring. The aluminum pipe was covered during measurements by a snap-on polypropylene cap. To reduce the possibility of increased temperature in the closed vessel, the unit was shaded using an angled section of galvanized sheeting. Controls were placed in the field adjacent to the treatment. The control systems were identical to the units utilized for collection of CO_2 evolved from soil except the volume of the controls was reduced to the equivalent volume above the soil in the closed treatment vessels (Fig. 2). The CO_2 in the soil effluent gases, absorbed as CO_3^{2-} in the traps, was analyzed (Stotzky, 1965) by titration (0.1-1.0 N HCl) of the unneutralized NaOH after precipitation of the CO_3^{2-} as the Ba^{2+} salt. Titrations were conducted utilizing an automatic, continuously recording titrimeter. A typical titration curve is illustrated in Fig. 3. Minimum detectable levels

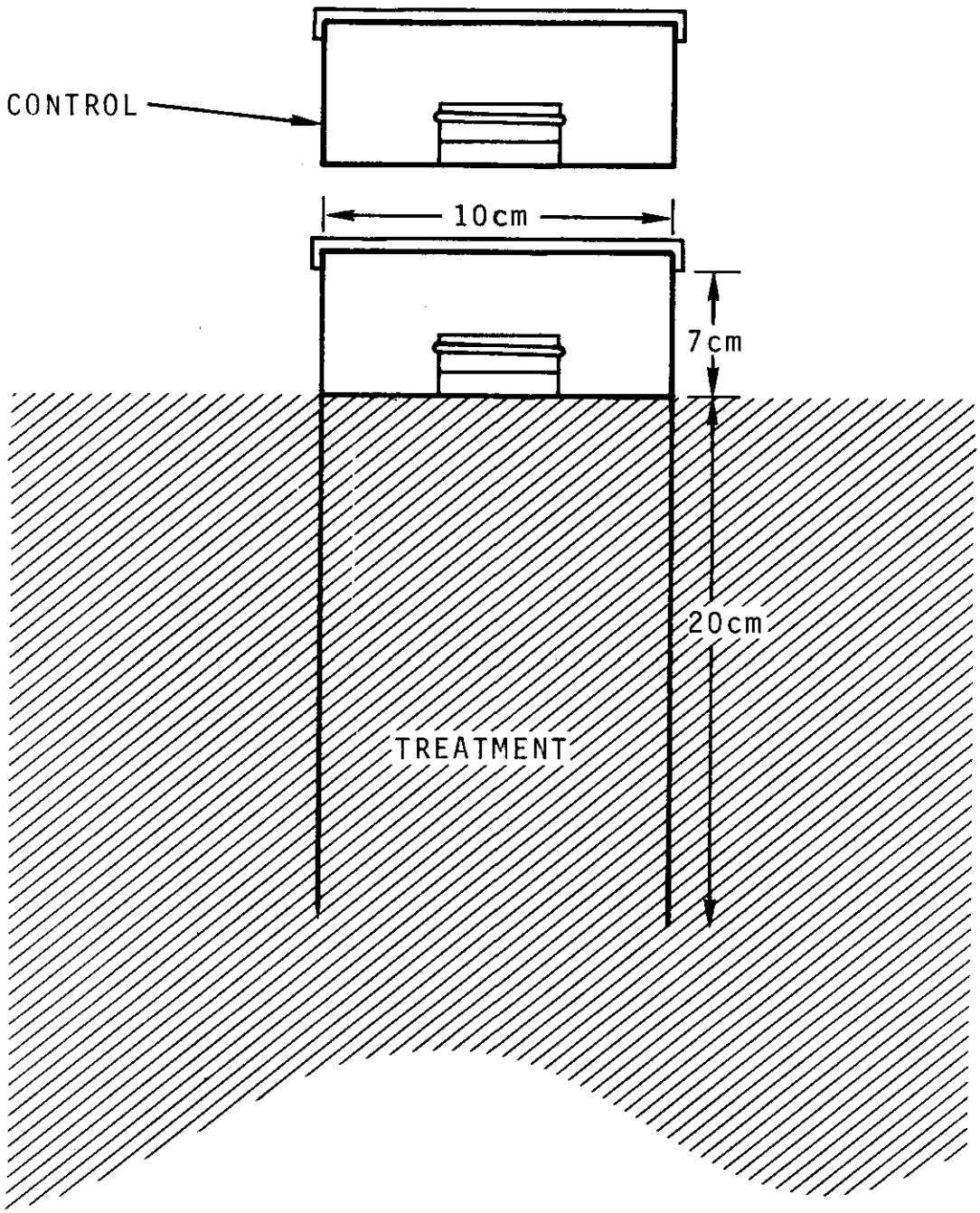

Figure 2. Apparatus for collection of carbon dioxide evolved from soil

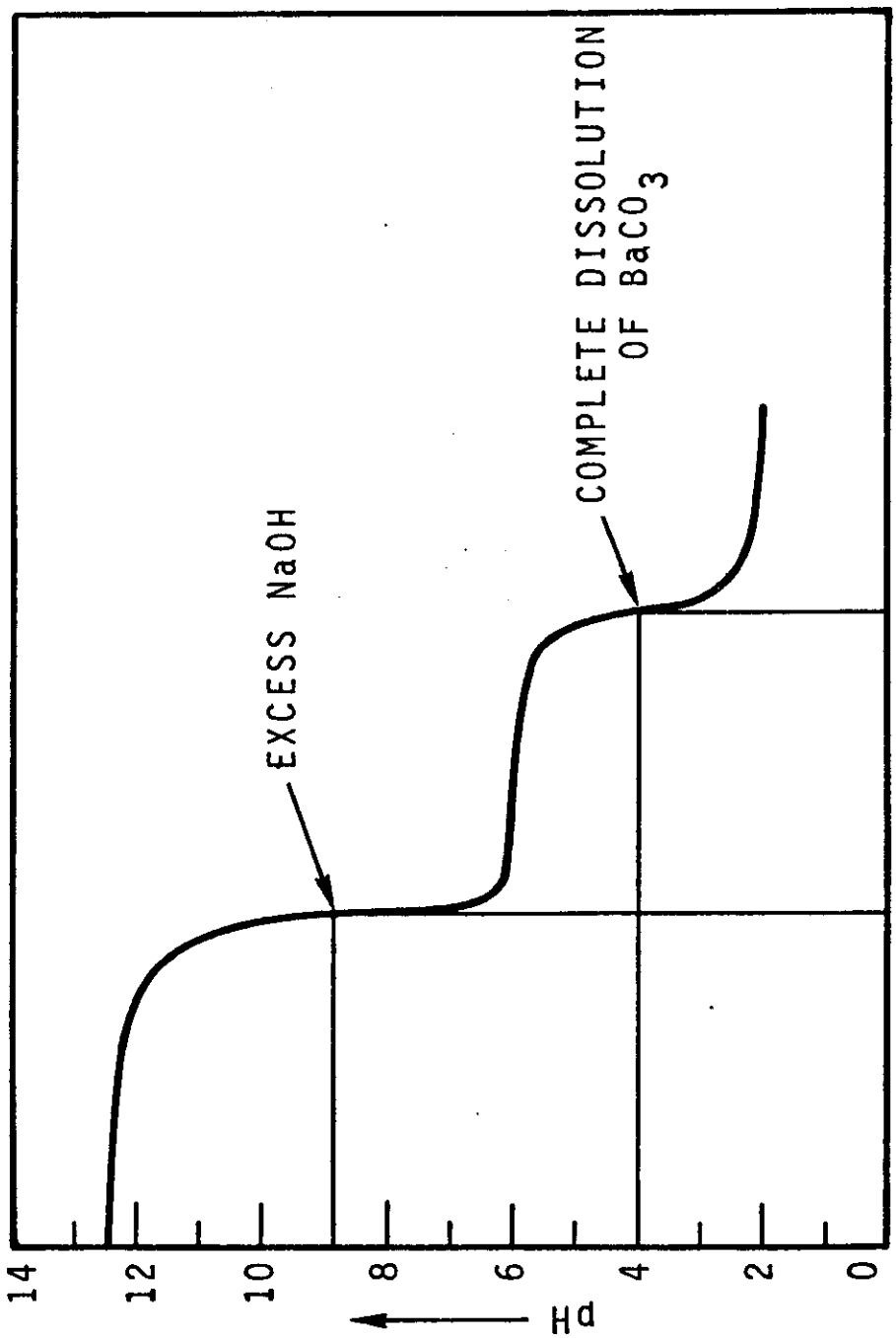

Figure 3. Titration curve for the determination of soil-evolved carbon dioxide collected in sodium hydroxide. Titration is performed after precipitation of carbonate as the barium salt. The amount of carbon dioxide collected, expressed in volume of standard hydrochloric acid, is equivalent to B minus A.

of soil evolved CO_2 were dependent primarily upon the concentration of NaOH employed for CO_2 collection and amounted to $\pm$ 1.1 and $\pm$ 11 mg CO_2 at 0.1 and 1.0 N NaOH, respectively. The CO_2 evolved per collection unit in 24 hours, ranged from approximately 25 to 100 mg in the polypropylene vessels (15 cm dia.) used in 1971 and from approximately 8 to 34 mg in the aluminum vessels (10 cm dia.) used in 1972.

Decomposition of Plant Tissues

To provide an estimate of the rate of plant tissue decomposition in soil, shoot and root tissues (Agropyron spicatum) were chopped (2-7 cm in length) and subsamples (1.0-3.0 g) placed in nylon mesh bags (15 cm x 15 cm). The bags (15 bags of each tissue) were buried in the soil (6-8 cm) at two locations on the grazed and at two locations on the ungrazed sections of the field plot. Thus, a total of 120 nylon bags (15 bags x 4 locations x 2 tissues) were buried at each time interval. The bags containing the tissue were buried on March 18, April 21 and June 4, 1971. A portion of the tissues buried in March were retrieved on April 21, May 26 and August 17, 1971, whereas a portion of tissues buried in April and June were retrieved on August 17, 1971. A random selection of tissues buried in 1971 were retrieved on June 6, 1972. On August 10, 1972, cellulose and shoot and root tissues (Agropyron spicatum) were buried in a similar manner. Sufficient quantities were placed in 1971 and 1972 to allow retrieval at yearly intervals for a period of 3 years from time of burial.

On retrieval, the tissues were removed from the nylon bags and subsamples were taken for gravimetric measurement of weight loss, based on

oven-dry (60°C) weight and for determination of elemental composition. Tissue weight change was calculated as follows:

$$\text{Percentage change in weight} = \frac{\text{Weight of original ash-free tissue} - \text{Weight of retrieved ash-free tissue}}{\text{Weight of original ash-free tissue}} \times 100$$

Elemental Analyses

Organic C, H, N and ash were determined on the original tissues and on retrieved tissues exhibiting maximum weight losses, i.e., tissues buried for five months or longer. The organic C, H and ash contents were measured as described by Wildung, et al., 1970, and N contents were determined by the Dumas method as described by Welcher, 1966.

Changes in tissue organic C and N were calculated as follows:

$$\text{Percentage change in C or N} = \frac{\text{C content of original ash-free tissue} - \text{C content of retrieved ash-free tissue}}{\text{C content of original ash-free tissue}} \times 100$$

RESULTS AND DISCUSSION

Evaluation of Methods

The polypropylene bottles used in 1971 performed well in providing a closed system for collection of soil-evolved CO_2. However, the bottles became brittle and cracked during the winter and aluminum pipe driven into the ground and covered with a snap-on polyropylene cap was used for CO_2 collection in the 1972 studies.

The mean CO_2 evolution rate using the original devices was nearly identical for grazed and ungrazed treatments. Installation of the aluminum

pipes early in 1972 resulted in a consistently, but not significantly, higher CO_2 evolution rate in the ungrazed plots likely due to the fact that the new containers more closely represented the field as it was altered by grazing over the past year. Because permanently placed collection vessels represent an unaltered microcosm, new units should be placed each year or portable units developed.

Although changes in soil water had marked influences on soil CO_2 evolution rate monitored during 1971 and early 1972, initial predictive models were improved when temperature was incorporated. It became apparent that temperature was an important parameter during the early spring, summer, late fall and winter. However, temperature effects were not as pronounced as water effects and the detection methods employed were insufficiently sensitive to determine changes in CO_2 evolution rate resulting from small changes in temperature. To improve sensitivity, the concentration of NaOH utilized for collection of CO_2 was adjusted according to expected CO_2 evolution rate. The rate was predicted from soil temperature and water data previously obtained and sufficient excess base was allowed to ensure that less than 40% of the base was neutralized. Acid concentrations utilized for titration of unneutralized base were adjusted accordingly. Potentiometric titrations were conducted using a continuously recording automatic titrimeter on a routine basis. These changes improved sensitivity by an approximate factor of 10, which allowed the detection of more subtle changes in the field.

In the 1971 studies, the CO_2 levels in the controls did not exceed the determined variation between replicate treatments, and therefore the

values for soil CO_2 evolution rate in 1971 were uncorrected for CO_2 present in the atmosphere within the vessels. However, with the improved sensitivity, it became necessary to correct for field controls, i.e. the CO_2 present in a capped vessel of volume equivalent to that above ground in the soil collection vessels. These modifications markedly improved correlations between temperature and CO_2 evolution rate and differences between grazed and ungrazed treatments appeared significant in the fall of 1972. Additional data to be collected in the spring of 1973 will assist in validation of these initial observations.

Subsurface (10 cm soil depth) soil temperatures under the shaded collection vessel and outside the shade canopy were approximately equivalent throughout the monitoring period. Surface soil (2 cm) temperatures outside the shade canopy seldom exceeded surface soil temperature under the canopy by 5°C. Measurements of soil in the morning (8 a.m.) before maximum ambient temperatures were reached likely served to minimize differences between shaded and unshaded surface temperatures. Subsurface soil temperatures were employed for all evaluations. However, most of the soil microbial activity likely occurs in the surface (0-3 cm) of the soil. If precise estimates of the influence of temperature on the microbial contributions to soil respiration are required, measurements of soil surface temperature should be employed.

Estimation of plant tissue decomposition by gravimetric determination of weight loss after field burial and retrieval was satisfactory provided degradation exceeded approximately 10% of the original tissue weight. If tissue degradation amounted to less than 10%, interpretations

were tenuous due to replicate variation. Variation may have arisen from subsampling errors (although 6 replicates were employed), the presence of fresh plant roots or from moisture in the interlayers of soil clay minerals retained by the roots after retrieval. Interlayer moisture may be considered stable at 60°C, the oven temperature at which the tissue was dried. In 1971, the decomposition of shoot tissues over the growing season was sufficient to allow valid comparisons between treatments, however root tissues decomposed more slowly; and evaluation of treatment effects on root decomposition over the same time interval was not feasible. In 1972, the burial period for both shoots and roots was extended to approximately 1 year; but after 1 year, decomposition of roots was still not sufficient to allow a comparison of treatment effects.

Seasonal Changes in Soil Temperature and Moisture

Soil temperature (Fig. 4), with the exception of several sharp decreases during rain storms, generally exhibited a gradual increase from 6.6°C in April to 31.0°C near the end of July, 1971. This temperature was maintained evidently through most of August. On September 1, 1971, the soil temperature had decreased to 19°C and it apparently continued to decrease to a low of 0.5°C in February. A similar temperature cycle occurred in 1972, except that the maximum recorded temperature (23.8°C in August) was lower than 1971.

Soil water content (Fig. 4) decreased from a high of 10.9% on April 1, to 2.5% at the end of May, 1971. In the interim, a light rainfall on May 13 increased the soil water from 2.3 to 2.9%. A rain storm added

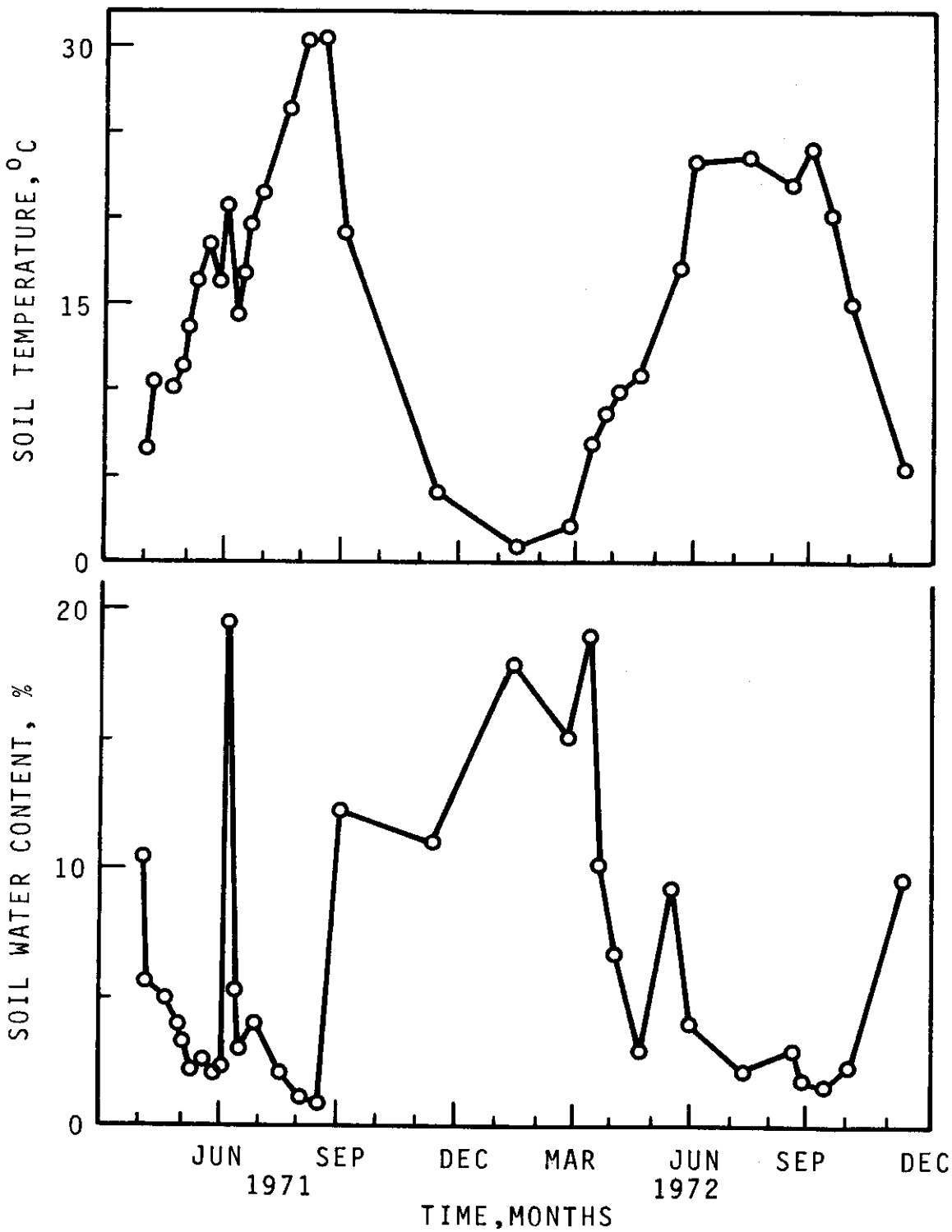

Figure 4. Seasonal changes in soil temperature and soil water on combined grazed and ungrazed treatments. Each value is the mean of 24 field replicates. Soil temperature and water were not significantly different for grazed and ungrazed fields.

approximately 2.5 cm of new water to the soil on June 3, raising the soil water content to near field water capacity (22%). Following the storm, surface soil water content decreased to 1.2% on August 12, due apparently to downward water movement, evapotranspiration from the surface and consumptive use by vegetation. Deviating from the usual climatic pattern in which July, August and September are dry months, a storm on September 1, which deposited approximately 1.3 cm of rainfall, raised the soil water level to 13.4%. Although records are not as detailed during the fall of 1971 and winter of 1972, soil water apparently increased through the fall reaching a maximum in the winter. The highest recorded maximum in 1972 occurred in March. This was followed by a general decrease during the summer but included a sharp increase in early May, 1972 as a result of a light rain. Records for 1972 were not as detailed as 1971, and it is likely that soil water content measured at more frequent intervals would reflect the several rains which occurred in the spring of 1972.

Influence of Soil Temperature and Moisture on Soil Respiration Rate

To determine the effect of soil temperature and soil water on soil respiration, simple correlations of temperature and water content versus soil CO_2 evolution during 1971 and 1972 were evaluated for the ungrazed treatment ($n = 31$). In contrast to data accumulated in 1971 (Wildung and Schmidt, 1971), in which there was a strong correlation between soil respiration rate and soil water, neither soil water nor temperature were significantly correlated ($P = 0.05$) with changes in soil respiration rate when data from 1971 and 1972 were combined. However, it was apparent from qualitative comparisons of these parameters (Figs. 4 and 5) that both soil

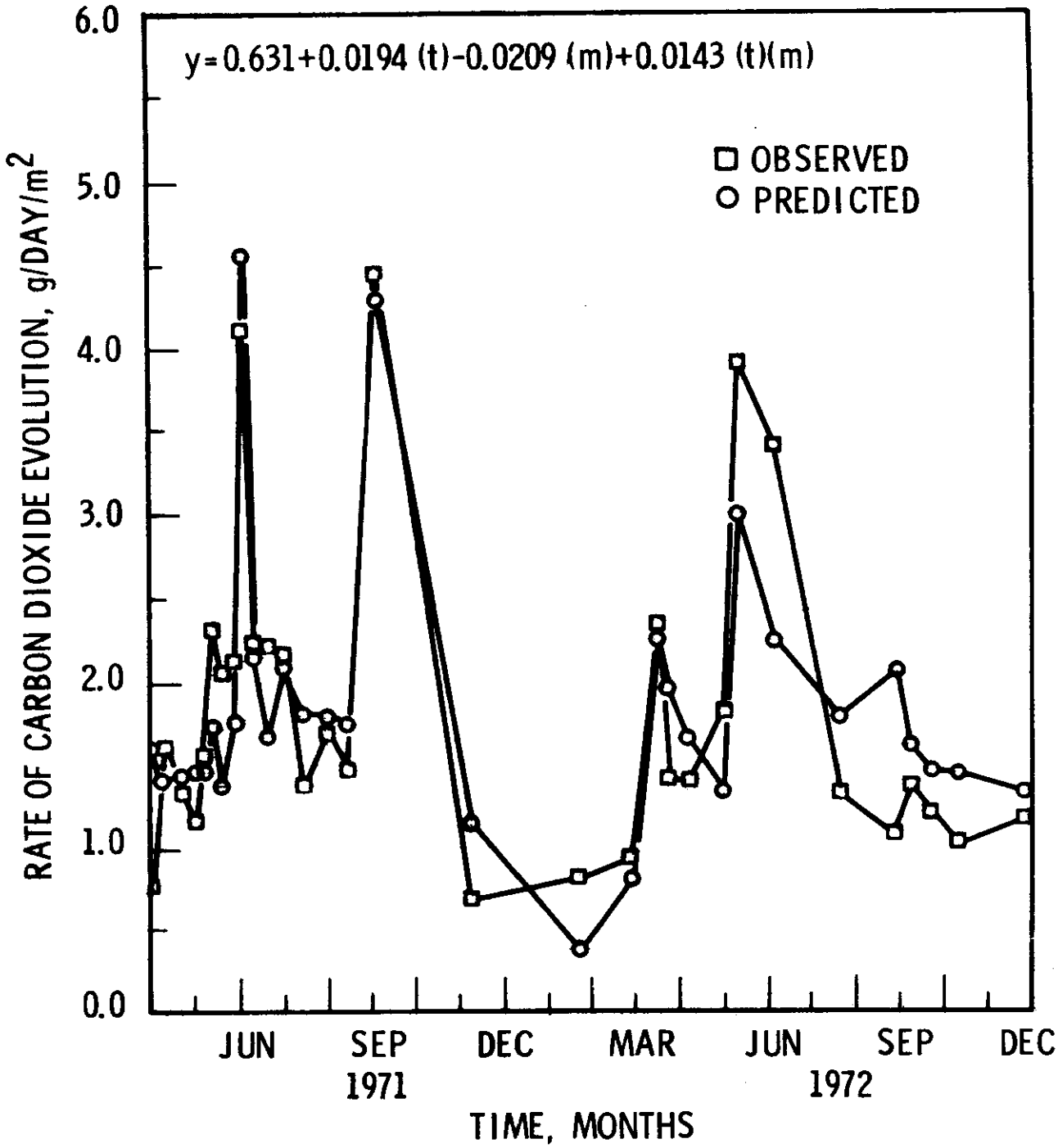

Figure 5. Multiple regression model (R = 0.86) describing the influence of soil temperature (t) and soil water content (m) on rate of carbon dioxide evolution (y) from ungrazed soil over a two-year period. Each observed value is the mean of 12 field replicates.

water and temperature played an important role in influencing soil respiration.

Increases in soil water content due to rainfall in the late spring and summer, when soil temperatures were above approximately 15°C (Fig. 4), resulted in marked increases (Fig. 5) in CO_2 evolution rate. If this water content was maintained for extended periods at these soil temperatures, total CO_2 evolution would have been much higher on an annual basis. However, soil water was inversely related to soil temperature ($r = 0.67$, $P < 0.01$) as a result of (i) climatic factors, i.e. rainfall was usually accompanied by reduced ambient temperatures, and (ii) increased evapotranspiration from soil at higher temperatures. The latter effect resulted in rapid decreases in soil water after a summer rainfall. Thus, over an annual period, marked effects of summer rains on soil respiration rate were less important.

It is likely that the effects of temperature and water content on soil microbiological activity and plant root respiration were complex and interrelated and that temperature and moisture were both highly important. Moisture was evidently the limiting factor in the late spring, summer and early fall, when temperatures were above approximately 15°C, and temperature a major factor in the late fall, winter and early spring, when water content was greater than approximately 50% soil water capacity (22%). Using multiple regression techniques, it was possible to explain a major portion (approximately 75%) of the variation ($R = 0.86$) in soil respiration rate during 1971 and 1972 on the basis of soil water and soil temperature (Fig. 5). The model appeared to have excellent predictive

capability and was sufficiently versatile to describe marked changes in soil respiration rate resulting from summer rains. A model using the same parameters and approximately equivalent coefficients performed equally well ($R = 0.91$) when applied to the grazed treatment (Fig. 6). To reduce residual variance, parameters other than temperature and moisture should be included, e.g., barometric pressure and ambient or soil surface (3 cm) temperature. Future studies will be oriented toward refinement of the model through identification and measurement of these parameters and validation of the model by measurement of soil respiration rate after manipulation of influential parameters in the field.

Influence of Grazing on Soil Respiration Rate

Comparison of soil respiration rates on grazed and ungrazed plots using the "t" test indicated that the treatments (Figs. 5, 6) were not significantly different ($P = 0.05$). Using the sign test, the treatments were not significantly different in 1971, but the grazed site was significantly lower ($P = 0.01$) than the ungrazed site in 1972. In contrast to the "t" test, the sign test, when applied to these data, takes direction of change with time into account.

Grazing may be expected to influence soil respiration rate by altering conditions which influence microbial activity and plant root respiration, e.g., soil fertility levels, availability of readily available sources of C, disturbance of surface soil structure and plant harvest. These effects should become more pronounced as grazing is continued. However, over the short-term, it is likely that changes in soil respiration rate would be most markedly influenced by changes in soil structure as this

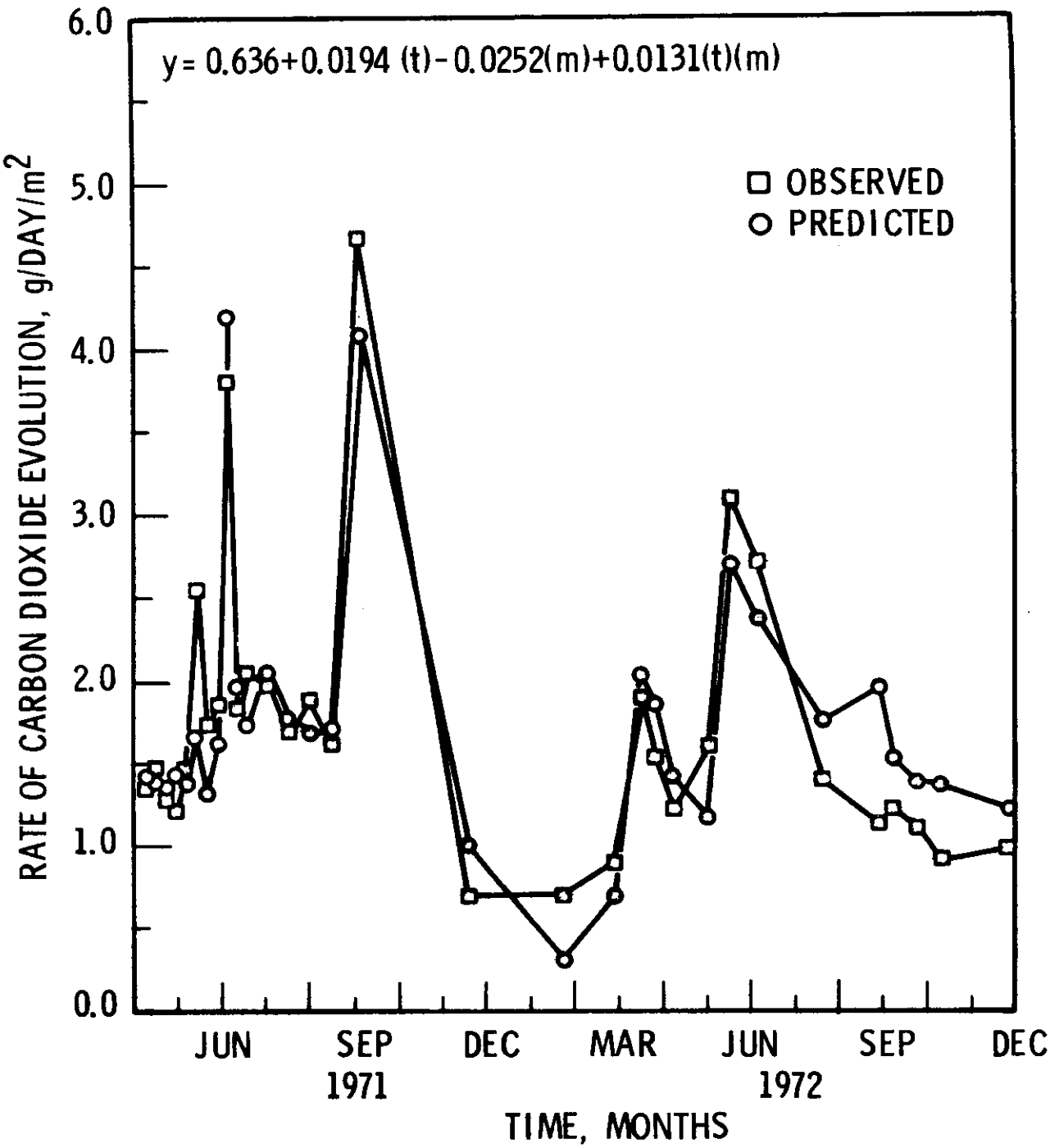

Figure 6. Multiple regression model (R = 0.91) describing the influence of soil temperature (t) and soil water content (m) on rate of carbon dioxide evolution (y) from grazed soil over a two-year period. Each observed value is the mean of 12 field replicates.

influences soil water holding capacity, temperature and CO_2 diffusion; and in total plant biomass, which is related to consumptive use of soil water and the rate of root respiration. It is difficult to quantify changes in soil structure. Soil water content and soil temperature on the grazed and ungrazed sites were not significantly different when all data were considered. However, the total, above-ground biomass of perennial grasses on the grazed and ungrazed sites (Rickard, 1972), not significantly different in spring, 1971, prior to initiation of the first grazing period, was approximately 25% lower on the grazed than the ungrazed sites in early spring, 1972, prior to initiation of the second grazing period. The differences between treatments were accentuated with grazing and amounted to approximately 50% in June, 1971 and 1972 after grazing was terminated. If reduction in live, above-ground biomass was accompanied by a reduction in live, below-ground biomass, the observed decrease in C flow on grazing may have resulted, in part, from a reduction in total root respiration. Future studies should be designed to test this hypothesis and determine the relative influence of other factors which may account for grazing effects on soil respiration rate.

Decomposition of Plant Tissues in Soil

Gravimetric measurements. Decomposition of Agropyron spicatum shoot tissues, measured gravimetrically, generally increased with burial time (Table 2). In 1971, when several burials and retrievals were made at intervals during the spring and summer, decomposition of shoots ranged from 11.2 to 26.6% and from 5.8 to 20.3% for the grazed and ungrazed treatments,

Table 2. Decomposition (weight loss) of shoot and root tissues (Agropyron spicatum) in soil.

Date of Burial	Date of Retrieval	Burial Time	Decomposition			
			Shoots		Roots	
			Grazed	Ungrazed	Grazed	Ungrazed
		days	----------%[1]----------			
			Retrieved[2] in 1971			
3-18-71	4-21-71	35	11.2 ± 0.5	5.8 ± 0.6	4.1 ± 1.6	6.9 ± 0.9
3-18-71	5-26-71	70	12.0 ± 1.6	10.5 ± 0.7	7.9 ± 1.1	1.7 ± 0.6
3-18-71	8-17-71	153	19.7 ± 0.9	20.3 ± 1.2	5.5 ± 1.5	6.7 ± 2.6
4-21-71	8-17-71	118	26.6 ± 4.4	13.4 ± 2.5	-13 ± 10	9.7 ± 7.3
6-4-71	8-17-71	74	14.5 ± 0.9	14.2 ± 2.1	0.5 ± 3.9	1.4 ± 4.0
			Retrieved[3] in 1972			
3-18-71	6-6-72	447	37.1 ± 5.8	29.8 ± 0.8	-1.2 ± 9.1	13.3 ± 2.3
4-21-71	6-6-72	413	45.8 ± 11.8	39.2 ± 10.2	4.8 ± 4.3	-6.2 ± 3.5
6-4-71	6-6-72	369	32.0 ± 1.6	35.0 ± 3.5	-11 ± 5	-21 ± 3

[1]Percentage lost based on oven-dry (60°C) ash-free weight

[2]$\bar{x}$ ± S.D., n = 6 (3 bags from 2 replicates)

[3]$\bar{x}$ ± S.D., n = 4 (2 bags from 2 replicates)

respectively. For shoots buried in March on the grazed treatment, total decomposition of tissues retrieved in August was significantly higher ($P = 0.05$) than decomposition for tissues retrieved in April and May. Decomposition of tissues buried in April and retrieved in August was significantly ($P = 0.05$) higher than tissues buried in March and retrieved in April. Decomposition of tissues buried in June and retrieved in August was significantly lower ($P = 0.05$) than tissue buried in April and retrieved in August. In the case of the ungrazed treatment, decomposition of tissues buried in March was significantly different ($P = 0.05$) for April, May and August retrievals, increasing with increased burial time. Decomposition of tissues buried in June and retrieved in August was significantly greater ($P = 0.05$) than tissues buried in March and retrieved in April. No other differences in shoot decomposition were significant within treatments and grazing did not appear to affect decomposition rate.

Shoot decomposition on grazed and ungrazed treatments increased by an approximate factor of 2, amounting to 29.8 to 45%, when length of burial time was extended through June, 1972. However, there were no significant differences in decomposition resulting from length of burial time or grazing treatment in the long-term studies.

Root tissues decomposed more slowly than shoot tissues (Table 2) and decomposition did not exceed 13% of the tissues originally buried after incubation for periods exceeding 1 year. There was considerable variation in decomposition as determined by these methods, as previously discussed. Grazing did not have a significant effect on root tissue decomposition.

Carbon, hydrogen and nitrogen measurements. Total organic C and H were determined for shoot and root tissues prior to burial on March 18, April 21 and June 4, 1971 and after retrieval on August 17, 1971. The results of analyses for tissues buried on March 18, 1971 have been previously reported (Wildung and Schmidt, 1971). The results of C, H and N analyses for tissues buried at the other time intervals in the spring of 1971 and recovered on June 6, 1972 are given in Tables 3 and 4.

As in the case of gravimetric analyses, there was considerable variation in the elemental analyses of retrieved tissue. In general, there did not appear to be a significant change in C, H or C/H ratios (Table 3) with tissue type, burial time or treatment except in the case of the June, 1971 burial. After recovery of these tissues from grazed and ungrazed treatments, organic C had decreased significantly, amounting to approximately 10 and 20% for shoot and root tissues, respectively.

The N contents of both shoot and root tissues (Table 4) generally increased on burial in the soil and generally were highest, regardless of treatment, in the tissues buried on June 4, 1971, the burial time which resulted in the largest reduction in organic C. It is noteworthy that this burial took place at a time when soil temperature and moisture (Fig. 4) were near optimum for microbial activity as indicated by a soil respiration rate (Figs. 5, 6) which approached the maximum for the year.

The increase in N content was accompanied by a corresponding decrease in C/N ratio, probably as a result of microbial conversion of tissue C to CO_2. However, it is possible that the tissues absorbed N, likely as NO_3-N, from the soil solution. The lack of a change in total C content of the

Table 3. Changes in carbon and hydrogen composition of shoot and root tissue (Agropyron spicatum) on decomposition in soil.

Date of Burial	Date of Retrieval	Grazed			Ungrazed		
		C	H	C/H	C	H	C/H
		----------%[1,2]----------			----------%[1,2]----------		
				Shoots			
Prior to Burial		46.9 ± 0.8	6.6 ± 0.2	7.1 ± 0.2	46.9 ± 0.8	6.6 ± 0.2	7.1 ± 0.2
3-18-71	6-6-72	43.9 ± 2.6	6.4 ± 0.1	6.9 ± 0.5	46.6 ± 0.4	6.2 ± 0.1	7.5 ± 0.1
4-21-71	6-6-72	37.4 ± 3.8	6.8 ± 0.2	5.6 ± 0.7	41.9 ± 1.1	8.1 ± 0.6	5.2 ± 0.3
6-4-71	6-6-72	38.7 ± 5.9	6.4 ± 0.3	6.0 ± 0.8	35.8 ± 2.9	7.3 ± 0.5	5.0 ± 0.5
				Roots			
Prior to Burial		48.8 ± 1.5	6.7 ± 0.2	7.2 ± 0.2	48.8 ± 1.5	6.7 ± 0.2	7.2 ± 0.2
3-18-71	6-6-72	36.7 ± 4.3	10.7 ± 3.6	4.6 ± 1.3	43.9 ± 1.6	6.6 ± 0.5	6.8 ± 0.6
4-21-71	6-6-72	47.4 ± 0.7	6.5 ± 0.2	7.4 ± 0.2	42.4 ± 4.5	6.5 ± 0.1	6.6 ± 0.7
6-4-71	6-6-72	30.9 ± 6.7	7.7 ± 0.4	4.2 ± 1.1	28.3 ± 5.2	7.9 ± 1.5	4.0 ± 1.1

[1]Based on oven-dry (60°C), ash-free weight

[2]$\bar{x}$ ± S.D., n = 4

Table 4. Changes in carbon and nitrogen composition of shoot and root tissue (Agropyron spicatum) on decomposition in soil.

Date of Burial	Date of Retrieval	Grazed C	Grazed N	Grazed C/N	Ungrazed C	Ungrazed N	Ungrazed C/N
		----------%[1,2]----------			----------%[1,2]----------		
				Shoots			
Prior to Burial		46.9 ± 0.8	0.7 ± 0.1	63.5 ± 2.2	46.9 ± 0.8	0.7 ± 0.1	63.5 ± 2.2
3-18-71	6-6-72	43.9 ± 2.6	1.0 ± 0.2	51.8 ± 10.6	46.6 ± 0.4	0.6 ± 0.1	85.0 ± 8.5
4-21-71	6-6-72	37.4 ± 3.8	1.8 ± 0.4	26.2 ± 7.9	41.9 ± 1.1	1.3 ± 0.1	33.6 ± 4.5
6-4-71	6-6-72	38.7 ± 5.9	1.3 ± 0.4	50.4 ± 26.0	35.8 ± 2.9	2.0 ± 0.5	24.9 ± 10.0
				Roots			
Prior to Burial		48.8 ± 1.5	0.5 ± 0.1	120.0 ± 11.5	48.8 ± 1.5	0.5 ± 0.1	120.0 ± 11.5
3-18-71	6-6-72	36.7 ± 4.3	2.0 ± 0.8	24.0 ± 9.4	43.9 ± 1.6	1.7 ± 1.1	32.9 ± 7.7
4-21-71	6-6-72	47.4 ± 0.7	1.7 ± 0.9	32.2 ± 5.8	42.4 ± 4.5	1.1 ± 0.1	38.6 ± 3.0
6-4-71	6-6-72	30.9 ± 6.7	3.0 ± 1.6	11.8 ± 3.5	28.3 ± 5.2	4.5 ± 2.6	12.7 ± 4.9

[1]Based on oven-dry (60°C), ash-free weight

[2]$\bar{x} \pm$ S.D., n = 4

tissue does not necessarily indicate that decomposition did not occur because the tissues consist of a number of components of varying C content. Decomposition can only be estimated by gravimetric means, i.e., directly, as reported in the previous section, or by calculation of the net C loss.

Decomposition, as measured by net C loss, of shoots on grazed and ungrazed fields after 12-15 months burial, ranged from 30 to 59% of the C in the tissue prior to burial (Table 5). Roots lost 8 to 31% of C in the original tissue after burial for the same time period (Table 5). Shoot and root decomposition measured by C loss, therefore, broadly agreed with gravimetric measurements of decomposition. However, as in the case of gravimetric measurements alone, variation between replicates for both shoot and root tissues was considerable and there were no significant differences in decomposition resulting from length of burial time or grazing.

Table 5. Decomposition (organic carbon loss) of shoot and root tissues (*Agropyron spicatum*) in soil.

Date of Burial	Date of Retrieval	Decomposition			
		Grazed		Ungrazed	
		Shoots	Roots	Shoots	Roots
		----------%[1,2]----------			
3-18-71	6-6-72	41 ± 12	26 ± 9	30 ± 1	22 ± 7
4-21-71	6-6-72	59 ± 16	8 ± 8	45 ± 20	8 ± 18
6-4-71	6-6-72	44 ± 18	30 ± 32	50 ± 10	31 ± 23

[1]Based on oven-dry (60°C) ash-free weight

[2]$\bar{x}$ ± S.D., n = 4

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APPENDIX I

FIELD DATA

CO_2 Evolution Collected at the ALE Site

The CO_2 evolution data were collected on form NREL-4E. The grams CO_2/24 hr/m^2 for each sample were calculated at the site. The IBP designation for CO_2 evolution data collected at the ALE Site is A2U4041. Examples of the data form and data follow.

GRASSLAND BIOME

U.S. INTERNATIONAL BIOLOGICAL PROGRAM

FIELD DATA SHEET--MICROBIOLOGY - CO_2 EVOLUTION

Data Type	Site	Initials	Date			Treatment	Replicate	Cylinder Area	Soil Temperature	Soil Water	Experimental	Hours CO_2 Trapped	Molarity HCl	Mean of Blanks	ml HCl	B-E	Mg CO_2	Mg CO_2/24 hr	g CO_2/24 hr/m^2
			Day	Month	Year														
1-2	3-4	5-7	8-9	10-11	12-13	14	15	17-19	20-23	25-28	30	32-35	37-41	43-47	49-53	55-59	61-65	67-71	73-77
4E																			

Data Type
4E CO_2 evolution

Site
01 ALE
02 Bison
03 Bridger
04 Cottonwood
05 Dickinson
06 Hays
07 San Joaquin
08 Jornada
09 Osage
10 Pantex
11 Pawnee
12

Treatment
1 Ungrazed
2 Lightly grazed
3 Moderately grazed
4 Heavily grazed
5 Ungrazed current year only
A Diet light
B Diet moderate
C Diet heavy
D ESA - O
E ESA - W
F ESA - N
G ESA - WN

Experimental
1 Experimental cylinder
2 Blank cylinder

NREL-4E NATURAL RESOURCE ECOLOGY LABORATORY - COLORADO STATE UNIVERSITY - PHONE (303) 491-5571 - FORT COLLINS, COLORADO 80521

EXAMPLE OF DATA

```
        1         2         3         4         5         6         7         8
12345678901234567890123456789012345678901234567890123456789012345678901234567890

4E01TG 08047111179.10.5 5.30 1 24.0                                      00.81
4E01TG 08047111179.10.5 5.30 1 24.0                                      00.94
4E01TG 08047111179.10.5 5.30 1 24.0                                      00.57
4E01TG 08047111179.10.5 5.30 1 24.0                                      01.20
4E01TG 08047111179.10.5 5.30 1 24.0                                      01.59
4E01TG 08047111179.10.5 5.30 1 24.0                                      00.78
4E01TG 08047112179.10.5 6.20 1 24.0                                      00.57
4E01TG 08047112179.10.5 6.20 1 24.0                                      00.70
4E01TG 08047112179.10.5 6.20 1 24.0                                      00.48
4E01TG 08047112179.10.5 6.20 1 24.0                                      01.31
4E01TG 08047112179.10.5 6.20 1 24.0                                      00.38
4E01TG 08047112179.10.5 6.20 1 24.0                                      -0.21
4E01TG 08047151179.10.5 5.30 1 24.0                                      00.71
4E01TG 08047151179.10.5 5.30 1 24.0                                      03.06
4E01TG 08047151179.10.5 5.30 1 24.0                                      01.85
4E01TG 08047151179.10.5 5.30 1 24.0                                      01.24
4E01TG 08047151179.10.5 5.30 1 24.0                                      01.34
4E01TG 08047151179.10.5 5.30 1 24.0                                      00.67
4E01TG 08047152179.10.5 5.10 1 24.0                                      02.38
4E01TG 08047152179.10.5 5.10 1 24.0                                      01.24
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4E01TG 08047152179.10.5 5.10 1 24.0                                      01.80
4E01TG 08047152179.10.5 5.10 1 24.0                                      01.18
4E01TG 08047152179.10.5 5.10 1 24.0                                      01.13
4E01TG 15047111179.10.1 5.20 1 24.0                                      01.68
4E01TG 15047111179.10.1 5.20 1 24.0                                      01.20
4E01TG 15047111179.10.1 5.20 1 24.0                                      01.58
4E01TG 15047111179.10.1 5.20 1 24.0                                      01.48
4E01TG 15047111179.10.1 5.20 1 24.0                                      02.46
4E01TG 15047111179.10.1 5.20 1 24.0                                      01.53
4E01TG 15047112179.10.1 4.60 1 24.0                                      01.33
4E01TG 15047112179.10.1 4.60 1 24.0                                      01.26
4E01TG 15047112179.10.1 4.60 1 24.0                                      01.54
4E01TG 15047112179.10.1 4.60 1 24.0                                      01.44
4E01TG 15047112179.10.1 4.60 1 24.0                                      01.25
4E01TG 15047112179.10.1 4.60 1 24.0                                      02.03
4E01TG 15047151179.10.1 5.10 1 24.0                                      01.52
4E01TG 15047151179.10.1 5.10 1 24.0                                      01.86
4E01TG 15047151179.10.1 5.10 1 24.0                                      01.57
4E01TG 15047151179.10.1 5.10 1 24.0                                      01.28
4E01TG 15047151179.10.1 5.10 1 24.0                                      01.73
4E01TG 15047151179.10.1 5.10 1 24.0                                      01.34
4E01TG 15047152179.10.1 5.10 1 24.0                                      01.24
4E01TG 15047152179.10.1 5.10 1 24.0                                      01.40
4E01TG 15047152179.10.1 5.10 1 24.0                                      01.28
4E01TG 15047152179.10.1 5.10 1 24.0                                      01.26
4E01TG 15047152179.10.1 5.10 1 24.0                                      01.38
4E01TG 15047152179.10.1 5.10 1 24.0                                      01.70
```