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1975 PROGRESS REPORT
[FINAL]

DECOMPOSITION AND MINERALIZATION IN AN *ARTEMISIA TRIDENTATA* COMMUNITY IN NORTHERN NEVADA

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ABSTRACT

Surface stem and buried leaf, stem and root litter which were placed in the field in 1973 were recovered and weighed. For buried litter, the order of weight loss was leaf, stem, root. Buried stem samples lost more weight than surface stem samples. Leaf litter analyzed in the lab using a Gilson differential respirometer evolved different quantities of CO_2 according to the temperature and moisture combinations used. Wet, old leaf litter at 35 C evolved the most; young, dry leaf litter at 5 C the least. CO_2 evolution proceeded at small, steady rates under low temperaturres as well as under "dry" conditions. Mixed litter, representing the combination of litter types found in the field, generated rates of CO_2 evolution most often paralleling the rates for old litter. These lab rates reflect combinations of environmental conditions in the field which may be used to interpret decomposition in situ.

INTRODUCTION

The purpose of this project is to determine the rate of decomposition of big sagebrush (*Artemisia tridentata* Nutt.) litter under field and experimental conditions. Although big sagebrush is a dominant shrub in the western United States, little work has been done on the decomposition of its litter. Some work has been done in the field (Comanor and Prusso 1973, 1974; Mack 1971), but no attempt appears to have been made to further refine these rates in the laboratory.

In this last year of the project, emphasis was on the decomposition rate of big sagebrush organs (leaf, stem, root) under controlled laboratory conditions. Since the literature indicates a slow decomposition rate for buried litter, root and stem litter samples were buried in the field in 1973. These samples were recovered in 1974 and 1975. Stem litter placed on the soil surface in 1973 was also recovered in 1974 and 1975. The results from both these studies are presented in this report.

METHODS

Laboratory Studies

This work was done in the Rock Valley Validation Site laboratory at the Nevada Test Site, Mercury, Nevada. Fresh big sagebrush litter was taken from shrubs near Reno and Austin, Nevada. Older litter was obtained from mounds below sagebrush shrubs. The older litter was brown to black in color and whole to fragmented. Some rock, grass, stem and bark debris was unavoidably contained in samples of old litter. After laboratory drying, as much of this foreign material as possible was separated from the sagebrush leaf litter. In this paper, the fresh litter "harvested" from shrubs is termed "young" litter; the sorted leaf litter from below the shrubs is termed "old" litter. "Mixed" litter refers to an equal mixture of the two.

Air-dried 0.50-g samples of each litter type were wrapped in porous cloth and stored at room temperature in groups within large plastic bags. Samples for each time-course "run" were chosen at random from these collections. From three to eight samples of each litter type were analyzed at one time under the same laboratory conditions.

Samples were run in a Gilson differential respirometer. In this instrument CO_2 evolved is trapped in an alkali solution (1 cc of 10% KOH) in the reaction vessel sidearm. Oxygen uptake, in microliters, is determined manometrically, usually at 30-min intervals, for the duration of the run. Since oxygen uptake is considered equal to CO_2 evolution, we will refer to our results as "CO_2 evolution" in the text. Early work determined that 6-hr runs provided repeatable data. The data obtained were corrected to STP. In the Gilson the sample environment is closely controlled. Temperatures selected for the runs were 5, 15, 25 and 35 C.

Water potentials were more difficult to maintain. These were determined using a soil psychrometer and a Wescor HR-33T microvoltmeter. After the samples were placed into the reaction vessels, they were wet using a hypodermic needle filled to predetermined levels with distilled water. For the "wet" samples, 1 cc of distilled water was used. The resulting moisture potential was less than —0.1 bar (the detection limit of the psychrometer probe). The detection limit of the "dry" samples was —77 bars; all dry samples used were more negative than this potential. Intermediate water potentials were obtained by wetting the samples with a quantity of water (about 0.5 cc) between that used for wet and dry samples. The litter at these intermediate moisture potentials is termed "moist" in the text. The amounts used established a beginning moisture potential of between —29 and —40 bars. Final moisture potentials varied also, but as measured, were between —40 and —60 bars. Moisture potentials were determined on samples equivalent to those used in the reaction vessels. Moisture potential values for these samples were considered representative for the other samples of the same litter type analyzed. Litter moisture potentials were determined after equilibration before the start of each run. At the end of each run selected reaction vessels were checked for moisture potentials.

Later a second technique was employed. This used the Wescor C-52 sample chamber psychrometer and the dewpoint microvoltmeter. Here, extra leaf samples of each type were again replicated in a vessel. From this vessel about four leaves were taken and placed in the sample chamber. After a 30-min equilibration period water potentials for these leaves were determined. Final water potentials were determined in the same manner, using leaves from the Gilson sample vessels. The DSCODE for these data is A3UCH11.

Field Studies

Field studies were carried out at Plot 03 located 10 km north of Reno, Nevada, at 1530 m. Sagebrush covers 19% of the ground in the plot. Big sagebrush litter samples from this area were air-dried in the lab and sewn into nylon mesh bags; bag mesh size was 1 mm^2. Stem litter was placed in 1-dm^2 bags on litter mounds below shrubs, in sets of six. Litter for burial was placed into sections of a larger bag. Buried litter consisted of leaf, large root, small root, large stem, small stem and twig samples. Each of these samples weighed 2.00 g. Replicate samples were buried under shrub canopies at 5 and 10 cm. Additional details, as well as litter size class information, are available in the 1973 progress report (Comanor and Prusso 1974).

Samples, on recovery, were brought into the lab and air-dried. After removal from the mesh bags, extraneous material (chiefly soil particles in the case of buried samples) was removed from the samples. The litter was then weighed. The error estimate of this process is in the range of 5-10% (Comanor 1975).

The data for both surface and burial samples are on A3UCH01.

RESULTS

Laboratory Studies

Mean CO_2 evolution rates were compared at the end of each 6-hr run. With several exceptions, the CO_2 evolution for any litter type decreased with a change of moisture potential from wet, to moist, to dry (Table 1). For most of the exceptions the moist litter evolved less than the dry litter at the same temperature: 25 C (young); 15 C (mixed); and 5 C (old, mixed). In two of the moist litter runs the values were greater than those for the wet conditions (35 C, mixed; 25 C, stem). The trend is also for a decrease in CO_2 evolution for any litter type as the temperature decreases. Several exceptions occur, however. Stems have a greater rate of CO_2 evolution than roots. Young leaves evolve less CO_2 than either mixed or old leaves. Old leaf litter has higher rates than mixed leaf litter an equal number of times that the reverse holds true. No pattern of temperature or moisture control emerges. Old exceeds mixed in one-half the cases, regardless of moisture potential. Alternatively, old exceeds mixed at 35 and 5 C (Table 1). At 25 and 15 C the situation is reversed.

At any temperature the moisture potential is a controlling factor. This may be clearly seen for young leaf litter (Fig. 1). In most cases the wet leaf litter (the litter with a moisture potential not measurable above —0.1 bar) evolved more CO_2 than the moist litter (with moisture potentials between —30 and —60 bars), which evolved more CO_2 than dry litter (with a moisture potential less than —77 bars). CO_2 evolution decreased during the runs for the high (35 C) and average (25 C) temperatures for young litter at the moisture potentials used (Fig. 1). At 15 C, CO_2 evolution rates were essentially steady. Here the wet litter had a higher respiration rate than the dry litter at both the beginning and end of the runs. The highest values obtained for young, wet litter were at 35 C. The values at 25 C were lower, approaching the final values for the cooler (15 C) temperature.

Moisture is more important at the high temperatures. CO_2 evolution rates for wet, young litter decrease markedly from 35 to 25 C, but less so from 25 to 15 C. The CO_2 evolution for old, moist and old, dry litter follows the same patterns: decreasing rates occurring with decreasing temperatures (Fig. 2). The rates for old, wet litter are always greater than the rates for old, moist litter, while old, dry litter evolves the least.

Substrate age is also a controlling factor. At 35 and 25 C young, wet litter CO_2 evolution, although initially higher, ends up similar to that for old, dry litter (Fig. 3).

Mixed litter (equal amounts of young and old litter) has CO_2 evolution characteristics generally between those of young and old litter. This is clearly shown for the 35 C runs for the mixed, wet litter (Fig. 4). The mixed, moist litter at 35 C evolves more CO_2 than either the young or old, moist litter; its value is close to that for mixed, wet litter. At 25 C the mixed, moist litter CO_2 evolution is also close to that for mixed, wet litter at that temperature. The mixed, dry litter, on the other hand, is closest to the old, dry litter at 25 C. The mixed litter curves at 15 C resemble those of young and old litter in their generally flattened appearance. However, the values for the three moisture potentials are greater, respectively, than those for the same moisture potentials for either old or young litter.

Table 1. CO_2 evolution rates (means and ranges) for five different big sagebrush litter types at four temperature and three moisture potential combinations. Data were taken at the end of the 6-hr experimental period and are expressed as g CO_2 x 10^{-4}·g dry wt^{-1}·hr^{-1}. Ranges are in parentheses

Litter type	Temp. (°C)	N	Moisture potential[a] Wet	Moist	Dry
Young[b]	35	3[c]	(4.1- 4.6) 4.3	(1.7-4.2) 2.5	(0.3-1.4) 1.0
Old	"	4	(5.7-12.4) 9.9	(2.3-8.6) 6.1	(4.4-5.7) 4.9
Mixed	"	3[c]	(7.4-10.0) 6.2	(7.3-8.8) 7.8	(2.3-3.3) 2.7
Stem	"	3	(4.0- 6.9) 5.0	(0.7-1.7) 1.3	(t -0.3) 0.2
Root	"	3	(0.7- 1.4) 1.1	(0.1-1.0) 0.5	(t -0.2) 0.1
Young	25	3[c]	(2.9- 3.1) 2.6	(0.1-2.8) 1.1	(0.4-3.3) 1.2
Old	"	3[c]	(8.1- 9.2) 8.5	(3.3-7.1) 3.8	(3.4-4.6) 2.2
Mixed	"	4[c]	(4.4- 9.4) 5.9	(0.2-7.9) 4.5	(2.3-2.4) 2.3
Stem	"	3	(2.5- 3.6) 2.9	(2.5-6.9) 4.6	(2.3-7.4) 2.7
Root	"	4	(0.9- 1.6) 1.2	--	(0.1-0.3) 0.2
Young	15	3[c]	(2.3- 2.4) 2.3	(0.8-2.3) 1.4	(0.3-1.2) 0.4
Old	"	3	(1.7- 5.0) 3.5	(1.9-3.7) 2.8	(0.1-1.0) 0.5
Mixed	"	4	(4.6- 8.1) 5.7	(0.4-2.3) 1.2	(0.9-3.6) 1.9
Stem	"	3	(1.7- 4.8) 3.5	--	(0.1-2.5) 1.3
Root	"	3	(1.1- 1.8) 1.4	--	(0.5-0.7) 0.6
Young	5	3	(0.8- 1.3) 1.0	(0.7-1.2) 1.0	(0 -0.1) 0.1
Old	"	3	(2.2- 4.3) 3.2	(1.5-1.9) 1.7	(0.1-9.2) 3.1
Mixed	"	3	(1.8- 4.1) 3.3	(1.1-1.7) 1.1	(0.3-4.2) 1.6
Stem	"	3	(0.9- 1.8) 1.2	--	(0 - 0) 0
Root	"	3	(0.6- 1.0) 0.8	--	(t -0.7) 0.3

[a] See Methods Section for details of moisture measurement.
[b] Young, old and mixed are leaf litter.
[c] N is 6-9 for the moist samples.

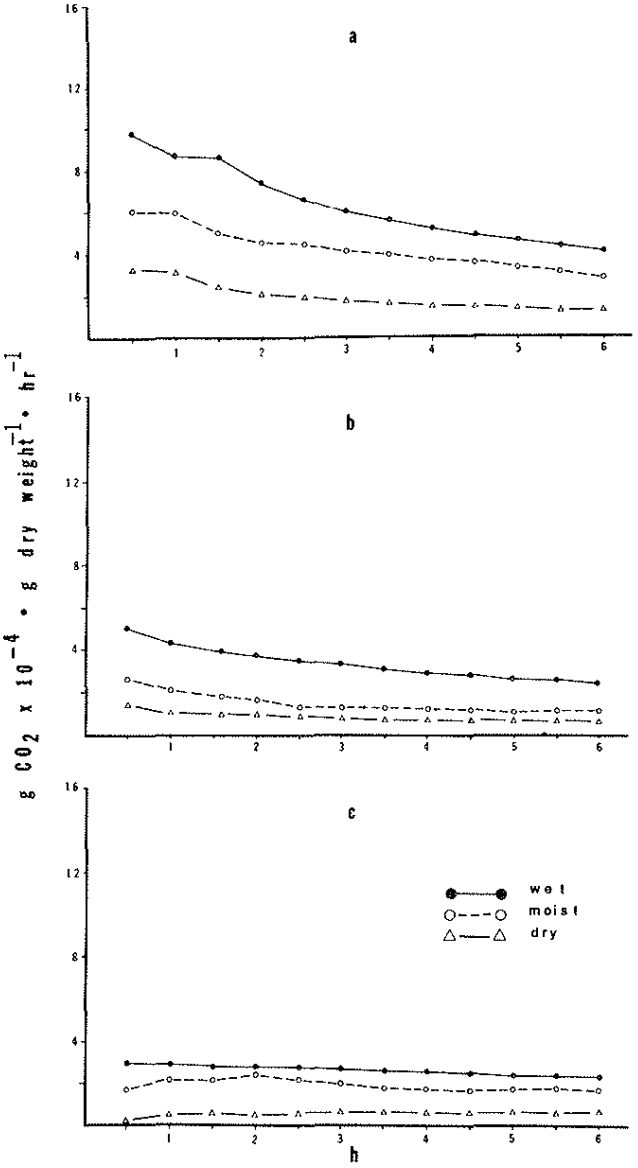

Figure 1. CO_2 evolution rates for young big sagebrush leaf litter at 35, 25 and 15 C and under wet, moist and dry moisture conditions.

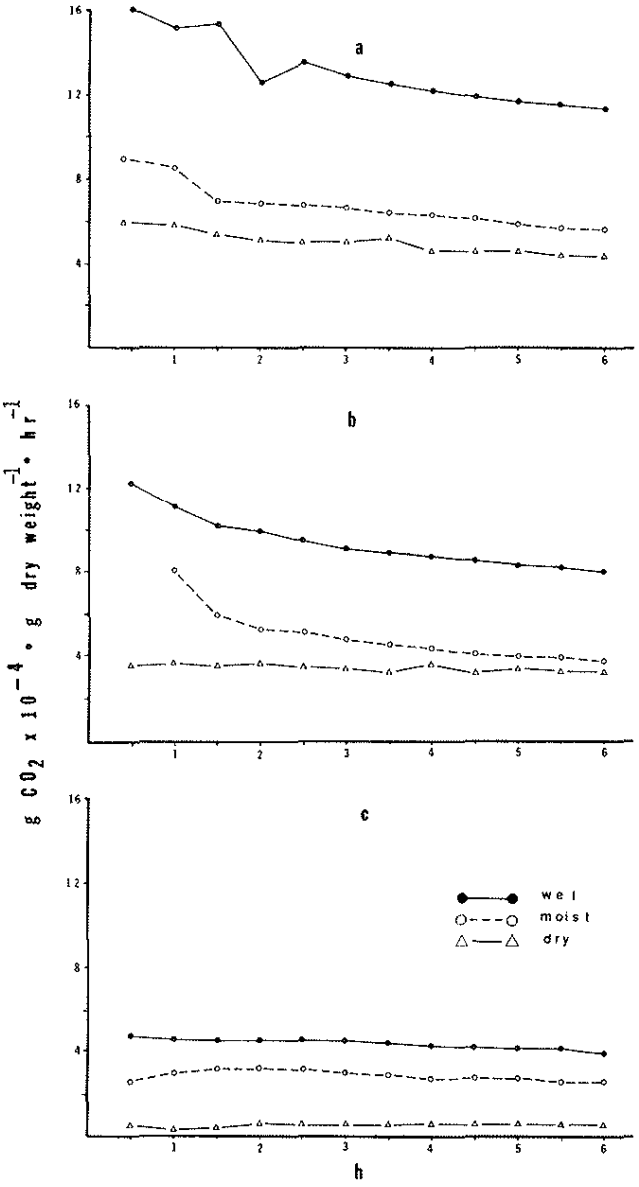

Figure 2. CO_2 evolution rates for old big sagebrush leaf litter at 35, 25 and 15 C and under wet, moist and dry moisture conditions.

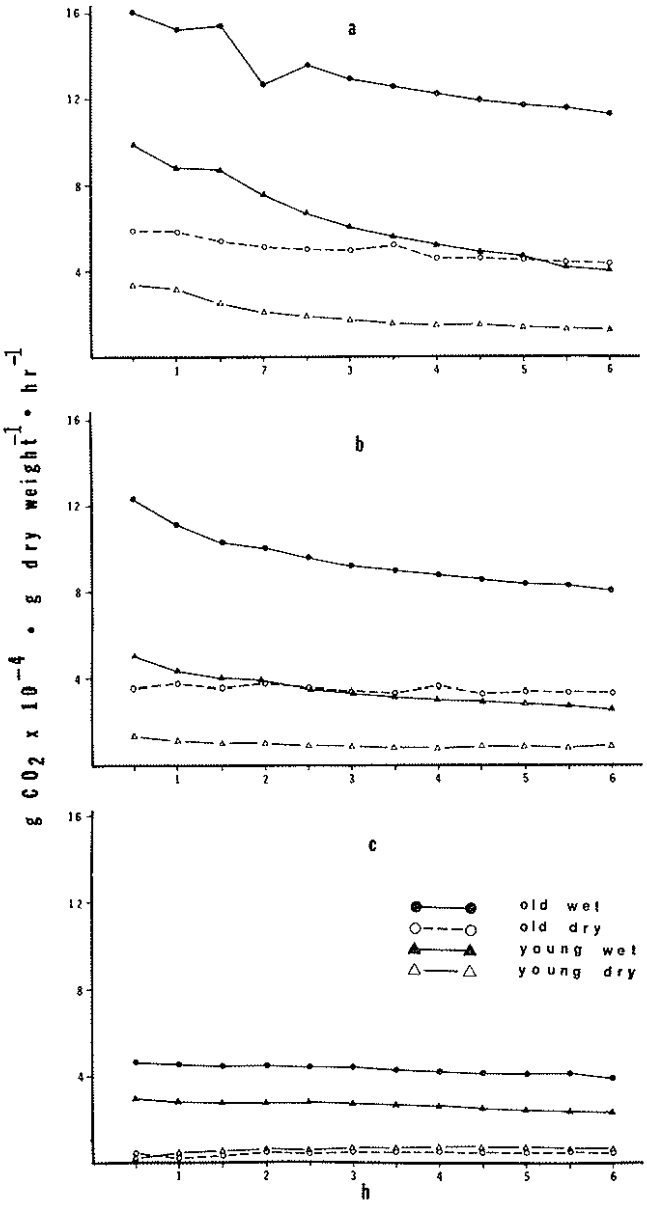

Figure 3. A comparison of old and young big sagebrush leaf litter under wet vs. dry conditions for temperatures of 35, 25 and 15 C.

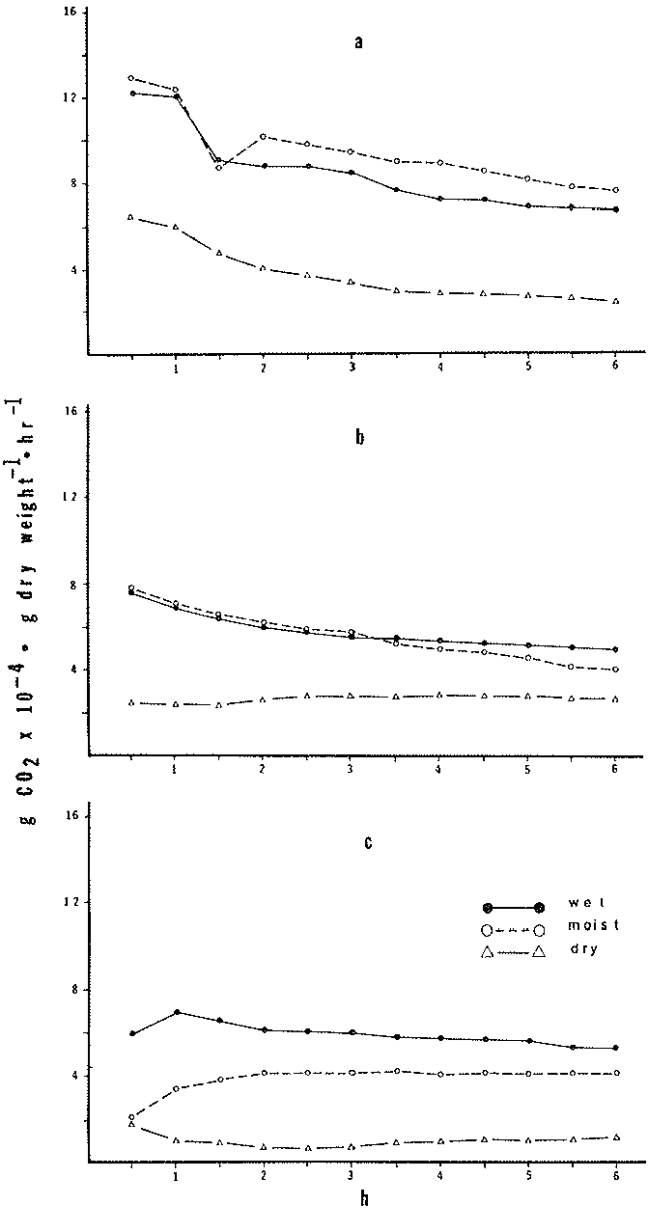

Figure 4. CO_2 evolution rates for mixed young and old big sagebrush leaf litter at 35, 25 and 15 C and under wet, moist and dry moisture conditions.

Statistical comparisons were made between pairs of experimental results at the ends of the 6-hr runs. In the old litter (Fig. 2), the differences between wet and dry moisture conditions at both 35 and 25 C are significant (t-test, unequal variances, $P<.05$). The same holds true for the young litter (Fig. 1) for these temperature-moisture combinations, although the differences are less. Many of the CO_2 evolution rates at the end of 6 hr are not significantly different from one another. No significant differences were found (using the t-test, as above) for the following combinations for old litter: 35 C, wet vs. moist, moist vs. dry; 25 C, moist vs. dry; 15 C, all comparisons. For young litter (Fig. 1) the 25 C, wet vs. moist, and moist vs. dry conditions were not significantly different. For the 15 C temperature for young litter, only the moist vs. dry moisture conditions were not significantly different.

The significance of the three experimental variables used was determined a three-way analysis-of-variance program on the university CDC-6400 computer. Temperature, moisture potential and age, as well as their interactions, were *each* found to significantly affect CO_2 evolution values ($P<.005$) (Table 2).

Field Studies

Stem litter placed in the field in October 1973 was recovered in January 1974, October 1974 and June 1975. The rate of weight loss shows an essentially linear relationship with time (Fig. 5). The coefficient of determination (r^2) is 0.995. The regression equation is

$$r = 2.575 + 0.4435x$$

If the rate of weight loss were projected out five years, the weight loss for surface stem litter would be approximately 30% of the original weight (Fig. 5).

Buried litter placed in the field in September 1973 was recovered in January 1974 and April 1975. Weight loss was greatest for the buried leaf litter samples (Table 3). After 20 months in the field, buried stem litter lost more weight than buried root litter. Increasing sizes of stems showed a decreasing weight loss for this period. Weight loss for small vs. large roots was in the same range of weight loss, however. Weight loss for certain litter types (stems and roots) was initially small. There appear to be very small differences in weight loss, which can be attributed to the 5-cm difference in burial depth. A three-way analysis of variance indicated that weight loss was significantly related to litter type ($P<.01$) and time in the field ($P<.05$), but not to the 5-cm vs. 10-cm burial depth used in this study.

DISCUSSION

CO_2 Evolution under Controlled Conditions

Initially it might seem that young litter (with its diversity of organic and inorganic compounds) should decompose more rapidly than older litter, which with time in the field, has lost its soluble and easily decomposible compounds. The results clearly show a more rapid rate of CO_2 evolution for older litter than younger litter (Fig. 3). For any combination of moisture and temperature conditions it appears that old litter will decompose more rapidly than young litter (Table 1). Three explanations seem plausible.

Table 2. Three-way analysis-of-variance results for CO_2 evolution of big sagebrush leaf litter in the laboratory under controlled conditions

Factors	*df*	*F*	
Temperature	2	105	***
Age	1	215	***
Moisture	2	107	***
Temperature x age	2	30	***
Temperature x moisture	4	5.58	***
Age x moisture	2	17.8	***
Temperature x age x moisture	4	5.14	***

First, the older litter is more broken-down (physically) than the young litter. This would make access into the leaf by fungal mycelia easier than if the leaf were intact. Further, the addition of more interstices among the leaves in the litter, as well as greater surface area/leaf biomass, should increase its water-holding capacity. Big sagebrush also is noted for the variety of its polyphenol compounds (Holbo and Mozingo 1965). These compounds could inhibit colonization of the leaf litter for some time. Decomposition would proceed only after leaching and/or breakdown of these compounds occurs through some means.

CO_2 evolution (and therefore decomposition) of the litter at 15 C shows essentially no change during the time-course of these runs, regardless of the moisture potential used (Figs. 1-4). These results would basically fit a model for zero-order kinetics. The patterns of CO_2 evolution, reflecting activity rates for the organisms active in the litter, represent a gradient of environmental response, from zero-order kinetics at the low (15 C) temperature to a first-order model for the 35 C temperatures. The response of the litter-inhabiting microorganisms at 15 C indicates the presence of cold-tolerant populations of decomposers in the litter. This suggests that decomposition occurs in the field during the winter months when temperatures are above freezing, even beneath a snow cover (Bleak 1970), and more so during periods of snow melt.

The rates of CO_2 evolution for mixed litter seem closer to the rates for old litter than for young litter (Table 1). It seems reasonable to assume that litter-inhabiting organisms from both litter types are present and active in such litter. The litter would represent a substrate utilized by two "groups" of decomposer organisms, with their preferences for different classes of compounds. However, since the total mass of either litter type is less than that for a comparative sample of "pure" old or young litter, the total rate of CO_2 evolution is limited, and is normally not much greater than the old litter, which is the more readily decomposible substrate of the two. This argument assumes a lack of competitive interaction due to the specialized nature of the microorganisms, as discussed.

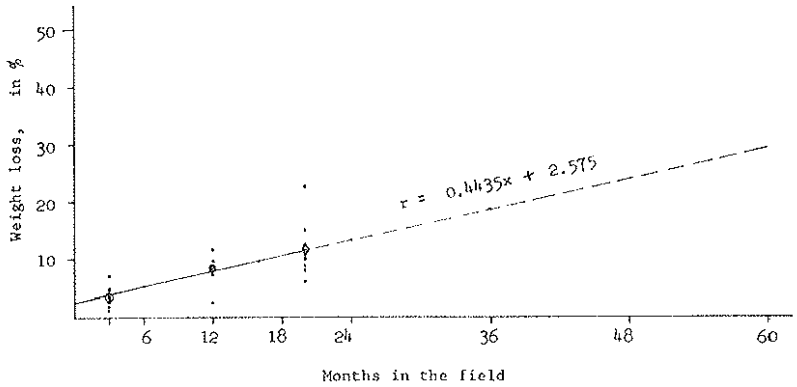

Figure 5. Percent weight loss of surface stem big sagebrush litter in the field during 1973-75.

It is interesting to note that sometimes the moist litter and the dry litter may be nearly identical at the end of the runs (i.e., 25 C; Figs. 1 and 2). Two factors are operative here. The first seems, very simply, to be a depletion of growth water by the active microorganisms. Second, the "dry" litter is never completely dry, as the experimental apparatus requires that it too be moistened. It is, however, drier than —77 bars; this moisture potential may be considered dry for all practical purposes.

Weight Loss for Litter in the Field

The weight loss for stem samples on the soil-litter surface below sagebrush shrub canopies was less than 10% in one year (Fig. 5). This is a much lower weight loss than for leaf litter under the same environmental conditions. For sagebrush leaf litter in the same plot area during an overlapping period of time the weight loss was approximately 25% (Comanor 1975). For an earlier year, in another plot, the weight loss for leaf litter was even greater (ca. 50%). Projecting the weight loss through time by the use of the linear regression equation developed, a 50% weight loss would not occur even after five years. This indicates that stem litter has a long residence time in the field, a fact obvious to observers in the Great Basin.

Rates of weight loss for buried litter were determined by litter type and time in the field. The large rates for leaf litter (Table 3) may be significant to the cycling of carbon and mineral elements in the big sagebrush community. In the shrub interspace soil cracks may develop and some leaf litter will enter these. Subsequent breakdown of this litter will add carbon to the soil in an area which is, quite often, lacking much plant cover. Breakdown rates for leaf litter under such circumstances will be less than those presented in Table 3, since the table rates were obtained below shrub canopies, where environmental conditions are more favorable to microbial activity throughout the year.

The weight loss for stem litter is greater under conditions of burial than on the surface. This may be attributed to the more constant and moist conditions obtaining within the soil. These results suggest that the breakdown of dead stems on the litter mound is enhanced as burial through soil and/or litter movement (cf. litter fall) occurs. Cycling of stem C into the soil from stem and leaf (as well as root) breakdown should proceed more rapidly beneath the shrub canopy, representing, in essence, a more-or-less closed (unitized) system.

Table 3. Percent weight loss of buried big sagebrush litter samples in the field. The six litter types were buried at 5 and 10 cm and recovered after 4 and 19 months

Litter type[a]	Depth (cm)	Weight loss (%; 4 months)[b]	Weight loss (%; 19 months)[b]
Leaves	5	32	46
	10	31	57
Large roots	5	0.2	19
	10	0.8	18
Small roots	5	3.5	12
	10	2	21.5
Large stems	5	0.3	25
	10	0	36
Small stems	5	7	35.5
	10	5	38
Twigs	5	14	44
	10	13	52

[a] See Comanor and Prusso (1974) for the description and size of the six litter types.
[b] Samples were buried on September 15, 1973, and recovered on January 17, 1974, and April 13, 1975.
The percent weight loss is based on an original weight of 2.00 g; air-dried.

Root weight loss is the least for the three plant organs considered. It must be pointed out here that no small roots were included in this analysis. Rootlets and small roots would be expected to have a greater rate of decomposition and turnover, perhaps exceeding stem material since they lack peridermis.

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