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THE EFFECT OF SOIL DRYING ON HUMUS DECOMPOSITION AND NITROGEN AVAILABILITY

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INTRODUCTION

Preliminary experiments with the macro-respirometer (Birch and Friend [3]) showed that when a soil was successively dried and rewetted decomposition after each rewetting followed a uniform pattern (see, for example, Figs. 1 and 2). Repetition of a similar pattern has since been found to occur under field conditions (Fig. 5) and this has important consequences on humus decomposition and nitrogen mineralisation. The effect of climate in relation to this pattern is discussed later.

One of the main problems in this work has been to explain why so little of the decomposable humus complex is decomposed after each rewetting since adverse physical (moisture, aeration) or chemical (toxic products) conditions appear not to be involved. It was tentatively concluded (Birch and Friend [3]) that successive dryings effected, on each occasion the release of small amounts of decomposable material from within the clay lattice where it was protected from microbial attack. Another possibility was that drying increased the amount of humus subsequently going into solution following which it was rapidly decomposed. More organic material can generally be extracted from a dry soil than a moist one and several workers (see Chase and Gray [6]) have ascribed the flush of decomposition that follows the wetting of a dry soil to this. From the experiments to be described it appears that these hypotheses are untenable. Humus decomposition is shown largely to involve direct microbial attack of the solid substrate, with repetition of the decomposition pattern depending on repetition of a similar

bacterial cycle, involving on each occasion a proportion only of the total utilisible substrate. Possible mechanisms to explain this behaviour are discussed.

EXPERIMENTAL

The macro-respirometer used in the following experiments has already been described (Birch and Friend [3]). Its sensitivity and simplicity of construction and operation render it particularly suitable for studying decomposition in soils for periods ranging from hours to months. Soils retain their mosture, and oxygen is automatically replaced as it is used up, the volume being simultaneously shown by a burette reading. About 20 minutes are required to record the daily rate of decompositions of 36 samples or treatments, and to reset the apparatus. The respirometer vessels were maintained at 25°C. The oven-dried soils were inoculated with 0.1 g fresh soil on rewetting but this appears to have little extra effect on subsequent decomposition compared with non-inoculation. Presumably the surviving population largely governs the subsequent course of decomposition.

Experiment 1. *The effect of air-drying and rewetting on decomposition*

Three 50-g samples of air-dry soil (6.2% C, 0.6% N) were brought to field capacity and put in the respirometer. After 10 days soils A and B were again air dried, rewetted and returned. The treatment was repeated twice more with A and once more with B after which B was oven dried for 24 hours at 100°C and rewetted. Soil C was used as a control to calculate the extra carbon mineralised after the 2nd, 3rd and 4th rewetting of A and B.

The pattern of decomposition (smoothed out) is shown in Fig. 1, and Table I summarises data not shown there.

TABLE I

Soil	Stage	Extra C mineralised mg/100 g air-dry soil	k
A	2	10.0	0.23
	3	10.0	0.24
	4	11.0	0.20
B	2	7.0	0.25
	3	11.0	0.26
	4	80.0	0.21

The k values were calculated from the equation $k = 1/t \log a/(a-x)$ where a is the gas uptake for the 5 day period after rewetting and x the uptake for t days (up to 5). For $t = 1, 2, 3$ and 4 the k values (averaged in Table I) for each flush of decomposition were reasonably constant indicating that the course of respiration followed a first-order reaction.

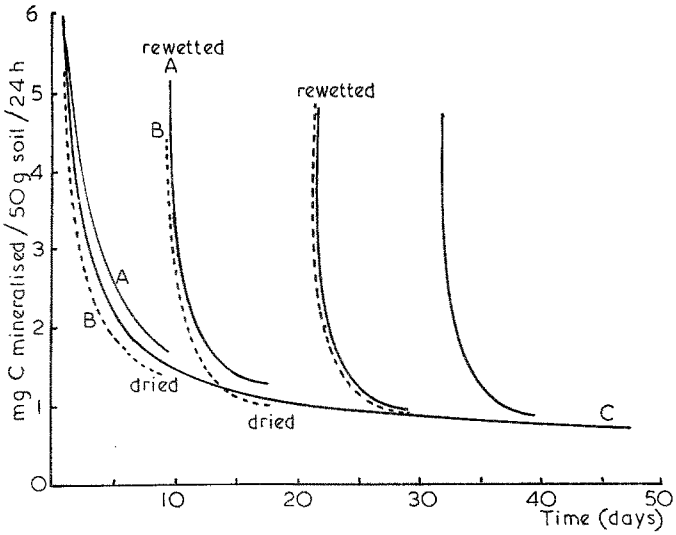

Fig. 1. The pattern of decomposition following each successive air-drying and rewetting of a soil.

The rapid decline in the rate of decomposition is not due to a shift in pH since this was found to be negligible. The development of toxic products could be responsible, but this appears unlikely (Expt. 11). Moreover washing the soil to remove possible soluble toxic compounds does nothing to enhance decomposition. When the course of decomposition follows a first-order reaction the concentration of substrate is often the limiting factor. Subsequent experiments show, however, that subtrate concentration, *i.e.* organic material in the soil solution is not involved. The rapid fall-off in the rate of decomposition could be due to adverse conditions in the respirometer. When, however, soil samples were taken from the respirometer exposed to the atmosphere and then returned there was no subsequent increase in the rate of decomposition. Moreover aeration and moisture conditions in the respirometer are virtually ideal.

Experiment 2. *To determine how often the drying and rewetting effect can be successively repeated.*

35 g of oven-dry soil (6.4% C, 0.7% N, pH 6.4) were brought to field capacity (15 ml water) and put in the respirometer. When the flush of decomposition was over the sample was again oven dried at 100°C for 48 hours and the procedure repeated. The results so far are shown (smoothed out) in Fig. 2. Oven-drying was employed because the magnitude of decomposition following this is greater than after air-drying (see Expt. 1) thus reducing the number of treatments required completely to exhaust the decomposable carbon reserve.

After the 43rd oven-drying and rewetting about 38 per cent of the total soil carbon has been oxidized, with a gradual decline, now levelling off, in the magnitude of each successive decomposition. The k values for each flush of decomposition (calculated as in Expt. 2) ranged in a random fashion from 0.22 to 0.27. The ratio of carbon to nitrogen mineralised during the first 18 treatments was 17.5 : 1. The magnitude of decomposition on rewetting was independent of the stage at which the previous drying took place (Fig. 2, points R and R'). This experiment is still proceeding to determine what proportion of the total soil carbon can be decomposed by this method.

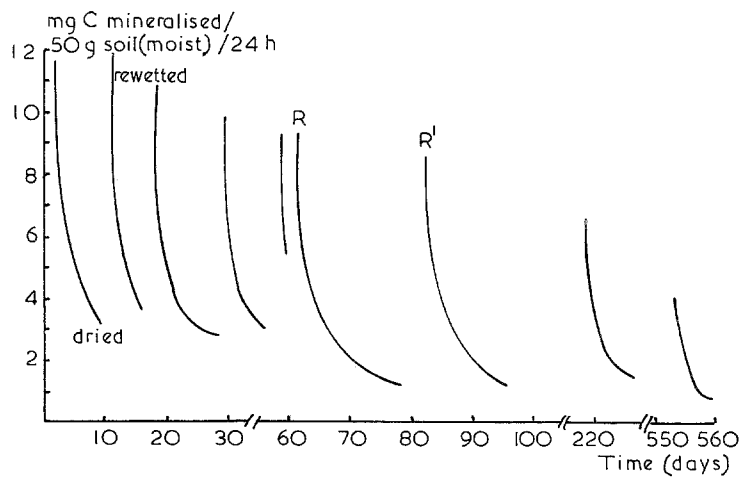

Fig. 2. The pattern of decomposition following successive oven-drying and rewetting (34 intermediate curves omitted).

In a parallel experiment using an acid soil (4.2% C, 0.24% N, pH 4.8) the magnitude of each successive flush of decomposition

fell off much more rapidly, and after the 12th treatment was very small. At this stage the carbon in the soil was reduced to 3.80 per cent indicating that only about 9.5 per cent of the original carbon was of a decomposable nature. The remainder must refer to undecomposable residues accumulated under acid conditions in the field. Microbial activity may also be reduced at the low pH but this did not affect decomposition after the first dryings and rewettings and it appears most probable that the residual material is inert to microbial attack.

Experiment 3. *To determine if successive oven-drying and rewettings, in the absence of intermediate decomposition, has a cumulative effect.*

40 g of oven-dry soil (A) were brought to field capacity and put in the respirometer. After 8 hours, and before decomposition began, the soil was removed and oven dried. This procedure was repeated twice more after which the soil was again oven dried, rewetted and allowed to decompose. A duplicate sample (B) was heated for periods equal to A (but without intermediate wetting) and then rewetted. Soil A therefore received four drying and rewetting treatments and Soil B one.

The magnitudes of decomposition for the six-day period after rewetting were A 54 mg C, B 53 mg C/100 g soil, a non-significant difference.

This experiment shows that the flush of decomposition following the wetting of a dry soil is not due to the effect of drying on the physical or chemical properties of the organic substrate, otherwise a cumulative effect would be expected. Drying affects the course of decomposition on rewetting rather than the decomposability of the substrate. This state of dryness is unaffected by previous dryness and rewettings and soils A and B start from the same state when allowed to decompose. Similarly with points R and R′ in Fig. 2 (Expt. 2). Here, however, R′ is slightly lower than R because of the slightly lower carbon content of the soil at this stage.

Experiment 4. *The effect of drying and rewetting on mineralisation of nitrogen.*

(a) Air-drying.

Three 40-g portions (B, C and D) of air-dry soil (7.7% C, 0.60% N) were brought to field capacity and put in the respirometer. After 10 days B was extracted for the determination of ammonia nitrogen and nitrate nitrogen

using a slight modification of Richardson's [17] method. Samples C and D were air dried at about 25°C for 2 days and returned to the respirometer. After 10 days C was extracted as for B, while D was again air dried, rewetted and returned to the respirometer. 10 days later this was extracted.

The results are given in Table II expressed on an air-dry basis.

TABLE II

Sample	No. of treatments	N in soil, ppm	
		NH_4–N	NO_3–N
A	0	30.0	182.0
B	1	10.0	202.0
C	2	10.0	222.0
D	3	10.0	244.9

Each air-drying gives, after rewetting an increment of about 20 ppm nitrate nitrogen. Assuming an acre 6″ of soil to weigh two million pounds this is equivalent to about 200 lb. of sulphate of ammonia per acre.

(b) Oven-drying.

This experiment was similar to the above, with oven-drying (100°C for 24 h) substituted for air-drying.

The results (Table III) are expressed on an air-dry basis, and the last column refers to the amounts of carbon and nitrogen mineralised during the breakdown period.

TABLE III

Sample	No. of treatments	N in soil, ppm		Ratio of C to N mineralised
		NO_3–N	NH_4–N	
A	0	167	29	
B	1	151	202	9.4
C	2	161	343	8.3
D	3	161	428	14.1

C : N ratios ranging from 10 to 20 have frequently been obtained with other soils for carbon and nitrogen mineralised during the active decomposition period following air- and oven-drying. Oven-drying greatly enhances nitrogen mineralisation on rewetting compared with air-drying.

Experiment 5. *The effect of different bases on humus solubility and decomposition.*

100-g portions of soil (6.5% C, 0.6% N, B.E.C. 30 me/100 g soil) were converted to the Ca, Mg, K and Na soils by shaking with 250 ml of *N* $CaCl_2$, $MgCl_2$ *etc.* The soils were then filtered under suction, washed with 200 ml of water and air dried for 48 hours. 30-g samples of each were then treated with 10 ml water and 1 g of fresh soil (as an inoculum) and put in the respirometer. Separate 10-g samples were extracted with 40 ml of water, and total nitrogen and mineral nitrogen were determined on the filtrates. Duplicate 30-g and 10-g samples were dried at 100°C for 24 hours and then treated as above except that 12 ml of water were added prior to putting them in the respirometer. After 16 days in the respirometer the samples were removed and again air dried (7 days at 25°C), or oven dried (24 hours at 100°C). The soils were then rewetted as before and put in the respirometer for 10 days. The results are summarised in Table IV. Organic nitrogen refers to total nitrogen (Kjeldahl's method) minus mineral nitrogen (direct distillation of extract with magnesium oxide) per 10 ml of extract. Milligrams C decomposed (1) is for 30 g soil after the 1st wetting and 16 days incubation and (2) after the 2nd rewetting and 10 days incubation.

TABLE IV

Group	Air-dry				Oven-dry			
Base	Ca	Mg	K	Na	Ca	Mg	K	Na
pH	6.30	6.30	6.60	7.09	6.29	6.33	6.77	6.91
mg soluble org. N	0.15	0.12	0.26	0.44	0.21	0.20	0.40	0.43
mg C decomposed (1)	34.3	40.7	38.6	35.9	46.1	56.8-	44.5	48.2
mg C decomposed (2)	15.6	15.4	15.1	17.2	30.5	40.2	31.5	33.6

These results show that while more organic material can be extracted from an oven-dry than an air-dry soil this is not related to the greater decomposition that occurs after oven-drying. Thus, between groups, the oven-dry Ca and Mg soils have less than half the amount of soluble organic material as in the air-dry Na soil but their magnitudes of decomposition are much greater. Moreover within each group the range of solubilities is wide but the magnitudes of decomposition are fairly uniform. Since the organic-matter content of the soils is also uniform, being little affected by the different treatments it appears that the organic matter itself is decomposed and that preliminary solution in water is not involved. The decomposition differences within groups could be due to the effect of the bases on the physical condition of the soil and therefore the accessibility of the organic matter. The decomposition

differences between groups, which is not due to solubility or total organic matter, could be due to the improved physical conditions of the soil after oven-drying or to the effect of oven-drying on subsequent microbial activity.

Experiment 6. *The decomposition of aqueous soil extract.*

100 g of oven-dry soil (as in Expt. 2) were shaken with 200 ml of water and filtered. The filtrate contained 1.50 mg organic N per 100 ml. Half the filtrate was evaporated to quarter the volume. Separate 30-g portions of another soil (2.4% C, pH 6.4), air-dry, were then treated as follows: – A, 10 ml water; B, 10 ml soil extract; C, 10 ml concentrated soil extract, and then put in the respirometer. These volumes brought the soil to field capacity. As a control 10 ml of extract were added to 100 g medium-grade sand plus 0.1 g soil as an inoculum.

The magnitudes of decomposition for the 6-day period after wetting were A 4.7 mg C, B 5.2 mg C, C 5.5 mg C per 30 g soil. Decomposition in the sand was negligible.

It is evident that the flush of decomposition following the wetting of the dry soil in Expt. 2 is not due to the solution of organic material. If this were so B or C above should differ from A by over 20 mg. The extract itself, as shown by its behaviour in sand, appears to be too dilute for microbial activity. The relative uniformity of the values for A, B and C support Expt. 5 and indicate that the humus fraction itself is attacked.

Experiment 7. *The relationship between decomposition and the percent carbon in the soil.*

(a) Different soils. Fig. 3 shows the relationship, which is highly significant, between the mg C decomposed/100 g soil (Y) (for the four-day period following the wetting of the oven-dry soil) and the percent carbon in the soil (X) The equation relating the two is

$$Y = 4.3\,X + 1.15$$

There is one obviously discrepant soil which has not been included in calculating this equation. This is similar to the acid soil cited in the second part of Expt. 2 and contains a high proportion of undecomposable carbon. Otherwise these results are in general agreement with those of Bunt and Rovira [5] who found that the

amount of readily decomposable material was generally proportional to the total organic matter content of the soil.

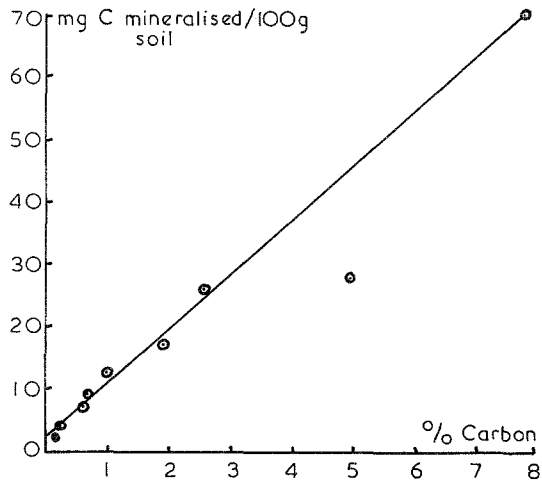

Fig. 3. The relationship between % C in the soil and the amount mineralised during the 4-day period after rewetting.

(b) Same soil. This soil has received various F.Y.M. additions over the last 26 years resulting in a range of values for percent C. Air-dry samples of the soils were brought to field capacity and put in the respirometer for 6 days. The resulting magnitudes of decomposition following very closely the percent C in the soil, are shown in Table V.

TABLE V

% *C*	mg C decomposed/100 g soil
0.920	8.00
0.962	8.29
1.196	13.93
1.214	14.54
1.410	19.03

The equation relating the two sets of values is highly significant.

$$Y \text{ (mg C decomposed)} = 23.1\ X \text{ (\% C)} - 13.6$$

The steeper slope of this regression line, compared with that for different soils, is probably due to the greater decomposibility of the humus derived from recently added F.Y.M.

Experiment 8. *The effect of wetting in two stages compared with one.*

35-g portions of oven-dry soil (similar to that in Expt. 2) were brought to 2.9, 5.7, 8.6, 11.4, 14.3, 17.1, 21.4, 25.7, 30.0 and 34.3 per cent moisture (field capacity) and put in the respirometer for 5 days. All the soils (except the last) were then brought at once to field capacity and returned to the respirometer for a further 5 days.

The patterns of decomposition are shown in Fig. 4, (with omissions to avoid overcrowding), while the magnitudes of decomposition for each of the two stages are given in Table VI.

TABLE VI

Moisture content, %	2.9	5.7	8.6	11.4	14.3	17.1	21.4	25.7	30.0	34.3
mg C decomposed (Stage 1)	1.8	2.4	3.0	4.2	9.0	14.4	21.0	24.6	27.0	33.6
mg C decomposed (Stage 2)	33.0	33.0	33.6	33.0	26.4	22.2	18.0	10.2	12.6	11.4
mg C decomposed (total)	34.8	35.4	36.6	37.2	35.4	36.6	37.0	34.8	39.6	45.0

It will be noted that the total magnitudes of decompositions are almost the same in all instances. The sample wetted in one stage to field capacity is a little higher than the others, but the trend of the graphs in Fig. 4 indicates that this superiority would be lessened had the samples been kept longer in the respirometer after the second stage wetting.

In this experiment decomposition during Stage 1 is directly proportional to the moisture content above 14.3 per cent, while decomposition up to 11.4 per cent moisture is small. It appears that only above a critical moisture content (in this instance about 11 per cent) is water available for microbial activity. The proportionality that then exists between decomposition and moisture content may reflect the ability of increasing moisture contents to support an increasingly large microbial population. When the soil is brought from sub-optimal moisture conditions (Stage 1) to optimal conditions (Stage 2) the restriction on the maximum population possible no longer obtains and the deficit in decomposition is then made good. It is likely that under field conditions (Expt. 10) the flush of decomposition at the start of the rains will be of the same

magnitude whether the soil is brought at once to field capacity or whether this is achieved somewhat gradually.

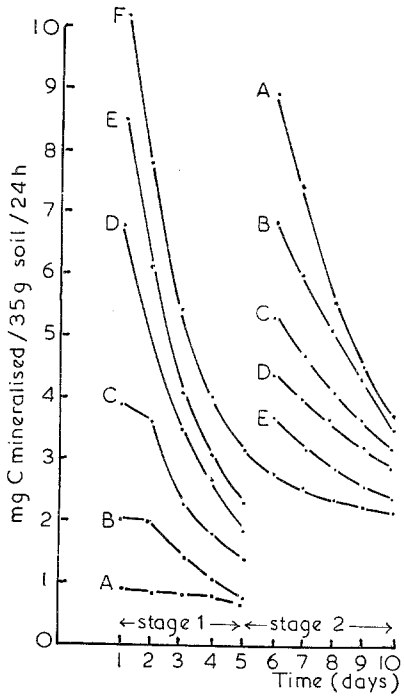

Fig. 4. The pattern of decomposition following two-stage wetting. Soil F at field capacity (34.3% moisture) throughout. Soils A, B, C, D, and E, stage 1, contained 11.4, 14.3, 17.1, 21.4 and 25.7% moisture; on the fifth day they were brought to field capacity.

Experiment 9. *The decomposition of leaf in subsoils and sand, and the subsequent effect of drying and rewetting.*

Two subsoils were selected with the following characteristics.

Soil	Depth	%N	%C	% Clay	me/100 g soil		pH
					T.E.B.	B.E.C.	
10612	22–39″	0.040	0.11	54.4	17.6	23.3	5.8
11612	10–23″	0.064	0.48	32.0	4.8	9.2	5.7

25 g were mixed with 50 g of medium-grade, acid-washed sand, brought to field capacity and treated with 0.4 g of powdered cotton leaf (40.0% C, 4.0% N). 75 g of sand alone (S) were similarly treated, and the samples put in the respirometer.

Rapid decomposition occurred in each instance, falling to a slow and almost steady rate after about 10 days. A further 0.4 g of leaf was then added, with similar results. Altogether five additions were made in this way. After each of these similar patterns of decomposition occurred, the magnitude however increasing with successive additions. This is shown in Table VII, where mg C decomposed refers to the 9 day period following the addition of 0.4 g leaf (160 mg C). Table VII shows also the overall decomposition after the 5 additions of leaf.

TABLE VII

Sample	mg C mineralised after additions						mg C added + mg C in sample	Decomposed %
	1	2	3	4	5	Total		
10612	40.9	67.2	75.4	85.9	98.2	367.6	828	44.4
11612	60.3	71.0	75.4	94.6	101.9	403.2	920	43.8
Sand	68.0	73.8	70.6	75.4	90.2	378.0	800	47.3

There is little to choose between the decomposition occurring in the different media.

The samples were then air dried at 20–25°C for 18 days after which they were restored to field capacity and put in the respirometer. The familiar flush of decomposition occurred in all instances. When this was over the samples were dried at 100°C, with similar results on rewetting, and these occurred again after a further oven-drying and rewetting. This experiment is still proceeding. The results so far given are in Table VIII and refer to the mg C mineralised during the first 6 days after rewetting. The corresponding k values are also given. Treatments 1, 2, 3 refer to the first, second and third drying and rewettings.

TABLE VIII

Sample	mg C mineralised after treatments			k values after treatments		
	1	2	3	1	2	3
10612	25.0	18.6	13.2	0.18	0.17	0.23
11612	24.4	14.4	13.2	0.21	0.17	0.22
Sand	15.0	18.6	12.0	0.20	0.22	0.21

The magnitude of the drying effect decreases following successive treatments which indicates a decline in the amount of material

involved. The k values, however, remain fairly constant and are similar to those reported in previous experiments for decomposition following the wetting of a dry soil. The uniformity of behaviour with both sands and soils indicates that the drying effect is little affected by the medium in which the organic matter is present.

Experiment 10. *To determine the seasonal course of decomposition in the field.*

The macro-respirometer is very suitable for measuring the magnitude of decomposition occurring in the field at any particular time. Thus, a soil put in the respirometer immediately after sampling will remain under conditions similar to those in the field with regard to the microbial population and moisture, particularly during the early period in the respirometer. The main difference between respirometer and the field conditions is that of temperature which, in the respirometer, remains steady at 25°C. In comparative studies, however, as in the present experiment, this is of minor importance.

A plot of fallow virgin land, which had recently been under wattle and a subsequent volunteer growth of grass was selected. It contained 0.66% N and 6.0% C. Immediately after sampling the soil was passed through a 2-mm sieve and 50 g placed in the respirometer. A duplicate sample was used for moisture determination. The magnitude of decomposition was then followed in the respirometer and the average daily oxygen uptake for the first two days (expressed as mg C in Fig. 5) was taken as a comparative measure of the rate of decomposition occurring in the field at the time of sampling.

Sampling started at the beginning of a wet season and continued at intervals of a few days throughout a series of alternate wet and dry periods. The results are shown in Fig. 5, and refer to soils containing 30 per cent moisture in the field at the time of sampling, thus putting the data on a comparable basis since the magnitude of decomposition also varies with the moisture content of the soil.

The main feature of interest is the marked decrease in the rate of decomposition in the field as the wet season continues, and the recovery in the rate of decomposition when rain falls again after a dry period. This conforms with the behaviour of soils on wetting and drying under laboratory conditions and reveals an interesting and important pattern of decomposition under natural conditions.

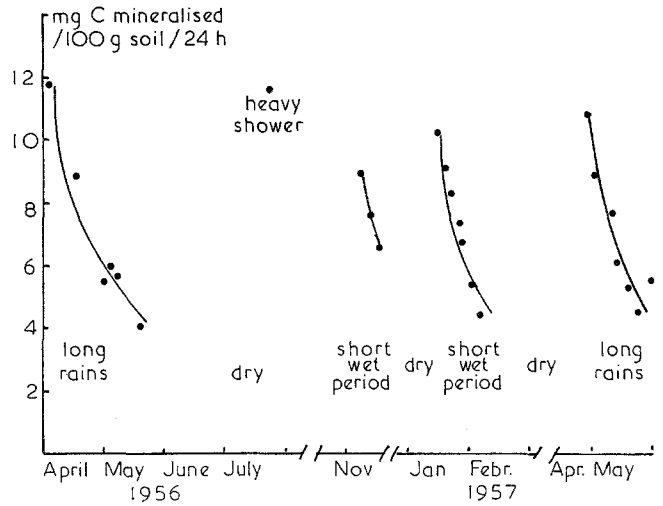

Fig. 5. The seasonal pattern of decomposition in the field.

Experiment 11. *To test for the development of toxic conditions during decomposition.*

Three 35-g portions A, B and C of oven-dry soil (as in Expt. 2) were each brought to field capacity with 15 ml water and put in the respirometer. After 6 days, when the flush of decomposition was over, a further 10 g of soil were brought to field capacity and added to A, and 20 g, similarly treated to B, Sample C received no additional treatment and served as a control. The soils were then kept for a further 6 days in the respirometer.

The results are summarised in Table IX.

TABLE IX

Sample	mg C decomposed			
	1st 6 days	2nd 6 days	2nd 6 days minus control	Column 4 calculated to 35 g
A	26.3	18.0	8.0	28.0
B	26.8	27.0	17.0	29.8
C	26.0	10.0	0	

It is seen from a comparison of columns 2 and 5 that the magnitude of decomposition that follows the wetting of a dry soil is not affected by the presence of soil in which decomposition has already occurred. The pattern of decomposition was also unaffected. Evi-

dently decomposition is not accompanied either by development of toxic conditions or of a microbial population inimical to those active during the early period after rewetting, otherwise the values for column 5 should be less than those for column 2. The effect of drying or subsequent decomposition cannot then be ascribed to destruction of toxic conditions or the elimination of one group of micro-organisms that competes with another.

DISCUSSION

This paper deals mainly with the decomposition of humus rather than of macro organic matter (leaf litter *etc.*). Since humus accounts for by far the largest proportion of soil carbon and nitrogen its decomposition behaviour is of particular importance. One of the main factors governing decomposition is the drying and wetting cycle of the soil the frequency and effectiveness of which is determined by climate and various agricultural practices. Some aspects of this cycle will now be discussed in relation to (a) nitrogen availability, (b) humus decomposition and (c) the mechanism involved.

a. Nitrogen availability. Under both laboratory and field conditions when a dry soil is moistened a characteristic pattern of decomposition occurs, as in Figs. 1 and 2. The magnitude of decomposition largely depends on the percent carbon in the soil and the conditions (hot or cold) under which the soil is dried. Decomposition is accompanied by nitrogen mineralisation (Expt. 4). Winsor and Pollard [18] also found that air-drying soils generally increased the amount of carbon and nitrogen subsequently mineralised, and various reports in the literature confirm this.

Maximum nitrate production will, then, occur at the start of the rains particularly in tropical soils subject to well defined wet and dry seasons. Once this initial flush of decomposition is over a period of slow decomposition and nitrogen mineralisation sets in. Early planting, an empirical procedure widely used by the peasant cultivator in East Africa, aims at having the crop planted when the rains begin. This practice, which has much to commend it, ensures that the crop gets part at least of the nitrate produced during the flush of decomposition that then occurs. Some of the nitrate is subsequently leached away and will not be available to

crops planted later in the rainy season, which usually make poorer growth although moisture is adequate.

This pattern of nitrogen mineralisation has an obvious bearing on soil-fertility studies and emphasises the dynamic aspect of nitrate supply. This is greater at the start of the rains than later on and, with some soils, may shift from an adequate to an inadequate level. Conventional methods for determining available soil nitrogen take no account of this decline. In addition to a changing rate of supply during a wet period there will be seasonal differences, depending on rainfall, in the amount of nitrogen mineralised in a given soil. Low rainfall which is generally more intermittant than high rainfall will be associated with a greater frequency of the drying and wetting cycle and therefore with greater nitrate production. In this connection nitrogen responses in East Africa, where these occur, are more common in wet than dry years. Similarly Glover [9] has reported that maize yields decline as seasonal rainfall increases above about 30 inches a year. Further, any circumstances that affect the intensity or prolongation of soil drying prior to the main rains, such as dry-seasons rains, will affect the amount of nitrate then produced. Rainfall is therefore an important factor to consider in soil-fertility studies and in the interpretation of the results of nitrogen-fertiliser trials. An appreciation of the pattern of nitrate production may also be of value in irrigation where, to some extent, the drying and wetting cycle can be controlled.

Any practice that intensifies soil drying should lead to more nitrate production when the rains begin. The beneficial effect of soil burning is related to this, and Experiment 2 shows that each of several successive burns should be effective. Analyses here have shown that burning has very little direct effect on humus destruction so that loss of humus due to burning depends largely on the increased decomposition that follows when burned soils are wetted. Since this is usually small in relation to the total humus reserve successive burnings should be effective over many years provided that physical deterioration of the soil and surface erosion do not set in.

The fact that humus can undergo marked decomposition for only a relatively short period (Expts. 1 and 10) in spite of its inherent decomposability helps to explain the persistence of nitrogen in the soil. The general lack of response to nitrogen in the

wheat-growing areas of Kenya is referable to this and Cornish [7] has reported similar behaviour for the stoney and mallee soils of the South Australian wheat belt. These observations agree with the pattern of decomposition already described in which the amount of material decomposed in any one cycle is generally small in comparison with the total amount present, but significant as regards the amount of nitrogen mineralised. The prolonged breakdown of this fraction compared with the rapid decomposition of the organic matter (leaf residues *etc.*) from which it is derived may partly account for the residual responses to organic manures obtained on the sandy tropical soils at Ukiriguru, Tanganyika. (Peat and Brown [14]).

The importance of drying on soil fertility has been reported, among others, by Lebedjantzev [12]. It appears from present studies that nitrogen mineralisation following the wetting of a dry soil is one of the main factors involved. Mineralisation of organic phosphorus can also occur but probably to a much smaller extent and in this instance fixation by the soil can also take place. The amounts of bases and trace elements (*e.g.* manganese) that go into solution are also affected by drying. Here the effect is due to physical rather than biological changes in the soil, but it serves to emphasise the dynamic aspect of soil fertility already mentioned, where conditions at the start of the rains, with regard to nutrient supply, are very different to those obtaining later in the wet season.

b. Humus decomposition. Expt. 10 shows that under field conditions a relatively high rate of decomposition occurs when a dry soil is wetted falling later to a slower and more constant rate as moist conditions continue. This pattern is repetitive and the frequency with which it occurs will be an important factor in the rundown of soil carbon. Since low rainfall, as pointed out earlier is usually associated with a greater frequency of wet and dry periods than high rainfall it should, above a certain lower limit, be conducive to an accelerated loss of soil carbon. A fairly general and direct relationship should therefore obtain between rainfall and the carbon, or total nitrogen, content of soils. In this connection Birch and Friend [4] found that the regression equations for total nitrogen on rainfall were remarkably alike for East African and North American (Middle West) soils. Another example is the similarity between the total nitrogen and humidity factor relationship found by Jenny [10]

for North America, and Prescott [16] for Australia. No doubt these relationships also involve the direct effect of rainfall on vegetative growth and subsequent humus production, but their marked similarity in spite of different temperature and vegetation conditions indicates the operation also of a common factor, the wetting and drying cycle, on humus decomposition.

Any agricultural practice that enhances soil drying such as burning, exposure by ploughing, wide spaces, intertilled cropping or bare fallowing should hasten the loss of soil carbon and numerous reports confirm this (see, for example, Mann and Barnes [13]). On the other hand crops affording shade will tend to conserve carbon. The high carbon level of constantly moist soils may also be due, partly, to the absence of the wetting and drying cycle. Anaerobic conditions cannot always be held reponsible for provided the soils are not waterlogged aerobic decomposition can occur, as pointed out by Allison *et al.* [1].

In addition to the pattern of decomposition mentioned above a third stage may be recognised under field conditions, namely the almost complete absence of decomposition under dry conditions when microbial activity is virtually negligible. The cycle of decomposition where wet and dry seasons prevail is therefore the simple one shown in Fig. 5 where relatively rapid decomposition (Stage 1) is succeeded by slower decomposition (Stage 2) under wet conditions and by virtually no decomposition (Stage 3) when dry conditions are restored.

c. The mechanism involved. The uniform pattern of decomposition following each successive drying and rewetting also occurs in a sand medium (Expt. 9). In other experiments not reported in the text it has also been found to occur with plant material alone and with commercial dried yeast (which usually contains added organic substrate). The presence of soil is therefore not essential to the drying effect, nor is the rapid decline in the rate of decomposition after rewetting necessarily due to physical changes in the soil (*e.g.* swelling of the colloids with alteration of the pore space) or inactivation of enzymes by adsorption. Since solubility of humus is also not involved (Expt. 5) the problem is more or less restricted to the effect of drying, or heating, on microbial behaviour.

Spores are resistant to adverse conditions such as drying and heating and their subsequent germination and multiplication after

each successive drying and rewetting should follow a fairly uniform pattern. A prominent feature of the early phase of a bacterial culture (*i.e.* the phase of physiological youth) is high metabolic activity which is very much greater than that of later generations developing after the period of maximum multiplication. This activity is characterised by high oxygen uptake and carbon-dioxide and ammonia production. Enzyme activity, an important factor in the breakdown of solid substrate, is also at a maximum during the early stages of growth as shown by Wooldridge and Glass [19]. The high initial rate of decomposition could, then, be due to the high metabolic activity associated with physiological youth, this activity declining as the culture ages and passes into the resting stage. A sequence of this behaviour would be expected each time a soil is dried and rewetted, for with the amount of substrate a more or less constant factor (though gradually declining) one has, on each occassion, a repetition under virtually uniform conditions of a bacterial cycle involving similar micro-organisms, namely those that survive the drying or heating treatments. With a given soil the magnitude of each successive flush of decomposition will decline as the organic reserve diminishes. With different soils the magnitude will depend largely on percent carbon (Expt. 7). Provided each drying leaves spores for germination and multiplication on rewetting the magnitude of decomposition should be independent of the number of times the soil is wetted and dried without intermediate decomposition (Expt. 3) and of the stage at which the soil is dried during the preceding flush of decomposition (Expt. 2) though here the carbon lost during the preceding flush will slightly reduce the magnitude of that following.

The rapid decline in the rate of decomposition after each rewetting cannot be explained by substrate exhaustion, since substrate is present in an amount considerably in excess of that required for a single flush of decomposition. It also appears improbable, from what has been said in Expt. 1, that the development of toxic conditions in the medium is responsible. Porter [15] states that the reasons for the slowing-down process in a bacterial culture are not well understood at present and factors other than mere exhaustion of the food supply and the accumulation of toxic metabolic products appear to be involved. Bail [2] has suggested that the crowding of the bacteria in a culture may cause the cessation of growth, there being

a maximum level of population that the medium can support. Such conditions could conceivably be reached in the limited volume of soil solution available for the bacteria. Bail considered that bacteria destroyed by heat do not consume the available biological space, thus permitting the recurrence he observed of the bacterial culture cycle in the same medium after heating, a behaviour similar to that after oven-drying and rewetting a soil.,

A further possibility is that the rapid decline in the rate of decomposition is due to the fact that micro-organisms active in the decomposition of substrate just after wetting have soon to compete with later-developing less active ones. This would infer the presence of several resistant species which, on rewetting interact on each occassion in a remarkably uniform manner (Expt. 2) conforming approximately to a first-order reaction. Evidence for such behaviour is contra-indicated by Expt. 11 which shows that the population present when the flush of decomposition is over does nothing to interfere with the normal pattern of decomposition of an oven-dried soil when this is introduced. Chase and Gray [6] found that when a dry soil was rewetted respiratory activity conformed to two superimposed first-order reactions. From this they concluded that after a dried soil has been remoistened there is present in addition to the more slowly decomposable humus complex a limited supply of readily available water-soluble organic matter and that this is responsible for the initial flush of decomposition on rewetting. It is however doubtful from Expts. 5 and 6 if water-soluble material plays a significant rate in this respect. The decline in the rate of decomposition appears, in the present work to be due to a decline in microbial activity. It is not possible to state the reasons for this decline, but it may be relevant that the logarithmic death phase in a bacterial culture also conforms to a first-order reaction, as does the decline in the rate of decomposition as shown by the k values in Expt. 2. The period over which these were calculated may, however, include part of a succeeding phase which would account for the fact that the first-order equation is not exactly followed

It has frequently been observed in these studies that prolonged air-drying results in greater decomposition on rewetting than short air-drying although the precentage loss of water is almost the same. Also vacuum-drying for five days over phosphorus pentoxide was hardly more effective than air-drying over the same period

in spite of the greater dehydration of the soil. Vacuum-drying and oven-drying were almost the same as regards moisture losses, but oven-drying resulted in a much greater magnitude of decomposition on rewetting and was as effective at 60°C as at 100°C. Since drying does not affect the inherent decomposibility of humus (Expt. 3) the drying effect must be due primarily to microbial changes. Curran and Evans [8] postulate that following heat shock spores are stimulated to intense metabolic activity, which could partly explain the marked decomposition that follows oven-drying. The enhanced effect of prolonged over short air-drying is difficult to explain. It is apparently not due to the increasing elimination of a competing microflora as the soil dries out since, without drying, this has no effect on the decomposition of added soil (Expt. 11). It is conceivable that prolonged drying progressively affects the physical conditions of the soil (shrinking of colloids *etc.*) leading to a greater exposure of organic surface for subsequent microbial attack. In this case vacuum-drying would be expected to have effects of similar magnitude, but this does not occur. In discussing the question of heat shock Knaysi [11] says that the effect has been attributed to the elimination of vegetative cells among which may be undesirable or weak variants. A similar result may be obtained with prolonged air-drying. Whatever the mechanism toxic conditions and substrate solubility seem definitely to be ruled out. The drying of soils appears largely to involve changes in microbial behaviour and this aspect of the problem is now being further studied.

The similarity in decomposition patterns under laboratory and field conditions indicates similar microbial behaviour in the field though here the situation is somewhat complicated by the simultaneous decomposition of leaf litter *etc.*, which was sieved out in the laboratory samples. The general pattern of behaviour is however almost as uniform and repetitive as under laboratory conditions and can usefully be applied to problems involving humus build-up and decomposition, and nitrogen mineralisation.

SUMMARY

Respirometer experiments show that when a dry soil is moistened a characteristic pattern of decomposition occurs in which an initial period of relatively rapid decomposition (Stage 1) falls, during a few days, to a slow steady rate (Stage 2). This pattern is repetitive with successive dryings and rewettings

and is common to all soils so far investigated. The magnitude of decomposition depends in the percent carbon in the soil and on the drying conditions, air-drying being less effective than oven-drying. Decomposition during Stage 1 conforms approximately to a first-order reaction and proportionate amounts of nitrogen are mineralised. A similar pattern of decomposition occurs under field conditions throughout successive wet and dry seasons.

Evidence is presented to show that decomposition involves direct microbial attack of the solid organic substrate and that the recurrent pattern of decomposition is due to the state in which the microbial population is left after drying and its subsequent behaviour on rewetting. The rapid decline in the rate of decomposition on rewetting (Stage 1) appears not to involve (1) the development of toxic conditions, (b) physical changes in the soil (since similar patterns of decomposition also occur with organic material alone or in sand) or (c) rapid decomposition of organic material made soluble by drying.

The operation and repetition of this pattern of decomposition in the field has important consequences in the rundown of soil carbon and the mineralisation of soil nitrogen particularly where well-defined wet and dry seasons occur. These consequences are discussed in relation to climate and certain agricultural practices.

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