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Decomposition of Elephant Dung in an Arid, Tropical Environment

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Summary. Carbon dioxide evolution from elephant dung and bare soil was measured in relation to the chemical composition of the decomposing organic material, temperature and moisture.

Carbon mineralisation from the dung was extremely rapid during the first 48 hours after deposition but micro-organism activity became progressively more limited by moisture after this initial period, and was at a comparatively low rate after two weeks when the dung was dry. Under high moisture controlled conditions CO_2 evolution from the dung was primarily temperature limited, but a decrease in the carbon mineralisation rate and the temperature response over the 14 day experimental period suggested that the availability of carbon and nutrient resources also became limiting to micro-organism activity.

Carbon dioxide evolution from the soil was negligible under normal conditions but both the soil and dry dung showed a rapid increase in CO_2 evolution rates following the addition of water.

The implication of these results for the dynamics of soil organic matter during the wet and dry seasons and for the ecology of dung beetles is discussed.

Introduction

In natural ecosystems, litter fall and the feeding activities of herbivores are the two main processes by which minerals contained in the above ground parts of plants are returned to the soil. Little quantitative information is available on either of these processes for tropical savannahs. Coe (1972) has estimated that the elephant population in Tsavo National Park, Kenya, could be consuming as much as 22% of the available above ground net primary production and producing about 154 kg of dung/km²/day (wet wt.). A comparison of the chemical composition of this dung (Dougall, 1963; Weir, 1972) with that of the major food plants of elephants (Napier-Bax and Sheldrick, 1963) shows that many of the important minerals, such as nitrogen, phosphorus and potassium, occur at a higher percentage in the dung than in the food material. There are two main reasons for this. First, energy sources in the food plants are removed, resulting in a proportional increase in the unassimilated minerals.

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Second, the animals may show intraspecific selection for parts of the food plant which have the highest nutritive quality (leaves selected in preference to woody materials and young leaves in preference to old, etc.). In ecosystems such as Tsavo, where grazing and browsing animals eat a major part of plant net production the mineralisation of dung influences the plant community.

During the wet season in Tsavo dung beetles rapidly remove and bury a large proportion of the elephant dung. During the dry seasons dung beetles become relatively scarce and dried dung accumulates on the surface of the soil. In this study we investigate the influence of temperature, moisture and chemical composition on elephant dung decomposition during the dry season.

Study Area

This study was carried out near the southern boundary of Tsavo National Park (East), approximately 2.5 km from the township of Voi, at an altitude of 1600 ft. The local vegetation was Scattered-Tree Woodland (Greenway, 1969) which has probably been derived from *Commiphora* Woodland by extensive elephant browsing (pers. comm., J. B. Sale). The experimental site was located in an open area between scattered *Commiphora* and *Acacia* trees. The soil is a dark red sandy loam (Butler, 1959) with patchy grass cover. The site was surrounded by a thick thorn hedge to reduce disturbance of apparatus by large mammals. The mean annual rainfall at Voi, over a period of 64 years, is about 538 mm (22 inches), but with considerable year to year variation between the maximum recorded rainfall during this period of 1201 mm (47.3 inches) and the minimum rainfall of 184 mm (7.2 inches) (Anon, 1964). This study was made in July 1972, approximately mid-way between the "long" rains (March to May) and the "short" rains (October to December). No measurable amounts of rain fell during the study period.

Materials and Methods

Carbon Dioxide Evolution

Carbon dioxide evolution from elephant dung and soil was measured using the absorption respirometers described by Anderson (1973a). These consist of 10 cm long, open ended, perspex cylinders, with an internal bore of 5.8 cm, which were left inserted in the dung or soil throughout the experiment. The cylinders are capped for short periods of time with closely-fitting lids bearing a small plastic dish. The lids have an access hole, which can be closed with a greased glass plate, through which 0.1 N potassium hydroxide can be added to the dish once the lid is in place. The respirometers were shaded with white cards during CO_2 determinations to prevent excessive heating when the cylinders were capped due to a "greenhouse" effect. At the end of the exposure period excess barium chloride is added to the potassium hydroxide and the solution titrated in the field with standard hydrochloric acid. The amount of carbon dioxide absorbed by the potassium hydroxide is

calculated by the difference between the mean of a number of blank determinations and the titre for the experimental reading assuming that 1 ml of decinormal hydrochloric acid is equivalent to 2.2 mg absorbed carbon dioxide.

Elephant dung was obtained from the orphan elephants raised by Major and Mrs. D. L. W. Sheldrick. The four elephants are kept in a stockade overnight and deposit large amounts of dung during this period. Much of this dung is trampled under these confined conditions and so dung found in discrete heaps at dawn is unlikely to be more than a few hours old.

Fresh dung was collected at 7 a.m. on 30th June (day 1). Six approximately 4.5 kg (wet wt.) piles of dung were made up on bare soil on the experimental site. The following experimental series and replicates were set up:

i) "Exposed" Dung. The respirometer cylinders were cut into the dung piles with a sharp knife and then carefully removed and weighed to establish the initial weight of dung they contained. The cylinders were replaced in position so that the surface of the dung in the respirometer was level with the surface of the dung in the main pile and the base of the cylinders were in contact with the underlying soil. These cylinders were only capped during CO_2 determinations and were therefore subject to approximately the same temperature and desiccation regime as the dung piles.

ii) "Enclosed" Dung. Two cylinders were cut into the dung and then removed and weighed as described above. The lower ends of the cylinders were then sealed with tightly fitting perspex blocks and the respirometers replaced in the dung piles. The lids were placed on both cylinders and left in place throughout the experiment, except during CO_2 determinations, to reduce moisture losses. The access hole in each lid was left open to allow geaseous exchange and to ensure that pressure equilibrium was established with the atmosphere. The respirometers were also shaded with white cards in between experiments to prevent heating of the dung by a greenhouse effect.

iii) Soil Respirometers. Six soil respirometers were set up by inserting the cylinders 2.5 cm into bare soil, 50 cm from each of the dung piles.

A certain amount of CO_2 is present in the air enclosed in the respirometers when the cylinders are capped. This source of error was negligible in the dung respirometers where there was little dead-space between the dung and the lid and where the rate of CO_2 evolution was high. The rate of CO_2 evolution from the soil, however, was extremely low and a large dead-space was present above the soil. A correction factor for the CO_2 contained in this dead-space was obtained by setting up two respirometers in which tightly fitting perspex blocks were used to blank off approximately the same volume of each cylinder as that filled by soil in the soil respirometers. Measurements of the enclosed CO_2 were initially made simultaneously with the experimental series but abandoned after it was found that the correction factor was constant at 0.1 mg CO_2 per soil respirometer.

Measurements of CO_2 evolution from soil and dung were made at approximately two hour intervals between 09.00 and 20.00 for the first two days of the experiment and thereafter at 09.00, 13.00 and 18.00 hours until day 14.

iv) Watering Experiments. Watering experiments were carried out on the exposed dung and soil respirometers on days 17 and 26; the enclosed dung samples were removed on day 14 for water content determinations and chemical analysis.

On day 17, normal CO_2 measurements were made on the exposed dung and soil respirometers at 09.24 hours. At 10.00, 32.5 ml of water (equivalent to half an inch of rain) was slowly added to each respirometer, carbon dioxide evolution from the re-wetted samples was measured at 10.37, 12.14 and 18.54 h.

On day 26 control measurements of CO_2 evolution were made at 09.00 followed by 32.5 ml of water per respirometer at 9.50. Carbon dioxide measurements were made at 10.20 and 11.36. At 12.00 a further 32.5 ml of water was added to each respirometer and further CO_2 evolution measurements were made at 13.38 and 18.00.

Dung and Soil Temperatures

Temperature measurements of the dung surface, centre, dung/soil interface, exposed soil surface and soil at a depth of 3 cm were made at hourly intervals throughout the experiment by an automatic temperature recorder with thermistor probes (Grant Instruments Ltd., Cambridge).

Dung and soil temperatures were also recorded within each respirometer at the beginning and end of each series of CO_2 measurements using a thermistor thermometer with needle probes (Grant Instruments Ltd.). The probes were inserted 3 cm into the centre of the dung and 1.5 to 2 cm into the soil.

Dung Moisture Content

Large faecal masses in the dung piles were lifted, a small sample of dung removed from the bottom of each pile and the faecal masses carefully replaced. Sampling was not carried out more than twice beneath any faecal mass as this could have accelerated the desiccation of the dung. Sampling was carried out once or twice a day for the first seven days of the experiment and subsequently on days 10, 11 and 13.

Moisture content measurements were made for the outside 2 cm of the dung piles on days 1 to 4, 7, 10 and 13.

Dung samples were rapidly sealed in tubes and oven dried at 105° C. Moisture content was expressed as percentage wet weight.

The extent to which the dung in the exposed respirometers was drying out was noted on five occasions during the course of the experiment. The cylinders were carefully lifted out of the dung pile and the proportions of dry, pale coloured dung and moist, dark dung were noted.

Water losses from the enclosed dung respirometers could not be expected to conform to the dung pile drying rates and so only initial (day 1) and final (day 14) moisture content determinations could be made for this series of experiments.

Chemical Composition of Dung

A sample of fresh dung was taken from each of the six dung piles on day 1. Soil samples were collected from the surface 2 cm of soil beside the soil respirometers on day 3. Dung samples were removed from the exposed and enclosed dung respirometers on day 14. The samples were oven dried at 105° C and stored in tightly stoppered tubes. Subsequently, the samples were finely ground in a hammermill (Glen Creston, Stanmore) and samples of a similar date and origin were thoroughly mixed together. Chemical analysis of the dung and soil was carried out by the Ministry of Agriculture, Fisheries and Food, Agricultural Development and Advisory Service (ADAS).

Results

Soil and Dung Temperatures

An operations fault in the continuous temperature recorder was not discovered until after the end of the experiment. The nighttime records

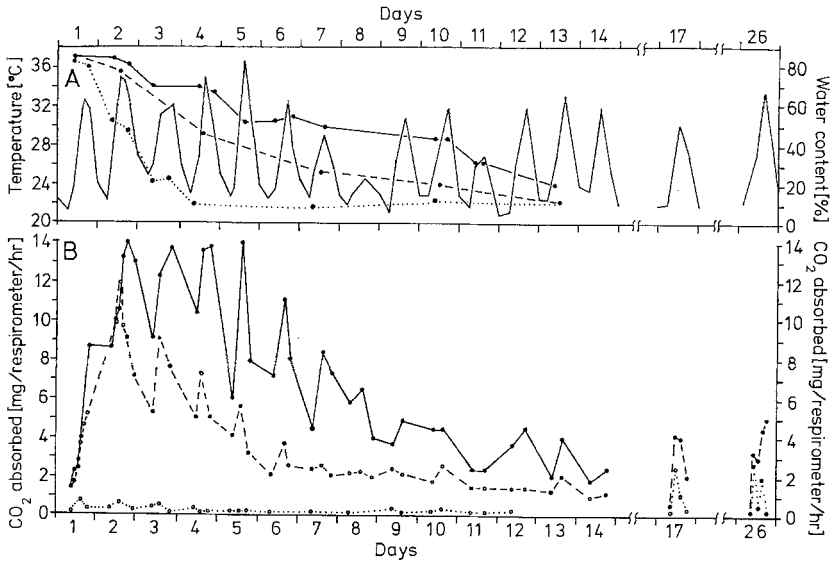

Fig. 1 A and B. Carbon dioxide evolution from dung and soil in relation to temperature and moisture. A Mean diurnal temperature fluctuations in the centre of the exposed dung (—). Mean percentage moisture content of dung at the bottom of the piles (•—•), on the dung surface (•···•) and the integrated mean moisture content of the dung in the "enclosed" respirometers (•---•). B Mean CO_2 evolution rates from the "enclosed" dung (•—•), the "exposed" dung (•---•) and from bare soil (•···•)

of soil and dung temperatures were complete but daytime records were irregular and therefore unreliable.

The diurnal temperature fluctuations shown in Fig. 1 A for the exposed dung respirometers are composites of the dung temperature measurements made at 09.00, 13.00 and 18.00 during CO_2 determinations and of the temperatures recorded in the centre of the dung at 06.00 and 24.00 by the chart recorder.

Soil surface temperatures are not shown since these were usually 47° C to 50° C at midday and exceeded the 45° C maximum on both thermister thermometers.

The minimum night temperatures in the centre of the dung were fairly constant at 21° C to 23° C throughout the study period. The sun rose at approximately 07.00 and dung temperatures then rose steadily to their recorded maxima at 13.00 to 15.00 h. By 18.00 the dung temperatures were often only a few degrees below the maximum temperature, but then decreased rapidly after sunset at 19.00 to the nighttime minima about an hour before dawn.

The maximum daytime dung temperatures recorded were 32° C to 34° C on 8 out of the first 14 days of the experiment. The absolute maximum dung temperature, 37.0° C, was recorded on day 5 when soil temperatures exceeded 55° C. The minimum daytime temperature of 22.9° C was recorded on day 8 under heavy cloud cover.

Daytime temperatures in the enclosed dung respirometers were consistently 1° C to 2° C below the exposed dung respirometer values owing to shading.

Dung Moisture Content

Moisture content determinations could not be made directly on dung in the respirometers as this would have necessitated removing material and disturbing the dung microclimates. It was intended to measure moisture losses from the experimental dung by weighing the respirometers but this was found impracticable for a variety of reasons. Instead, an integrated mean moisture value was calculated for the exposed respirometer dung from the moisture content determinations on the unconfined dung. It was necessary to assume that moisture losses from the exposed respirometers approximated to those from the dung piles themselves. The integrated mean moisture value was calculated by taking the overall mean for the sum of dung moisture contents allocated according to the proportions of dry and damp dung which could be seen through the transparent walls of the respirometers. This method could not be applied to the covered respirometers since the bottom of the cylinders was sealed to reduce water losses. On day 14 the mean moisture contents for the dung in these two respirometers were 71.4% and 69.3%.

Dung mean moisture contents and the integrated mean moisture values are shown in Fig. 1 A.

The moisture content of dung at the bottom of the piles fell from 84.0% to 70.0% over 13 days. The dung surface dried rapidly from 82.1% on day 1 to 10.0% on day 4 and remained at approximately 10% for the rest of the experiment. On days 2 and 3 the main dung piles and the dung in the exposed respirometers were colonised by small dung beetles (*Onitis* spp., *Onthophagous* spp., *Aphodius* spp.: Scarabaeidae, Coleoptera). The burrowing activities of these beetles resulted in the dung becoming loosely packed and aerated, and presumably accelerated rates of water loss from the dung.

Carbon Dioxide Evolution Rates

The exposed and enclosed respirometers all contained 65 g to 75 g of dung. Variations in CO_2 evolution rates between respirometers were not correlated with the weight of dung they contained and so rates of CO_2 evolution have not been corrected to a unit weight basis. Carbon dioxide

evolution from the dung is expressed as milligrams CO_2 absorbed/respirometer/hour.

i) Exposed Dung. Mean rates of carbon dioxide evolution from the fresh dung increased rapidly over the first day of the experiment (Fig. 1 B) from 1.45 mg/h at 09.00 hours, to 5.17 mg/hour at 19.00 hours. Carbon dioxide evolution rates continued to increase on day 2 from 8.69 mg/h at 09.00 to the maximum recorded rate of 12.08 mg/h at 13.26 when the highest dung temperatures of the day were recorded. Thereafter CO_2 evolution rates followed the diurnal temperature pattern but with a decreasing response to daytime temperature rises as the dung dried out (Fig. 1 A). By day 7, CO_2 evolution rates had decreased to about 2.5 mg/h and showed a further more gradual decline over the last 7 days of the experiment to approximately 1 mg/h on day 14.

ii) Enclosed Dung. Rates of CO_2 evolution in the moisture controlled respirometers showed similar rapid increases to the exposed dung during the first two days of the experiment to a maximum recorded rate of 13.95 mg/h at 17.15 on day 2. During days 3 to 7 of the experiment the diurnal patterns of CO_2 evolution closely followed the recorded temperature fluctuations. The relationship between temperature and CO_2 evolution rates during this period is shown in Fig. 2. Log rates of CO_2 evolution were a linear function of temperature (log rate $CO_2 = -0.1547 + 0.0409$ temp., $r = 0.80$) and showed a Q_{10} relationship of 2.58 between 22° C and 32° C.

Carbon dioxide evolution rates decreased markedly from day 8 to the end of the experiment and also showed a poor temperature response. The final mean moisture content of the dung in these respirometers on day 14 was 70.4% which suggests that, unlike the exposed respirometer series, moisture was not the factor limiting dung decomposition over this period.

Carbon dioxide evolution rates from both series of respirometers on day 1 did not show a response to decreases in dung temperatures during the afternoon and evening. The most likely explanation for this phenomenon is that the microbial populations were in the logarithmic growth phase during the first 24 hours or so of the experiment and so the decrease in population metabolism associated with the reduction of dung temperatures was masked by the rising metabolic demand of the developing microbial populations.

iii) Soil. Carbon dioxide evolution rates were extremely low and ranged between 0.2 mg/h and 0.6 mg/h with a mean rate of 0.3 mg/h for the duration of the experiment. No relationship between CO_2 evolution rates and soil temperatures was detectable for this series of readings.

iv) Watering Experiments. Rates of CO_2 evolution from the exposed dung and soil before and after wetting are shown in Table 1 and Fig. 1 B.

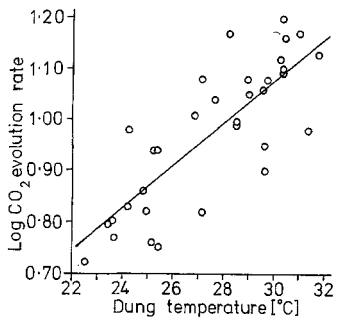

Fig. 2. Rates of CO_2 evolution from the "enclosed" dung in relation to the dung temperature

a) Day 17: The dung and soil showed an extremely rapid response to watering. Rates of CO_2 evolution increased approximately 7-fold in the dung and 8-fold in the soil, to 4.08 mg/h and 2.49 mg/h respectively, during a period of less than an hour after watering.

Carbon dioxide evolution from the soil declined rapidly during the day to the pre-watering level by late evening. The dung maintained the increased CO_2 evolution rates for a longer period of time than the soil and by sunset the mean rate was still 3.5 times higher than the pre-watering rate.

b) Day 26: Carbon dioxide evolution from the soil and dung showed a rapid response to watering as on 17 and after less than 1 hour the CO_2 eolution rates were close to those recorded in the first experiment after a similar time period. The increased rates of CO_2 evolution were maintained by the dung for about 1 hour but the mean soil rate decreased over the same period of time to near the pre-wetting value.

A further watering was carried out at midday. The dung CO_2 evolution rates continued to rise over the rest of the day, despite a decrease in dung temperatures, suggesting that the dung micro-organisms had entered an active growth phase as on day 1 of the experiment. The soil showed a reduced response to watering than in the morning, and by 18.00 had decreased once more to the pre-watering level.

v) Chemical Composition of Dung and Soil. The results of the chemical analysis of dung and soil samples are shown in Table 2. The nitrogen, phosphorus and potassium contents of the dung are considerably higher than the values for wild elephant dung given by Dougal (1963) of1.11%, 0.25% and 0.58% respectively. This is probably the result of these elephants being fed lucerne as well as natural browse when they are confined in the stockade at night (Coe, 1972).

Table 1. Watering experiments

Respirometer series	Experimental day	Time	CO_2 evolution rate (mg^2/respirometer/h)
Exposed dung	17	09.24	0.59
		(watered 10.00)	
		10.37	4.08
		12.14	4.03
		18.54	2.04
Soil	17	09.24	0.31
		(watered 10.00)	
		10.37	2.49
		12.14	1.04
		18.54	0.45
Exposed dung	26	09.00	0.32
		(watered 09.50)	
		10.20	3.22
		11.36	2.99
		(watered 12.00)	
		13.38	4.44
		18.00	4.68
Soil	26	09.00	0.32
		(watered 09.50)	
		10.20	2.69
		11.36	0.62
		(watered 12.00)	
		13.38	1.95
		18.00	0.23

Table 2. Chemical analysis of dung and soil (percentage composition by weight)

Sample	Collection date	Nitrogen (%)	Phosphorus (%)	Potassium (%)	Magnesium (%)	Organic carbon (%)	C:N ratio
Fresh dung	day 1	1.39	0.39	0.90	0.33	49.82	36:1
Exposed dung	day 14	1.04	0.25	1.05	0.28	51.56	50:1
Enclosed dung	day 14	1.29	0.32	0.89	0.34	50.46	39:1
Soil	day 3	0.15				2.30	15:1

The percentage mineral composition of the dung has been calculated on a weight basis. As carbon losses occur in the form of CO_2, mineral elements which do not have a gaseous phase or which are efficiently conserved by the microflora, such as nitrogen, should increase in their percentage composition. The decreases in nitrogen, phosphorus and

possibly magnesium content of the exposed dung by day 14 therefore reflect real reductions in the amounts of these elements. The increase in percent potassium content suggests that potassium was not lost during decomposition and may have shown a real increase due to the contamination of the dung by dust and soil. The slight increase in carbon content may not be significant but is also indicative of the differential removal of other elements. The decreases of nitrogen, phosphorus and magnesium could be caused by the activities of the dung fauna or by leaching. Nitrogen could also have been lost by denitrification and/or ammonification but it is more likely that it was conserved by incorporation into microbial tissues. Leaching can be largely discounted in this study, because of the lack of rain, although there was some uptake of dung moisture by the soil. The possibility that nitrogen, potassium and magnesium rich material was removed selectively by the dung fauna must be considered.

The dung beetles are selective in the dung material they remove. Elephant dung has two readily recognisable components. The first, which forms the bulk of the dung, is made up of pale coloured, fibrous plant materials, particularly large fragments of chewed wood. The second dung component is a finely divided, dark green/brown substance which appears to be derived from partly digested plant materials, gut secretions, etc. It was noticeable that after the exposed dung and the main dung piles had been sorted by the dung beetles, it was largely this fraction which had been removed. Inspection of the dung balls of these small scarabaeids from other sources supported this observation.

The relatively constant composition of the dung in the enclosed respirometers cannot be satisfactorily explained. The mean initial weight of material these respirometers contained, corrected to an oven-dry weight basis, was 10.50 g of dung/respirometer. After 14 days the mean weight loss from this material was 1.60 g oven dry material/respirometer. Losses of this magnitude, presumably in the form of carbon evolved as CO_2, should have resulted in significant percentage increases of nitrogen, phosphorus, potassium and magnesium. Seepage of liquid dung materials containing these elements could not have occurred as the base of the respirometers was tightly sealed. Beetles were excluded from the enclosed respirometers but the possibility that the activities of other dung invertebrates resulted in mineral losses (e.g. the emergence of coprophagous Diptera) cannot be discounted.

The area under the graph of CO_2 evolved from the enclosed dung (Fig. 1 B) is equivalent to 2.84 g CO_2 or 0.77 g carbon. Calculated mean losses of 0.80 g carbon/respirometer agree remarkably well with this figure. The close agreement of these values may be fortuitous but do suggest that the measurements of CO_2 evolved from dung in this study

reasonably reflect the true pattern of CO_2 evolution from the experimental material.

Discussion

A number of factors affect terrestrial decomposition processes. The rapidity with which a given substrate is oxidised by micro-organisms will depend on its chemical composition and on the biotic and abiotic properties of the surrounding environment. Temperature, moisture, available minerals, carbon/nitrogen ratio, oxygen availability and pH are the chief abiotic environmental influences on decomposition rates. Biotic factors, such as the feeding and burrowing activities of animals associated with the decomposing material, can also influence energy and mineral flux pathways.

In a temperate region where adequate rainfall in fairly evenly distributed throughout the year, temperature is the dominant variable determining the decomposition rate of soil organic matter (Anderson, 1973a). Under these conditions, up to an annual mean temperature of about 20° C, the accumulation of soil organic matter tends to be the rule rather than the exception (Mohr and van Baren, 1954). In those tropical regions with an annual mean temperature of 20° C to 25° C, or above, decomposition processes are very rapid and the accumulation of organic matter is exceptional unless limited by lack of moisture, waterlogging or the biochemical composition of the plant material. These climatic regions are generally associated with a monsoon climate and decomposition processes are moisture limited during the dry season. However, decomposition is so rapid when water is available that most organic matter accumulated in the soil during the dry season is mineralised during the rains.

Moisture limitation for soil micro-organisms and the extremely high decomposition rates of soil organic matter, when water is available, have been demonstrated in this study. The watering of bare soil resulted in a rapid increase in the rate of CO_2 evolution. The maximum mean soil "respiration" rate recorded of 2.69 mg/respirometer/hr, equivalent to 1.03 g CO_2/mg/hr, was among the lowest values for soil and dung recorded in this study but was nearly twice the maximum mean summer rate recorded for a well-developed temperate woodland soil (Anderson, 1973a).

The effect of moisture on dung decomposition is demonstrated by the results from the exposed dung series (Fig. 1B). The high rates of CO_2 evolution on day 2 decreased by over 75% as the integrated moisture index fell from 80.0% to 46.5% on day 4 (Fig. 1A). Similar relationship between micro-organism activity and the moisture content of the decomposing substrate, when temperature is not limiting, have been shown by Douglas and Tedrow (1959), Haber (1963), Parkinson and Coups

(1963) and many others. Micro-organism activity is rarely completely inhibited by moisture availability. Clark (1967) has shown that low rates of CO_2 evolution were detectable from soils air dried in the laboratory to a moisture content of 3%. In the same study, however, no detectable amounts of CO_2 were produced from soils with an organic content of approximately 1%, air dried to a moisture content of 1% i.e. similar soil conditions to those recorded in this study.

The reduction in CO_2 evolution rates from the exposed dung during the course of the experiment may not simply be a function of decreasing moisture content. The results for the covered respirometers (Fig. 1 B) suggest that the availability of energy and nutrient resources for heterotrophic micro-organisms may also be a contributory factor in determining the rate of dung decomposition under these conditions. Carbon sources, such as simple sugars, starch and, to a lesser extent, hemi-, celluloses, are rapidly utilised during the early stages of decomposition but the micro-organisms become progressively carbon limited as the relatively decomposition-resistant materials (cellulose, lignin, cutins, suberins, etc.) form an increasingly large proportion of the residual material (Alexander, 1961; Minderman, 1968; Waksman and Diehm, in Waksman, 1952). This change in the biochemical nature of the substrate may also be reflected by changes in the microflora. On days 6 to 10 the surface of the dung in these respirometers was covered with fructifications of a large *Pilobolus* species (Fungi, Phycomycetes). The decline in the rate of carbon mineralisation may also be caused by the decreased availability of other minerals such as nitrogen as a result of their immobilisation by micro-organisms. Both biotic factors (invertebrates comminuting the substrate and lysing microbial tissues) and abiotic factors (particularly the wetting and drying of the substrate) are important in recycling the limiting minerals (Anderson, 1973 b). The stimulatory effect which drying and re-wetting soil has on microbial activity and the decomposition of organic matter is well known. Stevenson (1956), Soulides and Allison (1961) and van Schreven (1967) attribute the effect to the release of minerals and readily assimilatable energy sources from the organic substrate. Witkamp (1963, 1964, 1969) suggested that the drying of litter resulted in the lysis and release of minerals immobilised in senescent microbial tissues. The increased respiration from dry dung and soil, after wetting (Fig. 1, Table 1), may therefore reflect the stimulation of microbial activity by moisture and readily available minerals.

Conclusions

In the wet and dry seasons at Tsavo, there are significantly different pathways of dung energy and nutrient flux through the decoposer community.

During the dry seasons, elephant dung is not extensively utilised by dung beetles and the main pathways of energy and nutrient flux are through micro-organisms. Decomposition is largely moisture limited during this period. The desiccation rates of dung masses will depend on the microclimate of the area in which they are deposited, the size of the dung piles and physical disturbance of the dung. The dung piles set up in this study were equivalent to those produced by an 8 year old elephant (Coe, 1972). Dung piles of mature elephants or of single faecal masses will clearly dry out at different rates. Desiccation rates are accelerated by disturbance of the dung by beetles, birds, baboons and trampling by large mammals.

When the rains start mineralisation is extremely rapid as temperature is then the main factor limiting decomposition rates. Diurnal moisture fluctuations will occur in the soil during this period, but this probably serves to accentuate decomposition rates by reducing microbial immobilisation of minerals. Leaching rates, however, will also be rapid under these conditions in well-drained soils (Bartholomew, 1972) and growth of shallow rooted plants must be vigorous to utilise minerals made available by dung and litter decomposition.

During the wet seasons dung beetles utilise a significant proportion of the dung produced by large mammals. The rates of dung removed by beetles can be extremely high: a 1.5 kg pile of dung was removed by 16000 beetles (biomass 477 g) during the course of 2 h January 6, (1973). In the present study the dung piles remained discrete after more than two weeks.

The dung is used as a food resource for adult beetles and larvae. In the former case feeding occurs either within the dung pile itself or the dung material is removed to shallow excavations where only about 20% of the material may be consumed. In the latter case oviposition takes place in dung buried in chambers excavated below or near to the dung pile and during the course of larval development most of the dung is utilised. The life cycle of the small scarabaeids, such as those species mentioned above, may be completed in a period of a few weeks. However, some of the species such as *Scarabeus*, *Catharsius* and *Heliocopris* (mean live weights 5 g, 7 g and 10 g respectively) may take up to a year to complete development.

The rapid mineralisation rates of the dung poses an interesting problem as to how the dung is conserved over a sufficiently long period of time to allow larval development of the larger species. There would appear to be three main hypotheses which could be put forward to account for this phenomenon. The first is that the decomposition of the dung balls follows the pattern shown by the covered respirometers where, after an initially high rate of carbon mineralisation, the decom-

position rates of the remaining materials are relatively slow and nitrogen is immobilised in microbial tissues. The second hypothesis is that the decomposition rate of the dung is reduced by the depth at which the ball is buried. The larval chambers of *Heliocopris dilloni* Guer, for example, have been recovered from as much as 2 m below the soil surface where the soil temperature is about 24° C and shows little seasonal and diurnal variation. Many smaller dung beetle species, however, construct their chambers less than 0.5 m below the surface where decomposition would be more rapid. The third possibility is that the adult beetles incorporate a bacteriostatic substance into the dung when the material is sorted for dung ball construction.

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References

Alexander, M.: Introduction to soil microbiology. New York: Wiley 1961

Anderson, J. M.: Carbon dioxide evolution from two temperate deciduous woodland soils. J. App. Ecol. **10**, 359–376 (1973a)

Anderson, J. M.: The breakdown and decomposition of Sweet Chestnut (*Castanea sativa* Mill.) and Beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. I. Breakdown, leaching and decomposition. Oecologia (Berl.) **12**, 251–274 (1973b)

Anon, A.: Collected climatological statistics for East African stations. Pt. 1. Kenya and Seychelles. E. A. Met. Dept. of E. A. Common Services Organisation. Nairobi (1964)

Bartholomew, W. V.: Soils of the humid tropics. Washington: National Academy of Sciences 1972

Butler, R. J.: Atlas of Kenya. Nairobi: The survey of Kenya 1959

Clark, F. E.: Bacteria in the soil. In: Soil biology, A. Burges, F. Raw, Eds., p. 15–49. London-New York: Academic Press 1967

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Coe, M. J.: Defaecation by African elephants [*Loxodonta africana africana* (Blumenbach)]. E. Afr. Wildl. J. **10**, 165–174 (1972)

Dougall, H. W.: On the chemical composition of elephant faeces. E. Afr. Wildl. J. **1**, 123 (1963)

Douglas, L. A., Tedrow, J. C. F.: Organic matter decomposition in arctic soils. Soil Sci. **88**, 305–312 (1959)

Greenway, P. J.: A check list of plants recorded in Tsavo National Park (East). J. E. A. Nat. Hist. Soc. Nat Mus. **27**, 169–209 (1969)

Haber, W.: Ein ökologischer Zugang zur Bodenmikrobiologie. In: Soil organisms, J. Doeksen, J. van der Drift, Eds., p. 190–196. Amsterdam: North Holland 1963

Minderman, G.: Addition, decomposition and accumulation of organic matter in forests. J. Ecol. **56**, 355–362 (1968)
Mohr, E. C. J., Baren, F. A. van: Tropical soils. The Hague: N. V. Uitgeverij W. van Hoeve 1954
Napier-Bax, P., Sheldrick, D. L. W.: Some preliminary observations on the food of elephant in Tsavo National Park (East) of Kenya. E. A. Wildl. J. **1**, 40–53 (1963)
Parkinson, D., Coups, E.: Microbial activity in a podzol. In: Soil organisms, J. Doeksen, J. van der Drift, Eds., p. 167–175. Amsterdam: North Holland 1963
Schreven, D. A. van: The effect of intermittent drying and wetting of a calcareous soil on carbon and nitrogen mineralisation. Plant and Soil **26**, 14–32 (1967)
Soulides, D. A., Allison, F. E.: Effect of drying and freezing soils on carbon dioxide production, available mineral nutrients, aggregation and bacterial populations. Soil Sci. **91**, 291–298 (1961)
Stevenson, I. L.: Some observations on the microbial activity in remoistened air-dried soils. Plant and Soil **8**, 170–182 (1956)
Waksman, S. A.: Soil microbiology. New York: Wiley 1952
Weir, J. S.: Mineral content of elephant dung. E. A. Wildl. J. **10**, 229–230 (1972)
Witkamp, M.: Microbial populations of leaf litter in relation to environmental conditions and decomposition. Ecology **44**, 370–377 (1963)
Witkamp, M.: Environmental influences on microbial populations and activity of the forest floor. 8th Int. Cong. Soil Sci. Bucharest, Romania, 647–654 (1964)
Witkamp, M.: Environmental effects on microbial turnover of some mineral elements. I. Abiotic factors. Soil Biol. Biochem. **1**, 167–176 (1969)

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