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Dung decomposition and pedoturbation in a seasonally dry tropical pasture

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Abstract Rates of dung decomposition and the associated accumulation of soil transported to the surface were compared for dung deposited during a dry and a wet season in a Costa Rican pasture. Average decomposition rates for the first 140 days after deposition were significantly lower for dung patches deposited at the beginning of the dry season than for patches deposited at the beginning of the wet season (0.73 vs. 1.50 g/day^{-1} on a dry weight basis). A strong linear relationship was found between dung removal and soil accumulation at the original soil surface, with an average of 2.0 g soil accumulated for every gram of dung which was removed. This relationship was not affected by deposition season. The lack of a seasonal difference, along with the relatively low decomposition rates during the wet season, were explained by the dominance of termites in the dung patches throughout the year. Evidence of dung beetle activity was never recorded during the dry season and was found in only 18 of the 45 dung patches recovered during the wet season.

Key words Decomposition · Termites · Cattle dung · Pedoturbation · Tropical pastures · Soil restoration

Introduction

The deposition of dung in pastures and its subsequent decomposition has a variety of important effects in pasture ecosystems. Cattle dung decomposition has been shown to affect nutrient cycling (MacDiarmid and Watkin 1972; Calafiori and Alves 1981; Omaliko 1984; Buschbacher 1987), soil physical properties (Brussard and Hijdra 1986; Herrick and Lal 1995), plant primary productivity (Bornemissza and Williams 1970; MacDiarmid and Watkin 1972; Calafiori and Alves 1981), animal grazing patterns (Omaliko 1981; Jones and Ratcliff 1983; Anderson et al. 1984), invertebrate populations (Matthiessen and Hayles 1983; Edwards and Aschenborn 1987; Grodowitz et al. 1987; Doube et al. 1988), and seed germination (Wicklow and Zak 1983).

Dung decomposition may also be associated with soil transport, both within the profile and to the soil surface (pedoturbation). Soil contamination of dung during decomposition has been reported widely (Holter 1979; Dickinson et al. 1981; Whitford et al. 1982), but the extent of soil transport to the surface has rarely been quantified. Depending on the source and fate of the soil, these decomposition processes could make a significant contribution to both pedogenesis and soil erosion.

The net impact of dung decomposition on pedoturbation and soil properties depends on the rates and mechanisms of decomposition within a particular pasture ecosystem. Both rates and mechanisms of dung decomposition vary widely. The time required to remove most or all dung from the soil surface ranges from less than a day in Africa (Edwards and Aschenborn 1987) to over 10 years in North American alpine areas. Higher rates of decomposition and/or burial have been shown to limit fly-breeding (Edwards and Aschenborn 1987), increase plant productivity (Bornemissza and Williams 1970; Fincher et al. 1981), and reduce the length of time during which surrounding vegetation is rejected by grazers (Marsh and Campling 1970).

Differences in decomposition rates can often be explained by different mechanisms and the relative activity of various decomposers (Tyndale-Biscoe 1994). Even within a single group of dung decomposers, Coleoptera larvae, a variety of different behaviours are represented (Bornemissza 1969). Each of these behaviours can be expected to have very different impacts on the fate of the dung and the nutrients it contains, on the creation of biopores, and on rates of soil transport and accumulation at the surface.

Despite the presence of large and steadily increasing populations of grazing animals in Latin America, there has

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been relatively little research on dung decomposition. Furthermore, very little published information is available on the potential relationship between dung decomposition and pedoturbation. The current study was designed to (1) compare cattle dung decomposition and soil accumulation rates during a dry and a wet season, (2) determine the relationship between dung decomposition and the mass of soil accumulated at the original soil surface, and (3) interpret differences in decomposition and soil accumulation based on observations of macroinvertebrate decomposer activity.

Table 1 Characteristics of dung patches on day of deposition for each of two seasonal depositions. Means followed by the same letter are not significantly different (P>0.05, N=3). *EC* electrical conductivity

Season	Dry matter (%)	Dry weight (g)	pH	EC (S m^{-1})	N (%)	P (%)
Dry	22.0a	330	8.1a	0.71a	1.20a	0.40a
Wet	17.6b	265	7.8b	0.69b	1.22a	0.37b

Materials and methods

Location

The study was conducted in a pasture at Hacienda La Pacifica, 5 km north of Cañas Guanacaste, Costa Rica (85°9′14.5″ W and 10°28′36.8″ N). The loam-textured soil was classified as a Typic Argiustoll (Soil Survey Staff 1994). Precipitation is limited to a single wet season (Fig. 1) and totalled 950 mm for the study year. This is approximately 22% below the 1220 mm predicted for the site based on long-term trends and averages (Hagnauer 1993). The 0.5-ha experimental site was located in a grazed, non-irrigated pasture 100 m from the nearest forested windbreak, and over 500 m from the nearest patch with an interior forest microclimate. The pasture was dominated by jaragua (*Hyparrhenia rufa*), a C4 perennial grass, and had not been tilled or fertilized for 20 years. The grass height was maintained at 9–53 cm by cutting. More information on the site has been given by Herrick and Lal (1995).

Dung production and deposition

Dung was collected from five 2-year-old steers housed in stables located 5 km from the field site. The stables were fitted with troughs to keep dung and urine separate. The cattle were fed a low-quality diet of African stargrass (*Cynodon nlemfluensis*) with an in vitro digestibility of 33%, which is similar to that of typical jaragua pastures in the area. Dung collected over a 24-h period was homogenized and subsampled for later chemical characterization and dry-matter content determination (Table 1).

Individual 1500-g portions (wet weight) were transported to the pasture and were randomly deposited a minimum of 1 m from other dung patches during an early dry-season deposition (February, 1991) and an early wet-season deposition (June, 1991). This yielded patches 21 cm in diameter (20–22 cm) and 4.3 cm high (4.0–4.8 cm). Cattle were excluded from the fenced site for the duration of the study, but were frequently present in the surrounding pasture.

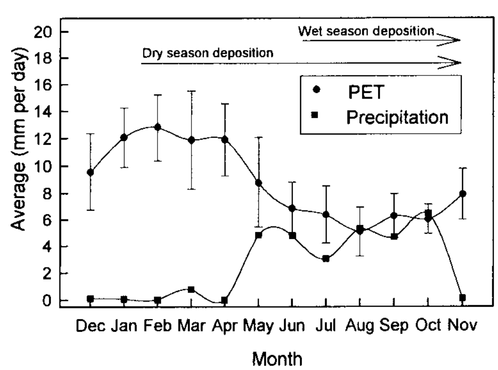

Fig. 1 Monthly average potential evapotranspiration (*PET*±1 SEM; n=number of days in month) and precipitation at the study site during the study period. Daily PET was calculated from on-site measurements of temperature, relative humidity, short-wave radiation, and wind speed using a modified Penman equation

Decomposition and soil accumulation

All dung, soil, and litter above the original soil surface were collected from nine randomly selected dung patches 12, 60, and 140 days after each deposition, and 270 days after the dry-season deposition. The 270-day dry-season deposition collection was completed in November 1991, and coincided with the 140-day wet-season deposition collection. The samples were oven-dried at 70 °C and stored in plastic bags. Decomposition was defined as the disappearance of dung from the soil surface. Determinations of the proportion of dung and soil in each sample followed Herrick (1995). This method is based on the relative moisture-holding capacity of the two materials. All data were corrected for normal seasonal variations in litter and surface soil by subtracting values from untreated plots sampled on the respective collection dates.

Macro-invertebrates

Invertebrates larger than 3 mm in any dimension were identified to Order during field collection of the dung and aboveground soil and litter, and the number of each was estimated. Invertebrate density in the surface 7 cm of soil was estimated from 5-cm diameter cores (two each from 0–3 and 4–7 cm). Similar estimates were made in control plots. The presence of invertebrate species not found in the samples was also noted, along with indications of previous activity, such as soil piles, buried dung balls, and dung beetle fecal pellets.

Results

Dung decomposition

All results are reported on an oven-dry weight basis. Average decomposition rates for the first 140 days after dung deposition for the wet-season deposition dung patches were more than double those for the dry-season deposition patches (1.50±0.06 vs. 0.73±0.09 g day^{-1}) despite the initially higher dry mass of the dry-season patches (Table 1). The proportion of dung remaining at the end of each of the first three periods (12, 60, and 140 days after deposition) was correspondingly lower for the wet-season deposition patches (Fig. 2a; analysis of variance, P<0.05, n=9). By the end of the wet season (270 and 140 days after deposition for the dry- and wet-season deposition, respectively), the proportion of dung remaining was similar for both depositions.

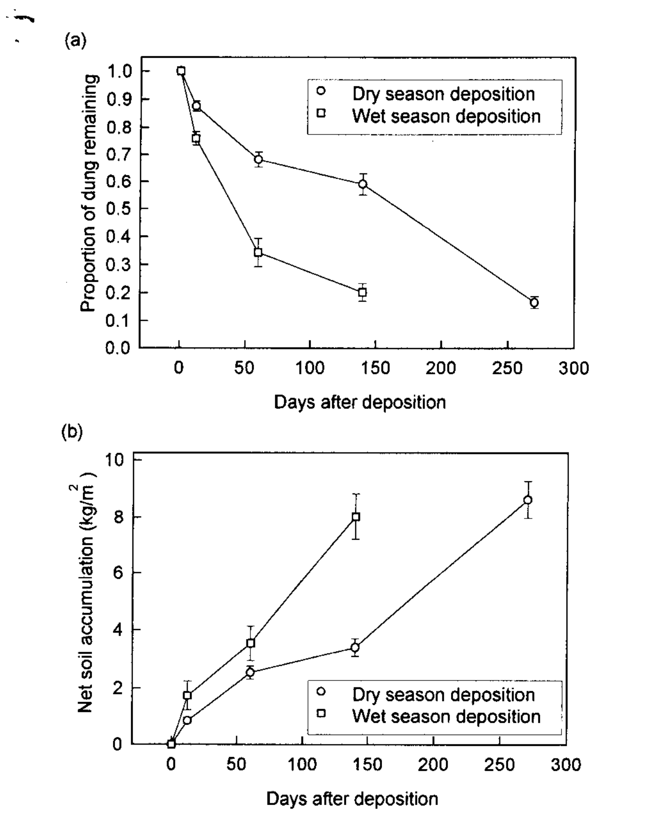

Fig. 2 Proportion of dung remaining on an oven-dry weight basis (**a**), and soil accumulated at the soil surface within 3 cm of the patch edge (**b**), for dry- and wet-season depositions. *Error bars* represent 1 SEM (n=9)

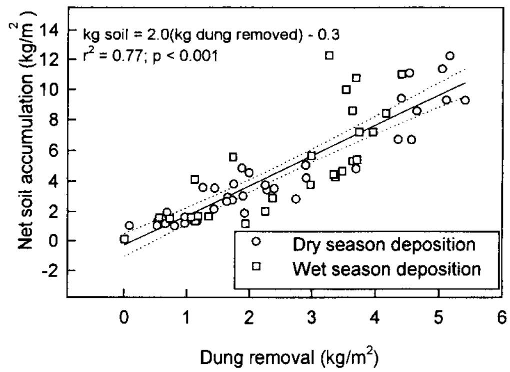

Fig. 3 Soil accumulation within 3 cm of the patch edge as a function of dung removal. Regression is based on all collections for both depositions. Data were converted to kg m^{-2} for both parameters

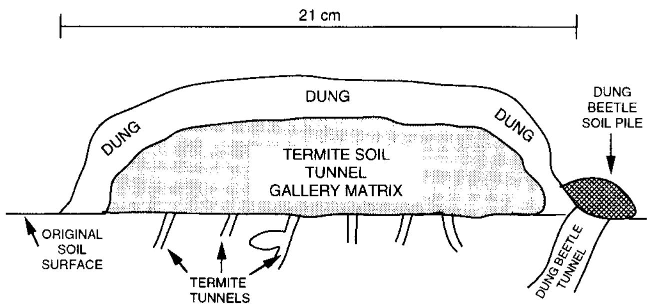

Fig. 4 Cross-section of dung patch with approximately 60% of dung removed. Illustration shows gradual replacement of dung by a matrix of soil, termite carton, and galleries. Even in the most highly decomposed patches, a thin surface crust was maintained until it was physically disturbed.

Soil accumulation

Soil accumulation at the original soil surface followed a similar pattern to that of dung decomposition, with consistently more soil associated with wet-season deposition dung patches on each collection day (Fig. 2b). Average accumulation rates for the first 140 days for the soil surface within 3 cm of the patch edge were 57.3±5.7 g m^{-2} day^{-1} for wet vs. 24.2±2.2 g m^{-2} day^{-1} for dry). The mass of soil associated with dung patches from both depositions was similar by the end of the wet season (Fig. 2b).

Decomposition vs. accumulation

There was a highly significant positive correlation between the mass of dung removed from a dung patch and the mass of soil accumulated on the original soil surface (Fig. 3). Approximately 2 g soil accumulated on the surface for every gram of dung (dry-weight basis) removed. This figure can be used to estimate the average annual soil accumulation on a hectare basis. If it is conservatively assumed that no further soil accumulation is associated with removal of the 20% of the dung remaining at the end of the wet season, decomposition of the dung deposited by two animals, each producing 2100 g dry dung per day (Buschbacher 1987), would generate 2450 kg ha^{-1} yearh^{-1} of soil accumulation.

Deposition season did not have a significant effect on the relationship between dung removal and soil accumulation (regression with deposition season as indicator variable; P>0.1; n=63). The similarity between the two deposition seasons was particularly strong early in the decomposition process, when environmental conditions were most different (Figs. 1 and 3). The pattern of decomposition and accumulation observed was similar for all 63 patches sampled (Figs. 3, 4), except for the appearance of soil piles at the edges of several wet-season patches (Table 2).

Macro-invertebrate activity

The soil-dwelling termites *Amitermes beaumontii* and *Hoplotermes* sp. nov. were the two most frequently encountered macro-invertebrates in both dung patch and control plots and were recovered on all five collection dates (Table 2). At least one of the two species was encountered in 60 of the 63 dung patch plots and in 21 of the 45 control plots samples. Average soil termite densities in the surface 7 cm (corrected for dung volume in the dung patch plots) were significantly higher in the dung patch plots than in the control plots for three of the four dry-season deposition collections and two of the three wet-season deposition collections.

Table 2 Average soil termite densities within 7 cm of the soil surface in dung patch and control plots, and number of dung patches (out of nine possible) with evidence of dung beetle activity. Termite densities in patch plots include termites in the dung and within 3 cm of the original edge of the dung patch. Densities within each sampling date which are not followed by the same letter are significantly different (Kruskal Wallis; $N=9$; $P<0.05$). Total number of patches with dung beetle activity may be less than the sum of activity types due to multiple signs of activity in some patches

Treatment	Patch age (days)	Termite density (termites l^{-1})	Dung beetle activity (no. of patches)				
			Soil piles	Adults	Larva	Dung balls	Total
Dry-season patch	12	39a	0	0	0	0	0
Control		1b	0	0	0	0	0
Dry-season patch	60	32a	0	0	0	0	0
Control		8b	0	0	0	0	0
Dry-season patch	140	87a	0	1	4	0	4
Wet-season patch	12	47a	3	0	0	3	5
Control		1b	0	0	0	0	0
Wet-season patch	60	77a	3	0	3	0	6
Control		14a	0	0	0	0	0
Dry-season patch	268	32ab	0	0	1	0	1
Wet-season	140	41a	2	0	0	0	2
Control		0b	0	0	0	0	0

Dung beetle activity appeared to be relatively low and transient in both dry- and wet-season deposition patches (Table 2). Evidence of dung beetle activity was not recorded in any of the 18 patches collected during the dry season and in only 18 of 45 patches recovered during the wet season. Millipedes were also occasionally found at the dung–soil interface, but never in the soil.

Discussion

Decomposition rates in both seasons were intermediate between the highest rates recorded for tropical ecosystems and the lowest rates measured in temperate ecosystems. In general, the highest dung removal rates are associated with high populations of dung beetles while the lowest are recorded in systems or under conditions in which there is little or no activity of dung beetles, earthworms, and termites (Holter 1979; Anderson et al. 1984; Edwards and Aschenborn 1987; Holter and Hendriksen 1988; Tyndale-Biscoe 1994). For example, Coe (1977) reported that a 2-kg pile of elephant dung can be removed in 2 h, in Kenya, while insecticide-treated cattle dung deposited in a California rangeland may last as long as 4 years (Anderson et al. 1984).

The 5–9 months required for the removal of 80–85% of the dung in the current study is similar to the period required for the removal of a similar proportion of cattle dung in an irrigated pasture in California (Anderson et al. 1984), and is significantly longer than the 1 month required during the dry season in a similar system in Nigeria (Omaliko 1981), and the 3 months necessary for termites to completely remove elephant dung in Kenya (Coe 1977). However, Whitford et al. (1982), who studied a system in the Chihuahuan Desert dominated by soil-dwelling termites, reported that an average of only 47% of the dung was removed over a period of 4 months. In the only Latin American study found in which cattle dung decomposition rates were reported, Buschbacher (1987) measured an 11.5% mass reduction during the first 14 days after deposition.

While overall decomposition rates were relatively low in the present study compared with other tropical systems, there was much less difference between dry- and wet-season decomposition rates than has been found in other regions (Omaliko 1981; Whitford et al. 1982). Janzen (1983) suggested that decomposition of horse and cattle dung in the seasonally wet region of Costa Rica is minimal during the dry season and is completed within a few days after dung beetles return during the wet season. The discrepancy between the results of the present study and Janzen's observations, which were made over a number of years and were supported by data on dung beetle populations, may be explained by one or more of the following factors. The first is that most of Janzen's (1983) work was based in Santa Rosa National Park, while the current study was located in a heavily grazed pasture over 500 m from the nearest forest patch. Large areas of open pasture were relatively uncommon in Guanacaste prior to European colonization; consequently, the dominant dung beetle fauna may be better adapted to the more heavily vegetated conditions in the National Park. The second possible explanation is that cattle (a ruminant) dung was used in the current study, while most of Janzen's work was based on horse dung. Dung quality and structure could affect both termite and dung beetle colonization and consumption rates. The denser cattle dung may provide a more effective barrier to evaporative moisture losses than horse dung, maintaining a higher internal relative humidity and thereby permitting higher levels of termite activity during the dry season. A third possible explanation is that dung beetle activity was relatively low during the study year due to below-normal precipitation. While this may have had some impact it is unlikely that the effect was as dramatic as that reported by Tyndale-Biscoe (1994) because the precipitation was relatively evenly distributed: the maximum period between precipitation events of at least 5 mm for the first 3 months following the wet-season deposition was less than 5 days, with the exception of one 6-day drought.

High levels of termite use of cattle dung were also recorded by Omaliko (1981) in Nigeria. However, Omaliko's report that there was virtually no wet-season termite activity stands in sharp contrast to the current study in which high levels of termite activity were found throughout the year. In fact, this continuous termite presence, together with the low levels of dung beetle activity and the lack of a deposition-season difference in the relationship between dung removal and soil accumulation, suggest that termites were the most important macro-invertebrate decomposers during both seasons. This hypothesis is further supported by the observation that material defecated by dung beetle larvae appeared to have been reprocessed by the termites.

The high levels of soil accumulation recorded were perhaps the most interesting and surprising results of the study. Even the minimum estimate of 2450 kg ha^{-1} $year^{-1}$ of soil accumulation associated with dung produced by two animal units per hectare is two to three times the rate previously reported for termites. A surface accumulation rate of 0.086 mm $year^{-1}$ (approximately 1200 kg ha^{-1} $year^{-1}$) was reported by Lee and Wood (1971), while Nutting et al. (1985) reported that two subterranean termites move 744 kg ha^{-1} of soil to the surface annually in a Sonoran Desert system. The fate of the material brought to the surface is, however, currently unknown.

In conclusion, the high levels of termite activity and soil transport to the surface found in the present study have potential implications for the restoration and maintenance of tropical pasture soils. In addition to the previously reported impacts on infiltration and bulk density, the movement of 2.5 t ha^{-1} $year^{-1}$ could play a significant role in pedogenesis. These high levels of pedoturbation could also have an impact on the distribution and availability of nutrients contained in the dung itself. Future studies should address the relative impacts of type and distribution of organic matter additions to pastures to determine whether the soil accumulation patterns identified are unique to the highly concentrated, discrete inputs provided by cattle dung.

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