

Variations in soil properties, species composition, diversity and biomass of herbaceous species due to ruminant dung residue in a seasonally dry tropical environment of India

PREETI VERMA, R. SAGAR, NITU GIRI, RANJANA PATEL, HARIOM VERMA, D.K. SINGH AND KULDEEP KUMAR

Department of Botany, Banaras Hindu University, Varanasi, India. www.bhu.ac.in/science/botany

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Abstract

Ruminants directly or indirectly influence nutrient cycling and vegetation structure in grassland ecosystems. We assessed the impact of natural cattle dung deposition on soil attributes and the resulting effects on species composition, species diversity and biomass of herbaceous vegetation in a natural grassland in the seasonally dry tropical environment of Banaras Hindu University, India. For this 72 plots of 1 × 1 m [12 locations × 2 treatments (dung residue and control) × 3 replicates] were selected in January 2013 and soil and vegetation samples collected. A total of 74 species belonging to 66 genera and 25 families were recorded. Principal Component Analysis (PCA) ordination revealed that the dung residue (DP) and control (CP) plots were distinctly different in terms of soil attributes and species composition. The *k*-dominance plot showed greater species diversity in DPs than CPs, with higher soil nutrients and moisture and lower soil pH in DPs than CPs. Similarly, DPs showed more herbaceous species and greater biomass than CPs. This trend can be explained by the positive responses of forbs, erect plants, annuals, large-statured, non-native and non-leguminous species to dung residue, while increased biomass can be partly due to cattle preferentially not grazing areas adjacent to a dung pat. Overall, the study showed that deposition of dung during grazing by cattle stimulates growth of pasture species and increases species diversity. Therefore cattle dung could be used as a sustainable alternative to chemical fertilizers to manage soil pH, species composition and diversity, and forage production in the seasonally dry tropical grasslands of India, which are nutrient- and moisture-limited.

Resumen

Los rumiantes directa o indirectamente influyen en el ciclo de nutrientes y en la estructura de la vegetación en los ecosistemas de pastizales. En el estudio se evaluó el impacto de la deposición natural de heces de bovinos en las características del suelo, la composición y diversidad de especies y en la biomasa de la vegetación herbácea de un pastizal nativo en ambiente tropical seco estacional de Banaras Hindu University, India. Para el efecto fueron seleccionadas 72 parcelas de 1 × 1 m [12 sitios x 2 tratamientos (residuo de heces y control) x 3 repeticiones]. Al comienzo del ensayo, en enero de 2013, se recolectaron muestras de suelo y vegetación. Se registraron un total de 74 especies pertenecientes a 66 géneros y 25 familias. Los Análisis de Componentes Principales (PCA) mostraron que las características de suelo y la composición de especies fueron diferentes entre los sitios con residuo de heces (DP) y el control (CP). La curva *k*-dominancia mostró una mayor diversidad de especies en las DPs que en las CPs, con niveles más altos de nutrientes y humedad en el suelo, y pH más bajo en DPs que en CPs. Del mismo modo, los DPs mostraron mayor número de especies herbáceas y mayor biomasa que los CPs. Esta tendencia se explica por las respuestas positivas de las especies herbáceas, erectas, anuales, de porte alto, no nativas y no leguminosas, a residuo de heces, mientras que el aumento de la biomasa puede deberse, en parte, a que el ganado prefiere no pastar en áreas adyacentes a residuos de heces. En general, el estudio mostró que la deposición de heces durante el pastoreo por el ganado bovino estimula el crecimiento de las especies y aumenta su diversidad. Por tanto las heces podrían ser utilizadas como una alternativa sostenible a los fertilizantes químicos para manejar el pH del suelo, la composición y diversidad de las especies y la producción de forraje en los pastizales tropicales en ecosistemas estacionales secos de la India, que presentan limitaciones de fertilidad y escasa humedad.

Correspondence: R. Sagar, Department of Botany, Banaras Hindu University, Varanasi-221005, India.
E-mail: sagar@bhu.ac.in

Introduction

Grasslands occupy roughly 25% ($33 \times 10^6 \text{ km}^2$) of the total land surface of the Earth (Shantz 1954) and about 18% of the total land area in India (Singh et al. 2006), the second most populous country globally. With the continuously growing human population, agricultural production per unit area has increased to fulfill the greater food requirements by increased use of N-based chemical fertilizers (Shukla et al. 1998). Usage of N-fertilizer has increased from 0.06 million tonnes in 1952 to 9.5 million tonnes in 1995, increasing the release of global warming gases into the atmosphere (Galloway et al. 2008; Zhou et al. 2010) and causing changes in soil, water and vegetation (Giles 2005). Therefore, an alternative to chemical N-fertilizer, which has the capacity to enhance forage production and species diversity with little or no negative effect on the environment, is needed.

The effects of dung on pasture ecosystems have been studied extensively with respect to nutrient cycling (Dickinson and Craig 1990) and species composition in temperate grasslands (MacDiarmid and Watkin 1971; Castle and MacDaid 1972). Such studies, with particular emphasis on biodiversity and biomass of plants, are lacking in tropical grasslands. We assumed that plants with different traits will respond differentially to dung residue and competitive interactions may be changed. Further, we hypothesized that dung residue may promote herbaceous biomass production and species diversity of certain plant species (Steinauer and Collins 1995), because moist dung is a nutrient-rich microhabitat that facilitates seed germination and seedling establishment of competitively superior species (Brown and Archer 1987).

The objectives of the present studies were to assess the effects of deposition of ruminant dung on soil and vegetation attributes in a seasonally dry tropical environment in India. Specifically, we examined the effects of ruminant dung deposition on: (1) community composition; (2) species diversity and biomass; and (3) diversity of plant functional groups in natural grasslands of Banaras Hindu University, Varanasi, India.

Material and Methods

Study sites

The study was conducted at 12 locations (INH - International Hostel; SUK - Sukanya; KAS - Kasturba; SNPG - Sarojani Nayadu; MMV - Mahila Maha Vidhyalay; BG - Botanical Garden; MB - Madhuban; MC - Meera

Colony; AG-1 - Agriculture Farm-1; AG-2 - Agriculture Farm-2; AG-3 - Agriculture Farm-3; and GB - Gandhi Bhawan) at the Banaras Hindu University ($24^{\circ}18' \text{ N}$, $83^{\circ}03' \text{ E}$; 76 masl), Varanasi, India, during January–March 2013. The grassland studied is representative of the unmanaged rangelands in the region. The area is a part of the Indo-Gangetic Plains characterized by a tropical monsoon climate. The year is made up of a cold winter (November–February), a hot summer (April–June) and a warm rainy season (July–September). October and March are transitional months between rainy and winter, and winter and summer seasons, respectively. During the study period, mean maximum temperature was 25.9° C (range $18\text{--}34.4^{\circ} \text{ C}$), while mean minimum temperature was 11.2° C (range $4.9\text{--}16.6^{\circ} \text{ C}$). The soil is characterized as Banaras Type III, which is a well-drained, pale brown, silty loam (Buol et al. 2003). In general, the soil is moderately fertile, being low in available nitrogen and medium in available phosphorus and potassium with neutral to alkaline pH (Sagar et al. 2008).

Study design

For sampling, 12 locations were selected visually to represent the entire range of variations in terms of soil, vegetation and ruminant dung residue. Within each location, 3 homogeneous dung residue (DP) pats of one month age (because in the dry season dung completely disappears within 2 months; Holter 1979) and 3 adjacent control (CP) spots with no dung were selected. Around each pat and control spot, a plot of $1 \times 1 \text{ m}$ in size was established, because a single release of cattle excrement on soil roughly occupies this area (Haynes and Williams 1993). Cow and buffalo dung pats are easily decomposed and scattered by the activity of dung beetles to cover 1 m^2 area within a month (R. Sagar personal observation). Thus, a total of 72 plots (12 locations \times 2 treatments \times 3 replicates) were sampled.

Soil sampling and analysis

From each plot, 3 soil samples (0–10 cm depth) were randomly collected, using a corer of 100 cm^3 capacity. These samples were mixed and gently homogenized. Large roots, fine roots, wood and litter were removed from the composite soil samples carefully and the soil sieved through a 2 mm mesh screen. One part of each sample was weighed and oven-dried at 105° C to determine soil moisture content, bulk density and porosity, while a second portion was air-dried for analysis of soil

pH, total soil carbon (total-C), total soil phosphorus (total-P), total soil nitrogen (total-N: inorganic-N + organic-N), ammonium nitrogen ($\text{NH}_4^+\text{-N}$) and nitrate nitrogen ($\text{NO}_3^-\text{-N}$). The sum of $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ is referred to as mineral-N or inorganic-N.

Soil moisture was measured by the gravimetric method. Soil bulk density (g/cm^3) was determined by using the corer method (stainless steel cylinders with a volume of 100 cm^3) (Piper 1944) and was calculated as the dry weight of soil divided by the soil volume (Su and Zhao 2003). Soil porosity was calculated by subtracting the ratio of soil bulk density and particle density (ca. 2.65) from its maximum value of 1 (Sagar and Verma 2010). Soil pH was determined by using a glass electrode (1:2, soil:water ratio). Total soil-C was analyzed by the Walkley (1947) and total soil-N by the Jackson (1958) methods. $\text{NH}_4^+\text{-N}$ was determined by the phenate method (APHA 1985), $\text{NO}_3^-\text{-N}$ by the PDSA method (Jackson 1958) and organic-N by the Jackson (1958) method. Soil phosphorus was analyzed by Allen's method (Allen et al. 1974).

The nutrient concentration (kg/ha) at each location was calculated by multiplying soil bulk density (g/cm^3) by the determined nutrient value (mg/kg). Inputs of soil moisture, pH and nutrients at each location due to ruminant dung were calculated by subtracting the values of control plots (CPs) from the values of the dung residue plots (DPs).

Vegetation sampling and analyses

For each established $1 \times 1 \text{ m}$ plot, the numbers of individual plants were recorded by species and above-ground live biomass of each species was clipped at the soil surface. All samples were oven-dried at $80 \text{ }^\circ\text{C}$ to constant mass and weighed.

Six plant functional attributes pertaining to the various life forms (grasses, sedges and forbs), growth forms (erect, prostrate, procumbent and decumbent), life span (annual, biennial and perennial), relative height (tall, medium and short), N-fixing ability (leguminous forbs and non-leguminous forbs) and origin and distribution (native, non-native and cosmopolitan) were selected. We selected these traits because of their differentiating role of morphology, phenology, competitive ability and taxonomy (Diekmann and Falkengren-Grerup 2002). Species were classed as medium height if 45–90 cm tall, while those below and above this range were grouped as short and tall categories, respectively. Other traits were determined with the help of Flora of Raipur, Durg and Rajnandangaon (Verma et al. 1985) and Flora of the

upper Gangetic plain (Duthie 1903). The biomass of each functional attribute was computed by summing the biomass of all species in each category.

The Importance Value Index (IVI) of each herbaceous species for each location was calculated by summing the relative frequency, relative density and relative biomass (Mueller-Dombois and Ellenberg 1974). The alpha-diversity (H') and its components, i.e. species richness (number of species/ m^2), evenness (E ; distribution of importance values among the species), and beta diversity in terms of habitat heterogeneity (β) were calculated for each location. The following equations were used to calculate the species diversity indices:

$$H' = -\sum_{i=1}^s p_i \ln p_i \quad (\text{Shannon and Weaver 1949})$$

$$E = \frac{H'}{\ln S} \quad (\text{Pielou 1966})$$

$$\beta = \frac{Sc}{\bar{S}} \quad (\text{Whittaker 1972})$$

where:

p_i = the proportion of importance value belonging to species ' i '; S = number of species; Sc = total number of species in the pooled sample; and \bar{S} = average number of species per sample. The diversities of DPs and CPs were compared using the k -dominance plots in which percent cumulative importance values were plotted against log species rank (Platt et al. 1984).

Statistical analyses

Analysis of variance (ANOVA) procedures of SPSS package (SPSS 1997) were used to examine the effects of trait, treatment and location on the soil and vegetation parameters. Paired 't'-test was used to understand the notable variations in the means of soil and vegetation parameters between the treatments. A Tukey's HSD (honestly significant difference) test was used to determine the significance of differences in the soil and vegetation variables among the locations and the traits. The locations of DPs and CPs were ordinated by PCA, using PC-ORD software (McCune and Mefford 1999). Pearson correlation coefficient was established between the soil variables with the help of SPSS package (SPSS 1997). In addition, stepwise regression was used to find out the main soil variables to explain the variability in species and biomass in DPs and CPs with the help of SPSS software (SPSS 1997).

Results

Soil moisture, porosity, pH and nutrient concentrations

Across DP and CP locations, soil moisture, porosity, pH, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, mineral-N, organic-N and total-N ranged from 3.7 to 21%, 48 to 76%, 7.4 to 7.8, 0.9 to 5.4 kg/ha, 0.6 to 3.0 kg/ha, 1.6 to 8.4 kg/ha, 527 to 1,059 kg/ha and 529 to 1,064 kg/ha, respectively. The mean values for soil moisture ($t = 18.33$, $P \leq 0.0001$), porosity ($t = 12.86$, $P \leq 0.0001$), $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, mineral-N, organic-N and total-N were significantly higher in DPs than in CPs (Tables 1–3). Contrastingly, the mean values for soil pH ($t = 17.44$, $P \leq 0.0001$) were higher in CPs than in DPs (Tables 1–3). ANOVA showed significant differences in these variables due to locations, treatments and location \times treatment (Table 3). Similarly, total-C, total-P and C:N ratio varied significantly due to location, treatment and location \times treatment (Table 3), with values approximately 2-fold greater in DPs than CPs (Tables 1 and 2). PCA ordination based on component soil attributes distinctly categorized DPs and CPs (Figure 1).

Pearson correlation analysis showed significant relationships between C:N ratio and $\text{NH}_4^+\text{-N}$ ($r = -0.58$, $P \leq 0.05$), $\text{NO}_3^-\text{-N}$ ($r = -0.59$, $P \leq 0.05$), mineral-N ($r = -0.68$, $P \leq 0.05$), organic-N ($r = -0.67$, $P \leq 0.05$), total-N ($r = -0.66$, $P \leq 0.05$), total-C ($r = 0.91$, $P \leq 0.001$) and total-P ($r = 0.67$, $P \leq 0.05$) in DPs, while in CPs, only total-C ($r = 0.97$, $P \leq 0.001$) and total-P ($r = -0.59$, $P \leq 0.05$) were significantly related with C:N ratio.

Nutrient inputs due to dung deposition

The subtraction of nutrient concentration of CPs from that of DPs is referred to here as nutrient input due to ruminant dung. ANOVA suggested that soil $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, mineral-N, organic-N, total-N, total-C, total-P and C:N ratio contributed by ruminant dung varied substantially due to location (Table 3). Across the locations, the changes of these nutrients displayed the following ranges: 1.3–3.0, 0.9–1.9, 2.2–4.5, 124–502, 127–506, 3,928–10,718, 27–60 kg/ha and 0.1–12.2, respectively (Tables 1 and 2). Similarly, soil moisture (5.3–12.9%), porosity (0.0–14%) and pH (-0.09 to -0.33) inputs or outputs (depending on a particular case) also varied with the location (Table 3).

Table 1. Mean soil physico-chemical characteristics (\pm s.e.) of different off dung pat locations (CPs).

Location	Moisture (%)	Porosity (%)	pH	$\text{NH}_4^+\text{-N}$	$\text{NO}_3^-\text{-N}$	Mineral-N	Organic-N	Total-N	Total-C	C:N ratio	Total-P (kg/ha)
				(kg/ha)							
INH	3.7a (0.1)	48a (2.2)	7.8e (0.0)	2.1b (0.1)	1.3g (0.0)	3.4c (0.2)	719c (33)	722cd (33)	949a (33)	1.3a (0.0)	73ab (3)
KAS	4.1ab (0.0)	52ab (0.1)	7.8de (0.0)	1.9b (0.0)	1.3e (0.0)	3.1bc (0.0)	744c (4)	747cd (4)	989a (2)	1.3a (0.0)	76ab (1)
SUK	4.7cd (0.1)	57bc (0.1)	7.8bcd (0.0)	1.8b (0.0)	1.2e (0.0)	2.9bc (0.0)	684bc (3)	687bcd (3)	922a (3)	1.3a (0.0)	77b (0.15)
SNPG	3.9a (0.1)	51a (0.2)	7.7e (0.0)	1.9b (0.0)	1.4fg (0.0)	3.3c (0.0)	731c (17)	734cd (17)	997a (11)	1.4a (0.0)	74ab (0.95)
MMV	5.1def (0.1)	62cd (2.3)	7.7cde (0.0)	3.0c (0.2)	1.2e (0.1)	4.2d (0.3)	762c (43)	766d (43)	5,934d (365)	7.7b (0.1)	74ab (4.48)
BG	5.5f (0.0)	65de (0.2)	7.7bcd (0.0)	1.9b (0.0)	0.8bc (0.0)	2.7b (0.1)	744c (9)	747cd (9)	5,549cd (33)	7.4b (0.1)	74ab (0.9)
MB	5.3ef (0.1)	64d (0.1)	7.7bcd (0.0)	2.9c (0.0)	1.1de (0.0)	4.0d (0.0)	696bc (12)	700bcd (12)	4,999bc (30)	7.2b (0.2)	70ab (0.2)
MC	4.9de (0.1)	63d (1.3)	7.7bcd (0.0)	2.9c (0.1)	1.1efg (0.0)	4.1d (0.2)	761c (29)	765cd (29)	5,770d (190)	7.6b (0.1)	74ab (2.9)
AG-1	5.3ef (0.1)	69ef (0.2)	7.6ab (0.0)	1.3a (0.0)	0.7ab (0.0)	2.0a (0.0)	527a (25)	529a (25)	6,022d (255)	11.4cd (0.1)	66ab (1.0)
AG-2	6.1g (0.1)	70f (0.3)	7.5a (0.0)	0.9a (0.0)	0.6a (0.0)	1.6a (0.0)	557bc (5)	558ab (5)	4,706b (55)	8.4b (0.1)	65a (0.8)
AG-3	5.3ef (0.2)	65de (0.2)	7.7bcd (0.1)	2.1b (0.0)	0.9cd (0.0)	3.0bc (0.0)	610abc (3)	613abc (3)	5,661cd (25)	9.2bc (0.1)	66ab (0.4)
GB	4.4bc (0.2)	48a (1.1)	7.8de (0.0)	3.1c (0.1)	1.4g (0.0)	4.5d (0.1)	661abc (75)	666abcd (75)	8,519e (180)	13.2d (1.6)	73ab (3.68)

INH = International Hostel, KAS = Kasturba, SUK = Sukanya, SNPG = Sarojani Nayadu, MMV = Mahila Maha Vidhyalay, BG = Botanical Garden, MB = Madhuban, MC = Meera Colony, AG-1 = Agriculture Farm-1, AG-2 = Agriculture Farm-2 AG-3 = Agriculture Farm-3 and GB = Gandhi Bhawan.

Table 2. Mean soil physico-chemical characteristics (\pm s.e.) of different dung pat locations (DPs).

Location	Moisture (%)	Porosity (%)	pH	NH ₄ ⁺ -N	NO ₃ ⁻ -N	Mineral-N Organic-N Total-N			Total-C	C:N ratio	Total-P (kg/ha)
						(kg/ha)					
INH	9.0a (0.0)	53a (0.1)	7.6d (0.0)	3.8ab (0.0)	2.8de (0.0)	6.5abc (0.0)	843a (13)	849a (13)	9,632ab (38)	11.4b (0.2)	133f (0.6)
KAS	10.1a (0.0)	55a (0.1)	7.6d (0.0)	3.8abc (0.0)	2.5bcd (0.0)	6.3abc (0.0)	906a (13)	912a (13)	11,226bcd (10)	12.3bc (0.2)	131f (0.6)
SUK	12.2b (0.1)	58ab (0.3)	7.6d (0.0)	3.8ab (0.0)	2.5abcd (0.0)	6.2ab (0.0)	907a (11)	913a (11)	10,941abc (78)	12.0bc (0.2)	123cdef (1)
SNPG	9.3a (0.0)	54a (0.2)	7.6d (0.0)	3.8abcd (0.0)	2.7cde (0.0)	6.5abc (0.1)	860a (16)	867a (16)	11,715cd (71)	13.5bc (0.3)	133f (0.8)
MMV	14.7c (0.3)	62bc (2.0)	7.5c (0.0)	5.4g (0.3)	3.0e (0.2)	8.4e (0.4)	909a (44)	917a (45)	12,315cd (644)	13.4bc (0.1)	138f (7)
BG	18.4fg (0.6)	71ef (0.5)	7.4a (0.0)	4.4de (0.1)	2.3ab (0.0)	6.7bc (0.1)	917ab (12)	924ab (12)	10,963bcd (167)	11.9bc (0.1)	106abc (1)
MB	16.3de (0.3)	68de (0.7)	7.4ab (0.0)	4.8efg (0.1)	2.5abcd (0.1)	7.3cd (0.2)	916ab (28)	923ab (28)	11,126bcd (203)	12.1bc (0.6)	114cde (2)
MC	15.8cd (0.2)	65cd (1.2)	7.5bc (0.0)	5.3fg (0.2)	2.7cde (0.1)	8.0de (0.3)	889a (32)	897a (32)	12,548d (429)	14.0c (0.8)	127def (4)
AG-1	19.5gh (0.3)	74fg (0.2)	7.4ab (0.0)	4.3bcde (0.0)	2.2a (0.0)	6.4abc (0.0)	892a (51)	899a (51)	10,785bcd (369)	12.1bc (0.7)	95ab (1)
AG-2	21.0h (0.6)	76g (0.3)	7.4a (0.0)	3.6a (0.1)	2.1a (0.0)	5.7a (0.0)	1,059b (21)	1,064b (21)	8,913a (91)	8.4a (0.3)	92a (2)
AG-3	17.5ef (0.3)	69def (1.1)	7.4ab (0.0)	4.6ef (0.2)	2.4abc (0.1)	7.0bcd (0.3)	883a (34)	890a (34)	10,726bc (366)	12.1bc (0.6)	110bcd (3)
GB	14.5c (0.3)	62bc (2.2)	7.5bc (0.0)	4.4cde (0.2)	2.3ab (0.1)	6.7bc (0.3)	961ab (31)	967ab (31)	12,447cd (690)	12.9bc (0.8)	132f (6)

Means within columns followed by different letters are significantly different at $P \leq 0.05$. INH = International Hostel, KAS = Kasturba, SUK = Sukanya, SNPG = Sarojani Nayadu, MMV = Mahila Maha Vidhyalay, BG = Botanical Garden, MB = Madhuban, MC = Meera Colony, AG-1 = Agriculture Farm-1, AG-2 = Agriculture Farm-2 AG-3 = Agriculture Farm-3 and GB = Gandhi Bhawan.

Table 3. Summary of ANOVA (F -values and degrees of freedom) of different soil and vegetation parameters due to location and treatment (DP and CP).

Variable	Location	Treatment	Location \times Treatment
	$F_{11,48} =$	$F_{1,48} =$	$F_{11,48} =$
Soil moisture	215***	1,177***	109***
Porosity	111***	107***	5.97***
pH	49***	1,021***	8.46***
NH ₄ ⁺ -N	74***	2,768***	11.36***
NO ₃ ⁻ -N	40***	4,175***	8.63***
Mineral-N	50***	3,345***	9.38***
Organic-N	3.19**	367***	7.73***
Total-N	3.25**	377***	7.74***
Total-C	69***	3,965***	41.94***
C:N ratio	43.3***	902***	45.60***
Total-P	21.7***	1,636***	9.91***
Richness	26.48***	1,718***	5.37***
Evenness	3.42**	22***	5.85***
Shannon index	23.17***	1,080***	7.35***
Beta diversity	8.5***	253***	2.91**
Biomass	139***	761***	46.15***

** = $P \leq 0.001$; *** = $P \leq 0.0001$.

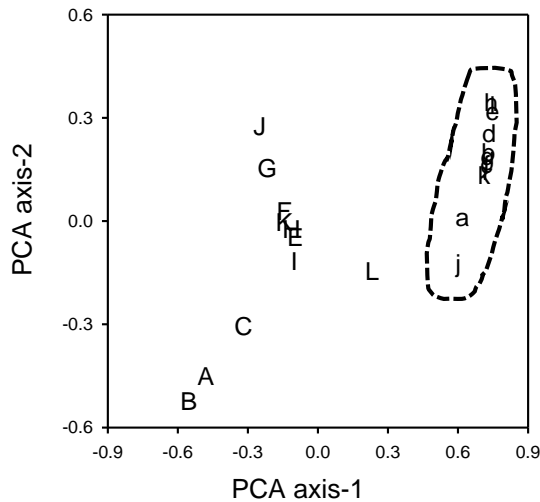


Figure 1. PCA ordination of different off dung pat (capital letters) and dung pat (small letters) locations (CPs resp. DPs) on the basis of nutrient concentrations. The letters within the dotted line represent the dung pat locations. In the ordination diagram A and a = International Hostel, B and b = Sukanya, C and c = Kasturba, D and d = Sarojani Nayadu, E and e = Mahila MahaVidhyalay, F and f = Botanical Garden, G and g = Gandhi Bhawan, H and h = Madhuban, I and i = Meera Colony, J and j = Agriculture Farm-1, K and k = Agriculture Farm-2, L and l = Agriculture Farm-3.

Species composition

A total of 74 species belonging to 66 genera and 25 families was recorded from seventy-two 1×1 m plots (Table 4). The families Asteraceae and Poaceae had the highest number of species (10), followed by Fabaceae (7) and Amaranthaceae (6), with 12 families being represented by a single species. The DPs had 72 species and CPs had 52 species. Twenty-three species were exclusively present in DPs, while only 2 species were restricted to CPs, and 49 species were common to both DPs and CPs (Table 4).

On the basis of biomass, *Cynodon dactylon* was the dominant species for both DPs and CPs. The second and third most common species in DPs were *Echinochloa crus-galli* and *Urena lobata*, respectively, while *Malvastrum tricuspidatum* was the second and *Oxalis corniculata* the third most common species in CPs (Table 4). PCA ordination based on component species of these 2 treatments also showed differences in species composition of DPs and CPs (Figure 2).

Species diversity and biomass

Across locations, the mean species number, evenness, Shannon index and beta diversity per plot varied from 3 to 17, 0.70 to 0.97, 1.05 to 2.62 and 1.07 to 3.14, respectively (Tables 5 and 6). ANOVA suggested that these diversity indices differed substantially due to location, treatment and location \times treatment (Table 3). Mean

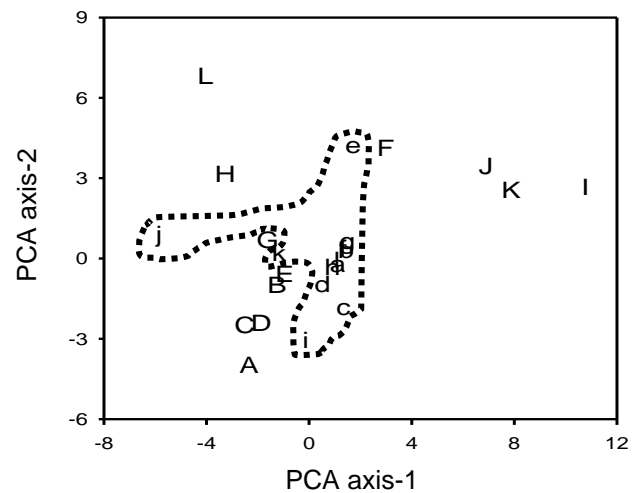


Figure 2. PCA ordination of different dung (capital letters) and off dung pat (small letters) locations (CPs resp. DPs) on the basis of relative biomass of herbaceous species. The letters within the dotted line represent the off dung pat locations. Stepwise regression showed that the soil phosphorus explained PCA axis-1 in CPs, while soil phosphorus and soil pH, respectively, explained PCA axes-1 and -2 in DPs. In the ordination diagram A and a = International Hostel, B and b = Sukanya, C and c = Kasturba, D and d = Sarojani Nayadu, E and e = Mahila MahaVidhyalay, F and f = Botanical Garden, G and g = Gandhi Bhawan, H and h = Madhuban, I and i = Meera Colony, J and j = Agriculture Farm-1, K and k = Agriculture Farm-2, L and l = Agriculture Farm-3.

values for species number and Shannon index were higher in DPs than in CPs. On the other hand, mean values for evenness and beta diversity were lower in DPs than in CPs (Tables 5 and 6). Thus, dung inputs by ruminants promoted species diversity and restricted the distribution of individuals among the species. The k -dominance plots for DPs and CPs are illustrated in Figure 3, in which the uppermost line (DPs) represented greater diversity than the bottom line (CPs).

On the basis of stepwise regression analysis, soil moisture explained 97% of the variation in species number and soil porosity explained 85% of the variation in Shannon index and 69% of the variation in beta diversity in CPs, while none of the soil variables explained the variability in species evenness. In contrast with these patterns, soil pH independently accounted for 85% of the variation in species number and, together with $\text{NO}_3\text{-N}$, explained 91% of the variation in species number in DPs. Similarly, soil pH also accounted for variation in Shannon index, while soil moisture accounted for variation in species evenness and beta diversity (Table 7). Linear regression analysis showed significant negative relationships between soil pH and species number in both DPs and CPs (Figure 4). Further, the higher determination coefficient (R^2) in DPs than in CPs (0.92 vs. 0.55) suggested that soil pH had a greater influence on species number in areas where dung was deposited.

Table 4. Species and biomass (g DM/ha) of herbaceous species of different dung pat and off dung pat locations (CPs resp. DPs).

Species ¹	Family	Dung pat (DP)		Off dung pat (CP)	
		Biomass	Sites occupied	Biomass	Sites occupied
<i>Abutilon indicum</i> (L.) Sweet E,L,Pe,NLF,N	Malvaceae	46	BG, MC, AG-1, AG-2, AG-3	13	MB
<i>Acalypha indica</i> L. E,M,A,NLF,N	Euphorbiaceae	17	INH, SUK, MMV, BG, MB	4	SNPG
<i>Achyranthes aspera</i> L. E,L,Bi,NLF,N	Amaranthaceae	38	INH, SUK, BG, MB, MC, GB	8	KAS, MB
<i>Aerva sanguinolenta</i> (L.) Blume E,L,Pe,NLF,N	Amaranthaceae	13	INH, SUK, MMV, MB,	14	MMV, BG, GB
<i>Aeschynomene indica</i> L. E,M,Bi,LF,NN	Fabaceae	9	AG-1,AG-2	0	
<i>Ageratum conyzoides</i> L. E,L,A,NLF,NN	Asteraceae	35	SUK, MMV, BG, MB, MC, GB	10	AG-2
<i>Alternanthera sessilis</i> (L.) R. Br. ex DC. P,L,A,NLF,NN	Amaranthaceae	17	BG, MB, MC, AG-1	24	MMV, BG, GB
<i>Alysicarpus vaginalis</i> (L.) DC. De,L,Pe,LF,N	Fabaceae	16	AG-2, AG-3	4	AG-2
<i>Amaranthus spinosus</i> L. E,L,A,NLF,NN	Amaranthaceae	33	BG, AG-1, AG-2, AG-3	0	
<i>Amaranthus viridis</i> L. E,M,A,NLF,NN	Amaranthaceae	16	BG, MB, MC, GB	14	BG, MB
<i>Ammannia baccifera</i> L. E,L,A,NLF,N	Lythraceae	12	GB	54	KAS, SUK, SNPG, MC, AG-1
<i>Anagallis arvensis</i> L. E,M,A,NLF,NN	Primulaceae	12	AG-1, AG-3	0	
<i>Argemone mexicana</i> L. E,L,A,NLF,NN	Papaveraceae	22	BG, MC, AG-1, AG-3	0	
<i>Atylosia marmorata</i> R. Br. ex Benth. P,L,A,LF,NN	Fabaceae	3	MMV, BG, MB	34	BG, MB, AG-2, AG-3, GB
<i>Biophytum sensitivum</i> (L.) DC. E,L,A,NLF,NN	Oxalidaceae	16	AG-3	0	
<i>Caesulia axillaris</i> Roxb. De,L,A,NLF,N	Asteraceae	12	MC, GB	0	
<i>Chenopodium album</i> L. E,L,A,NLF,NN	Amaranthaceae	33	BG, AG-1, AG-2, AG-3	0	
<i>Commelina benghalensis</i> L. Pro,L,A,NLF,NN	Commelinaceae	53	MMV, BG, AG-1	0	
<i>Convolvulus prostratus</i> Forssk. P,S,Pe,NLF,N	Convolvulaceae	11	INH, SUK, MMV, MB	1	MC
<i>Croton bonplandianus</i> Baill. E,M,Pe,NLF,NN	Euphorbiaceae	12	MC	6	MC
<i>Cynodon dactylon</i> (L.) Pers. P,S,Pe,G,COS	Poaceae	194	INH, SUK, SNPG, MMV, BG, MB, MC, AG-AG-2, AG-3, GB	105	INH, KAS, SUK, SNPG, MMV, BG, MB, MC
<i>Cyperus cyperoides</i> (L.) Kuntze P,M,Pe,Se,NN	Cyperaceae	29	KAS, SNPG, MB, MC, GB	1	MB
<i>Cyperus rotundus</i> L. P,M,Pe,Se,COS	Cyperaceae	43	INH, SUK, SNPG, MB, MC	28	INH, KAS, MMV, MC
<i>Dactyloctenium aegyptium</i> (L.) Willd. De,S,A,G,NN	Poaceae	56	INH, SUK, SNPG, MMV, BG, MB, MC, GB	2	MMV, MB
<i>Desmodium triflorum</i> (L.) DC. E,L,Pe,LF,NN	Fabaceae	0		34	MMV, BG, MB, AG-1
<i>Dichanthium annulatum</i> (Forssk.) Stapf E,S,Pe,G,NN	Poaceae	77	INH, SUK, SNPG, MMV, BG, AG- 1, AG-2, AG-3, GB	9	MB
<i>Digitaria ciliaris</i> (Retz.) Koeler De,S,A,G,NN	Poaceae	48	INH, KAS, SUK, SNPG, MMV, MC	14	AG-1, AG-3
<i>Echinochloa colona</i> (L.) Link De,M,A,G,NN	Poaceae	50	INH, KAS, SNPG, AG-AG-2, AG-3	8	AG-2
<i>Echinochloa crus-galli</i> (L.) Beauv. De,L,A,G,NN	Poaceae	134	SNPG, MMV, BG, MB, MC, AG-1, AG-2, AG-3, GB	0	

Continued

Species ¹	Family	Dung pat (DP)		Off dung pat (CP)	
		Biomass	Sites occupied	Biomass	Sites occupied
<i>Eclipta alba</i> (L.) Hassk. P,S,A,NLF,NN	Asteraceae	28	INH, SUK, SNPG, MB, MC, GB	10	GB
<i>Eleusine indica</i> (L.) Gaertn. E,M,A,G,NN	Poaceae	19	INH, KAS, SUK, SNPG	2	MMV
<i>Eragrostis tenella</i> (L.) P. Beauv. ex Roem. & Schult. E,L,Pe,G,NN	Poaceae	53	INH, KAS, SUK, SNPG, MMV, MB, MC, AG-1, AG-2, AG-3	10	SUK, AG-1
<i>Euphorbia dracunculoides</i> Lam. E,L,Bi,NLF,NN	Euphorbiaceae	34	AG-1, AG-3	16	AG-1, AG-2
<i>Euphorbia hirta</i> L. Pr,L,A,NLF,NN	Euphorbiaceae	62	INH, KAS, SUK, SNPG, MMV, BG, MB, AG-1, AG-2, AG-3	5	MMV
<i>Evolvulus nummularius</i> (L.) L. P,S,Pe,NLF,NN	Convolvulaceae	22	INH, MMV, BG, MB, GB	7	KAS, SUK, GB
<i>Evolvulus alsinoides</i> (L.) L. Pr,S,A,NLF,NN	Convolvulaceae	42	INH, KAS, SNPG, MMV	1	AG-2
<i>Gomphrena celosioides</i> Mart. E,M,A,NLF,NN	Amaranthaceae	49	KAS, SNPG, MMV, MB, MC	0	
<i>Gnaphalium luteoalbum</i> L. De,M,A,NLF,NN	Asteraceae	31	KAS, SNPG, MMV,	0	
<i>Heliotropium indicum</i> L. E,M,A,NLF,NN	Boraginaceae	16	MB, MC, GB	0	
<i>Herpestis monnieri</i> (L.) Kunth E,M,Pe,NLF,N	Plantaginaceae	20	AG-1, AG-2, AG-3, GB	8	SUK, MC
<i>Hyptis suaveolens</i> (L.) Poit. P,L,A,NLF,NN	Lamiaceae	19	AG-1, AG-3, GB	5	GB
<i>Imperata cylindrica</i> (L.) P. Beauv. E,L,Pe,G,NN	Poaceae	36	AG-1, AG-2, AG-3	5	BG
<i>Indigofera linifolia</i> (L. f.) Retz. Pr,M,A,LF,NN	Fabaceae	13	SNPG, AG-1, AG-2, AG-3	6	AG-1
<i>Lathyrus aphaca</i> L. E,M,A,LF,NN	Fabaceae	8	AG-2	3	AG-2
<i>Launaea procumbens</i> (Roxb.) Ramayya & Rajagopal P,S,Pe,NLF,N	Asteraceae	38	KAS, SNPG, MMV, BG, MB	16	MMV, AG-1, AG-2
<i>Leucas aspera</i> (Willd.) Link E,M,A,NLF,NN	Lamiaceae	33	BG, MB, MC, GB	1	AG-1
<i>Lindenbergia indica</i> (L.) Vatke E,L,A,NLF,N	Orobanchaceae	12	GB	15	MMV, BG
<i>Malvastrum tricuspidatum</i> (R. Br.) A. Gray E,L,Pe,NLF,NN	Malvaceae	55	SUK, SNPG, BG, MB, MC, AG-1, AG-2, AG-3	62	INH, BG, MC, AG-1, 1GB
<i>Melilotus albus</i> Medik. E,L,Bi,LF,NN	Fabaceae	28	AG-1, AG-2	13	AG-1, AG-2
<i>Nicotiana alata</i> Link & Otto E,M,Pe,NLF,NN	Solanaceae	2	GB	3	MB
<i>Oldenlandia corymbosa</i> L. P,M,A,NLF,NN	Rubiaceae	2	KAS, SUK, SNPG	12	SNPG, AG-1, AG-2
<i>Oplismenus compositus</i> (L.) P. Beauv. P,S,Pe,G,NN	Poaceae	32	KAS, SUK, SNPG, MMV, BG, AG- 1, AG-2, AG-3	19	KAS, MMV, AG-3, GB
<i>Oxalis corniculata</i> L. Pr,S,Pe,NLF,NN	Oxalidaceae	12	AG-1, AG-3	55	INH, KAS, SUK, SNPG, BG, MB, AG-1
<i>Parthenium hysterophorus</i> L. E,L,Pe,NLF,NN	Asteraceae	66	MC, AG-2, AG-3, GB	0	
<i>Paspalum flavidum</i> (Retz.) A. Camus P,L,Pe,G,NN	Poaceae	0		4	AG-2
<i>Peristrophe bicalyculata</i> (Retz.) Nees. E,L,Pe,NLF,NN	Acanthaceae	6	GB	0	
<i>Phyla nodiflora</i> (L.) Greene P,L,A,NLF,NN	Verbenaceae	2	MC	0	

Continued

Species ¹	Family	Dung pat (DP)		Off dung pat (CP)	
		Biomass	Sites occupied	Biomass	Sites occupied
<i>Portulaca oleracea</i> L. ^{P,S,A,NLF,NN}	Portulacaceae	66	INH, KAS, SUK, SNPG, MMV, MB	0	
<i>Ranunculus sceleratus</i> L. ^{E,L,A,NLF,NN}	Ranunculaceae	32	AG-1, AG-2, AG-3	0	
<i>Rorippa dubia</i> (Pers.) H. Hara ^{E,M,A,NLF,N}	Brassicaceae	28	AG-1, AG-2, AG-3	14	INH, SUK
<i>Ruellia tuberosa</i> L. ^{E,M,Bi,NLF,NN}	Acanthaceae	4	GB	1	MC
<i>Rumex dentatus</i> L. ^{E,L,Bi,NLF,N}	Polygonaceae	25	AG-1, AG-2, AG-3	0	
<i>Rungia pectinata</i> (L.) Nees ^{Pr,M,A,NLF,N}	Acanthaceae	4	GB	21	INH, SUK, BG, AG-3
<i>Rungia parviflora</i> Nees ^{Pr,M,A,NLF,NN}	Acanthaceae	26	KAS, SUK, SNPG, BG, MB, AG-1, AG-2, AG-3	0	
<i>Scoparia dulcis</i> L. ^{E,M,Pe,NLF,NN}	Plantaginaceae	22	SUK, SNPG, MMV AG-3, GB	1	AG-3
<i>Sida acuta</i> Burm. f. ^{E,L,Bi,NLF,NN}	Malvaceae	57	KAS, SUK, SNPG, GB	47	INH, KAS, SNPG, BG, MC, AG-3
<i>Sida cordifolia</i> L. ^{E,S,Pe,NLF,NN}	Malvaceae	121	INH, KAS, SUK, SNPG, MMV, BG, MB, MC, GB	0	
<i>Solanum nigrum</i> L. ^{E,L,A,NLF,NN}	Solanaceae	22	MC, AG-2	17	MC, AG-2, AG-3
<i>Sonchus oleraceus</i> L. ^{E,L,A,NLF,NN}	Asteraceae	47	AG-1, AG-2, AG-3	21	AG-1, AG-2, AG-3
<i>Spilanthes acmella</i> (L.) L. ^{E,M,Pe,NLF,NN}	Asteraceae	21	BG, MB, MC, GB	0	
<i>Tridax procumbens</i> L. ^{Pr,M,Pe,NLF,NN}	Asteraceae	16	SUK, SNPG, MB, MC	15	SUK, SNPG
<i>Uraria picta</i> (Jacq.) Desv. ex DC. ^{E,L,Pe,LF,N}	Fabaceae	20	AG-2, AG-3	0	
<i>Urena lobata</i> L. ^{E,L,Pe,NLF,NN}	Malvaceae	162	KAS, SNPG, MMV, BG, MB, MC, AG-1, AG-2, AG-3, GB	0	
<i>Vernonia cinerea</i> (L.) Less. ^{E,M,A,NLF,NN}	Asteraceae	9	SUK, MB, GB	6	MMV

¹Nomenclature according to the Tropicos taxonomic database (www.tropicos.org).

Abbreviations used: E = Erect, P = Prostrate, De = Decumbent, Pr = Procumbent; L = Tall, M = Medium, S = Short height; A = Annual, Bi = Biennial, Pe = Perennial; G = Grasses, Se = Sedges, NLF = Non-leguminous forb, LF = leguminous forb; N = Native, NN = Non-native, COS = Cosmopolitan; INH = International Hostel, SUK = Sukanya, KAS = Kasturba, SNPG = Sarojani Nayadu, MMV = Mahila MahaVidhyalay, BG = Botanical Garden, GB = Gandhi Bhawan, MB = Madhuban, MC = Meera Colony, AG-1 = Agriculture Farm-1, AG-2 = Agriculture Farm-2 and AG-3 = Agriculture Farm-3.

Across species, locations and treatments, herbaceous biomass varied between 0.4 and 194 g/m² (Table 4) and from 14.6 to 93 g/m² across locations and treatments (Tables 5 and 6). ANOVA showed substantial variation in herbaceous biomass owing to location, treatment and coupling of location and treatment (Table 3). Step-wise regression suggested that soil moisture explained much of the variation in herbaceous biomass in both treatments (DP and CP), with greater values in DP than in CP (Tables 5–7). Thus, greater soil moisture availability together with soil nutrients provided greater biomass accumulation in this dry tropical grassland.

Plant functional attributes

ANOVA revealed significant variation in species number and biomass of plants with different functional attributes due to trait, location and treatment and their interactions (Table 8). The differences in mean species number and biomass among plants with different traits in DPs and CPs, analyzed by the HSD test, are presented in Table 9. Forbs plus erect, annual, tall, non-native and non-leguminous plants predominated in both DPs and CPs, while mean values for species number and biomass for plants with different traits were greater in DPs than in CPs (Table 9).

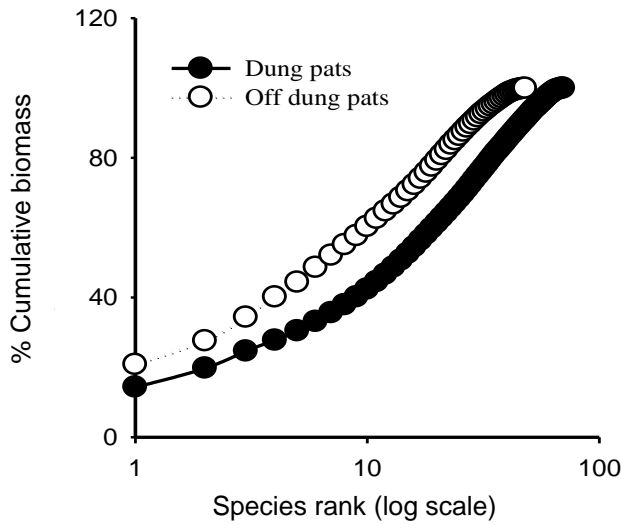


Figure 3. The k-dominance plot in which total percentage cumulative biomass is plotted against log species rank for dung and off dung pats (DPs resp. CPs).

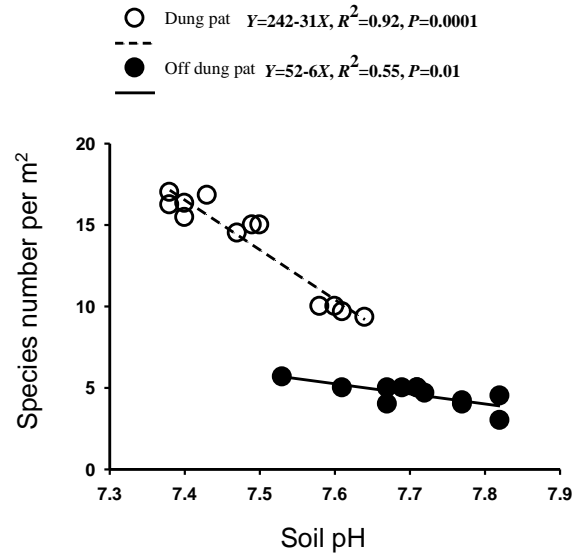


Figure 4. Linear relationships between soil pH (X) and species number (Y) at dung and off dung pat locations (CP resp. DP).

Table 5. Mean values for vegetation parameters (\pm s.e.) at different off dung pat locations (CPs).

Location	Species number	Evenness	Shannon index	Beta diversity	Biomass (g DM/m ²)
INH	4.5ab (0.00)	0.96ab (0.03)	1.05a (0.04)	1.76a (0.19)	14.7a (0.13)
KAS	4.2ab (0.33)	0.89ab (0.04)	1.14ab (0.06)	1.80ab (0.10)	17.0a (0.58)
SUK	4.0ab (0.00)	0.90ab (0.03)	1.24abc (0.05)	2.11ab (0.06)	22.5bc (0.29)
SNPG	3.0a (0.00)	0.97b (0.00)	1.07a (0.00)	2.51abc (0.09)	14.6a (0.15)
MMV	4.7bc (0.33)	0.96ab (0.01)	1.40bc (0.07)	2.32abc (0.05)	24.8d (0.17)
BG	5.0c (0.00)	0.93ab (0.01)	1.49c (0.02)	2.63abc (0.13)	28.3d (0.88)
MB	5.0c (0.00)	0.89ab (0.01)	1.44bc (0.02)	2.69abc (0.27)	24.5c (0.29)
MC	5.00c (0.00)	0.78a (0.08)	1.26abc (0.12)	2.77bc (0.26)	23.0bc (0.29)
AG-1	5.00c (0.00)	0.92ab (0.02)	1.48c (0.03)	3.09c (0.31)	29.0d (0.58)
AG-2	5.67d (0.33)	0.79a (0.02)	1.41bc (0.04)	3.14c (0.14)	30.0d (0.58)
AG-3	5.00c (0.00)	0.91ab (0.04)	1.46c (0.07)	3.13c (0.32)	24.0c (0.58)
GB	4.00abc (0.58)	0.85ab (0.05)	1.14ab (0.08)	2.27abc (0.08)	21.2b (0.44)

INH = International Hostel, KAS = Kasturba, SUK = Sukanya, SNPG = Sarojani Nayadu, MMV = Mahila Maha Vidhyalay, BG = Botanical Garden, MB = Madhuban, MC = Meera Colony, AG-1 = Agriculture Farm-1, AG-2 = Agriculture Farm-2, AG-3 = Agriculture Farm-3 and GB = Gandhi Bhawan.

Table 6. Mean values for vegetation parameters (\pm s.e.) at different dung pat locations (DPs).

Location	Species number	Evenness	Shannon index	Beta diversity	Biomass (g DM/m ²)
INH	9.3a (0.33)	0.75ab (0.01)	1.69a (0.04)	1.18ab (0.10)	44a (1.4)
KAS	10.0a (0.00)	0.70a (0.02)	1.63a (0.05)	1.46abc (0.08)	50a (0.3)
SUK	10.0a (0.00)	0.82abcd (0.04)	1.90ab (0.10)	1.39abc (0.11)	53a (1.3)
SNPG	9.7a (0.33)	0.84bcd (0.00)	1.92abc (0.04)	1.07a (0.07)	48a (0.3)
MMV	15.0b (0.58)	0.83abcd (0.05)	2.25cd (0.13)	1.53abc (0.20)	68b (2.7)
BG	17.0c (0.33)	0.81abcd (0.01)	2.27cde (0.01)	1.65abc (0.13)	88de (3.1)
MB	16.33bc (0.88)	0.82abcd (0.04)	2.22bcd (0.11)	1.21ab (0.07)	77c (1.8)
MC	15.00b (0.58)	0.80abcd (0.01)	2.16bcd (0.03)	1.29ab (0.26)	74bc (1.1)
AG-1	15.46b (1.00)	0.91cd (0.01)	2.49de (0.05)	1.59abc (0.08)	93e (2.7)
AG-2	16.24bc (1.45)	0.93d (0.01)	2.44de (0.08)	2.01c (0.10)	93e (1.6)
AG-3	16.82bc (0.88)	0.89cd (0.01)	2.33de (0.04)	1.79bc (0.13)	79cd (2.2)
GB	14.50b (0.58)	0.92cd (0.01)	2.62e (0.05)	1.27ab (0.11)	74bc (1.1)

Means within columns followed by different letters are significantly different at $P \leq 0.05$. INH = International Hostel, KAS = Kasturba, SUK = Sukanya, SNPG = Sarojani Nayadu, MMV = Mahila Maha Vidhyalay, BG = Botanical Garden, MB = Madhuban, MC = Meera Colony, AG-1 = Agriculture Farm-1, AG-2 = Agriculture Farm-2 AG-3 = Agriculture Farm-3 and GB = Gandhi Bhawan.

Table 7. Products of stepwise regressions between different soil and vegetation variables in off dung (CP) and dung pats (DP) for herbaceous vegetation.

Off dung pat (CP)				Dung pat (DP)			
Models	Regression equations	R ²	P	Models	Regression equations	R ²	P
1	$SR = -0.58 + 0.31M$	0.97	≤ 0.0001	1	$SR = 38 - 4.7pH$	0.85	≤ 0.0001
				2	$SR = 44 - 5.7pH + 0.6Ni$	0.91	≤ 0.0001
1	No relation	-	-	1	$E = 0.67 + 0.01M$	0.46	≤ 0.02
1	$Sh = 0.15 + 0.02Por$	0.85	≤ 0.0001	1	$Sh = 22.06 - 2.7pH$	0.70	≤ 0.001
1	$\beta = -0.47 + 0.05Por$	0.69	≤ 0.001	1	$\beta = 0.69 + 0.05M$	0.56	≤ 0.005
2	$\beta = 4.45 + 0.03Por - 0.05P$	0.81	≤ 0.001				
1	$B = -11.07 + 7.0M$	0.82	≤ 0.0001	1	$B = 5.87 + 4.32M$	0.97	≤ 0.0001

In the equations, *S*, *E*, *Sh*, β , *B*, *M*, *Por*, *P*, *pH* and *Ni* represent species number, evenness, Shannon index, beta diversity, biomass, soil moisture, soil porosity, soil phosphorus, soil pH and soil nitrate nitrogen, respectively.

Table 8. Summary of ANOVA on herbaceous species number and biomass of different trait categories.

Sources	Dependent variables	Df	F	
			Species	Biomass
Trait	Life form	2	525***	324***
	Growth form	3	303***	97***
	Life span	2	172***	105***
	Height	2	40***	34***
	Nativity	2	664***	339***
	N-fixing ability	1	231***	179***
Location	Life form	11	4.20***	4.71***
	Growth form	11	4.59***	2.97**
	Life span	11	4.19***	4.77***
	Height	11	4.17***	3.59***
	Nativity	11	4.60***	5.32***
	N-fixing ability	11	3.02**	2.41*
Treatment	Life form	1	365***	236***
	Growth form	1	425***	143***
	Life span	1	299***	203***
	Height	1	364***	144***
	Nativity	1	427***	244***
	N-fixing ability	1	92***	70***
Trait × Location	Life form	22	7.15***	5.16***
	Growth form	33	6.90***	3.74***
	Life span	22	2.73***	2.41**
	Height	22	10.85***	6.01***
	Nativity	22	6.00***	8.04***
	N-fixing ability	11	2.32*	1.45 ^{NS}
Location × Treatment	Life form	11	1.69 ^{NS}	1.86*
	Growth form	11	1.75 ^{NS}	1.44 ^{NS}
	Life span	11	1.94*	2.49**
	Height	11	1.82*	1.31 ^{NS}
	Nativity	11	2.00*	2.28*
	N-fixing activity	11	1.26 ^{NS}	0.95 ^{NS}
Trait × Treatment	Life form	2	111***	71***
	Growth form	3	97***	32***
	Life span	2	49***	29***
	Height	2	5.96**	9.01***
	Nativity	2	270***	146***
	N-fixing activity	1	77***	49***
Trait × Location × Treatment	Life form	22	4.11***	2.63***
	Growth form	33	5.34***	2.42***
	Life span	22	1.97*	0.86 ^{NS}
	Height	22	4.48***	3.00***
	Nativity	22	2.39**	2.59***
	N-fixing activity	11	1.90*	1.64 ^{NS}
Error	Life form	143		
	Growth form	192		
	Life span	143		
	Height	144		
	Nativity	144		
	N-fixing activity	96		

* = P≤0.01, ** = P≤0.001, *** = P≤0.0001 and ^{NS} = non-significant.

Table 9. Mean species number (per m²) and biomass (g DM/m²) (\pm s.e.) of plants with different functional traits in dung pat (DP) and off dung pat (CP) locations.

Plant functional attribute	Trait	Off dung pats		Dung pats		% Increase/decrease	
		Species	Biomass	Species	Biomass	Species	Biomass
Life form	Grasses	1.00b (0.12)	6.19b (0.75)	3.93b (0.28)	24.10b (2)	293	289
	Sedges	0.12a (0.06)	0.61a (0.31)	0.26a (0.11)	1.13a (0.53)	117	85
	Forbs	3.30c (0.21)	16.00c (1.31)	9.26c (0.55)	44.85c (2)	181	180
Growth form	Erect	2.12b (0.20)	11.00b (1.25)	8.00c (0.47)	37.50c (3)	277	241
	Prostrate	1.58b (0.19)	7.09b (1.00)	3.73b (0.24)	22.00b (2)	136	210
	Procumbent	0.47a (0.10)	2.78a (0.62)	1.08a (0.16)	8.08a (1)	130	191
	Decumbent	0.25a (0.07)	1.93a (0.33)	1.58a (0.15)	3.50ab (1)	132	81
Life span	Annual	1.81b (0.21)	9.80b (1.21)	7.19c (0.38)	35.08b (2)	297	257
	Biennial	0.36a (0.10)	1.97a (0.61)	0.80a (0.16)	4.00a (1)	122	103
	Perennial	2.25b (0.22)	11.00b (1.29)	5.40b (0.26)	31.00b (2)	140	182
Height	Tall	2.08c (0.20)	10.80b (1.31)	7.60b (0.54)	45.00b (4)	265	317
	Medium	0.97a (0.11)	5.00a (0.9)	3.02a (0.24)	19.02a (1)	211	280
	Short	1.37b (0.13)	7.00a (1.20)	2.77a (0.38)	15.06a (2)	102	115
Nativity	Native	0.94a (0.14)	4.55a (0.72)	1.42a (0.22)	10.50a (1)	51	131
	Non-native	2.90b (0.26)	14.72b (1.40)	11.00b (0.50)	54.00b (4)	279	267
	Cosmopolitan	0.58a (0.12)	3.53a (0.76)	0.97a (0.10)	7.30a (2)	67	107
N-fixing activity	Leguminous forbs	0.81a (0.12)	6.00a (0.66)	0.36a (0.37)	4.90a (2)	-56	-17
	Non-leguminous forbs	2.49b (0.18)	10.00b (1.27)	8.64b (0.58)	39.95b (3)	247	300

Within parameters, means within columns followed by different letters are significantly different ($P \leq 0.05$).

Discussion

Soil properties

While ruminants depend on grasslands, they control their structure and cycling of energy and nutrients (Augustine and McNaughton 1998) through foraging, trampling and dung and urine inputs, which are important sources of moisture and nutrients for plant establishment and growth on drier locations (Bakker et al. 2004; Williams and Haynes 2006). The greater soil moisture and porosity in DPs compared with CPs in this study may be due to

increased physical mixing of soil by micro- and macro-organisms (dung beetles, earthworms, termites, bacteria and fungi) in DPs (Lovell and Jarvis 1996; Williams and Haynes 2006). The study suggests that dung inputs to the soil by ruminants may improve physical properties, water infiltration and water holding capacity of the soil (Brouwer and Powell 1998).

The lower soil pH in DPs than in CPs may be due to the release of carbonic acids during decomposition of dung residues in the presence of adequate soil moisture and temperature (Rao et al. 2009; Verma et al. 2013). Williams and Haynes (2006) suggest that dung with suf-

ficient soil moisture absorbs greater solar heat, which raises the temperature of underlying soil, and accelerates the decomposition process of dung residue (Stanford et al. 1973), resulting in increased release of carbonic acids. Other studies have also suggested that application of ruminant manure to acidic soils increases the level of acidity (Bussink and Oenema 1998; Whalen et al. 2000).

The negative relationships of C:N ratio with $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, mineral-N, total-N and total-C suggested greater rates of N and C mineralization in DPs compared with CPs. High levels of nutrients in dung residue (undigested food with lignified plant tissues and cell wall, gut microorganisms, secretions and cellular debris from the gut mucosa; Church 1969) might have determined the rates of C- and N-mineralization. It has been suggested that organic matter rich in N (low C:N ratio) has greater C- and N-mineralization than organic matter with low N concentration (Vourlitis et al. 2007; Rao et al. 2009; Verma et al. 2013). In temperate grazed grassland, the return of animal dung can contribute 260 kg N/ha (Schnyder et al. 2010) and 22,500 kg C/ha (Whitehead 1986) and in intensively managed systems may boost concentrations of these elements to a much higher level than in unmanaged grasslands (Lovell and Jarvis 1996). In the present study, the total-N (232 kg/ha) and total-C (6,860 kg/ha) contributed by ruminant dung residue to the soil were lower than the values reported by Schnyder et al. (2010) for N and by Whitehead (1986) for C. It reflected lower nutrient mineralization and C:N ratio in the tropics than in temperate grasslands. Differences in forage quality in the 2 different climates could explain the differences.

Composition, diversity and biomass of plant functional traits

Based on the diversity indices and *k*-dominance analyses, the study showed comparatively higher species diversity in DPs than in CPs. In different situations, other studies have also emphasized that diversity can be unequivocally compared only when the *k*-dominance plots from the locations to be compared do not overlap. In this circumstance, the lowest line will correspond to the most diverse community and the uppermost line will represent the least diversity (Sagar and Singh 2005; Sagar et al. 2012; Verma et al. 2013). This pattern can be explained because of cumulative effects of 2 mechanisms: (1) grazers might have added viable seeds of grasses, forbs and woody species via their digestive tracts to the soil; and (2) the dung might have provided sufficient moisture and nutrients for the germination and establishment of the deposited as well as remaining

seeds at the respective microsites. Seeds of grasses, forbs and woody species can remain viable even after passing through the digestive tracts of ruminants (Thomson et al. 1990; Gardener et al. 1993). It appears that the dung residue created favorable environmental conditions to the microsites for the germination of seeds and subsequent seedling establishment due to increased soil fertility, increased water holding capacity and reduced competition with existing species (Ocumpaugh et al. 1996). Further, nutrients from dung residue may either suppress or destroy some existing species and create gaps and resource availability for other species (Watt 1947; Coffin and Lauenroth 1988). Our experience and observations indicate that livestock preferentially graze areas with no dung in a pasture and avoid pasture adjacent to dung pats. Consequently, areas where dung is deposited carry a much higher biomass of pasture because of differential grazing pressure on dung and non-dung areas. Therefore, the apparent difference between the two plots (DPs and CPs) would over-estimate the increase in growth as a result of dung deposition.

Soil pH is an important attribute affecting species diversity because of its relationship with the availability of nutrients and toxic elements (Pausas and Austin 2001). In unmanaged grassland, Grime (1973) reported maximum species diversity at a range of soil pH of 6.1–6.5; species diversity declined as soils became more acidic or alkaline because few species were adapted to highly acidic or alkaline soils. Both low and high soil pH and nutrients can limit seed germination and plant performance (Van den Berg et al. 2005). In this alkaline soil, dung residue lowered soil pH and resulted in the accumulation of a larger number of species. Evidently, the negative relationships between soil pH and the parameters of species diversity in DPs promoted species diversity due to decreased soil pH as reported by Verma et al. (2013) in a nitrogen-amendment experiment.

In an N-deposition study, Lauenroth et al. (1978) reported variation in community structure mainly due to changes in several dominant groups. While factors like rooting depth, N-use efficiency and association with mycorrhizae can affect responses of plants to changed nutrient conditions (Ren et al. 2011), soil water and annual rainfall are vital factors which can interact with N to influence ecosystem functioning (Chen et al. 2011). When water and N were added separately to shortgrass steppe in North America, above-ground biomass increased by 250 and 100%, respectively, but the increase was 700% when water and N were added together (Lauenroth et al. 2008). In the present study, dung deposits increased the tall, erect, annual, non-native and non-leguminous forbs. This is not surprising as the native vegetation would

have evolved largely in the absence of additional nutrients. It has been reported that weedy and ruderal species are successful invaders in N-rich environments (Sharma et al. 2005; Gaertner et al. 2012); hence they dominated in DPs compared with CPs. According to Diekmann and Falkengren-Grerup (2002), tall species are typically favored by N-deposition at the cost of short species, and can overgrow and shade the short-statured species. Short-statured species are excluded due to light limitation (Stevens et al. 2006). In this study, most forbs were erect in growth habit and hence, adapted to compete for light, which may be a reason for the greater increment in species number and biomass of forbs in DPs than CPs. Nevertheless, N-fixing species normally compete for light less effectively than non-N-fixing species (Haynes 1980). Thus, the study suggests that the natural attributes of forbs allowed them to take advantage of the higher nutrient levels due to dung deposition. Similarly, with the help of a meta-analysis including data from 304 studies and 456 terrestrial plant species, Xia and Wan (2008) also reported 54% increase in the herbaceous biomass due to fertilizing with N.

Overall, the study revealed that the seasonally dry tropical grasslands, which experience relatively high soil pH and low soil moisture and nutrients, benefit from ruminant dung deposition, through reduction in soil pH, and increase in soil moisture and nutrients. These conditions favored seed germination and seedling establishment of opportunistic plants, which led to increased diversity and biomass of herbaceous species in the dry tropical pasture studies. While it is well known that application of ruminant dung can benefit a pasture by increasing dry matter yields, this study has shown that the species composition in available forage can be changed as well, which can also affect nutritional value, depending on the species' palatability. It is important to return dung to pastures or croplands, where animals are housed or placed in corrals at night, to ensure the sustainable use of the pastures/grasslands. The study suggested that dung could be a substitute for chemical fertilizers to increase soil nutrients and herbaceous species diversity. However, further study of diversity-productivity relationships is vital before a clear understanding of full benefits of fertilizing with dung is available to make recommendations for the sustainable management of seasonally dry tropical ecosystems.

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