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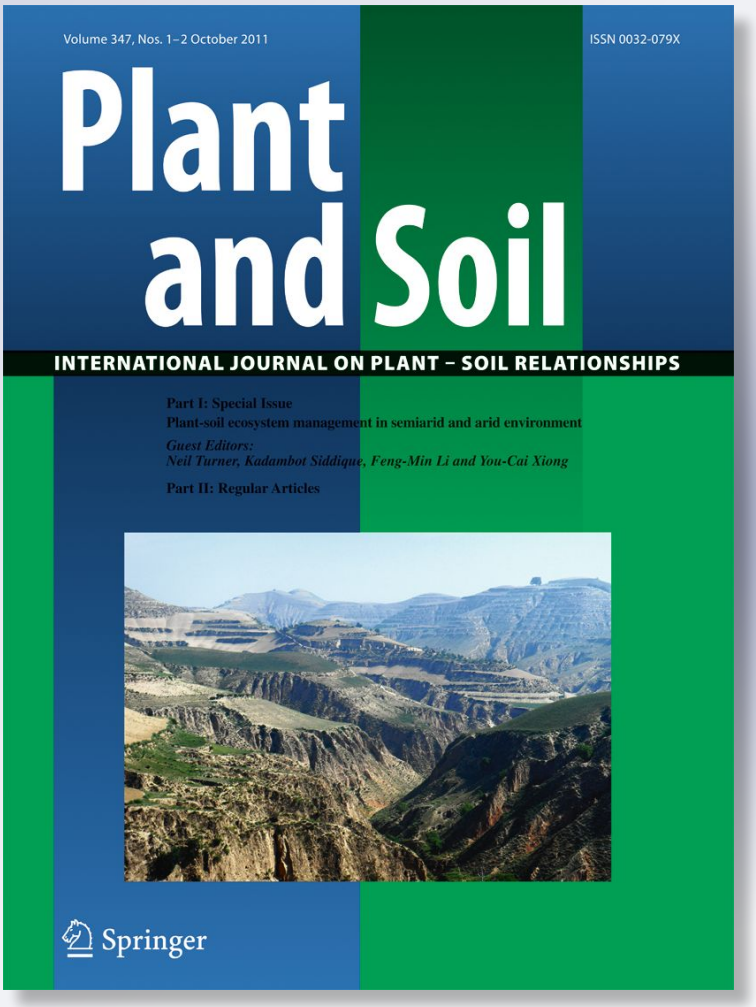

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REGULAR ARTICLE

Herbaceous production in South India—limiting factors and implications for large herbivores

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Abstract This study's goal was to better understand the growth pattern and limitations of the herbaceous production that supports South India's rich large herbivore grazer assemblage. We conducted a fully factorial nitrogen and water (three levels each) treatment field experiment in the herbivore rich South Indian Western Ghats region to determine the seasonal pattern and the extent to which nitrogen and water availability limit herbaceous production. Graminoid production was found to be nitrogen limited. Despite low rainfall, additional water did not significantly increase overall biomass production nor extend growth in the dry season. Accumulated standing biomass was highest in the late wet season (November) and lowest in the dry season (May). Leaf nitrogen was highest in the early wet season (June) and lowest in the late dry season (March). Grazing had a positive effect on grass production by extending the growing season. Biomass production and graminoid leaf nitrogen concentration levels in the study area were similar to other tropical areas in the world. Also similar to other tropical large herbivore areas, the dry season poses an annual challenge for large herbivores in the study area —particularly the smaller bodied species—to satisfy their nutrient requirements.

Keywords Graminoids · Leaf nitrogen · Plant available moisture · Plant biomass · Soil nitrogen · Western Ghats

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Introduction

The two factors that most limit the quantity and quality of herbaceous production are moisture and soil nutrients (Hopkins 2000; Pandey and Singh 1992). Both the amount and the temporal (seasonal as well as annual) variation in moisture availability affect herbaceous growth (Le Houérou et al. 1988; Milchunas et al. 1994, 1995), while nitrogen stands out from among the list of soil nutrients as limiting herbaceous production most frequently (Chapin 1980; Parsons and Chapman 2000).

Understanding the phenology and what affects the biomass and quality of the herbaceous layer has helped comprehend herbivore ecology in Africa, a region where the herbaceous layer is the major resource component supporting the world's richest and most diverse large herbivore assemblage (Coughenour et al. 1985a, b; Prins 1988; Prins and Loth 1988). Examples

of how plant production is understood to impact herbivore ecology are: the timing of parturition in multiple populations of large herbivore species coinciding with the season of highest plant quality (Post 2003); the mass migration of herbivores (like in East Africa's Serengeti-Mara ecosystem) tracking spatiotemporal variation in plant quantity and quality (Bell 1970; Boone et al. 2006; Frank et al. 1998; Vesey-Fitzgerald 1960); and the positive relation of large herbivore species diversity patterns in East and West Africa with the spatial distribution of herbaceous quantity and quality (Coe et al. 1976; Klop and Prins 2008; Olff et al. 2002).

India supports a rich and diverse large herbivore species assemblage, of which many are grazers (Prater 1985). North (excluding its dry Western region) and South India do not differ significantly with respect to annual rainfall. However, the North is richer in soil nutrients because of the constant replenishment of rich alluvial soil from multiple rivers originating in the Himalayas. Studies have found the biomass production of the herbaceous layer in North India is relatively high when compared to other tropical regions, and that this production was most affected by available moisture and grazing (Pandey and Singh 1991, 1992). This study's goal was to investigate whether important factors like nitrogen, water, and grazing impact herbaceous production in South India.

We conducted a field experiment in the herbivore rich Western Ghats region, South India, to assess the seasonal variation in biomass and leaf nutrient concentration, and to better understand the limiting potential of water and nitrogen on herbaceous production. Based on our understanding of herbaceous production and quality from other tropical regions with seasonal cyclic water availability (Bacon 2004; Deshmukh 1986; Kamnalrut and Evernson 1992) we tested the prediction that leaf nitrogen concentration would peak in the early wet season and then continuously decrease, reaching its lowest level in the dry season.

Materials and methods

Experiment design

We conducted a field experiment (August 2006-August 2007) on a grassy meadow located in a wildlife resort (elevation 1070 m) that bordered the Nilgiri Biosphere, South India (11°55′ N, 76°63′ E). The Nilgiri Biosphere hosts a diverse assemblage of herbivores including Asian elephant (*Elephas maximus*), gaur (*Bos gaurus*), sambar (*Cervus unicolor*), chital (*Axis axis*), muntjac (*Muntiacus muntjak*) and four-horned antelope (*Tetracerus quadricornis*); gaur are known to rely the most, and muntjac the least on grazing (Prater 1985). The study site's annual rainfall cycle is monsoon driven and includes a six-month wet (June-November) and a six-month dry (December-May) season. The wet season is bimodal in nature as two different monsoons contribute to the precipitation: the Southwest monsoon (May-July) followed by the Northeast monsoon (September-November). The rainfall during our 12-month study period was 730 mm (Fig. 1; recorded in Masinagudi 2 km north of the experiment site), which was below the last 15-year (1991–2005) average of 860 mm. Mean monthly temperature was 24°C, reaching a high of 34-35°C in April-May and a low of 5-6°C in December-January. We found the soils at the experiment site to be slightly acidic (5.02±0.14 95% CI, n=5), low in nitrogen concentration (0.12±0.07% CI, n=5), and having a sandy loam surface with a gravelly clay substrate.

The experiment design included watering and fertilization of plots inside fenced exclosures (7.5× 4.5 m) (that excluded large herbivores, but not rodents and hares). Each of the five exclosures contained nine 2×1 m treatments plots (inter-plot spacing was 0.5 m) of a fully factorial 3×3 (three treatment levels of two factors) randomized block design. The three treatment levels of the two factors were: Factor 1 (Moisture) with levels (i) no additional water (control), (ii) addition of 300 mm spread over the wet season, treated in equal parts every 3 days, (iii) addition of 300 mm spread over the entire year, treated in equal parts every 3 days; and Factor 2 (Nitrogen, added in the form of NH_4NO_3) with levels (i) no addition of N (control), (ii) addition of 7 gN m^{-2} yr^{-1}, and (iii) addition of 21 gN m^{-2} yr^{-1}. The reason we chose to add 300 mm in our water treatments to simulate a wet year, was because the difference between the annual average and wettest year (1991–2005) was 300 mm. We chose the two levels of nitrogen from the range of fertilization levels suggested by Tilman (1987). The nitrogen (NH_4NO_3) treatments were applied in three dosages over the growing season—25% on June 25, 50% on August 23, and 25% on October 3 2006—and water was added to the treatment plots in the morning using a watering can with a perforated nozzle.

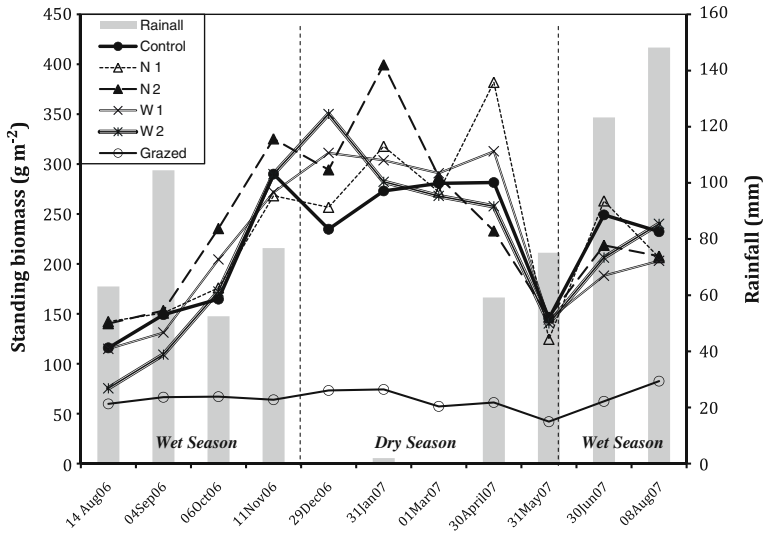

Fig. 1 Means (n=5 for each treatment on each sampling occasion) of standing biomass of the herbaceous layer found in the control, N1 (Nitrogen Level 1 = additional 7 gm^{-2}), N2 (Nitrogen level 2 = additional 21 gm^{-2}), W1 (Water level plots = additional 300 mm during the wet season), W2 (Water Level 2 = additional 300 mm during the whole year) in plots that were fenced (i.e., free of grazing) and plots that were heavily grazed (i.e., outside the fences) in South India, August 2006-August 2007. Rainfall was measured in Masinagudi, 2 km north of experiment location

Samples (n=5 for each treatment on each sampling occasion) of above ground standing biomass were collected by clipping a 0.05 m^2 (0.5×0.1 m) patch of the herbaceous layer to ground level from each treatment plot from all five exclosures on 11 occasions (average inter-cropping period=33 days) over the 12-month study period (14 August 2006-08 August 2007). To understand the effect of grazing, we collected (n=5; each 0.05 m^2) clipped samples from an area grazed heavily by cattle ~50 m from each fenced plot. Clipped samples were separated into green leaf, dry leaf, green stem, dry stem, forb leaf and forb stem, and then dried in the sun till weights reached a steady state. The dry masses of separated categories were weighed using an electronic balance to a tenth of a gram. Over 98% of the herbaceous biomass sampled were grasses, of which the dominant species were the perennials *Bothriochloa pertusa*, *Heteropogon contortus*, *Eragrostis atropurpurea*, and *Digitaria spp*., and to lesser extent *Sporobolus indicus* and *Themeda tremula*. The dominant species were equally distributed in the five exclosures.

Nitrogen concentration of the leaf component of the grasses (the green leaf component was analyzed except in the late dry season when only dead biomass was available) was measured in four different seasons—late wet (06 Oct 2006), mid dry (31 Jan 2007), late dry (01 Mar 2007), and early wet (30 Jun 2007)—using an automated dry combustion nitrogen analyzer at the National Institute of Animal Nutrition and Physiology, Bangalore, India.

A sample of the top 10 cm of the soil was collected from each of the five fenced plots (n=5) prior to the experiment. And the end of the experiment soil samples were collected from all the control plots and plots that were treated with either only water or nitrogen (n=25: 5 control, 10 from plots that were treated with only water, and 10 from plots that were treated with only nitrogen; we did not collect samples from the plots that were treated with both nitrogen and water). We measured the following soil properties: total nitrogen concentration (% dry mass of soil determined using the Kjeldahl method that measured total Kjeldahl nitrogen—which is organic nitrogen, ammonia and ammonium—and nitrate-N and nitrite-N); organic carbon concentration (% dry mass of soil determined using the Walkley-Black method); and pH and electric conductivity (EC%), (determined using a potentiometer, Carter and Gregorich 2008).

Statistical analysis

Two way repeated-measures ANOVA tests were used to detect whether the addition of nitrogen and water

affected: 1) herbaceous biomass production, based on the 11 measurements over the year; and 2) graminoid leaf nitrogen concentration, that were measured in four seasons. A one-way repeated measures ANOVA test was used to detect whether standing biomass differed between the grazed and ungrazed (untreated control) plots. In the repeated-measures ANOVA analysis of standing biomass, the Mauchly's test indicated that the assumption of sphericity had been violated (χ_{54}^2= 110.53, P<0.001). Therefore, the degrees of freedom were corrected using the Greenhouse-Geisser estimate of sphericity (ε=0.64), and the results of the standing biomass analysis are Greenhouse-Geisser estimates (Table 1). In the repeated-measures ANOVA analysis of leaf nitrogen concentration (expressed as% dry mass), however, the Mauchly's test indicated that the assumption of sphericity was not violated (χ_5^2=9.68, P=0.09), and therefore this analysis' results did not need correction and are reported assuming sphericity to be true. All statistical tests were done using SPSS *v*.18.

Results

Herbaceous growth (estimated by the difference between two successive monthly biomass measurements of the ungrazed control plots) occurred between May and December, i.e. during the rainy season and a short period of the immediate cool winter (Fig. 1). There was no growth of the herbaceous layer in the dry season within the exclosures, even in plots that received additional water. The highest rate of daily biomass change (calculated by dividing the difference in biomass by the number of days between two successive sampling occasions) was recorded in the month of October (0.81% day^{-1}). The proportion of herbaceous leaf biomass was highest in September and lowest in January in the control plots (Fig. 2a). Ungrazed standing biomass (within the exclosures) was highest in the late wet season (October) and lowest in the late dry season (May) (Fig. 1). In January leaf biomass was only 40% of total biomass, and its live component only 10% (Figs. 2a&b).

The range of standing crop biomass found in the control plots within the exclosures was 116–320 g m^{-2} (Appendix Table 5). Standing crop biomass was significantly greater within the exclosure (the control ungrazed plots) than the grazed plots ($F_{1,8}$= 75.56, P<0.001), and varied unimodally over time across all treatments (Fig. 1). The addition of nitrogen increased biomass production, but the addition of water and the addition of a combination water and nitrogen did not impact biomass production during the experiment (Table 1). The positive effect of nitrogen on biomass production was significant when comparing nitrogen level 0 (no addition) to both level 1 (P=0.05) and level 2 (P< 0.002), while the difference between levels 1 and 2 was not significant (P=0.20). The differences in biomass production between the different water treatment levels were insignificant: between levels 0 and level 1 (P=0.14); levels 0 and 2 (P=0.55); and levels 1 and 2 (P=0.40).

In the absence of grazing the live(green)% of the leaf component in graminoid biomass was 100% for the first half of the wet season (May-August), had declined to 0% by the late dry season (March), and was again back at 100% with the onset of a new wet season (Fig. 2b). Grazing appeared to stimulate new leaf production, as the live component in leaf biomass was higher for a longer duration in the grazed plots than the ungrazed plots (Fig. 2b). The reason for the lack of confidence interval bars in the line graph depicting green leaf% in the grazed plots (Fig. 2b) is because on most sampling

Table 1 Results of 2-way repeated measures ANOVA of above ground primary production standing biomass from a fully factorial 3×3 treatment (the two factors = nitrogen and water) grazing exclosure experiment in South India. Statistics reported are corrected Greenhouse-Geisser estimates of the ANOVA model. Significant values are reported in bold font. The data was repeatedly measured on 11 occasions between August 2006 and July 2007 (average inter-cropping period=33 days). The results presented below are of the main effects; see Results for intra factor level differences

Source	df	F	P
Intercept	1	519.34	**< 0.001**
Block	1	11.23	**0.002**
Nitrogen	2	5.45	**0.009**
Water	2	1.01	0.35
Nitrogen * Water	4	0.65	0.63
Error	34		
Time	10	18.98	**< 0.001**
Time * Block	10	3.86	**0.001**
Time * Nitrogen	20	1.37	0.18
Time * Water	20	1.72	0.06
Time * Nitrogen * Water	40	1.33	0.14
Error	340		

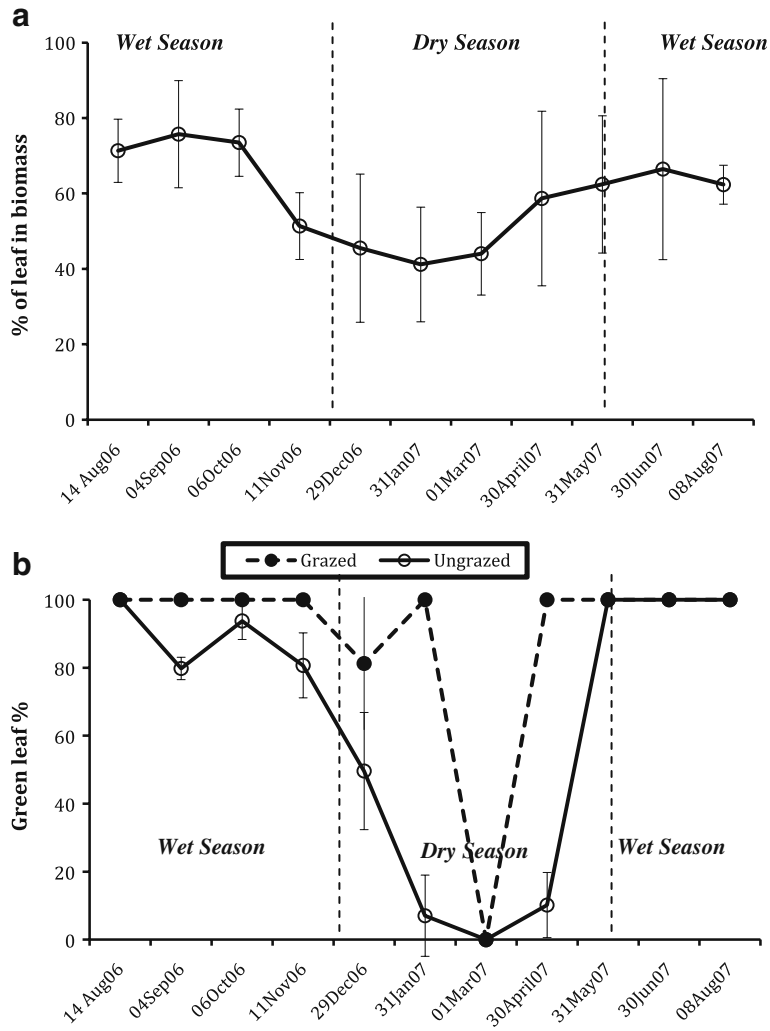

Fig. 2 Mean (± 95% CI) a) Leaf%, and b) Live leaf% in the standing biomass of the herbaceous layer found in the control (untreated) plots within grazing exclosures of a water and nitrogen treatment experiment in South India. In (b), live leaf% found in ungrazed (within exclosures) plots is compared to grazed plots (outside exclosures)

occasions all five samples had the same amount of green leaf%.

Leaf nitrogen varied significantly between the seasons (0.92–2.10%) and was highest in the early wet season and lowest in the late dry season, lending support for our prediction (Fig. 3; Appendix Table 6). The addition of nitrogen, but not water had a significant positive effect on leaf nitrogen concentration (Table 2). The effect of additional nitrogen on leaf nitrogen concentration was positive and significant between plots that received 21 gN m^{-2} yr^{-1} (level 2) and those that received both no nitrogen (level 0; P=0.001) and 7 gN m^{-2} yr^{-1} (level 1; P=0.002), but the difference between levels 0 and 1 was insignificant (P=0.49). The response of leaf nitrogen to the water treatments was insignificant when comparing any two levels: between levels 0 and 1 (P=0.45), between levels 0 and 2 (P=0.20), and between levels 1 and 2 (P=0.05).

Using a one-way ANOVA, we found no significant difference in the total N (0.11–0.24% dry mass of soil), organic C (0.84–2.15% dry mass of soil), and pH (5.06–6.5) properties in the soil sampled prior to the experiment and with the post-experiment soil properties found in the control and main effects plots (Appendix Table 7). We did find, though, that electrical conductivity (0.04–0.33 mhos cm^{-1}) was higher in the soils in plots that were treated with nitrogen (0.14±0.06 95% CI) than the pre-experiment (0.06±0.02 95% CI) and the post-experiment control (0.06±0.02 95% CI) and water treated (0.07±0.02 95% CI) plots.

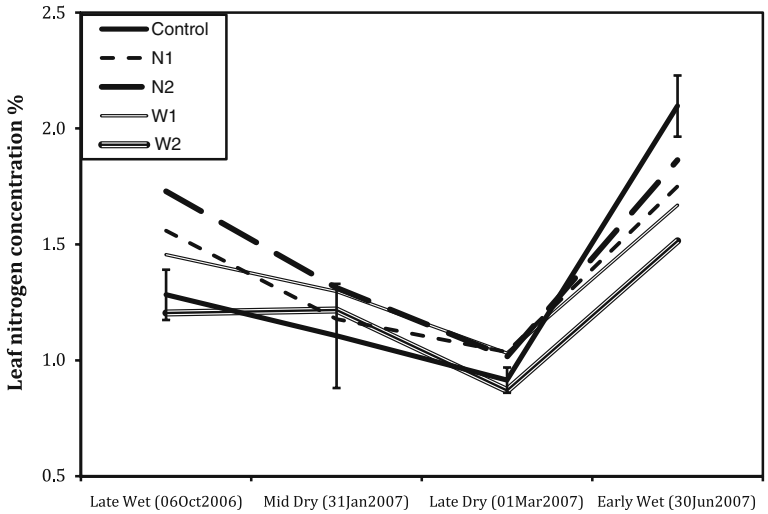

Fig. 3 Means (n=5 for each treatment on each sampling occasion) of the nitrogen concentration of the green leaves of the herbaceous layer found in the control, N1 (Nitrogen Level 1 = additional 7 gm^{-2}), N2 (Nitrogen level 2 = additional 21 gm^{-2}), W1 (Water level plots = additional 300 mm during the wet season), and W2 (Water Level 2 = additional 300 mm during the whole year) plots that were part of a fully factorial fenced (i.e., free of grazing) field based experiment in South India, August 2006-August 2007. For the control, the means ± 95% CI have been plotted

Discussion

We found herbaceous production in the study area to be nitrogen limited, highlighted by the positive response in biomass to the addition of even small amounts of nitrogen (7 gN m^{-2} yr^{-1}). The absence of a positive response in soil nitrogen levels to the nitrogen treatments indicated that the herbaceous layer rapidly absorbed the added nitrogen. Both these responses—the additional biomass production and the rapid absorption of nitrogen—were recorded despite below average annual precipitation during the study period, conditions, it could be argued, that should have favored herbaceous growth responding more to the water than the nitrogen treatments.

As predicted, plant nitrogen was at its highest during the early wet season and lowest in the late dry season. It appears that the large herbivore assemblage in the study copes with graminoid quality conditions similar to those found in Africa (Table 3). As a function of body mass based resource consumption principles, smaller-bodied herbivore species have a greater need for higher quality forage than do larger-bodied herbivores (Bell 1970; Van Soest 1994). Therefore, like in Africa, the smaller-bodied grazer species in the study area (like chital) should strive to maximize their intake of high quality herbaceous forage found in the fresh graminoid flush of the early wet season. Our results (Figs. 2a-b) also show that after January, the beginning of the dry season, the herbaceous layer has a lower proportion of leaves and high fiber (stem) content. Therefore, satisfying nutri-

Table 2 Results of a 2-way repeated measures ANOVA of graminoid leaf nitrogen concentration from a fully factorial 3×3 treatment (the two factors = nitrogen and water) grazing exclosure experiment in South India. Significant values are reported in bold font. The data was repeatedly measured on four different seasons (late wet, mid dry, late dry, early wet) between August 2006 and July 2007. The results presented below are of the main effects; see Results for intra factor level differences

Source	df	F	P
Intercept	1	1,084.25	**< 0.001**
Block	1	5.75	0.023
Nitrogen	2	9.21	**0.001**
Water	2	2.10	0.15
Nitrogen*Water	4	0.45	0.78
Error	29		
Season	3	35.20	**< 0.001**
Season * Block	3	5.79	**0.001**
Season * Nitrogen	6	1.80	0.11
Season * Water	6	3.80	**0.002**
Season * Nitrogen * Water	12	2.07	**0.027**
Error	87		

Table 3 Leaf nitrogen concentration of grass species/herbaceous layer in tropical ecosystems around the world (listed below on increasing lower-end of nitrogen range)

Location	Leaf nitrogen (%)	Source
Global review	1–6	Mattson 1980
Mkwaja North, Tanzania (5°43′ S, 38°47′ E)	0.4–2.4	Treydte et al. 2006
Tarangire National Park, Tanzania (3°35′ S, 35°55′ E)	0.53–3.5	Voeten and Prins 1999
Greater Kruger Park, South Africa (24°17-78′ S, 30°66′-31°26′ E	0.6–1.9	Treydte et al. 2008
Boucle du Baoule, Mali (13°45′ N, 9°20′ E)	0.76–4.5	de Bie 1991
Lake Manyara National Park, Tanzania (3°30′ S, 35°45′ E)	0.8–3.8	Prins and Beekman 1989
Hyparrhenia filipendula (Africa)	0.85–2.1	Coughenour et al. 1985a
Masinagudi, India, South India (11°55′ N, 76°63′ E)	0.92–2.1	This study
Themeda triandra (Africa)	0.96–1.6	Coughenour et al. 1985b
Floodplain grassland, Amazon (3°15′ S, 60°00′ W)	1.5–2.5	Piedade et al. 1992
Water treated grasslands, Amboseli, Kenya (2º 30′ S; 37º 15′ E)	2.6–4.1	Georgiadis et al. 1989

tional requirements by grazing would be challenge for smaller-bodied grazer species during the dry season when grasses have low nitrogen concentration and high fiber content.

Larger-bodied herbivore roughage grazers, like the gaur, also benefit from the high quality forage of the wet reason. However, Illius and Gordon (1987) found that the intake of ruminants over 500 kg can be limited in swards below 60 mm height. This is because short graminoid swards constrain the bite depth of larger species—despite their having larger bite areas—more than they do the bite depth of smaller species relative to their respective metabolic requirements. This difference has the potential to reduce the competition between chital and gaur for graminoid resources during the early wet season. Therefore, while species like the gaur do build body reserves by harvesting the higher quality forage found in the wet season, the short flush of the early wet season (April-May) is less attractive to the gaur than it is for the chital.

Chital and sambar parturition are known to occur in seasonal annual cycles (chital parturition peaks in the dry season and sambar parturition peaks in the early wet season) while parturition of the much larger gaur occurs throughout the year (Prater 1985; Raman 1998; Schaller 1967). Therefore, chital appear to time their parturition to allow lactating females, while sambar appear to time their parturition to allow calves to benefit from the high quality forage in the early wet season (Post 2003). With respect to gaur—given that larger-bodied species are capable of subsisting on lower quality forage—their non-seasonal parturition may be a function of them not being constrained by the quality of forage available in the study area, i.e., if we consider the average body mass of a female gaur to be 600 kg (Prater 1985); the nitrogen requirements for maintenance, pregnancy and lactation to be $0.65 \times W^{0.75}$, $0.78 \times W^{0.75}$, and $1.01 \times W^{0.75}$ respectively (Agricultural Research Council Working Party 1980); that ruminant herbivores consume about 2% of their body mass on a dry matter basis every day (Murray 1995), and the daily required nutrient concentration of a ruminant to be daily requirements divided by daily intake; we get female gaur needing 0.66% N for maintenance, 0.79% N for pregnancy, and 1.02% N for lactation; all of which are below, or only slightly higher than the lower bound (0.92%) of the nitrogen concentration range found in the study area.

The standing biomass estimates within the exclosures were comparable to biomass levels found within exclosures in savannas and other tropical habitats of Africa and Asia (Table 4). We know that large-sized herbivores require a minimum amount of biomass to persist in an area, i.e., while smaller-bodied species are constrained by forage quality, larger-bodied species are constrained by forage quantity. Therefore, the similarity in productivity levels in the study area with areas in Africa that support large herbivores offers insight into how the study area manages to support populations of megaherbivores like elephant and gaur. Biomass estimates from the study site were lower, however, when compared to sites in North

Table 4 Above-ground biomass estimates of herbaceous layer in tropical ecosystems around the world (listed based on increasing biomass level)

Location	Highest above-ground biomass (g m^{-2})	Rainfall (mm y^{-1})	Source
Boucle du Baoule, Mali (13°45′ N, 9°20′ E)	300	900	de Bie 1991
Bandipur, South India (11°47′ N, 76°23′ E)	300	1,100	Devidas and Puyravaud 1995
Kaputei plains, Kenya (1°30′ N, 36°40′ E)	309	900	Owaga 1980
Masinagudi, South India (11°55′ N, 76°63′ E)	320	860	This study
Nairobi National Park, Kenya (1°20′ N, 36°50′ E)	332	850	Deshmukh 1986
Nairobi National Park, Kenya (1°20′ N, 36°50′ E)	338	950	Kinyamario and Macharia 1992
Ban Klong Hoi Khong, Thailand (6° N, 100° E)	347	2,100	Kamnalrut and Evernson 1992
Lamto savannas, Ivory Coast (5°02′ N, 6°13′ E)	420	1,300	Menaut and Cesar 1979
Guinea savannas, Nigeria (9°18′ N, 5°04′ E)	435	1,175	Ohiagu and Wood 1979
Pilbara,Northwest Australia (22°17′ N, 117°40′ E)	500	350	Bennett and Adams 2001
Vindhyan Plateau, Central India (24°18′ N, 82°59′ E)	741	1,035	Pandey and Singh 1992
Rudranath, North India (30°28′ N, 79°20′ E)	918	1,600	Ram et al. 1989
Kurukshetra, North India (29°58′ N, 76°51′ E)	1,740	800	Singh and Yadava 1974

India (Table 4). Annual rainfall is similar in both North and South India (Table 4, except for the much higher 1600 mm that Rudranath receives). However, North India has richer soil nutrients as a function of constant replenishment by alluvial deposits from multiple rivers originating in the Himalayas, and Central Indian soils are considered to be rich as a function of the volcanic activity of the Deccan Traps.

It was a little surprising that additional moisture did not affect graminoid production in the dry season. However, the vegetation cover within the exclosures was intact and quite dense for most of the experiment period. It is therefore possible that the water added during the water treatments was intercepted and not all of it reached the soil. Although the grass cover was thinner in the dry season, the impact of the water being intercepted would have been greater in the dry season as only significantly wet soil to a certain depth can have an affect on plant growth. It is also possible that because the water was added in small quantities over time it did not penetrate the soil and instead evaporated, while if the same amount of water came in the form of rainfall it would have come in shorter and heavier bursts and would have more likely penetrated the soil and aided in herbaceous production. However, we did not measure soil moisture, therefore it is unclear to what extent this potential experimental drawback might have had on the results.

The higher levels of soil electric conductivity found in plots treated with nitrogen is similar to what was found by Eghball (2002), and indicates that additional nitrogen increases the amount of soluble salts in soil. The insignificant effect of the treatments on the other soil properties, for e.g. a potential increase in soil nitrogen in plots that received nitrogen, might have been because of the relatively small sample size analyzed.

Although light to moderate grazing has been shown to increase primary production by 45% in Central India (Pandey and Singh 1992), the high grazing intensity on our grazed plots probably reduced biomass production, similar to what has been found in other sites (Milchunas and Lauenroth 1993). Grazing, however, extended the period of leaf production in the herbaceous layer in the study area—green leaf% remained higher and for a longer period in the grazed plots (Fig. 2a)—which is similar to what has been found in North Indian and African savannas (McNaughton 1984; Milchunas et al. 1995; Augustine et al. 2003).

In conclusion, this study provides evidence that herbaceous biomass production in the study area is limited by nitrogen availability and does not get affected by additional moisture even in a below

average rainfall year. We also found evidence that grazing can lengthen the period of leaf production in the area. Graminoid biomass and leaf nitrogen levels were found to be similar to other tropical areas around the world. In general, the low nitrogen and high fiber levels in the dry season can impact the ecology and biology of large herbivores, particularly the smaller-bodied species. This is relevant in the context of long-term conservation of these species, as the Nilgiri Biosphere, where this study was conducted, has the highest biomass of large herbivores in Asia.

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Appendices

Table 5 The standing biomass measurements (g) of 0.05 m^2 patches clipped from the different treatment plots within the five fenced experimental exclosures and grazed plots outside the exclosures. N1 = additional 7 gm^{-2}; N2 = additional 21 gm^{-2}; W1 = additional 300 mm during the wet season; and W2 = additional 300 mm during the whole year

Treatment	14Aug06	04Sep06	06Oct06	11Nov06	29Dec06	31Jan07	01Mar07	30Apr07	31May07	30Jun07	08Aug07
Fenced plots											
Control	4.4	10.6	8.3	21.9	11.0	15.3	12.6	18.3	5.3	16.5	27.1
	8.8	10.8	8.3	15.2	15.5	14.3	13.8	13.4	4.4	9.6	5.9
	5.4	5.1	9.8	20.3	16.7	15.8	14.4	19.9	9.6	12.7	12.4
	6.8	7.1	8.8	9.7	8.3	9.6	15.2	9.8	8.9	11.6	6.2
	3.6	3.7	6.0	5.4	7.2	13.3	14.2	9.0	8.2	11.9	6.5
N1	6.5	8.5	12.1	17.0	11.8	12.2	19.8	12.7	4.3	16.5	7.4
	4.0	4.5	5.5	7.5	12.3	18.8	9.1	11.4	4.8	11.0	11.5
	14.7	12.2	11.0	24.1	16.2	17.5	14.2	29.7	3.3	8.9	9.4
	6.8	7.2	10.5	8.5	12.9	13.6	9.9	23.4	8.2	17.1	8.5
	4.9	5.4	5.5	8.9	12.1	19.6	14.6	23.3	9.5	13.0	13.5
N1+W1	4.3	7.8	13.4	11.6	25.1	15.3	12.9	12.9	8.4	16.5	13.3
	6.0	8.7	16.5	14.4	13.6	16.6	20.5	20.5	3.0	9.6	16.2
	6.8	5.5	12.5	26.2	19.4	14.5	20.9	20.9	9.2	12.7	9.7
	7.2	9.8	8.5	18.1	17.6	14.2	10.4	10.4	8.9	11.6	8.0
	4.0	7.2	8.3	9.1	16.2	14.8	11.3	11.3	8.8	11.9	8.6
N1+W2	8.1	12.1	13.9	15.5	18.5	29.3	12.2	11.0	4.7	10.5	15.3
	7.0	9.8	15.8	17.0	13.8	15.3	15.3	20.3	6.3	10.5	13.8
	7.5	5.4	11.7	20.3	15.3	14.7	14.5	17.7	6.8	12.0	6.5
	6.9	6.1	8.1	11.8	14.4	18.0	16.3	13.2	12.6	4.5	16.1
	5.2	5.1	7.3	9.4	14.2	15.9	16.4	17.6	9.8	11.2	12.0
N2	6.2	7.4	16.0	19.0	12.9	23.8	14.6	10.8	7.7	12.8	12.4
	4.8	9.6	8.3	15.0	13.1	25.1	16.3	10.2	6.8	12.3	10.8
	9.4	9.2	19.8	21.0	16.9	25.0	15.4	11.6	5.2	12.9	7.3
	5.6	6.8	7.9	19.9	11.1	12.5	11.4	10.5	9.1	9.8	12.9
	9.3	5.3	7.3	7.8	18.7	15.4	13.6	10.9	7.3	7.6	6.5
N2+W1	5.4	13.9	13.7	23.7	25.5	26.0	23.0	14.0	6.6	8.1	19.2

Table 5 (continued)

Treatment	14Aug06	04Sep06	06Oct06	11Nov06	29Dec06	31Jan07	01Mar07	30Apr07	31May07	30Jun07	08Aug07
	7.6	13.2	11.1	29.3	25.7	21.8	23.9	32.4	5.8	11.7	25.8
	10.3	8.4	11.3	10.4	27.8	17.4	18.0	24.9	5.3	8.1	13.9
	6.8	6.4	7.2	12.8	12.5	12.0	9.1	12.5	10.3	10.0	11.4
	5.7	6.2	13.9	12.2	12.9	16.3	15.0	17.3	5.5	11.0	12.3
N2+W2	10.2	12.6	13.7	10.8	26.2	20.8	15.3	11.4	4.5	8.2	16.1
	3.5	5.6	15.8	12.2	22.3	20.2	23.5	16.6	8.1	10.9	8.2
	15.2	8.0	14.8	13.9	28.6	24.0	13.7	18.4	7.8	8.0	9.7
	9.0	7.1	8.0	15.3	15.3	9.6	13.7	16.3	9.5	8.9	7.7
	6.5	4.8	11.6	11.7	14.3	22.0	13.6	10.1	11.3	13.3	10.3
W1	4.7	7.4	11.9	11.2	13.5	12.2	15.4	11.4	8.0	7.8	10.1
	2.9	6.3	7.3	8.7	11.3	14.4	10.9	13.0	4.1	8.9	9.3
	7.4	5.5	13.3	18.5	21.7	19.0	14.2	20.4	4.0	8.3	10.5
	2.9	5.4	9.3	18.6	12.7	12.0	16.4	15.0	10.8	8.9	13.7
	8.0	6.9	7.0	11.0	13.1	14.3	14.2	18.8	8.4	12.7	6.1
W2	6.3	5.6	11.3	21.8	19.4	13.8	14.0	14.3	5.1	10.9	15.1
	2.8	3.1	8.3	11.1	20.1	14.0	11.4	10.5	5.0	12.9	7.6
	2.3	4.4	7.1	22.5	20.1	15.2	11.5	11.9	8.0	6.4	12.4
	3.1	8.7	–	7.8	13.0	12.4	15.5	13.9	8.4	11.0	11.1
	2.4	4.4	6.2	10.2	16.9	14.1	13.5	11.1	8.4	11.3	15.7
Non-fenced plots											
Grazed	3.1	3.1	2.6	1.5	0.7	1.3	0.8	1.2	1.2	1.2	3.6
	2.6	1.7	2.2	0.4	0.5	2.2	0.9	0.7	1.3	1.2	2.2
	4.5	3.7	1.5	0.7	0.6	2.1	0.8	1.0	0.5	2.0	2.5
	1.5	3.5	3.5	1.3	0.8	1.3	0.5	1.3	1.2	1.4	2.2
	2.5	2.5	1.7	0.8	1.9	1.3	0.8	1.3	1.4	2.6	2.3

Table 6 Measurements of the graminoid leaf nitrogen concentration found in different plots within the five experimental exclosures. N1 = additional 7 $g m^{-2}$; N2 = additional 21 $g m^{-2}$; W1 = additional 300 mm during the wet season; and W2 = additional 300 mm during the whole year

Treatment	06Oct2006	31Jan2007	01Mar2007	30Jun2007
Control	1.41	0.78	0.90	2.16
	1.42	0.90	0.98	2.06
	1.21	1.39	0.94	2.15
	1.23	1.22	–	1.86
	1.15	1.24	0.85	2.25
N1	1.78	1.12	1.20	1.91
	1.36	1.09	1.13	2.01
	1.86	1.26	0.93	2.11
	1.35	1.33	1.16	1.62
	1.45	1.10	0.76	1.10
N1+W1	0.95	1.01	–	1.77

Table 6 (continued)

Treatment	06Oct2006	31Jan2007	01Mar2007	30Jun2007
	1.32	1.31	1.10	1.82
	1.40	1.48	1.12	2.08
	1.34	1.48	1.19	1.80
	1.27	1.08	0.93	1.71
N1+W2	1.44	0.90	0.97	1.60
	1.36	1.18	0.75	1.76
	1.57	1.28	1.01	1.83
	–	1.38	1.00	1.75
	1.27	1.32	0.78	1.48
N2	1.83	1.04	1.04	1.86
	1.64	1.43	0.95	1.84
	1.42	1.22	0.78	2.10
	2.00	1.44	1.17	1.87
	1.75	1.44	1.14	1.66

Table 6 (continued)

Treatment	06Oct2006	31Jan2007	01Mar2007	30Jun2007
N2+W1	1.67	0.90	1.06	1.96
	2.12	1.33	1.21	1.93
	1.73	1.27	1.01	2.14
	1.43	1.69	1.54	2.00
	1.54	1.52	1.22	1.51
N2+W2	1.70	1.54	1.48	1.85
	1.82	1.61	1.20	1.72
	1.86	1.32	1.10	1.89
	1.34	1.65	1.10	1.73
	1.26	1.50	0.89	1.42
W1	1.73	1.54	1.50	1.65
	–	1.75	0.91	1.52
	1.36	1.11	0.95	1.93
	1.21	0.94	1.06	1.57
	1.52	1.15	0.75	1.67
W2	1.09	0.98	–	1.54
	1.41	1.42	1.11	1.40
	1.19	1.36	0.68	1.77
	1.13	1.24	0.90	1.51
	–	1.09	0.79	1.36

Table 7 Pre- and post-experiment soil properties. All control and the main-effect plots was sampled post-experiment (i.e. at the end of one year) from the five fenced exclosures. N1 = additional 7 gm^{-2}; N2 = additional 21 gm^{-2}; W1 = additional 300 mm during the wet season; and W2 = additional 300 mm during the whole year

Plot	Soil properties			
	pH	Electric conductivity	Organic carbon	Total nitrogen
Pre-experiment	5.90	0.07	1.12	0.12
	5.90	0.08	1.57	0.15
	6.20	0.06	1.32	0.11
	6.10	0.05	1.27	0.11
	6.00	0.05	1.42	0.12
Control	5.54	0.06	1.48	0.20
	6.34	0.07	1.88	0.17
	6.17	0.05	1.46	0.12
	5.88	0.04	1.65	0.14
	6.21	0.06	1.63	0.13
N1	5.06	0.04	1.73	0.15
	5.60	0.15	1.36	0.14
	6.49	0.09	1.98	0.24

Table 7 (continued)

Plot	Soil properties			
	pH	Electric conductivity	Organic carbon	Total nitrogen
	6.48	0.10	1.88	0.18
	5.58	0.24	1.33	0.12
N2	6.45	0.06	1.48	0.17
	5.54	0.23	1.51	0.15
	5.11	0.33	1.98	0.17
	6.03	0.06	1.41	0.14
	5.88	0.13	1.56	0.12
W1	6.07	0.07	2.15	0.19
	6.42	0.06	0.84	0.14
	6.48	0.07	2.10	0.17
	5.90	0.04	1.58	0.14
	6.04	0.05	1.36	0.11
W2	5.93	0.06	1.43	0.13
	6.17	0.05	1.56	0.13
	5.47	0.18	1.11	0.16
	6.01	0.05	1.11	0.11
	6.50	0.09	1.88	0.15

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