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A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant–soil water balance

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Summary

1. Large herbivores play a key role in creating spatial heterogeneity through the formation of grazing lawns. Recent research suggests that the currently accepted nutrient-based theory on the formation of these grazing lawns cannot universally explain their formation in all ecosystems where they are found.

2. We developed and investigated an alternative hypothesis on grazing lawn formation and maintenance based on herbivore effects on the plant–soil water balance. We propose that large herbivores change the soil water balance in grazing lawns through defoliation and soil compaction, causing a shift in vegetation composition towards a drought-tolerant plant community.

3. Investigating this idea in a tropical savanna, we indeed found profound differences in grazing lawn soil properties and water balance. In particular, defoliation increased soil temperatures and potential evaporation rates while soil compaction increased bulk density and decreased water infiltration rates, especially on fine-textured soils. Soil moisture was therefore generally much lower in grazing lawns than in adjacent bunch grass areas.

4. Furthermore, we found that grazing lawn species show drought-tolerant traits, with higher leaf sodium levels, suggesting evolutionary adaptation to these herbivore-induced dry conditions. However, leaf water potentials did not differ between grazing lawn and bunch grass species.

5. *Synthesis.* This study shows that large herbivores might form grazing lawns through previously underestimated effects on water balance. Thus, future studies on large herbivore effects on vegetation should increasingly focus on additional pathways of soil compaction and defoliation. While nutrient-based processes driving grazing lawn formation may operate during the wet season in savannas, we suggest that water balance-based processes are additionally important during the dry season.

Key-words: defoliation, herbivore-induced stress, landscape heterogeneity, plant–herbivore interactions, savannas, soil compaction, soil texture

Introduction

In grasslands, large herbivores play a key role in creating spatial heterogeneity through the formation of grazing lawns (McNaughton 1984). Grazing lawns persist in many different ecosystems and their importance for plant–herbivore interactions and as biodiversity hotspots has been widely shown (Bell 1971; Coppock *et al.* 1983; McNaughton 1984; Person

et al. 2003). They are characterized by high productivity and different plant species composition; with higher abundances of nutrient- and mineral-rich species that form keystone resources for grazing herbivores (McNaughton 1979, 1984; Augustine, McNaughton & Frank 2003). Grazing lawns have been shown to arise as a result of a positive feedback between grazing lawn grasses and grazing herbivores (McNaughton 1984). A strong history of research in the mechanisms of this feedback has firmly established the prevailing idea that grazing lawn grasses are more grazing tolerant and require more nutrients than bunch grasses and

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therefore persist under heavily grazed circumstances. The high-nutrient content of grazing lawn above-ground tissues is thought to result from three main processes (Fig. 1):

1 compensatory growth of plants keeps shoots in a physiologically young active stage (McNaughton 1976; Hik & Jeffries 1990; McNaughton, Banyikwa & McNaughton 1997; Ruess *et al.* 1997) and increases nutrient uptake per unit of root mass as a result of increased photosynthetic input (Ruess, McNaughton & Coughenour 1983; Coughenour *et al.* 1990; Coughenour 1991),

2 increased plant nutrient availability through local deposition of urine and dung (McNaughton 1979; Detling & Painter 1983; Ruess & McNaughton 1984; Holland & Detling 1990; Frank & McNaughton 1993; McNaughton *et al.* 1997; Frank & Groffman 1998; Augustine, McNaughton & Frank 2003),

3 promotion of litter quality through dominance of high-quality species, and this litter is decomposed faster, increasing soil nutrient turnover (Wedin & Tilman 1990, 1996; Grime *et al.* 1996; Olofsson & Oksanen 2002; Sjogersten, van der Wal & Woodin 2012).

The enhanced tissue nutrient concentrations of grazing lawn plants promotes repeated return of grazing herbivores, potentially resulting in a positive feedback between large grazing herbivores and nutrient-rich lawn grasses: both groups promote each other. On the other hand, low-quality bunch

grasses dominate on less nutrient-rich spots, which stay nutrient poor as the herbivores are deterred by the low tissue nutrient concentrations of the dominant plants. This nutrient-based mechanism has been proposed to explain why mosaics of bunch and lawn grasses are found in many grazing ecosystems, with locally higher grazer densities in lawn grass areas than bunch grass areas (McNaughton 1984; Augustine, McNaughton & Frank 2003).

Although this theory is generally accepted and supported by previous work, a number of studies suggest that these three processes (compensatory growth, increased nutrient addition and enhanced litter quality) alone cannot explain grazing lawn formation in all grazing ecosystems where these typical vegetation structures are found:

1 When grown without defoliation under similar conditions, grazing lawn species from both the Serengeti (Tanzania) and Hluhluwe-iMfolozi (South Africa) also contain higher foliar nutrient concentration than bunch grass species, and both groups show increased nutrient levels after defoliation (Anderson *et al.* 2013). Therefore, compensatory growth is not the only process explaining increased nutrient levels in grazing lawn species, although it could be seen as an additional effect to increase plant nutritional quality.

2 Positive, non-significant and negative feedback effects of large herbivores on nitrogen cycling have also been reported

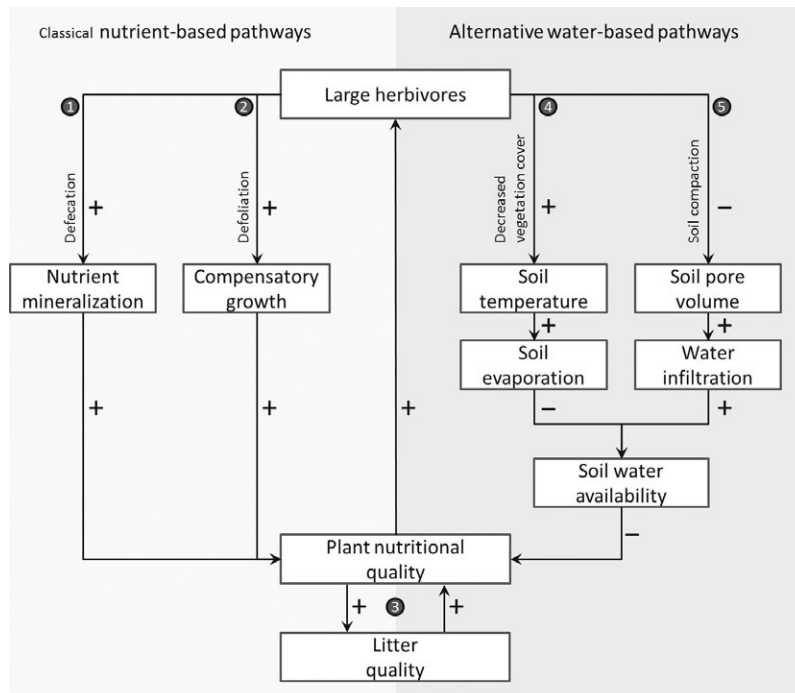


Fig. 1. Overview of the influence of large herbivores on grass nutritional quality (adapted with permission from Schrama *et al.* 2013). The diagram shows five main pathways by which herbivores affect grass nutritional quality. Pathways 1, 2 and 3 encompass the current accepted nutrient-based theory: (1) increased N-mineralization through defecation, (2) compensatory growth after defoliation and (3) increased litter quality through changes in plant community composition towards grazing-tolerant highly nutritious grass species. Pathways 4 and 5 are investigated in this study and operate in semi-arid systems through changes in water balance: (4) decreased vegetation cover through defoliation increases soil temperature and bare soil evaporation and (5) soil compaction decreases water infiltration. Together, pathways 4 and 5 decrease soil moisture which in turn increases grass nutritional quality, since plant adaptations to reduce evaporative water loss also reduces photosynthetic carbon fixation. This results in changes in plant carbon to nutrient ratios (Bremner & Dewit 1983; Ollif, Ritchie & Prins 2002).

(e.g. van Wijnen, van der Wal & Bakker 1999; Bakker *et al.* 2004; Stock, Bond & van de Vijver 2010; Schrama *et al.* 2012), indicating that other processes may play a role in the formation and maintenance of grazing lawns than just enhanced nutrient cycling (Schrama *et al.* 2013). However, while several studies report the deceleration of nitrogen cycling in grazing lawns under herbivory (Schrama *et al.* 2013), lower plant nutrient concentrations are not reported despite reductions in N mineralization. Hence, an alternative explanation is required for increased plant nitrogen concentrations in grazing lawns than promotion of N mineralization.

3 The nutrient-based theory on grazing lawn formation predicts a shift in community composition based on the assumption that lawn grasses are more tolerant to defoliation. Recently, a test of this underlying assumption under controlled laboratory conditions showed no difference between grazing lawn and bunch grass species in tolerance to defoliation (Anderson *et al.* 2013).

Coughenour (1985) indicates that grazing lawn species have traits associated with drought tolerance, like basal meristems, small stature, below-ground nutrient reserves and rapid growth. Interestingly, these very same traits enable plants to withstand grazing (Milchunas, Sala & Lauenroth 1988; Augustine & McNaughton 1998). Both water limiting conditions and high grazing pressure provides selection pressure for plants to evolve tolerance of loss of plant organs (Milchunas, Sala & Lauenroth 1988), and therefore, it has been hypothesized that tolerance to grazing and survival in semi-arid conditions have evolved together (Coughenour 1985). Furthermore, drought tolerance can be physiologically achieved by osmotic adjustment, for example through accumulation of sodium in the plant vacuoles (Jennings 1968; Girma & Krieg 1992; Gaxiola *et al.* 2001; Bartlett, Scoffoni & Sack 2012), as this increases plant turgor and plant water potential through higher osmotic potential differences between the plant and its direct surroundings (leaf boundary layer, rhizosphere). Lawn grasses have been shown to contain high levels of sodium which in turn is very attractive to large herbivores that are often sodium deficient in grazing ecosystems (Belovsky 1981; McNaughton 1988; Tracy & McNaughton 1995; McDowell 1997). In addition, plant adaptations to reduce evaporative water loss also reduces photosynthetic carbon fixation. This results in changes in plant carbon to nutrient ratios (Breman & Dewit 1983; Olf, Ritchie & Prins 2002), that could explain the high-nutrient concentrations found in grazed areas.

In this study, we therefore propose and investigate an alternative hypothesis on grazing lawn formation by large herbivores that is based on changes in plant water availability instead of nutrient cycling, resulting in an alternative feedback loop with a central emphasis on water balance. We suggest that herbivores not only modify nutrient dynamics but also the local water balance via different mechanisms, which can be grouped into two additional categories of herbivore-induced vegetation changes: (4) vegetation impacts and (5) trampling effects (Fig. 1):

4 Defoliation by herbivores opens up the vegetation and therefore decreases vegetation cover and increase the exposure of bare soil. Vegetation cover tends to reduce evaporation rates by shading the soil and reducing wind velocity (Thurrow 1991). Therefore, removal of above-ground biomass may strongly increase soil evaporation and temperature, especially in tropical ecosystems with high solar radiation, potentially reducing soil water availability for plants. Furthermore, decreased above-ground biomass reduces soil organic matter content, which is an important factor in aggregate formation and stability (Thurrow 1991). Reduced soil aggregation strongly affects macroporosity, with reduced infiltration rates and soil water content in poorly aggregated soils (Allison 1973). This may explain why vegetation cover in semi-arid ecosystems is a good predictor of infiltration capacity (Rietkerk & van de Koppel 1997).

Defoliation could also affect soil water condition indirectly through an alteration of vegetation transpiration demands. Transpiration may be reduced, if defoliation reduces leaf area. However, grazing-induced enhanced transpiration is also possible as a result of increased photosynthetic rates, due to increased leaf N, increased light, younger leaf age and reduced feedback inhibition (McNaughton 1979; Coughenour, McNaughton & Wallace 1984).

5 Trampling by large herbivores is known to have profound effects on soil physical conditions via soil compaction (Pietola, Horn & Yli-Halla 2005; Bilotta, Brazier & Haygarth 2007; Batey 2009). Compaction-induced changes in (semi-) arid ecosystems include a decrease in pore size (Kim *et al.* 2010), a reduced water holding capacity (Lipiec & Hatano 2003; Pietola, Horn & Yli-Halla 2005; Batey 2009), reduced infiltration rates (Hamza & Anderson 2005), an increased surface run-off (Batey 2009) and a reduced aggregate stability (Knoll & Hopkins 1959).

These mechanisms can create locally dry soil conditions in grazed areas as a result of reduced soil water availability through above-ground removal of vegetation and soil compaction by large herbivores. In turn, this can promote dominance of plant species with adaptations to drought, such as plant sodium accumulation and increased water use efficiency, which make these species very attractive to large herbivores. Altogether, this results in an alternative feedback loop with a central emphasis on water balance (Fig. 1, right side).

Two important factors affecting soil moisture and water balance in addition to herbivory are rainfall and soil texture. Rainfall sets the boundary condition how much water is available for infiltration in the first place. Furthermore, the effect of soil compaction is dependent on soil texture, with fine-textured soils being more sensitive to compaction than coarse-textured soils (Van Haveren 1983), and high-clay soils having naturally less water infiltration capacity under semi-arid conditions than sandy soils (Rietkerk *et al.* 2000, 2002). Therefore, it is expected that effects of grazers on the plant-soil water balance change across gradient of soil texture and rainfall.

Unfortunately, there are currently substantial differences in terminology in the literature on grazing lawn formation (e.g. lawn grasses vs. short grasses; grazing lawns vs. hotspots) and it is therefore crucial to clarify and position our terminology to put our study into context. We do so by describing the three successive processes involved in grazing lawn formation:

1 The first step is a concentration of high herbivore densities in specific areas, possibly mediated by edaphic factors as high soil fertility and low rainfall (Archibald 2008; Cromsigt & Olf 2008; Anderson *et al.* 2010), landscape features attractive to herbivores like water holes, wallows and rubbing posts (Cromsigt & Olf 2008), local fire events (Archibald *et al.* 2005; Archibald 2008) or risk-driven factors (Anderson *et al.* 2010; Hopcraft, Olf & Sinclair 2010).

2 Once herbivores are aggregated local feedbacks can arise between soil and vegetation characteristics, and herbivore abundance (Fig. 1) that change nutrient and water availability, and in turn affect plant physiology. This results in short-grazed grasses with higher plant quality and high herbivore concentrations, often referred to as grazing hotspots. Nevertheless, this could merely be a result of phenotypic plasticity and does not necessarily involve a change in plant species composition (Arnold, Anderson & Holdo 2014).

3 When these feedbacks are strong and persistent enough over time this might catalyze a turnover in plant species composition towards herbivore-induced stress adapted vegetation, possibly mediated by specific local environmental conditions (rainfall, geological grain size). These lawn-forming species have specific traits associated with herbivore-induced stress, as basal meristems, small stature, below-ground nutrient reserves, stolons/rhizomes and rapid growth (Coughenour 1985).

Here, we chose to study the effect of water balance in this last situation (different plant communities), since we expect that if the hypothesized pathways are present, we are most likely to find evidence here. Therefore, as a first attempt to investigate our water-balance hypothesis we compared water balance-related features on grazing lawns and adjacent bunch grass areas. Consequently, when referring to grazing lawns we mean a different plant community with specific traits as outlined above.

The objectives of this study were to investigate (i) how grazing lawns differ in soil physical conditions (compaction, water infiltration) compared to adjacent bunch grass areas, (ii) how these differences in soil physical factors play out over gradients of soil texture and rainfall and (iii) how these changes in water balance correlate to plant physiological responses.

Materials and methods

STUDY SITE AND SAMPLING DESIGN

We performed this study in Hluhluwe iMfolozi Park, South Africa, an ecosystem with steep gradients in rainfall and soil texture within a

relatively small area in combination with high grazer densities. For detailed description about the park and the methods described below, we refer to the online Supplementary Methods section of this paper (see Appendix S1 in Supporting Information).

We selected 24 study sites throughout the park that were separated at least 225 m, with a largest distance between sites of 31.1 km. Site selection was based on the amount of annual rainfall and on parent material (shale, dolerite or sandstone) based on geology maps of the park. These parent materials differ in soil texture with increasing geological grain size from shale to dolerite to sandstone, so as to obtain independent gradients of both rainfall and parent material texture. At every site, we chose three replicate plots of 10 × 10 m, representative for the area. At each replicate, we selected a lawn grass part and a bunch grass part, when present. Measurements were taken in the dry season (June–July) and in the wet season (November–January) of 2010.

RAINFALL

Rain gauge data from 17 weather stations was used to create a rainfall map for HiP (mostly on different locations than the study plots), containing rainfall data from 2001 to 2007. Subsequently, spatial coordinates of each site were used to extract interpolated estimates of rainfall from the map.

TEXTURE

Soil samples (approximately 150 g) were collected (see ‘Pore volume’ for collection details) at every replicate plot in the field in June 2010 and taken back to the Netherlands for a soil texture analysis at the Netherlands Institute for Sea Research, Texel. In order to determine the geological grain size distribution of the soil samples, organic matter and carbonate were removed from the samples. Median geological grain size of soils was determined using a Coulter LS 13 320 particle size analyzer and Autosampler, which measures particle sizes in the range of 0.04–2000 Fm in 126 size classes, using laser diffraction (750 nm) and PIDS (450, 600 and 900 nm) technology (McCave & Syvitski 1991).

VEGETATION HEIGHT

During the (wet) growing season, average height of both vegetation types (lawn and bunch) was measured for each replicate at each site.

SOIL TEMPERATURE

Soil temperature was measured for each site at one of the replicates in both vegetation types using Thermochron® iButton® DS1921G temperature loggers (Maxim Integrated Products Inc., San Jose, CA, USA). The iButtons® were placed in the soil at a depth of 10 cm. Temperatures were logged every day at 13.00 pm throughout the wet season study period.

POTENTIAL SOIL EVAPORATION

Potential soil evaporation was estimated during the dry season, with potential soil evaporation defined as the decrease in soil moisture over time after experimental water addition. At 15 sites, three replicates of soil moisture gypsum blocks (Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands) were buried 10 cm below the soil surface

in both lawn and bunch grass areas, thereby minimally disturbing the soil during the burial process. Gypsum blocks were left in the field for 3 days to allow the blocks to synchronize with soil moisture. Then 2 L of water were added to ensure complete saturation of the gypsum block and surrounding soil. Subsequently for 5 days in a row, decrease in soil moisture was measured, and this decrease was used as a relative estimate for potential evaporation rate. No rainfall was recorded for those days.

PORE VOLUME

During both the wet and the dry season, we measured bulk density as a proxy for pore volume, as pore volume decreases with bulk density. At every site, three soil samples were taken both in lawn and bunch grass areas. A pick (dry season) or spade (wet season) was used to break open the soil after which intact blocks of soil with undisturbed physical structure (approximately $5 \times 5 \times 5$ cm) were taken back to the research station. Plant parts were clipped from the sample when present, and pre-dried weight of the soil block was measured. The volume of the soil block was then determined by putting the samples in a glass cylinder filled with water, correcting for the amount of water taken up by the soil sample. Then the samples were oven dried for 48 h at 105 °C and weighed again. Bulk density (g cm^{-3}) was calculated as soil sample dry weight divided by original intact volume. Subsequently, samples were transported to the Netherlands for texture analysis.

WATER INFILTRATION

During both the dry and wet season, maximum infiltration rates were measured at each site with a single replicate for lawn and bunch grass areas. A double-ring infiltrometer (Bower 1986) was used with inner and outer rings of 15 and 30 cm in diameter, respectively. Infiltration rate was calculated as the drop in water level in centimetres per unit time, with a 1 cm h^{-1} drop corresponding to an infiltration rate of $10 \text{ mm water m}^2 \text{ h}^{-1}$.

SOIL WATER AVAILABILITY

During the dry season, soil water content was determined in combination with the bulk density measurements. Soil water content was calculated using soil pre-dried (FW) and dry weight (DW) as: $(FW_{\text{soil}} - DW_{\text{soil}}) / DW_{\text{soil}}$. However, in the wet season, this method was not applicable due to high fluctuations in soil moisture following rainfall events. Therefore, soil moisture was repetitively measured for each site at one of the replicates for the lawn and the bunch grass area, using gypsum blocks. Sites were measured every week on the same day across sites during the wet season of the study period.

PLANT LEAF WATER POTENTIALS

Plant leaf water potentials were measured for six common species at seven sites across the rainfall gradient between November 15 and January 13 (wet season); *Panicum maximum*, *Eragrostis curvula*, *Eragrostis superba*, *Themeda triandra*, *Urochloa mosambicensis* and *Sporobolus nitens*. Measurements were taken between 11.00 and 13.00, standardizing for midday measurements. Water potential was measured through use of a pressure chamber instrument (PMS Instrument Company), model 1000. Leaves were pressurized to a pressure of 40 bar, or until glistening was seen on the cut edge. Three measurements were taken for each species at every site.

LEAF SODIUM CONTENT

The three most abundant species of both grass types (lawn and bunch) were identified at each replicate and leaves were collected, dried and transported for sodium analysis in the laboratory, as an indicator for plant osmotic adjustment. There, vegetation samples were dried again at a temperature of 70 °C and ground with a Foss Cyclotec grinder with a sieve of 2 mm. Maximum 0.5 g sample was destructed with 8 mL 65% HNO_3 in a tube with Teflon inliner by pressurized microwave digestion using a CEM discover SPD (CEM Corporation, Matthews, NC, USA). After diluting the sample to 100 mL, leaf sodium content was measured by Atomic Absorption Spectrophotometry, using a Varian Spectra 220 FS. Measurements were optimized with 1% CsCl (Temminghoff & Houba 2004).

DATA ANALYSES

First, we analyzed differences between lawn and bunch grass areas irrespective of differences in rainfall and soil texture. We used generalized linear mixed models (GLMM) to deal with the nested design (spatial pseudoreplication), measurements over time (temporal pseudoreplication) and nonlinear behaviour of response variables. Water infiltration rates for both dry and wet season and dry season potential evaporation rates were determined fitting linear models for each measurement with time as the predictor. These infiltration and potential evaporation rates were used for further analyses. We compared dry and wet season water infiltration rates, dry season potential evaporation rates, dry season soil moisture content and bulk density and wet season penetration depth, vegetation height, plant sodium content and leaf water potential between vegetation types using a GLMM, with full models containing vegetation type as a fixed factor and site as random effect. Wet season soil temperature and soil moisture content were compared between growth forms using GLMMs with full models containing vegetation type as a fixed factor and site and time as random effects to deal with temporal pseudoreplication.

Secondly, we analyzed the effect of soil texture and rainfall on soil physical conditions related to soil compaction between vegetation types, that is bulk density and infiltration rate. To avoid spatial pseudoreplication, we averaged measurements of the replicates for all parameters, resulting in an average value for each vegetation type per site. To analyze soil texture, we constructed linear models with the full models containing vegetation type, geological grain size and their interaction effects. To analyze rainfall, we used the same models as for soil texture, using rainfall instead of geological grain size as a predictor. Model selection was done using backwards stepwise removal of non-significant fixed effects.

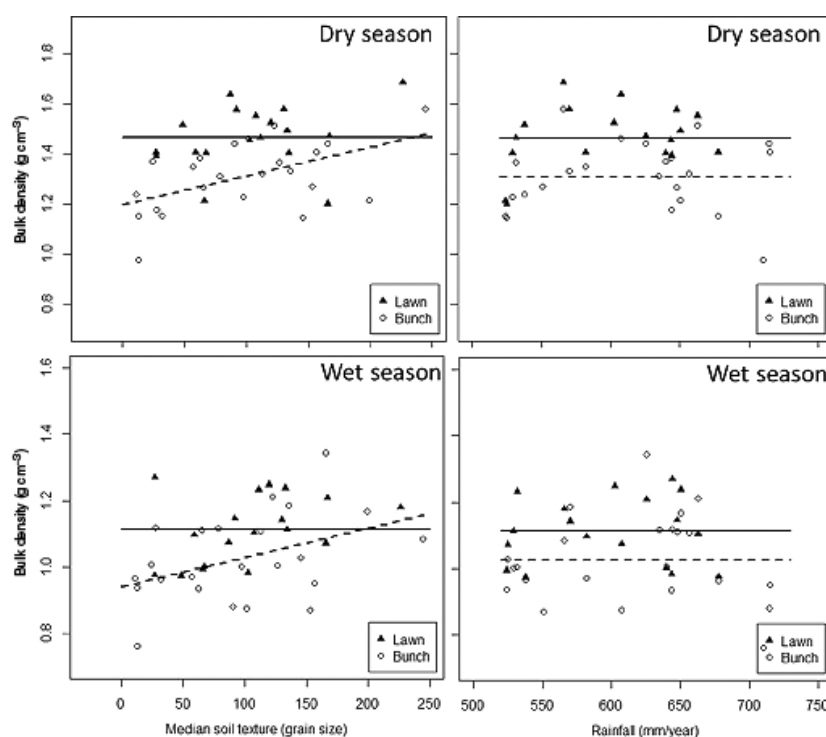
Results

SOIL PHYSICAL CONDITIONS

First, we investigated differences between lawn and bunch grass areas irrespective of differences in rainfall and soil texture. During the dry season, water evaporated significantly faster in grazing lawns than in bunch grasslands: approximately 90% of the water added to dry soil was evaporated in lawn grasslands after 2 days, while it took circa 3.5 days before the same amount evaporated in bunch grasslands (Table 1). Bulk densities were significantly higher for soils from grazing lawns than from bunch grasslands in both dry

Table 1. Generalized linear mixed-effect model results from various soil and vegetation parameters from African lawn and bunch grass areas (vegetation type) measured at 24 sites in Hluhluwe-iMfolozi Park (site was used as random factor)

Season	Parameter	Lawn	Bunch	Vegetation type
Dry	Potential soil evaporation index (%)	1.468 ± 0.068	1.095 ± 0.087	$F_{1,29} = 30.563, P < 0.0001$
Dry	Bulk density (g mL^{-1})	1.462 ± 0.019	1.315 ± 0.026	$F_{1,54} = 58.242, P < 0.0001$
Dry	Log infiltration (mm min^{-1})	-1.108 ± 0.231	0.736 ± 0.300	$F_{1,18} = 63.531, P < 0.0001$
Dry	Soil moisture (g g^{-1} soil)	0.064 ± 0.002	0.072 ± 0.008	$F_{1,54} = 8.374, P = 0.0055$
Wet	Vegetation height (cm)	6.000 ± 1.363	28.68 ± 1.484	$F_{1,71} = 276.7, P < 0.0001$
Wet	Soil temperature ($^{\circ}\text{C}$)	32.15 ± 0.766	27.07 ± 0.626	$F_{1,21} = 44.118, P < 0.0001$
Wet	Penetration depth (cm)	1.976 ± 0.148	3.499 ± 0.284	$F_{1,63} = 105.7, P < 0.0001$
Wet	Log infiltration (mm min^{-1})	-1.113 ± 0.389	0.111 ± 0.278	$F_{1,26} = 9.900, P = 0.0041$
Wet	Bulk density (g mL^{-1})	1.107 ± 0.022	1.026 ± 0.024	$F_{1,62} = 13.74, P < 0.0001$
Wet	Soil moisture ($\text{k}\Omega$)	48.21 ± 2.833	54.38 ± 2.934	$F = 4.746, P = 0.0297$

**Fig. 2.** Bulk densities of lawn grass (black triangles, black line) and bunch grass soils (open circles, dotted line) explained by median geological grain size and rainfall for wet and dry season measurements. Horizontal lines represent average bulk densities of non-significant correlations, while diagonal lines represent significant correlations from generalized linear mixed-effect models (see 'Methods').

and wet season, with the largest difference found in the dry season (Table 1). Water infiltration rates were on average twice as high in bunch grasslands than in lawn grass areas during the wet season, but this difference increased to more than 10 times for dry season infiltration rates (Table 1). Furthermore, infiltration rate significantly decreased with bulk density for the dry season (LMM: $F_{1,16} = 11.5, P < 0.01$) and for the wet season (LMM: $F_{1,25} = 5.66, P < 0.05$). All observations were used for these analyses, without separation between lawn and bunch areas, and thus showing a general pattern between infiltration rate and bulk density. Dry season soil moisture content was significantly higher in bunch grasslands than in lawn grasslands (Table 1). Also, wet season soil moisture was significantly higher in bunch grasslands than in lawn grasslands (Table 1). During the wet season, vegetation height was found to be significantly lower on grazing lawns than on bunch grass areas (Table 1). Furthermore, wet season daytime soil temperatures were on average 2.8 $^{\circ}\text{C}$ higher in

lawn grasslands than in bunch grasslands (Table 1). Wet season daytime soil temperature decreased significantly with an increase in vegetation height (GLMM: $F_{1,38} = 6.47, P < 0.05$). Again, all data points were used for these analyses, without separation between lawn and bunch areas, thus showing general relationships between soil temperature and vegetation height.

SOIL TEXTURE

Median geological soil grain size values ranged from 11 to 244 μm across the sites (see Table S1). Furthermore, we found no correlation between rainfall and geological grain size (LMM: $F_{1,22} = 0.86, P = 0.36$). To investigate the effect of soil texture on grazing lawn formation through soil compaction, we first evaluated the effect of geological grain size on differences in bulk density and infiltration rate between lawn and bunch grass soils (pathway 5 in Fig. 1). Bulk

density increased with geological grain size for bunch grass areas for both dry (LM: $F_{1,21} = 8.01$, $P = 0.01$; Fig. 2) and wet season (LM: $F_{1,21} = 4.60$, $P < 0.05$) in contrast with lawn grass areas where bulk density remained constant (dry: LM: $F_{1,16} = 1.4$, $P = 0.25$; wet: LM: $F_{1,16} = 2.93$, $P = 0.11$).

Furthermore, Fig. 3 shows how dry season infiltration rate decreased with geological grain size for bunch grass areas (LM: $F_{1,21} = 5.08$, $P < 0.05$), while for lawn grass areas we found no significant effect of geological grain size (LM: $F_{1,16} = 0.53$, $P = 0.47$). Results for wet season infiltration rates were different in comparison with dry season with a significant increase of infiltration rate for lawn grasses (LM: $F_{1,15} = 5.57$, $P < 0.05$), but not for bunch grasses (LM: $F_{1,18} = 1.14$, $P = 0.30$). However, for both seasons, the largest difference in infiltration rate was found for fine-textured soils.

RAINFALL

Annual rainfall ranged from 524 to 715 mm between the driest and wettest sites in this study. Figure 2 shows that annual rainfall did not affect bulk density in either season for neither lawn grass areas (dry: LM: $F_{1,16} = 1.52$, $P = 0.23$; wet: LM: $F_{1,16} = 0.06$, $P = 0.81$) and bunch grasses areas (dry: LM: $F_{1,21} = 0.06$, $P = 0.81$; wet: LM: $F_{1,21} = 0.03$, $P = 0.86$). However, infiltration rates were correlated with rainfall. Dry season infiltration rates (Fig. 3) decreased with rainfall for lawn grass areas (LM: $F_{1,16} = 4.80$, $P < 0.05$), but not for bunch grass areas (LM: $F_{1,21} = 0.02$, $P = 0.90$). For the wet season, we found the same pattern with decreasing infiltration rates for lawn grass

areas (LM: $F_{1,15} = 5.96$, $P < 0.05$), but not for bunch grass areas (LM: $F_{1,18} = 0.18$, $P = 0.67$).

PLANT PHYSIOLOGICAL ADAPTATIONS

Vegetation types differed significantly in their ecophysiological characteristics. Leaf sodium content was significantly higher on average for lawn grasses than bunch grasses (LMM: $F_{1,86} = 127.6$, $P < 0.0001$). In particular, the grazing lawn species *U. mosambicensis* and *S. nitens* that are more prevalent towards low rainfall areas have high leaf sodium concentrations (Fig. 4). *Digitaria longiflora*, a grazing lawn species typically found at higher rainfall areas relative to *U. mosambicensis* and *S. nitens* showed intermediate leaf sodium concentrations, but still higher than for most bunch grasses.

Leaf water potential was not significantly different between lawn grass and bunch grass species (LMM: $F_{1,29} = 2.326$, $P = 0.13$). On average, lawn grass water potential was 0.30 MPa lower than for bunch grasses. However, large interspecific differences were found (Table 2). *Themeda triandra* and *S. nitens* were found to have the lowest leaf water potentials followed by *E. curvula*, *U. mosambicensis* and *E. superba*. *Panicum maximum* had the highest water potentials measured.

Discussion

The objective of this study was to investigate the hypothesis that grazer effects on plant–soil water balance can explain grazing lawn formation, not only grazer effects on nutrient cycling. We suggested that grazers induce drought causing a

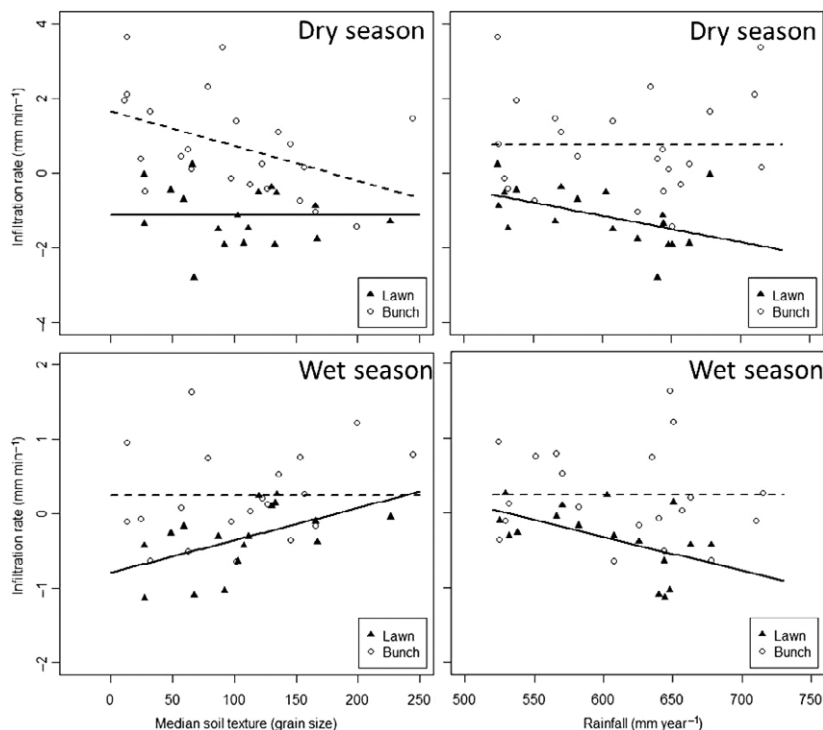


Fig. 3. Infiltration rates in lawn grass (black triangles, solid lines) and bunch grass soils (open circles, dashed lines) explained by median geological grain size and rainfall for wet and dry season measurements. Horizontal lines represent average infiltration rates of non-significant correlations, while diagonal lines represent significant correlations from generalized linear mixed-effect models (see 'Methods').

Fig. 4. Leaf sodium concentrations for the most dominant lawn and bunch grass species. Samples were taken across 24 sites. Number of samples taken per species are denoted above each boxplot. Letters indicate whether means significantly differ from each other (Tukey's test, $P < 0.05$).

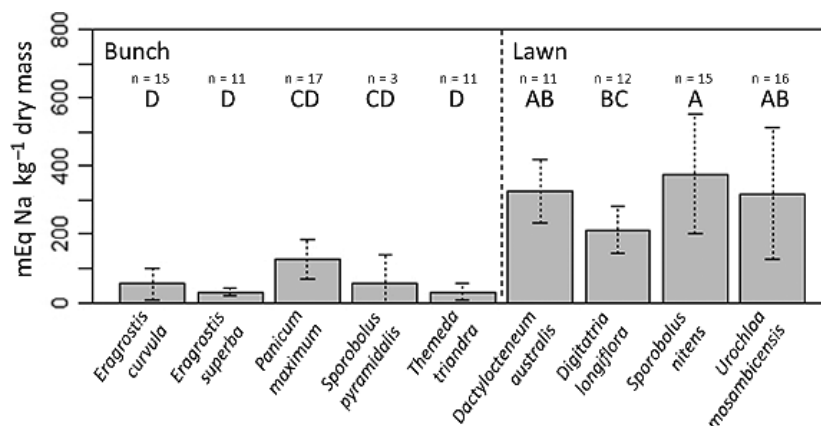


Table 2. Leaf water potentials (mean \pm SD) for six most dominant grass species (lawn and bunch) at seven selected sites that covered the rainfall gradient

Vegetation type	Species	Water potential (MPa) (mean \pm SD)
Bunch	<i>Themeda triandra</i>	-2.37 ± 1.18
Lawn	<i>Sporobolus nitens</i>	-2.21 ± 1.04
Bunch	<i>Eragrostis curvula</i>	-1.89 ± 0.42
Lawn	<i>Urochloa mosambicensis</i>	-1.75 ± 1.16
Bunch	<i>Eragrostis superba</i>	-1.62 ± 0.69
Bunch	<i>Panicum maximum</i>	-1.14 ± 0.21

shift in vegetation composition towards a drought-tolerant plant community, which then becomes secondarily attractive to herbivores through various physiological mechanisms. In a first attempt to find evidence for this hypothesis, we compared soil physical conditions and plant physiological adaptations related to water balance on and off grazing lawns. Indeed, we found that the grazing lawns of Hluhluwe-iMfolozi Park, that are known for their high herbivore visitation rates, showed profound differences in soil properties and soil water balance. In particular, bulk density, soil moisture, water infiltration and potential evaporation rates were very different between grazing lawns and bunch grass areas. Concomitant with these changes, we found that plant species characteristic for grazing lawns show drought tolerance-related traits, specifically higher leaf sodium levels (pointing at osmotic compensation). However, we did not find differences in leaf water potentials. We interpret this as evidence that our newly proposed pathway of grazer-plant-soil feedback through modification of the water balance (pathway 4 and 5 in Fig. 1) might be more important for grazing lawn formation than previously acknowledged.

IMPORTANCE OF DEFOLIATION

Investigating the relation between vegetation height and soil parameters, we found that grazing lawns had lower vegetation height compared with bunch grass areas. Furthermore, soil temperature and bare soil potential evaporation were both

found to be significantly higher on grazing lawns. Soil temperature decreased with vegetation height, suggesting direct effects of defoliation on soil temperature. Unfortunately, we could not correlate potential soil evaporation rate with soil temperature because these measurements were taken in a different season. However, Campbell (1971) did show that potential soil evaporation strongly depends on soil temperature. In combination with our results, this shows that vegetation cover reduces soil temperature and potentially affects soil evaporation rates. This strongly suggests that defoliation increased water limitation stress by warming up the soil, which is in agreement with findings by Thurow (1991).

IMPORTANCE OF SOIL COMPACTION

Secondly, we predicted higher bulk densities and lower infiltration rates for lawn grass areas as a result of soil compaction caused by herbivore trampling. Indeed, we found that bulk density was higher for grazing lawns compared with nearby bunch grass areas. This is in agreement with an earlier study by Kim *et al.* (2010) that used a medical CT scanner to analyze compacted and non-compacted soil, where compaction by grazers was found to decrease pore volume by 69%. Also, we found lower infiltration rates for lawn grass areas compared to bunch grass areas and this was directly related to differences in soil bulk density. Studies from agricultural research also show that increased bulk densities due to soil compaction results in reduced infiltration rates (Hamza & Anderson 2005). Furthermore, several studies on the effects of grazing/trampling on bulk densities and infiltration rates find similar results (Gifford & Hawkins 1978; McGinty, Smeins & Merrill 1979; McCalla, Blackburn & Merrill 1984; Belsky 1986; Thurow, Blackburn & Taylor 1986; Warren *et al.* 1986a,b; Mwendera & Saleem 1997; Castellano & Valone 2007; Du Toit, Snyman & Malan 2009). Trampling increases soil bulk density, decreases water infiltration rates and increases surface water run-off, resulting in drier conditions.

ROLE OF RAINFALL AND SOIL TEXTURE

We expected that the effect of soil compaction would be largest on fine-textured soil, because the fraction of small pores

becomes much larger in fine-textured soils (Van der Linden *et al.* 1989; Rasiah & Kay 1998). We indeed observed that the differences in bulk density and infiltration rate between lawn and bunch grass areas decreased with geological grain size. Therefore, the effect of soil compaction on soil properties such as bulk density and infiltration rate was highest on fine-textured soils. This can be explained by the fact that fine-textured soils tend to have better potential structural organization. Soil structure is determined by the degree to which soil particles are held together in individual clusters, termed aggregates (Thurrow 1991), which are often created by soil macrofauna such as earthworms. Aggregate stability increases with percentage clay (Kemper & Koch 1966; Throeh & Thompson 2005) and therefore, fine-textured soils have a higher potential soil structure, higher pore volume and lower bulk densities. However, trampling by grazing animals mechanically disrupts soil aggregates and reduces aggregate stability (Knoll & Hopkins 1959; Beckmann & Smith 1974; Thurrow 1991), as visualized in Fig. 5. Warren *et al.* (1986a, b) showed in an agricultural dryland setting that repeated high-intensity trampling decreased aggregate stability and increased bulk density which in turn reduced infiltration rates and increased surface run-off. This corresponds with the results from our study, where the largest effect of soil compaction is found at finer textures, because of the greatest change in soil structure. These results suggest that the relative importance of soil compaction in grazing lawn formation is highest with fine textures, while at coarse-textured soils other pathways (related to nutrient cycling) could be more important (pathways 1,2 and 4, Fig. 1).

PLANT RESPONSES

We expected that differences in water balance and soil properties would be related to differences in plant species traits

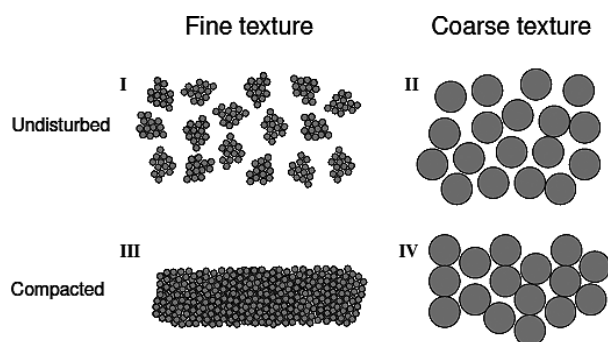


Fig. 5. Soil structure for fine and coarse-textured soils, both for undisturbed and compacted soils. I. Fine particles form soil aggregates, providing a good soil structure. Macropore size is large, resulting in high infiltration. II. Coarse-textured soils do not form aggregates. Soil structure is poor. However, because of the large particles, macropore size is still relatively high. Infiltration rates are intermediate. III. Due to compaction soil structure has broken down. Small particles are closely bound together and pore size is small. Infiltration rates are low. IV. Compaction has not much effect on coarse-textured soils. Soil structure is poor. Infiltration rates are intermediate.

through species sorting at the community level. Indeed, our results show physiological differences between lawn and bunch grasses, specifically in leaf sodium concentrations. Leaf sodium concentrations were much higher for lawn grass species than bunch grass species, consistent with other studies (McNaughton 1988; Verweij *et al.* 2006; Stock, Bond & van de Vijver 2010). Increased leaf sodium concentrations have often been attributed to local inherent soil differences (lawns forming on naturally sodic soils). Nevertheless, McNaughton (1988) found increased levels of foliar sodium concentrations in heavily grazed areas while soil sodium concentrations were not different between grazing lawns and surrounding bunch grasses, suggesting that these differences do not merely reflect soil salinity differences. Furthermore, our plots were paired and close to each other (2–5 m) with no differences in soil texture or elevation between the plots, making it unlikely that predisposed differences in soil sodium contents existed. Also, the observed differences between lawn and bunch grasses in tissue sodium concentration were retained under common greenhouse conditions (H. Olf, unpubl. results). Therefore, although we cannot directly link these increased leaf sodium concentrations to decreased water availability due to the correlative nature of our study, it does fit our hypothesis and strengthens our claim that osmotic adjustment should be considered.

Furthermore, plant water potentials did not differ between grazing lawn and bunch grass species. Large intraspecific differences were found resulting in high standard deviations, which is likely affected by the use of mid-day water potential measurements. Furthermore, this is caused by spatial and temporal variation, since leaf water potentials were measured at different sites and on different days. Interestingly, the bunch grass species *T. triandra* showed the lowest water potentials. This species often occurs on grazed patches in the Serengeti (Arnold, Anderson & Holdo 2014) and is known for its relatively high level of phenotypic plasticity and tolerance to grazing.

In this study, we have highlighted two previously overlooked effects of grazing by large herbivores on vegetation. We investigated two additional pathways and showed high correlations between herbivore grazed areas (grazing lawns) and local dry conditions through decreased vegetation cover and soil compaction. These additional pathways may be complementary to the prevailing pathways on nutrient cycling and we therefore urge to incorporate all pathways into future studies. Also, different mechanisms may dominate in different seasons, where herbivore-induced drought is a dry season mechanism, and herbivore-promoted nutrient cycling is likely more a wet season phenomenon. As soon as some process initiates herbivores to aggregate (as discussed in the introduction), multiple feedback mechanism start to take place. Subsequently, plant quality can increase through phenotypic plasticity of existing species or species turnover. However, this can be a result of either pathway. For example, Arnold, Anderson & Holdo (2014) found improved plant quality in hotspots in Serengeti and Kruger National Park, without profound changes in plant composition, nor differences in soil

chemistry. This suggests that not increased nutrient input, but compensatory growth or the pathways related to water balance might have improved plant quality (through phenotypic plasticity).

We suggest that the processes described in this study are more general and could play an important role in grazing lawn formation in ecosystems world-wide. However, the importance of the different pathways (Fig. 1) is expected to vary across gradients of geological grain size, moisture and between seasons. On the dry end of the rainfall gradient (this study), defoliation and soil compaction might induce drought stress and increase plant quality to herbivores through increased foliar sodium levels. However, in very wet systems soil compaction might create anoxic conditions, limiting plant growth through a different mechanism. Schrama *et al.* (2013) suggests that for very dry and wet soils, soil compaction by grazing herbivores results in negative feedback on N-mineralization, with an increased effect on fine-textured soils. We argue that especially under conditions where grazing lawn formation was not accompanied by a change in N cycling our alternative pathways could play an important role in creating stressful environments and adapted vegetation which in turn is attractive for large herbivores.

Lastly, soil compaction can affect N-mineralization (Schrama *et al.* 2012), which may result in interactive effects between the pathways. Also, grazing lawn formation through feedbacks on water availability can secondarily promote nutrient cycling through grazer attraction or vice versa, which makes it difficult to distinguish the effects of these processes. Our study should be seen as a first investigation and has shown that we should consider the proposed alternative pathways on grazing lawn formation through changes in water balance. We therefore call for further work that experimentally investigates the causes and effects and separates the relative importance of, and interactions between the different pathways of the grazing lawn hypothesis along main environmental gradients.

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Data accessibility

Data and R scripts available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.05f81> (Veldhuis *et al.* 2014).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary methods.

Table S1. Detailed texture information of the soil samples.