*Applied Vegetation Science* **17** (2014) 470–481

# Response of community-aggregated plant functional traits along grazing gradients: insights from African semi-arid grasslands

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**Keywords**
Continuous and rotational grazing; Forage quality; Functional ecology; Leaf carbon and nitrogen content; Numerical traits; Piospheres; Plant strategies; South Africa; Specific leaf area; Taxon-free method; Tenure system

**Abbreviations**
CO = commercial tenure system; CPFT = community-aggregated plant functional traits; CU = communal tenure system; GP = grazing pressure; MRPP = multi-response permutation procedure; RDA = redundancy analysis

**Nomenclature**
African Plant Database

Received 25 June 2013
Accepted 25 November 2013
Co-ordinating Editor: Lauchlan Fraser

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## Abstract

**Questions:** Plant communities fulfil key functions in the ecosystem, which can be characterized by their plant functional traits. In functional ecology, plant communities are considered to hold a set of trait attributes reflecting a specific plant strategy adapted to persist in the environment to which they are exposed. In semi-arid grasslands of the Republic of South Africa, we addressed the following questions: how are community-aggregated plant functional traits (CPFT) shaped by grazing gradients; which plant strategies are associated with the response of CPFTs; and are environmental factors, such as soil properties and grazing management, interrelated with the functional response of vegetation to grazing gradients?

**Location:** Semi-arid grasslands close to Thaba Nchu, Free State (Republic of South Africa).

**Methods:** Piosphere transects from a water point into the field were established to portray grazing gradients on two communal grazing areas with continuous grazing and two commercial farms with rotational grazing. Along each transect, six plots (5 × 5 m) were evenly distributed. The trait–transect sampling was applied to record 12 CPFT related to light capture and forage quality. A redundancy analysis was performed to derive relationship between CPFTs, grazing gradients and environmental conditions.

**Results:** Grazing intensity decreased along piosphere transects, from the water point into the field. Most CPFTs responded to this decreasing gradient of grazing intensity and so allowed derivation of trait syndromes that clearly reflect plant strategies of ruderal and competitive vegetation. Close to water points, plants had higher nitrogen concentrations, fewer cell wall components and higher specific leaf area, hence light capture might be faster and more efficient per leaf area and leaf mass. Plant communities exposed to intensive grazing were well adapted to defoliation, trampling and nutrient accumulation through fast growth rates and a quick return strategy.

**Conclusions:** In the sacrifice zone around water points, there is an ecological niche for vegetation communities exhibiting a strategy of fast growth, which is well adapted to intense and frequent grazing and is also associated with forage of high nutritional quality.

Doi: 10.1111/avsc.12092

## Introduction

Grasslands occupy approximately 40% of the Earth's terrestrial surface (Reynolds 2005). They provide many ecosystem services, with the supply of forage for domestic and wild herbivores being among the most important. Mismanagement of livestock farms, and especially overgrazing, has been widely identified as a major cause of grassland degradation and desertification in arid and semi-arid environments (Milton et al. 1994; Snyman & du Preez 2005; Ruppert et al. 2012). Sharp ecological thresholds in vegetation change may occur along local grazing gradients (Sasaki et al. 2008). Particularly steep grazing gradients may be found in close vicinity to water points. The piosphere, i.e. the extremely degraded area around water points, is induced by a high concentration and return rate of livestock that drink water, graze intensively, release excreta and trample the vegetation (Andrew 1988). Although piospheres have been frequently studied for understanding grazing effects on vegetation, other factors such as soil properties, can be coupled with grazing effects and in turn influence vegetation structure and composition (Linstädter & Baumann 2013). Hence, piosphere studies need to take into account the extent to which soil properties, management practices and grazing gradients co-vary.

Assessment of the state and degradation condition of South Africa's grassland vegetation is based on agronomic principles, and primarily aims at improving livestock production (Hardy et al. 1999). Changes in floristic composition and the response of indicator species or species groups along known grazing gradients (van der Westhuizen et al. 2005; Van Oudtshoorn 2009) may also be interpreted as a functional vegetation response to grazing. However, up to now few studies have directly addressed how grazing affects the expression of plant functional traits in grassland communities in South Africa's semi-arid grasslands.

In recent years, functional ecology has developed as a discipline that offers new opportunities in linking plant functional traits (Violle et al. 2007) to processes within communities, as influenced by both environment and management. Functional ecology puts into focus the functioning of plants in the ecosystem rather than the taxonomic classification of species. It also links the provision of ecosystem services to these functions (Lavorel et al. 2011). The functional approach improves our understanding of the underlying mechanisms that lead to temporal changes and spatial variations in floristic composition (McGill et al. 2006). Furthermore, certain traits have been identified as particularly sensitive to environmental change, such as those that are known to respond to nutrient gradients (Schellberg & Pontes 2012). Specific traits may not only respond to but also affect on ecosystem processes, and are thus called effect traits (Kazakou et al. 2009). Although there are differences between response and effect traits per definition, both trait types are related to each other and together constitute the community structure that influences major ecosystem functions (Suding et al. 2008).

As functional traits can be measured on practically any individual plant, the functional trait approach not only allows crossing species' boundaries but also scaling up of functional traits to higher levels of organization (Violle et al. 2007). In this sense, community-aggregated plant functional traits (CPFT) express an aggregation of trait values that enables the trait characterization of an entire plant community. CPFT have traditionally been calculated as the mean trait value weighted by the relative abundance of each species (Garnier et al. 2007). This so-called taxon-explicit method takes into account species' identity and provides a set of trait values for each species.

In contrast, taxon-free methods, which ignore species identity, have been recently tested (Gaucherand & Lavorel 2007). In rangeland studies, taxon-free methods have been applied to capture spatio-temporal patterns of CPFT, ignoring floristic composition, as affected by defoliation and trampling (Albert et al. 2010; Violle et al. 2012). Furthermore, taxon-free sampling allows rapid assessment of species-rich communities, as there is no need to identify species (Gaucherand & Lavorel 2007). It is also a valuable method for direct assessment of numerical trait responses, particularly along large environmental gradients. Most studies on grazing effects have either concentrated on categorical traits, applying taxon-explicit methods (Saatkamp et al. 2010; Wesuls et al. 2012), or defined plant functional types based on a set of numerical traits.

In this study, we hypothesized that (i) a variation in grazing intensity along local gradients leads to changes in CPFT, and that some of them are highly relevant for forage quality. Based on the assumption that CPFT can assist in better understanding functional interaction with grazing (defoliation, trampling and excreta) and vegetation, we also hypothesized that (ii) plant strategy in grasslands follows a pattern of CPFT along the grazing gradient. We finally hypothesized that (iii) among other variables, such as soil properties and range management practices (i.e. continuous and rotational grazing), the grazing intensity is the main explanatory factor driving the response of CPFT. Accordingly, the aims of this research were (i) to identify changes of CPFT with grazing intensity along piosphere transects, to (ii) link CPFT responses with plant strategies, and (iii) to describe trait response to grazing intensity under different soil conditions and management practices (i.e. continuous and rotational grazing) associated with tenure systems.

## Methods

### Study area

The study was performed in a grassland situated in South Africa's Free State, close to the town of Thaba Nchu (29°13′S, 26°47′E; 1490 m a.s.l.). The climate is semi-arid with a mean annual precipitation of 560 mm; rain primarily falls in summer (October–April) and determines the growing season. Maximum and minimum mean daily temperatures in January and July are 31 °C/15 °C and 16 °C/−2 °C, respectively, with 119 frost days per annum on average (Schulze 1979). Predominant soils are Lixisols (FAO 2006), which contain a mixture of clay minerals, dominated by montmorillonite and illite. Vegetation is classified as an *Eragrostis obtusa-Eragrostis lehmanniana* grassland (Cowling et al. 2004) and is dominated by perennial $C_4$ grasses such as *Themeda triandra* and *Eragrostis* spp. (see species list in Appendix S1).

### Data acquisition

We selected four farms that were representative of the two main tenure systems found in South Africa's grassland biome: communal grazing areas and commercial farms (see Table 1). Stocking rates were estimated based on direct interview of the headmen, most cattle owners from the communities and the owners of the commercial farms. During autumn 2010 (Mar–Jul), one transect along the piosphere caused by gradual animal grazing was identified at the unique and permanent water point of each study area (i.e. two grazing areas each on communal and commercial farms). Transect length was determined based on a visual assessment of a gradient of biomass uptake and biomass destruction induced by defoliation and trampling in relation to the distance to water points and varied among farms (see Table 1). Transects started at water points and ended at average field conditions, where changes in vegetation structure and composition were no longer visually detectable. Along each transect, six plots (5 × 5 m) were equally spaced. Hence, the six positions per piosphere transect were denominated as 1 (closest to the water point) to 6 (furthest from the water point).

At the end of the growing season, between March and April 2011, vegetation exposed to grazing was surveyed. In order to measure the grazing effect on vegetation structure under current grazing conditions, animal access to plots was not restricted. A trait–transect sampling (taxon-free method) was applied (Gaucherand & Lavorel 2007), using two lines 5 m long in each plot. In addition, species identity was recorded (Appendix S1). On each line, we sampled 13 points at a distance of 40 cm. Hence 26 points per plot were sampled, which complies with the sample size recommended of Cornelissen et al. (2003). At each point, direct measurements of traits were conducted on individual tillers (rooted individuals were considered on stoloniferous species) and stems (other than grasses, hereafter called tiller) that had flowered but had not been defoliated. We pooled a sample of 13 tillers per line and stored them in a cooler until laboratory measurements were taken. Leaf traits were measured on the youngest, healthy and fully expanded leaf of each individual tiller. After sampling, a strip of 5.0 × 0.5 m centred at each line was clipped to stubble height (2 cm). The material was oven-dried (48 hr, 68 °C), and dry matter of biomass samples and total dry biomass per unit area were calculated.

Two criteria were used in the selection of traits that were measured: published relevance of numerical traits for impact of grazing on vegetation functioning (Weiher et al. 1999; Diaz et al. 2007) and its significance for forage quality and animal intake. Furthermore, we considered their relevance in the description of plant strategies. Thus, 12 traits were measured on standing biomass. Values of numerical plant functional traits were averaged cross-wise in each plot (26 measurements). A list of plant functional traits is given in Table 2.

To obtain a surrogate for light absorption and potential leaf photosynthetic capacity, we used a handheld chlorophyll meter SPAD-502 (Konica 2009). In the field, at least three SPAD readings were taken in the centre of the fully expanded leaf when still attached to each individual tiller.

**Table 1.** Average characteristics of field conditions in transects.

| Farm Name | Land Tenure | Transect Length (m) | Bare Ground (%) | Stocking Rate (Ha·LSU$^{-1}$)$^{\ddagger}$ | Grazing Pressure (1–9) | Denomination | Litter and Moribund Biomass, % | Standing Biomass (g·m$^{-2}$) |
|---|---|---|---|---|---|---|---|---|
| Fransina | CO$^{\dagger}$ | 56 | $4.77^{a}$ | 5.15 | $3.33^{a}$ | Low | $3.61^{*b}$ | $293.90^{*b}$ |
| Middeldeel | CU$^{\dagger}$ | 70 | $30.12^{*c}$ | 4.35 | $5.67^{*b}$ | Moderate to severe | $0.85^{a}$ | $116.59^{a}$ |
| Rustdam | CO | 45 | $12.35^{b}$ | 4.92 | $6.00^{b}$ | Moderate to severe | $2.25^{*ab}$ | $136.39^{*a}$ |
| Sediba | CU | 45 | $17.25^{*c}$ | 5.98 | $6.83^{*b}$ | Severe | $0.87^{a}$ | $105.62^{a}$ |

Different letters indicates significant differences between farms (one-way ANOVA and LSD, $P < 0.05$).

*Significant differences between tenure systems (Student's *t*-test, $P < 0.05$).

$^{\dagger}$CO and CU = commercial farms and communal grazing areas as land tenure, respectively.

$^{\ddagger}$Stocking rate = ha per livestock unit.

**Table 2.** Community-aggregated plant functional traits (CPFT) measured on standing biomass, their description, abbreviations, and measurement units. Summary of results of ANOVA among transect positions.

| | CPFT | | ANOVA | |
|---|---|---|---|---|
| | Abbreviation | Unit | *F* | *P* |
| Leaf chlorophyll meter readings | $L_{SPAD}^{\dagger}$ | | 0.683 | 0.643 $^{NS}$ |
| Leaf area | $L_a$ | ($cm^2$) | 2.913 | 0.042 * |
| Leaf C content | $L_C$ | ($mg\cdot g^{-1}$) | 1.297 | 0.309 $^{NS}$ |
| Leaf C:N Ratio | $L_{C:N}$ | | 2.200 | 0.100 $^{NS}$ |
| Leaf N content | $L_N$ | ($mg\cdot g^{-1}$) | 2.763 | 0.051 $^{NS}$ |
| Leaf number per tiller | $L_n^{\dagger}$ | ($tiller^{-1}$) | 0.995 | 0.449 $^{NS}$ |
| Specific leaf area | $L_{SLA}$ | ($m^2\cdot kg^{-1}$) | 0.890 | 0.508 $^{NS}$ |
| Tiller C content | $T_C$ | ($mg\cdot g^{-1}$) | 0.077 | 0.995 $^{NS}$ |
| Tiller cell wall components (NDF) | $T_{CW}$ | ($mg\cdot g^{-1}$) | 1.762 | 0.172 $^{NS}$ |
| Tiller height | $T_h^{\dagger}$ | (cm) | 1.755 | 0.173 $^{NS}$ |
| Tiller N content | $T_N$ | ($mg\cdot g^{-1}$) | 2.890 | 0.044 * |
| Tiller weight | $T_w$ | (mg) | 4.261 | 0.010 * |

NDF, neutral detergent fibre; *F*, statistic F; *P*, probability; NS, not significant.

$*P < 0.05$; $**P < 0.01$.

$^{\dagger}$Measurements carried out on each individual tiller.

**Table 3.** Explanatory variables measured on the sward and on the soil, their description, abbreviations and measurements units.

| Feature | Variable | Abbreviation | Unit |
|---|---|---|---|
| Sward Characteristics | Bare ground | BG | (%) |
| | Grazing pressure | GP | |
| | Litter and moribund biomass | LM | (%) |
| | Standing biomass | SB | ($g\cdot m^{-2}$) |
| | Tiller density | TD | ($m^{-2}$) |
| Soil properties | Available water capacity (potential) | $S_{AWC}$ | ($100\ m^3\cdot m^{-3}$) |
| | Cation base saturation | $S_{CBS}$ | (%) |
| | Cation exchange capacity | $S_{CEC}$ | ($meq\cdot 100\ g^{-1}$) |
| | Soil acidity | $S_{pH}$ | |
| | Soil C content | $S_C$ | ($mg\cdot kg^{-1}$) |
| | Soil C:N ratio | $S_{C:N}$ | |
| | Soil N content | $S_N$ | ($mg\cdot kg^{-1}$) |
| | Soil content of plant available phosphorus | $S_P$ | ($mg\cdot kg^{-1}$) |

The highest value was recorded to avoid underestimates (e.g. for grasses with narrow leaves). Specific leaf area ($L_{SLA}$) was measured according to Garnier et al. (2001). Therefore, one leaf scan of the pooled samples (i.e. of 13 leaves) was conducted with a LI-3100C area meter (Li-Cor, Lincoln, NE, US). $L_{SLA}$ was calculated as the ratio of leaf area of fresh leaves to leaf dry mass (oven dried 48 hr, 68 °C). Pooled samples of tillers and leaves were ground and combusted for analysis in an autoanalyser (NA 1500; Carlo Erba, Milano, IT) to determine C and N content. Tillers were analysed for cell wall components ($T_{WC}$) via neutral detergent fibre analysis (Goering & Van Soest 1970).

Vegetation state at the plot level was assessed using five parameters, (i) a visual estimation of the ground cover of litter and moribund biomass, (ii) a visual estimation of bare ground cover, including stone cover, (iii) a measurement of the standing biomass of the two strips per plot, (iv) an estimation of tiller density as the ratio of standing biomass and tiller weight (Pontes et al. 2010), (v) a combination of parameters (i)–(iii), and (vi) a visual observation of the plot floristic composition in an expert assessment of grazing pressure (GP; Van Oudtshoorn 2009). The GP was denominated as follows: 1 (none), 2 (none to low), 3 (low), 4 (low to moderate), 5 (moderate), 6 (moderate to severe), 7 (severe), 8 (severe to extreme) and 9 (extreme) in accordance with Holecheck et al. (2006). Sward characteristics are listed in Table 3.

We collected and pooled five soil subsamples per plot (5 cm diameter at 0–20 cm depth). Samples were thoroughly mixed, air-dried, crushed and sieved (2 mm). Soil texture was determined by the pipette method and the sieve method (Committee 1990). Cation base saturation ($S_{CBS}$) and cation exchange capacity ($S_{CEC}$) were calculated based on atomic absorption spectroscopy. Soil acidity was measured in a 1:2.5 (v/v) water suspension. The soil C and N content was determined by combustion in an autoanalyser (NA 1500), and the C:N ratio calculated. The soil content of plant-available phosphorus (Olsen P) was determined colorimetrically (Murphy & Riley 1962). The potential available water capacity ($S_{AWC}$) was estimated via a pedotransfer function (Gaiser et al. 2000) for soils with a non-low active clay fraction

$$S_{AWC}\,[100\,m^3\cdot m^{-3}] = 0.093\,C\,[g\cdot kg^{-1}] + 0.254\,clay\,[\%] + 0.185\,silt\,[\%] \tag{1}$$

where C was total carbon and where the soil content of clay and silt was expressed as a percentage of soil texture. Soil samples were free of carbonates, so total C was used in place of the total organic C measurement required in the original equation. Soil properties are listed in Table 3.

## Data analysis

Redundancy analysis (RDA) was performed with CANOCO for Windows 4.5 (Wageningen UR, NL) with the following settings: (i) not standardized by samples, (ii) centred and (iii) standardized by CPFT (Lepš & Šmilauer 2003b). The explanatory power of environmental variables was assessed with a Monte Carlo permutation test (999 permutations) restricted by line transects (Lepš & Šmilauer 2003a).

A multi-response permutation procedure (MRPP) was performed with PC-ORD v 6 (MjM Software, Gleneden Beach, OR, US) to compare the CPFT response to grazing intensity among tenure systems. We grouped two lines per plot, two consecutive plots of transects as near (1 and 2), middle (3 and 4) and far (5 and 6), and the two farms of each tenure system. Multiple comparisons based on relative Euclidean distances were performed.

An ANOVA ($P < 0.05$) was conducted, and least significant differences (LSD) for comparisons among farms as well as Pearson's correlation coefficient (r) were calculated using SPSS 20 (IBM Corp., New York, NY, US). Comparisons among tenure system were performed with Student's *t*- test at a 5% significant level. We log10-transformed $L_N$, $L_{SLA}$, $T_N$, $T_W$ and $T_{wRE}$ to normalize the data.

## Results

### Response of CPFT along piosphere transects

Grazing pressure (GP) decreased with increasing distance from the water points, levelled off at mid-positions and became almost constant at the furthest position (Fig. 1a).

In contrast to the response of GP, standing biomass increased consistently with distance to water points (Fig. 1a). Where high GP occurred in areas close to the water point, only a small amount of biomass was measured. Hence, there was a strong correlation of the two morphological traits $T_h$ and $T_w$ and the standing biomass (Fig. 1a,b; $r = 0.879$ and 0.815, respectively, $P < 0.01$). In contrast, tiller density did not follow a clear trend along piosphere transects, ranging from 1266, 1499, 802, 792, 782–994 tillers·m$^{-2}$ from positions 1–6 (averaged across farms). Therefore, the increase in standing biomass was better explained by a corresponding increase in the above-mentioned traits of individual tillers than by changes in tiller density.

A trend towards lower $L_{SLA}$ was identified along transects, with high values in positions close to the water point (1) and low values further away (4 and 6; Fig. 2a). However, this trait exhibited high variability, as indicated by the error bars in the figure. A comparison of Fig. 2a,b indicates that $L_{SLA}$ and $L_N$ followed a similar pattern, with a positive correlation ($r = 0.609$, $P < 0.01$). While communities close to the water point had higher N content than those at more distant positions of the transect. Structural components of tillers ($T_{CW}$) behaved contrarily, with lower values close to the water point.

Ordination diagrams resulting from the RDA are presented in Fig. 3. The distribution of the sampled plots (Fig. 3a) indicates a gradual and ordered pattern from positions close to the water point (1) on the right side of the diagram to positions further away (6) on the left. A summary of the related statistics is given in Table 4.

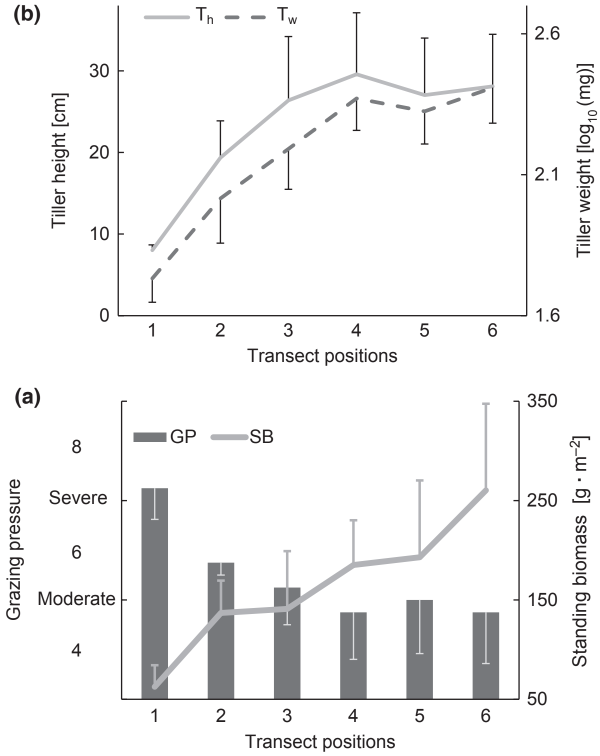


**Fig. 1.** (a) Variation in grazing pressure (GP) and standing biomass (SB) and (b) response of tiller height and weight along transect positions. Horizontal axes represent six evenly distributed positions along piosphere transects (Transect positions), from 1 (closest to water point) to 6 (furthest from water point, where no further vegetation changes were visually detectable). Error bars indicate SD. Abbreviations: $T_h$, tiller height; $T_w$, tiller weight.

Figure 3b presents CPFTs as the response variables of the RDA. Communities on the right side of the ordination diagram (Fig. 3a,b) represent higher $L_N$ and $T_N$, thus suggesting a better forage quality than those on the left side. Towards the left side, $L_{CN}$ and $T_{CW}$ represent higher values of structural components (NDF = cellulose, hemicelluloses and lignin), which generally indicate lower forage quality. Similarly, we identified heavier and taller tillers at low axis values on the left (Fig. 3b), which can be associated with higher amounts of biomass (as presented in Fig. 1a). Tiller height was positively correlated to tiller cell wall components ($r = 0.772$, $P < 0.01$; Fig. 3b). Thus, the response of CPFT displays a contrast of 'forage quality' vs 'forage quantity' along Axis 1. The second axis (Axis 2) mainly represents the response of $L_{SPAD}$ and less of other CPFTs. The location of $L_N$ in almost orthogonal direction to SPAD indicates a weak correlation of values with leaf N content and leaf photosynthetic capacity.

Doi: 10.1111/avsc.12092

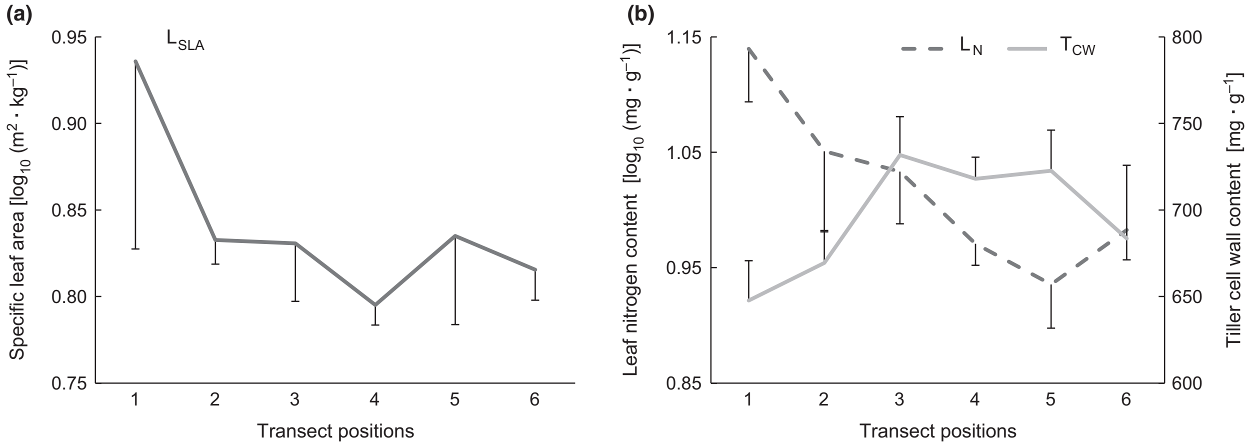
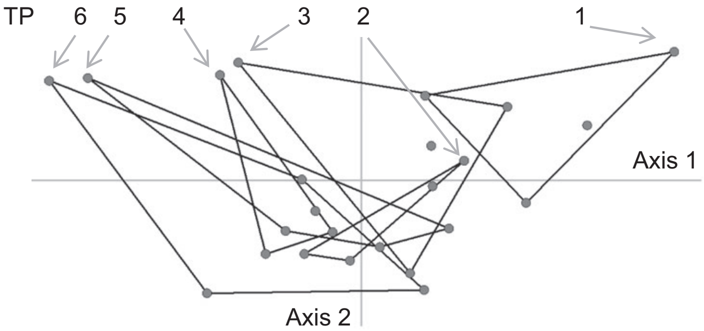


**Fig. 2.** **(a)** Specific leaf area and **(b)** comparison of leaf N with tiller cell wall components along transect positions. Horizontal axes represent six evenly distributed positions along piosphere transects (Transect positions), from 1 (closest to water point) to 6 (furthest from water point, where no further vegetation changes were visually detectable). Error bars indicate SD. Abbreviations: $L_{SLA}$, specific leaf area; $L_N$, leaf N content; $T_{CW}$, tiller cell wall components.

(a) **Sampled plots**



(b) **Response variables** (c) **Explanatory variables**

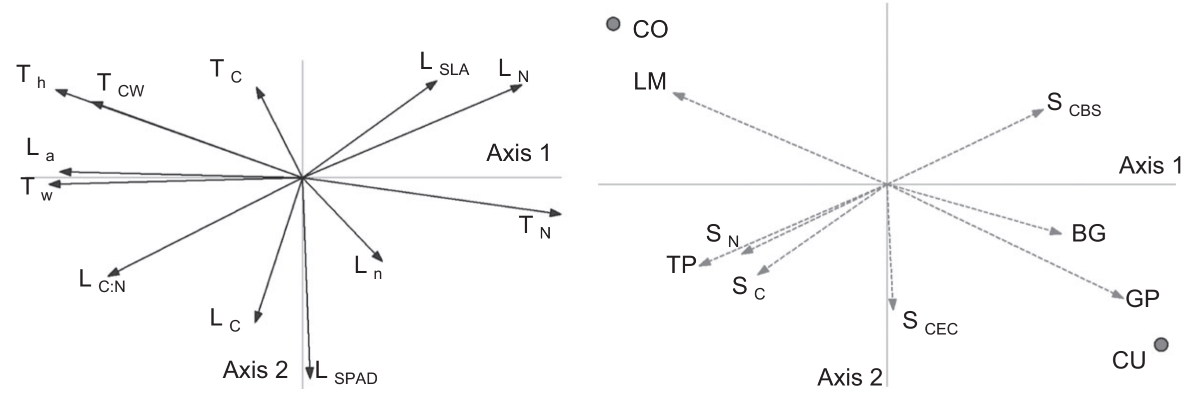


**Fig. 3.** Ordination diagrams derived from RDA based on community-aggregated plant functional traits (CPFT) measured on semi-arid grasslands of South Africa. **(a)** Sampled plots ($n$ = 24) of four farms and six positions of piosphere transects (TP). The enveloped lines indicate TP from 1 (closest to water point) to 6 (furthest from water point, where no further vegetation changes were visually detectable). **(b)** CPFT response variables and **(c)** most important explanatory variables. Abbreviations: CU, communal grazing areas, CO, commercial farm. See Tables 2 and 3 for further abbreviations and Table 4 for analysis details.

**Table 4.** Summary of results of redundancy analysis (RDA) of community-aggregated plant functional traits (CPFTs).

| Analysis | % axis 1 (all)* | *F* axis 1 (all)† | *P* axis 1 (all)‡ |
|---|---|---|---|
| RDA (Fig. 3) | 40.1 (66.6) | 6.683 (2.321) | 0.0010 (0.0010) |

*Trait variability explained by canonical Axis 1 and for all (4) axes in brackets.

†*F* = statistic F for Axis 1 and for all axes in brackets.

‡*P* = probability from the Monte Carlo permutation test for Axis 1 and for all axes in brackets.

## Explanatory variables of CPFT response

### *Effect of grazing intensity*

Grazing pressure, litter and moribund biomass, as well as bare ground, were the most important explanatory variables that varied along Axis 1 (Fig. 3c), which represent the gradient of grazing intensity. These variables best explained the grazing impact mainly as a consequence of defoliation. High values of grazing pressure corresponded with large values of bare ground on the right end of the ordination diagram, while a high cover of litter and moribund biomass (accumulation of ungrazed biomass) appeared under low grazing pressure at the opposite end.

### *Effect of soil properties*

The second axis of variation (Fig. 3c) was mostly explained by soil properties, particularly $S_{CEC}$. The redundancy analysis, where soil properties and other sward characteristics were analysed as explanatory variables, revealed a strong negative correlation of $S_{CBS}$ with $S_N$ ($r = 0.421$, $P < 0.05$), whereas $S_C$ and $S_N$ were positively correlated ($r = 0.776$, $P < 0.01$). The GP vector in this diagram also indicates that, on average for all transect plots, farms and tenures systems, soil N and C content increased when grazing pressure decreased at most distant piosphere positions.

### *Effect of tenure system*

The effect of tenure system as an explanatory variable of the functional response along the grazing gradient was evaluated with a MRPP. Table 5 shows that there were no differences between tenure systems in this respect, neither between positions near water points (1 and 2), nor in middle positions of transects (3 and 4). However, far positions (5 and 6) were significantly different from each other. Comparisons of grouped positions within each tenure system also indicate significant differences among positions near to water points (1 and 2) and the remaining positions. Nevertheless, differences among middle positions (3 and 4) and far positions (5 and 6) in both tenure systems were not significant.

# Discussion

## Methodology

Measuring CPFTs with the trait–transect procedure and taxon-free methodology had the advantage of accounting for variation in trait expression due to species richness, its relative abundance and species turnover. In addition, the trait–transect method also accounts for intraspecific trait

**Table 5.** Results of multi-response permutation procedure (MRPP) on grouped transect positions on communal (CU) and commercial (CO) farms around the town of Thaba Nchu, Free State (Republic of South Africa).

| Multiple comparisons (relative euclidean distance) | | | CU | | CO | *P* | *A*† | *T*‡ |
|---|---|---|---|---|---|---|---|---|
| Near CU | vs | Near CO | 1, 2 | vs | 1, 2 | 0.8376 $^{NS}$ | 8.89E-01 | −0.0312 |
| Middle CU | vs | Middle CO | 3, 4 | vs | 3, 4 | 0.1299 $^{NS}$ | −1.04E+08 | 0.0566 |
| Far CU | vs | Far CO | 5, 6 | vs | 5, 6 | 0.0083 ** | −3.72E+08 | 0.172 |
| Near CU | vs | Middle CU | 1, 2 vs 3, 4 | | | 0.0423 * | −2.14E+08 | 0.0704 |
| Near CU | vs | Far CU | 1, 2 vs 5, 6 | | | 0.0442 * | −2.14E+08 | 0.0697 |
| Middle CU | vs | Far CU | 3, 4 vs 5, 6 | | | 0.5131 $^{NS}$ | 2.89E-01 | −0.0094 |
| Near CO | vs | Middle CO | | | 1, 2 vs 3, 4 | 0.0147* | −3.19E+08 | 0.174 |
| Near CO | vs | Far CO | | | 1, 2 vs 5, 6 | 0.0011 ** | −5.77E+08 | 0.3004 |
| Middle CO | vs | Far CO | | | 3, 4 vs 5, 6 | 0.442 $^{NS}$ | 2.24E−01 | −0.0125 |
| Near CU | vs | Middle CO | 1, 2 | vs | 3, 4 | 0.0066 ** | −3.88E+08 | 0.205 |
| Near CU | vs | Far CO | 1, 2 | vs | 5, 6 | 0.0004 ** | −6.79E+08 | 0.3416 |
| Middle CU | vs | Far CO | 3, 4 | vs | 5, 6 | 0.011 * | −3.48E+08 | 0.1729 |
| Middle CU | vs | Near CO | 3, 4 | vs | 1, 2 | 0.1185 $^{NS}$ | −1.14E+08 | 0.0466 |
| Far CU | vs | Near CO | 5, 6 | vs | 1, 2 | 0.0872 $^{NS}$ | −1.42E+08 | 0.0546 |
| Far CU | vs | Middle CO | 5, 6 | vs | 3, 4 | 0.1305 $^{NS}$ | −1.05E+08 | 0.0532 |

*P*, probability, $*P < 0.05$; $**P < 0.01$; NS, not significant.

†*A* = statistic *A* chance-corrected within-group agreement as $\log_{10}$.

‡*T* = test statistic *T*, describes separation between groups.

variability that is relevant for trait studies (Violle et al. 2012) and which is at least partially neglected in other methods. However, our results suggest a low sensitivity of CPFTs captured with the taxon-free methodology in response to grazing pressure. We did not identify significant differences in most of our comparisons of CPFTs along the grazing gradient (Table 2). Moreover, we found no significant correlation between $L_{SPAD}$ and $L_N$ ($r = -0.204$, $P < 0.05$; Fig. 3b). In contrast to other studies (Kantety et al. 1996), our results did not show correspondence between $L_{SPAD}$ and leaf N content. We infer that this lack of correlation can be ascribed to the taxon-free method, which disregards the species-specific attributes that influence SPAD values, such as cell wall components and leaf thickness.

## Effects of grazing intensity

In accordance with our first hypothesis, our study provides evidence for a functional response of semi-arid vegetation to the effect of a grazing intensity along piospheres. The general response of 12 CPFTs along the gradients, as observed from the distribution of plots in the ordination diagram (Fig. 3a), followed an ordered pattern in accordance with increasing distance from water points (see TP in Fig. 3b). In more detailed observations, previous studies reported clear responses of community-aggregated single traits (Cruz et al. 2010; Wesuls et al. 2012) or responses of grass species' trait syndromes to grazing (Pontes et al. 2010). Our study also confirms that the response of individual traits to grazing may be highly variable (Saatkamp et al. 2010). In semi-arid grasslands of South Africa, we found both a correlation between CPFTs such as $T_h$ and $T_W$ (Fig. 1a) and complementary behaviour, such as for $L_N$ and $T_{CW}$ (Fig. 2b). We also identified an aggregated response of morphological traits (e.g. $T_h$, $T_w$, $L_a$ – taller and heavier tillers had larger leaves; Fig. 3b), which can be interpreted as a typical trait syndrome of plants subjected to grazing (Pontes et al. 2010). As expected (hypothesis 2), some morphological traits were closely related to physiological traits that also reflected forage quality. For example, specific leaf area (a morphological trait) was positively correlated with leaf N content (a physiological trait, also indicative of forage quality; see Fig. 2), and tiller height (a morphological trait) was positively correlated with tiller cell wall components (a physiological trait that also reflects plant grazing value). This indicates that our study successfully captured the intimate link between physiological attributes of plants and morphological characteristics. Our results also show that in South African grasslands, certain 'soft' morphological traits may be used as surrogates for 'hard' traits related to plant physiology and grazing value (Weiher et al. 1999).

The response of traits as described above, such as a positive correlation between $L_{SLA}$ and $L_N$, can thus be understood as plant strategies. Based on a proved relationship between six leaf traits, Wright et al. (2004) proposed the worldwide leaf economics spectrum. Plants vary in the velocity of receiving revenue from the invested nutrients and dry mass into leaves through internal partitioning. These authors reported that, on one side of the leaf economics spectrum, quick return strategies present high values of both $L_{SLA}$ and $L_N$, thus providing larger photosynthetic area and higher N content per unit mass. As leaf N is directly and positively correlated with chlorophyll content (Gaborcik 2003) and the key enzyme of the photosynthetic pathway (i.e. RuBisCO), its increased leaf concentration enhances photosynthetic capacity. In addition, Wright et al. (2004) also indicated that high values of $L_{SLA}$ and $L_N$ are accompanied by a relatively short leaf life span, determining rapid biomass dynamics and release of nutrients as litter.

In this study, vegetation communities located close to water points (positions 1 and 2) exhibited features related to the three strategies: quick return, fast growth and non-conservative nutrient use. Communities under high grazing intensity (close to water points) had high $L_{SLA}$ and $L_N$ and a high photosynthetic capacity, which is expected to give a rapid return on invested nutrients. Furthermore, these communities had low $L_{C:N}$, $L_C$ and $T_{CW,}$ which were negatively correlated with $L_{SLA}$, supporting higher rates of photosynthesis. Other studies confirmed that large values of $L_{SLA}$ and $L_N$ and low values of $L_{C:N}$, $L_C$ and $T_{CW}$ are usually measured in plants with high relative growth rates (Niemann et al. 1992; Poorter & Bergkotte 1992), and are therefore assigned to a fast growth strategy (Aerts & Chapin 1999). Finally, in these communities we found a lower content of structural cell wall components, which is generally expected in short-lived leaves (Wright et al. 2004). A short leaf life span is characteristic for the ruderal (R) and competitive (C) strategy of the CSR plant strategy scheme (Grime 1979). Hunt et al. (2004) also reported the plants of R and C communities generally have a short leaf life span, early leaf senescence, and lower recycling and internal partitioning, related to the nutrient-use strategy (Chapin 1980). More generally, our results underline that existing trait combinations describe adaptive corridors where allometric and physiological constraints are minimized from the organ to the whole plant level (Maire et al. 2013). In reference to livestock-mediated changes in forage quantity and quality, we found that communities closest to the water point (position 1) accumulated the smallest amounts of standing biomass (Fig. 1a) and were dominated by shorter and stoloniferous species (Appendix S1) compared to those communities at the opposite end of the grazing gradient. These short and dense swards produced more leaves per tiller and offered more tillers per biomass unit (data not shown). Although communities accumulated less biomass, we found that their forage quality was higher (larger N content, lower C:N ratio and less structural components). Cruz et al. (2010) reported that vegetation communities exposed to high grazing intensity present increased abundance of stoloniferous plant types associated with a non-conservative strategy (referred to as rapid capture strategy). They concluded that in such situations, there is a reduction in forage availability, which is incompatible with high animal production. However, a reduction in biomass may, at least partially, be compensated by a higher forage quality (see following section on implications).

At the other end of the grazing gradient, we found that communities distant from water points displayed features of slow return strategies, with lower $L_{SLA}$ and N content (both in leaves and tillers) and higher content of structural components than in communities close to water points. These communities had lower photosynthetic capacity per unit leaf area while their higher content of structural components matched slow nutrient turnover and a conservative strategy (Chapin 1980).

In confirmation of our third hypothesis, variables related to grazing were the strongest in explaining the overall response of CPFTs (Fig. 3c). However, we observed changes in soil properties, such as a higher $S_{AWC}$, at positions near the water point (positions 1, 2 and 3; Appendix S2) than at longer distances and also significantly higher $S_{CBS}$ close to the water point, which is likely an indication of higher water availability (because of cation import from higher relief areas via run-off). Water points built in areas of low relief create a common pattern of spatial variation in soil properties in relation to the water point location (Klintenberg & Verlinden 2008). As a consequence, areas close to water points are wetter, which could partly explain the unusually high abundance of desirable grasses that appears to partly mask degradation effects of intense grazing. However, $S_{AWC}$ was a weak explanatory variable in the RDA, presenting low correlation factors with Axes 1 and 2 for response variables (−0.03 and −0.06) and explanatory variables (−0.04 and −0.07). We found more N in plant tissues growing on the most N-poor soils (position 1. Appendix S2), thus displaying a contradictory gradient of N content on plants vs soils (Aan et al. 2006). Generally, soils along the piosphere transects had significantly higher concentrations of N and P than those outside piospheres (data not shown), indicating a livestock-mediated centripetal redistribution of nutrients within the rangeland landscape (Augustine 2003). Thus it would be more plausible if soils closest to water points had the highest N concentrations. Our data could be explained by a high N uptake rate of productive and ruderal plant communities at transect position 1, leading to a depletion of N stock. This depletion process is apparently more important than the enrichment of nutrients in the inner parts of the piospheres due to urine and dung from the animals (Kotzé et al. 2013).

Tenure systems were not distinguishable in their response of CPFT, neither among near nor among intermediate positions to water points (1, 2, 3 and 4). However, sites of the furthest transect positions (5 and 6) were significantly different (first section of Table 5). This latter difference can be better explained as a specific condition occurring on Fransina (one of the commercial farms) than as an effect of land tenure (see Appendix S3). For instance, similar stocking rates were observed amongst the four study farms, but Fransina presented significant differences in bare ground, grazing pressure, litter and moribund material and standing biomass compared to all the other farms, including Rustdam, which is also under commercial tenure (Table 1). Our results support previous findings that the timing of grazing (continuous vs rotational) may have little effect on CPFTs or on ecological functions of rangelands (Briske et al. 2008) when stocking rates are comparable. Considering that the grazing pressure on CU grasslands was once higher and has only gradually decreased since the early 1990s (C. Naumann, pers. comm.), our results imply that, during the past two decades, vegetation on CU farms was able to recover from historically higher grazing pressure.

We studied ‘response traits’ (Suding et al. 2008) to grazing intensity and identified the associated plant strategies at either end of the grazing gradient. However, beyond the response of the vegetation, we also conclude that potentially there were vegetation effects on ecosystem processes. The variation in nutrients and structural components of the biomass might influence nutrient turnover (Kazakou et al. 2009). For example, high N concentration (as found in communities close to water points) is known to accelerate litter decomposition. In contrast, increased cell wall components, which result in decelerated decomposition of dead plant material, were found at longest distances from water points. Tenure systems did not prove to be determining factors in differentiating plant communities according to their functional characteristics (CPFTs). So, it is evident that more research should be conducted to determine which farm peculiarities or range management practices modify CPFT responses.

## Implications

Our study on semi-arid rangeland sites in South Africa shows that under high grazing intensity, there is an ecological niche for plant species well adapted to intense and frequent grazing via plant strategies of quick return/fast growth/non-conservative nutrient use. As a condition for performing a quick return strategy, these communities require high concentration of leaf N, and accordingly, they produce tissues with lower levels of structural components. In turn, these overgrazed areas provide high-quality forage, to the benefit of animal performance. Although such communities accumulate comparatively low amounts of biomass, they may still play an important role in the provision of high-quality forage, which can be particularly important at the onset of the growing season when other grassland communities are not yet productive (Bollig & Schulte 1999). Moreover, a recent study from South Africa reports that, at least under non-drought conditions and comparatively moderate stocking rates, as in our study, the effects of livestock-mediated vegetation changes on secondary production may be masked by the presence of high forage quality plant species found under heavy grazing (Vetter & Bond 2012), mainly due to their high protein content and digestibility. Our taxon-free study supports these observations that forage quality improvements may compensate for declines in forage quantity, although it aggregates intra- and interspecific trait responses to grazing.

There is a need to develop range practices and ecological restoration programmes that lead to ensemble plant communities, taking into account their CPFTs and plant strategies. For instance, this could be used to achieve increased vegetation cover of areas where animal activities are concentrated, at water points, shaded areas, campsites, salt licks or human settlements (Andrew 1988), with functionally adapted vegetation of quick return/fast growth/non-conservative nutrient-use strategies. In contrast, the communities that were present at the far ends of transects comprise most of the rangeland area and provide high amounts of biomass. However, these communities exhibit slow return/slow growth/conservative nutrient-use strategies and require longer rest periods to regain the nutrients they once invested in leaf tissue. While these characteristics certainly limit the sustainable frequency and intensity of grazing on slow-return communities, areas with this vegetation have the advantage of accumulating high amounts of standing biomass. This natural fodder storage built up from palatable perennial plants may be crucial for animal nutrition during the annual period of resource scarcity at the end of the dry season (Wiegand et al. 2004). Hence, functional resource heterogeneity within a rangeland, where fast and slow return strategies are present, may improve its secondary productivity (Fynn 2012).

## Acknowledgements

We are grateful to the headmen and farmers for allowing us to carry out field research on their land and for their pleasant cooperation. Many thanks to Hermanus J. Fouché, Hennie Snyman and Hermias C. van der Westhuizen for support during study set-up. We also thank Chris C. du Preez, Elmarie Kotzé and Thomas Gaiser for helpful discussions on soil properties. Information on stocking rate was gratefully received from Christiane Naumann. The technical support of Petra Weber was invaluable, as were comments from Judith Schleicher. We also thank two anonymous referees for valuable comments. This research was partly funded through the collaborative research project FOR 1501 of the German Science Foundation (DFG). C.M. also acknowledges funding from the DAAD.

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## Supporting Information

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

**Appendix S1.** List of vascular plant species.

**Appendix S2.** Soil properties along transect positions.

**Appendix S3.** Distribution of sampled plots on the ordination diagram (RDA) grouped by farm.