Acta Oecologica 53 (2013) 1–10

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

# Positive versus negative environmental impacts of tree encroachment in South Africa

Séraphine Grellier [a,*], David Ward [b], Jean-Louis Janeau [c], Pascal Podwojewski [c], Simon Lorentz [d], Luc Abbadie [e], Christian Valentin [f], Sébastien Barot [g]

[a] University of Science and Technology of Hanoi, Hoang Quoc Viet, Cau Giay, Hanoi, Viet Nam
[b] School of Biological & Conservation Sciences, University of KwaZulu-Natal, Box X01, Scottsville 3209, South Africa
[c] IRD-Bioemco c/o School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Box X01, Scottsville 3209, South Africa
[d] Centre for Water Resources Research, University of KwaZulu-Natal, Box X01, Scottsville 3209, South Africa
[e] UMR Bioemco 7618, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris 05, France
[f] IRD-Bioemco, 32, av. H. Varagnat, 93143 Bondy Cedex, France
[g] IRD-Bioemco, École Normale Supérieure, 46 rue d'Ulm, 75230 Paris 05, France

ARTICLE INFO

*Article history:*
Received 2 January 2013
Accepted 5 August 2013
Available online

*Keywords:*
*Acacia sieberiana*
Grassland
Tree–grass interaction
*Senecio inaequidens*
Soil properties

ABSTRACT

Woody plant encroachment in grasslands is a worldwide phenomenon. Despite many studies, the consequences of woody plant encroachment on sub-canopy vegetation and soil properties are still unclear. To better understand the impacts of trees on grassland properties we examined the following questions using a mountainous sub-tropical grassland of South Africa encroached by an indigenous tree, *Acacia sieberiana* as a case study: (1) Do trees increase sub-canopy herbaceous diversity, quality and biomass and soil nitrogen content? (2) Do large trees have a stronger effect than medium-sized trees on grass and soil properties? (3) Does the impact of trees change with the presence of livestock and position of trees in a catena? We studied grass and non-graminoid species diversity and biomass, grass quality and soil properties during the wet season of 2009. Nitrogen in grass leaves, soil cation exchange capacity and calcium and magnesium ion concentrations in the soil increased under tall *Acacia* versus open areas. Medium-sized *Acacia* decreased the gross energy content, digestibility and neutral detergent fibre of grasses but increased the species richness of non-graminoids. Tall and medium *Acacia* trees were associated with the presence of *Senecio inaequidens*, an indigenous species that is toxic to horses and cattle. The presence of livestock resulted in a decrease in herbaceous root biomass and an increase in soil carbon and leaf biomass of grass under *Acacia*. Tree position in the catena did not modify the impact of trees on the herbaceous layer and soil properties. For management of livestock we recommend retaining tall *Acacia* trees and partially removing medium-sized *Acacia* trees because the latter had negative effects on grass quality.

## 1. Introduction

Grasslands and savannas cover 51% of the total land area of the earth (Asner et al., 2004) and almost 40% of the global population depends on these biomes (Reynolds et al., 2007). Any degradation occurring in these ecosystems will have a strong impact on local human populations, especially on rural livestock-dependent communities. Woody plant encroachment into grasslands and savannas is a widespread phenomenon (Ward, 2005; Wiegand et al., 2005; Bond, 2008; Graz, 2008; Van Auken, 2009) that reduces the area available for grazing and transforms grasslands into savannas or woodlands (Archer, 1995; Eldridge et al., 2011).

In the last 50 years, the phenomenon of woody plant encroachment has increased, and both positive and negative effects on grassland and savanna functions and properties have been reported (Scholes and Archer, 1997; Archer et al., 2001; Van Auken, 2009; Eldridge et al., 2011). The effects of encroachment are highly variable and, despite many studies (e.g. Treydte et al., 2007; Riginos et al., 2009; Ravi et al., 2010), the impact of woody plant encroachment in grasslands and savannas is still unclear. For example, trees increased grass biomass and soil nutrient content in Ethiopia (Abule et al., 2005), while they decreased grass cover and the ability to take up nutrients and fix carbon in grassland of the central USA (Lett and

---

[*] Corresponding author. Tel.: +84 4 37 91 69 60.
*E-mail addresses:* seraphine.grellier@usth.edu.vn, grellier_seraphine@yahoo.fr (S. Grellier).

1146-609X/$ – see front matter © 2013 Elsevier Masson SAS. All rights reserved.
http://dx.doi.org/10.1016/j.actao.2013.08.002

Knapp, 2003). Woody plant encroachment has been inconsistently linked to ecosystem degradation or desertification (Maestre et al., 2009; Eldridge et al., 2011). In arid and semi-arid areas where water limitation occurs, shading by trees can have more positive impacts on the herbaceous layer than in more humid areas (e.g. Belsky et al., 1993; Treydte et al., 2007). The impact of trees on grassland properties in wetter areas may be less conspicuous or more difficult to test experimentally (Treydte et al., 2007). Moreover, few studies have dealt with the impact of trees on non-graminoid herbaceous species (Belsky et al., 1993), which may also play an important role for pastoralism and biodiversity (Hector et al., 1999; Pfisterer et al., 2003; Schmidtke et al., 2010).

Since many studies have focused on woody plant encroachment in semi-arid and arid areas (Belsky et al., 1989; Abule et al., 2005; Ward, 2009), this study uses a mesic grassland in South Africa. The main goal was to better understand the impact of trees on the herbaceous layer and soil properties, with a focus on their effects on livestock grazing. Tree effects on the herbaceous layer and soil properties are expected to depend on the tree species and tree size/age (Treydte et al., 2007, 2009). *Acacia* species, as legumes, usually increase soil nitrogen (Kambatuku et al., 2011), with the magnitude of increase correlated with tree size (Ludwig et al., 2004). In addition, shading effects on the herbaceous layer change with canopy size (Belsky, 1994). We studied two other factors (catena position and the presence or absence of livestock) that may modify the impact of trees on the herbaceous layer and soil properties. While the effects of grazing have frequently been studied (e.g., Belsky et al., 1993; Abule et al., 2005; Mbatha and Ward, 2010; Dunne et al., 2011), their interaction with catena position is not known. Catena position is one of the determinants of soil depth and texture and therefore of soil properties (Oztas et al., 2003; Salako et al., 2006). Soil properties such as bulk density affect soil moisture (Famiglietti et al., 1998) or soil fertility which can drive ecosystem processes, modifying the effects of trees on the soil and herbaceous layer (Treydte et al., 2007). Livestock have a large impact on grassland (Mbatha and Ward, 2010; Dunne et al., 2011). Their presence, through grazing, trampling or dung fertilization may also modify the impact of trees on the herbaceous layer and soil properties. We aim, through this multi-factorial field study, to highlight mechanisms of the impacts of woody plant encroachment on the sub-canopy herbaceous layer and soil properties. Based on the previously cited literature, we tested the following predictions from the perspective of the impacts of grazing by cattle (the main herbivores at our study site):

1) The legume, *Acacia sieberiana* var. *woodii* (Burtt Davy) Keay & Brenan, increases the quality and biomass of the sub-canopy herbaceous layer and improves soil properties, especially by increasing soil N. We also predict that the array of herbaceous species may be modified under *A. sieberiana*, favouring some less palatable species for cattle grazing.
2) The stronger shading effect of large trees compared to medium-sized trees reduces herbaceous biomass but increases soil moisture. Soil nitrogen is higher under large trees than under medium-sized trees (Treydte et al., 2007), and large trees improve the quality of the herbaceous layer in terms of grass digestibility, nitrogen, phosphorus, and gross energy.
3) The impact of trees on grass growth is greater in the upper part of the catena on relatively unfertile soils than in the lower part where soils are more fertile.
4) Grazing masks the beneficial effects of trees on the herbaceous layer biomass due to removal of the aboveground grass layer. Livestock increase soil carbon and soil nitrogen under trees through dung and urine deposition (Belsky et al., 1989).

## 2. Materials and methods

### 2.1. Study site

The study site was located in Potshini, 8 km south-east of Bergville (28° 48′ 37″ S; 29° 21′ 19″ E), KwaZulu-Natal, South Africa (Fig. 1). The site was on a north-sloping watershed of the Tugela Basin (30,000 km$^2$) and is representative of the topography, vegetation, climate and human habitat of the KwaZulu-Natal Drakensberg foothills. The altitude of the study site varied between 1217 and 1452 m and covered an area of 2.5 km$^2$. The climate is broadly described as mesic and is sub-humid sub-tropical with two well marked seasons: a rainy summer period (October–April) and a dry winter period (May–September). The area has a mean annual precipitation (calculated over the last 65 years) of 750 ± 162 mm (Grellier et al., 2012) and mean annual temperatures were 16.5 and 16.1 °C in 2008 and 2009, respectively. Mucina and Rutherford (2006) classified the vegetation as Northern KwaZulu-Natal moist grassland, which is usually dominated by *Themeda triandra* Forssk and *Hyparrhenia hirta* (L.) Stapf. Encroachment by a single indigenous tree species, *A. sieberiana*, occurs in the watershed. Aerial photography of the site confirms tree encroachment over the last 30 years (Grellier et al., 2012). The general soil type is luvisol (World Reference Base, 1998).

We studied three areas with different geomorphologies along the catena (Fig. 1). These areas are distinguished mainly by their slope as well as geomorphological and ecological characteristics. The first area (hereafter referred to as Upslope) had a steep slope (17.5 ± 4.5°) and patches of doleritic rocks. The second area (hereafter referred to as Midslope) in the catena was not as steep (9.7 ± 2.5°), and the third area (hereafter referred to as Downslope), located at the bottom of the watershed had a gentle slope (5.9 ± 1.4°).

The site is a communally-owned grassland and follows two rotation periods regarding management of livestock (mostly cattle). During the maize-growing season and until harvest (a period of 8 months), the cattle are kept in the grassland areas (November–June). During the winter (for a period of 4 months), the cattle feed on the maize residues in the fields (July–October) located around the community settlement (separated from the grassland areas). There is no clear fire management protocol for this area, which is only affected by natural and accidental fires.

### 2.2. Experimental design

Our multi-factorial design included three treatments: position on the catena, presence-absence of an *Acacia* (and its size) and presence-absence of livestock. To study spatial variation at the landscape scale, we considered the three geomorphological areas described above (Upslope, Midslope, Downslope). To examine the effect of tree presence and size, we sampled 40 individual *Acacia* trees of two size classes, 20 tall *Acacia* trees (>3 m height) and 20 medium-sized *Acacia* trees (1–3 m height) according to their position in the catena, which were almost equally distributed in each of the three zones (Fig. 1). *Acacia* height was measured instead of age as dendrochronology could not be used due to large variation between seasons and associated tree rings observed in this sub-tropical tree. Moreover, size has been successfully used in previous studies (Treydte et al., 2009). The tall *Acacia* trees were on average (±standard deviation) 5.5 ± 1.0 m in height and they had a mean diameter at breast height (dbh) of 0.3 ± 0.1 m and a canopy radius of 4.7 ± 1.8 m. The medium *Acacia* trees were on average 2.6 ± 0.5 m tall, with a mean dbh of 0.08 ± 0.02 m and a canopy radius of 1.6 ± 0.3 m. As a comparison to areas under tree canopy (see below for details) we selected “open areas” in 24 locations away from *Acacia* in open grassland and distributed in the three areas of the catena. To

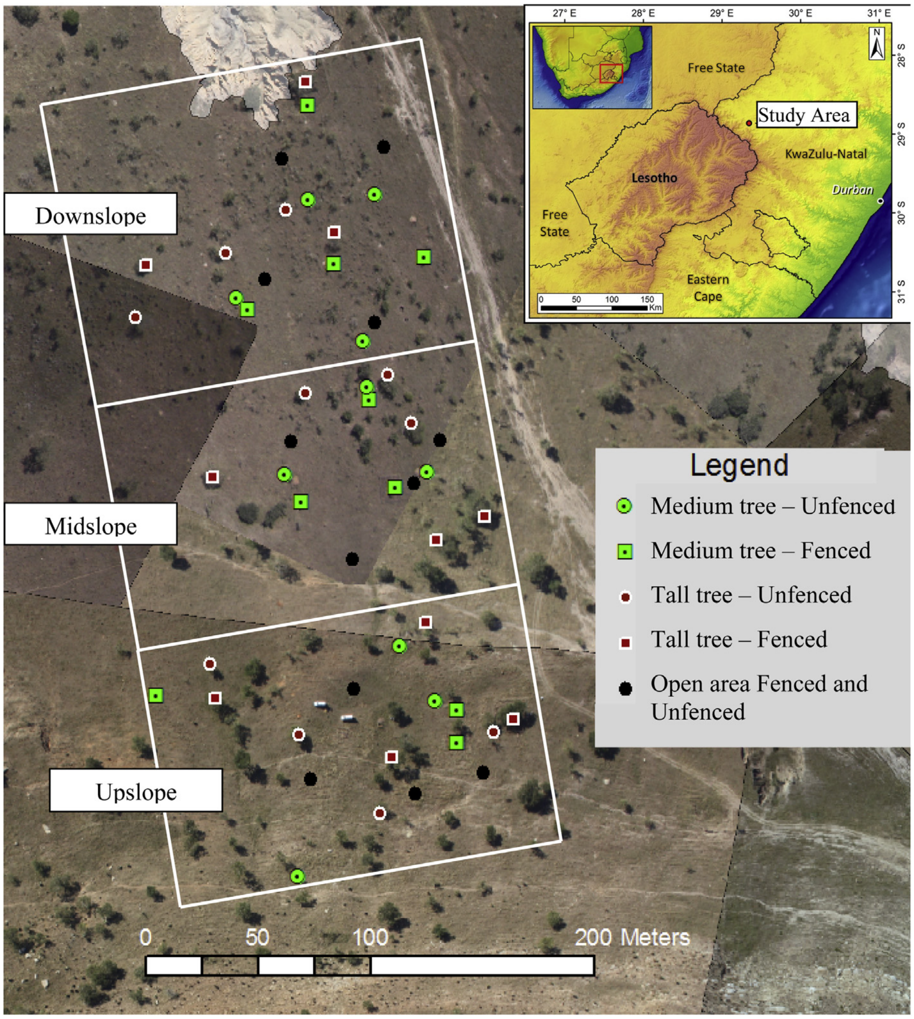

**Fig. 1.** Study area location and aerial view in 2009 with sampling points.

examine the effects of livestock presence, we fenced half of the locations for each treatment (tall *Acacia*–medium *Acacia*–open area) with 2 × 2 m fences in October 2008, six months prior to the initiation of sampling in April 2009. For each location ($n = 64$, locations in total for all combinations of treatments), one 50 × 50 cm plot was delimited for further soil and vegetation sampling. The plots were centred on the most shaded part under *Acacia* canopy, where the shading effects of *Acacia* were expected to be highest. Based on the north-facing slope of the site, this was always within half of the canopy radius southwards from the stem base.

### 2.3. Sample collection

Within each plot, herbaceous vegetation was clipped to ground level, and all non-graminoid species and grass species were separated. All species were identified and graminoid and non-graminoid species richness was calculated (species number). For the different grass species only, their percentage within the total graminoid biomass was estimated visually (see also Ward et al., 1993), while dry biomass of all non-graminoid species was measured. Green grass leaf material was separated for further analyses.

On the same plots, topsoil samples at depths of 0–20 cm were collected for chemical analysis. The determination of soil moisture ($SW_{0-10}$) and soil bulk density (BD) was performed by extracting undisturbed soil cores in 250 cm$^3$ cylinders (Baize, 1988) between 0 and 10 cm. Soil samples at 20–30 cm were collected to obtain $SW_{20-30}$. All soil samples were stored in closed plastic bags and weighed in the field.

Soil cores for determining root biomass were collected at 0–10 cm depth on the same plot with a cylinder 10 cm length and 15 cm diameter. These samples were passed through a 2 mm sieve and washed with clean water to separate roots and soil. Roots were dried at 70 °C for 48 h and weighed.

### 2.4. Analyses of vegetation and green grass leaves

All grass and non-graminoid biomass samples from the 50 × 50 cm plots were dried at 70 °C for 48 h, and then weighed. Green grass leaves were milled to pass through a 1 mm sieve prior to chemical analysis to measure variables linked to grass quality. Total nitrogen concentration in green grass leaves ($N_{grass}$) was analysed with a Leco FP2000 Nitrogen Analyzer using the Dumas combustion method from AOAC Official Method 990.03 (Kenneth, 1990). Phosphorus in green grass leaves ($P_{grass}$) was analysed by digestion with sulphuric acid, hydrogen peroxide and a selenium catalyst using a block digester at 360 °C. Digested samples were analysed using a Technicon autoanalyzer II to measure the absorbance of the phosphomolybdovanate complex at a wavelength of 420 nm. The $N_{grass}$:$P_{grass}$ ratio was calculated to test for nutrient limitation (Koerselman and Meuleman, 1996). Grass fibre content was analysed by assessing acid detergent fibre (ADF) content using a Dosi-Fibre machine according to the AOAC Official Method 973.18 (Kenneth, 1990) and neutral detergent fibre (NDF) content with the same machine using the method described by Van Soest et al. (1991). Gross energy (GE) contained in green grass leaves was measured using a digital data system isothermal CP500 bomb calorimeter. Dry matter digestibility was measured *in vitro* with cellulase as described by Zacharias (1986).

### 2.5. Soil analyses

Soil water content (SW) and BD samples were oven-dried at 105 °C for 24 h and weighed. Soil samples from 0 to 20 cm were air-dried and passed through a 2 mm sieve. Total soil nitrogen ($N_{soil}$) and total soil carbon ($C_{soil}$) were analysed by automated Dumas dry combustion method using a LECO CNS 2000 (Matejovic, 1996). Soil pH was determined in 1:2.5 soil:water suspension. Cation exchange capacity (CEC) was assessed with the Metson method (Metson, 1956); the exchangeable cations $Ca^{2+}$, $Mg^{2+}$, $K^{+}$, $Na^{+}$ and their sum were quantified with the ammonium acetate method at pH 7.0 (Association Française de Normalisation, 1992).

### 2.6. Statistical analyses

Response variables were grouped into three categories.

1) Description of the herbaceous community: grass dry biomass, non-graminoid dry biomass, green grass leaf biomass, grass species richness, and non-graminoid species richness, individual grass and non-graminoid species presence (for the most frequently observed species with a presence >15% and >5% of the plots, respectively).
2) Grass quality (measured from green grass leaves): dry matter digestibility, grass leaf nitrogen ($N_{grass}$), grass leaf phosphorus ($P_{grass}$), $N_{grass}$:$P_{grass}$ ratio, gross energy (GE), ADF, and NDF.
3) Soil properties: soil moisture at 0–10 cm ($SW_{0-10}$), soil moisture at 20–30 cm ($SW_{20-30}$ cm), bulk density (BD), total soil carbon ($C_{soil}$), total soil nitrogen ($N_{soil}$), pH, exchangeable $Na^{+}$, $Ca^{2+}$, $Mg^{2+}$, $K^{+}$, and cation exchange capacity (CEC).

Spatial auto-correlation was tested for all variables with a Mantel test based on distance matrixes prior to the analyses. The cations, $Ca^{2+}$ and $Mg^{2+}$ and CEC were the only variables that were spatially auto-correlated for the whole data set or for each zone of the catena. For each of the other non-correlated response variables described above, we tested for the effect of the presence or absence of trees (*Tree*), location along the catena (*Position*) and the presence or absence of livestock (*Livestock*) by a three-way ANOVA with *Tree*, *Position* and *Livestock* as factors. Normality of residuals and homogeneity of variances were tested for each model. Variables with non-normally distributed residuals or heterogeneous variances were log-transformed or square root transformed. For $Ca^{2+}$, $Mg^{2+}$ and CEC, we first tested the effect of *Position* with a one way ANOVA (using *lm* in R) to avoid masking the *Position* effect due to spatial auto-correlation. Variables with non-normally distributed residuals or heterogeneous variances were transformed. Thereafter, we used a second model on the residuals of the previous ANOVA to test for the effect of *Tree* and *Livestock* (using *lme* in R) taking into account the spatial auto-correlation as a random effect with an exponential distribution that best fit these data.

The presence/absence of the main grass and non-graminoid species were analysed separately by three-way factorial analyses of deviance (using a binomial model due to the binary format of the variables) with *Tree*, *Position* and *Livestock* as factors. Dominance of each grass species on a plot (i.e. where the grass species concerned was the most abundant) was analysed following the same method. The high frequency of zeroes in the results of dry biomass of non-graminoid species did not allow us to apply a generalized linear model to these data as model residuals were not normal whatever the transformations applied to the variable. We thus transformed these data into binary format to analyse the deviance of the highest biomass of non-graminoid species (i.e. greater than the third upper quartile) called “highest biomass” in the following section of the study.

Because of the considerable number of statistical tests in this study, and to avoid rejecting a null hypothesis when it is actually true (type I error), we applied adjusted Bonferroni corrections (Holm, 1979) to *p* values for each group of variables (vegetation quantity, grass quality and soil properties) for all analyses. Similarly, *post hoc t*-tests with Bonferroni corrections were always used to compare means between pairs of treatments for the significant factors. All models were simplified by keeping the lowest residual deviance and using the method described by Crawley (2009). All of the statistical models applied in this study used R version 2.11.1. (http://www.R-project.org).

## 3. Results

### 3.1. Effect of location on the herbaceous layer and soil properties

*Position* in the catena affected almost all of the soil variables, confirming that soil properties vary along the catena (Table 1) and validating our experimental design along the catena. Soil moisture $SW_{0-10}$ and $SW_{20-30}$ were lower Upslope (as results were similar for both SW, only $SW_{0-10}$ is displayed in Fig. 2) compared to Midslope and Downslope. Soil carbon ($C_{soil}$) had a similar pattern (Fig. 2). Total soil nitrogen ($N_{soil}$) was greater at the Midslope sites (Fig. 2). Contrastingly, BD was higher Upslope than Midslope (Fig. 2). CEC, as well as $Ca^{2+}$ and $Mg^{2+}$, had smaller values Downslope than Midslope and Upslope (Fig. 2). pH increased significantly from Downslope to Upslope (Fig. 2).

While soil properties changed along the catena, there were only a few significant effects of *Position* on the herbaceous layer and no significant interaction effect between the position and the presence or absence of trees (Table 2). The phosphorus concentration in green grass leaves ($P_{grass}$) was higher Midslope (0.082 ± 0.016%) than Downslope (0.068 ± 0.015%) (Table 2). In contrast, the $N_{grass}$:$P_{grass}$ ratio had significantly lower values Midslope (16.1 ± 2.7) than Downslope (18.9 ± 3.6).

**Table 1**
Outputs from a three-way ANOVA (*F* values) of soil variables (excepted $Ca^{2+}$, $Mg^{2+}$ and CEC) with *Tree* (Tall *Acacia*, Medium *Acacia*, Open Area), *Livestock* (Present, Absent) and *Position* in the catena (Upslope, Midslope, Downslope). The cations, $Na^{+}$ and $K^{+}$ do not appear in this table due to the absence of significant effects for all treatments. The only significant interaction was *Tree* × *Livestock* for Total $C_{soil}$, indicated in bold. The cations, $Ca^{2+}$ and $Mg^{2+}$ and CEC were analysed using two different models due to spatial auto-correlation. Stars indicate significant *p* values (*<0.05, **<0.01, ***<0.001). (t) indicates variables that have been transformed for statistical analyses. Each model was simplified so some *F* values are not displayed.

| Soil variables | Error d.f. | Tree | Livestock | Position |
|---|---|---|---|---|
| BD | 58 | 3.44 | $15.58^{***}$ | $5.26^{**}$ |
| Soil moisture $SW_{0-10}$ (t) | 61 | – | – | $24.52^{***}$ |
| Soil moisture $SW_{20-30}$ | 61 | – | – | $14.48^{***}$ |
| pH | 58 | $13.51^{***}$ | $5.67^{*}$ | $7.56^{**}$ |
| $Ca^{2+}$ | 61 | $7.61^{**}$ | – | $11.07^{***}$ |
| $Mg^{2+}$ | 61 | $11.87^{***}$ | – | $15.77^{***}$ |
| CEC | 61 | $7.87^{***}$ | – | $8.44^{***}$ |
| $C_{soil}$ | 56 | $\mathbf{3.70}^{*}$ | | $4.94^{**}$ |
| $N_{soil}$ (t) | 61 | – | – | $5.71^{**}$ |

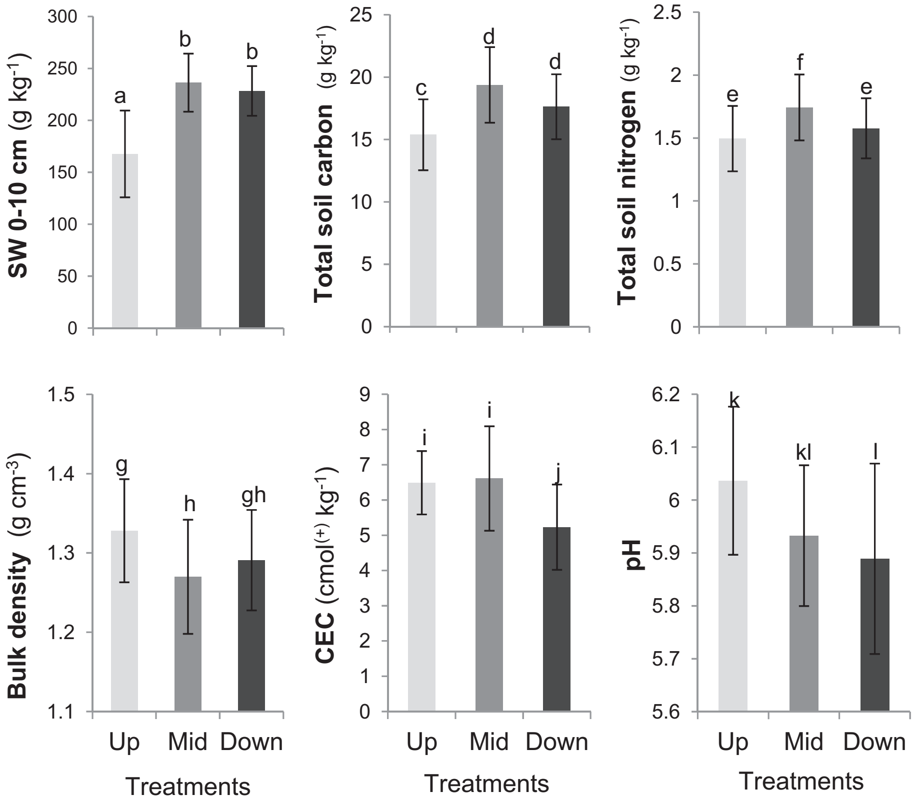

**Fig. 2.** Main significant effects of *Position* on explanatory variables. Means and standard deviations are displayed. Letters indicate significant *p* values among treatments ($p < 0.05$). *Up*: Upslope; *Mid*: Midslope; *Down*: Downslope; refer to position in the catena.

The grass species, *H. hirta* was twice as frequent Downslope than Upslope. This result was especially clear when livestock were present. The grass species, *Paspalum scrobiculatum* (L.) showed similar results, with a greater presence Downslope but, in this case, only when livestock were absent. Conversely, the grasses *Digitaria longiflora* (Retz.) Pers. and *Eragrostis curvula* (Schrad.) Nees were more frequently present Upslope than Midslope and Downslope (Table 3). There was no significant effect of *Position* on non-graminoid species.

**Table 2**

Outputs from a three-way ANOVA (*F* values) of vegetation variables with *Tree* (Tall *Acacia*, Medium *Acacia*, Open Area), *Livestock* (Present, Absent) and *Position* in the catena (Upslope, Midslope, Downslope). Only the *Tree*:*Livestock* interaction showed significant results and is thus presented here. Gross energy was analysed using a generalized linear model. Three-factor and four-factor interactions were not significant and are thus omitted. Stars indicate significant *p* values ($^{*}<0.05$, $^{**}<0.01$, $^{***}<0.001$). (t) indicates variables that have been transformed for statistical analyses. Each model was simplified so some *F* values are not displayed.

| | Error d.f. | Tree | Livestock | Position | Tree: Livestock |
|---|---|---|---|---|---|
| *Herbaceous quantity variables* | | | | | |
| Dry grass biomass (t) | 62 | – | $76.66^{***}$ | – | – |
| Green grass leaf biomass | 58 | 1.96 | 2.07 | – | $5.45^{*}$ |
| Grass species richness (t) | 62 | – | $4.64^{*}$ | – | – |
| Non-graminoid species richness | 61 | $6.10^{*}$ | – | – | – |
| Root biomass | 62 | $3.23^{*}$ | 0.35 | – | $3.64^{*}$ |
| *Graminoid leaf quality variables* | | | | | |
| Digestibility (t) | 60 | $4.64^{*}$ | $24.15^{***}$ | – | – |
| $N_{grass}$ | 58 | $30.23^{***}$ | $34.40^{***}$ | – | $5.99^{*}$ |
| $P_{grass}$ | 56 | 0.15 | $22.90^{***}$ | $4.58^{*}$ | $3.65^{*}$ |
| $N_{grass}$:$P_{grass}$ | 59 | $7.89^{**}$ | – | $4.76^{*}$ | – |
| Gross energy | 63 | $4.21^{*}$ | – | – | – |
| ADF | 62 | – | $45.79^{***}$ | – | – |
| NDF | 58 | – | – | – | $5.17^{**}$ |

### 3.2. Effects of A. sieberiana on the sub-canopy vegetation and soil properties

The effect of *A. sieberiana* on several characteristics of the sub-canopy vegetation was significant (Table 2). Non-graminoid species richness was greater under medium *Acacia* than in open areas (Fig. 3). Digestibility of green grass leaves was significantly greater under tall *Acacia* than medium *Acacia* (Fig. 3). $N_{grass}$ was significantly greater under *Acacia* than in open areas (Fig. 3). $N_{grass}$:$P_{grass}$ ratios were significantly lower for open areas than under *Acacia* (Fig. 3) whereas GE had lower values for medium *Acacia* than in open areas and tall *Acacia* (Fig. 3).

The grasses, *H. hirta* and *Sporobolus africanus* (Poir.) Robyns & Tournay were the two main grass species found in this grassland (Table 3). However, *Tree* had no significant effect on grass species (Table 3), whereas it had significant effects on non-graminoid species (Table 4). The dominant invasive species, *Richardia braziliensis* (Moq.) was present in all plots but it had the greatest biomass in open areas. The herb, *Sida dregei* Burtt Davey was more common under tall *Acacia*, as was the case with the herb *Senecio inaequidens* that was only found under *Acacia* (both tall and medium). *Hibiscus pedunculatus* L.f., a small woody shrub was only present under tall *Acacia* (Table 4).

The presence or absence of trees (*Tree*) impacted four soil variables significantly (Table 1). $Ca^{2+}$ and $Mg^{2+}$ followed the same pattern as CEC, with lower values in open areas and lower values under medium *Acacia* than under tall *Acacia* (Fig. 3). A different

**Table 3**
Outputs from a three-way factorial analyses of deviance (deviance values) for the seven most frequently observed grass species with *Tree* (Tall *Acacia*, Medium *Acacia*, Open Area), *Livestock* (Present, Absent) and *Position* in the catena (Upslope, Midslope, Downslope). *Tree* was not significant and is thus omitted. Significant interactions associated with *Livestock* × *Position* are indicated in bold. The number of plots where the species and dominant species were observed from a total of 64 plots is also indicated. Absence of value (−) means that it has not been included into the analyses due to very low occurrence. Stars indicate significant *p* values (*<0.05, **<0.01, ***<0.001). Each model was simplified so some deviance values are not displayed.

| Grass species | Presence/absence of grass species | | | | | Most dominant grass species | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Deviance values | | | % of plots for livestock | | Deviance values | | % of plots for livestock | |
| | Number of plots | Livestock | Position | Present | Absent | Number of plots | Livestock | Present | Absent |
| *Hyparrhenia hirta* | 50 | **8.40*** | | | | 30 | 6.48* | 62 | 31 |
| *Sporobolus africanus* | 48 | 20.10*** | – | 53 | 97 | 20 | 37.15*** | 0 | 62 |
| *Digitaria longiflora* | 30 | – | 16.45** | | | 1 | – | | |
| | | **9.37*** | | | | | | | |
| *Paspalum scrobiculatum* | 25 | **8.27*** | | | | 0 | – | | |
| *Eragrostis plana* | 23 | **5.78*** | | 50 | 21 | 5 | – | | |
| *Eragrostis curvula* | 18 | – | 9.77* | | | 5 | – | | |
| *Themeda triandra* | 14 | 6.95* | – | 34 | 12 | 3 | – | | |

pattern was observed for pH with lower values under *Acacia* than in open areas.

### 3.3. Effect of livestock on the herbaceous layer and soil properties

*Livestock* as well as the interaction *Tree* × *Livestock* significantly affected herbaceous quantity and quality (Table 2). Dry grass biomass was significantly higher in the absence of livestock than when it was present (Fig. 4). This effect was similar for grass species richness and ADF (Fig. 4). However, digestibility was significantly greater in the presence of livestock (Fig. 4). Moreover, $N_{grass}$ as well as $P_{grass}$ were significantly higher in the presence of livestock but only in open areas and medium *Acacia* (Table 5). Neutral detergent fibre (NDF) for grass from open areas was greater than for medium *Acacia* but only in the absence of livestock (Table 5). In the presence of livestock, green grass leaf biomass was significantly greater under tall *Acacia* than in open areas (Table 5) and root biomass showed an opposite pattern (Table 5).

The effect of livestock was significant for most grass species (Table 3). For the two most common species, we investigated the number of plots where the species were dominant (i.e. the greatest biomass among all grass species present on the plot). *H. hirta* was twice as dominant when livestock were absent than in the presence of livestock whereas *S. africanus* was the most abundant in the presence of livestock and was never dominant in the absence of livestock (Table 3). The presence of *Eragrostis plana* (Nees) and *T. triandra* was more frequent in the absence of livestock. *S. africanus* showed the opposite pattern, being present with greater frequency in the presence of livestock (Table 3). *Centella asiatica* (L.) Urban was the only non-graminoid species that was

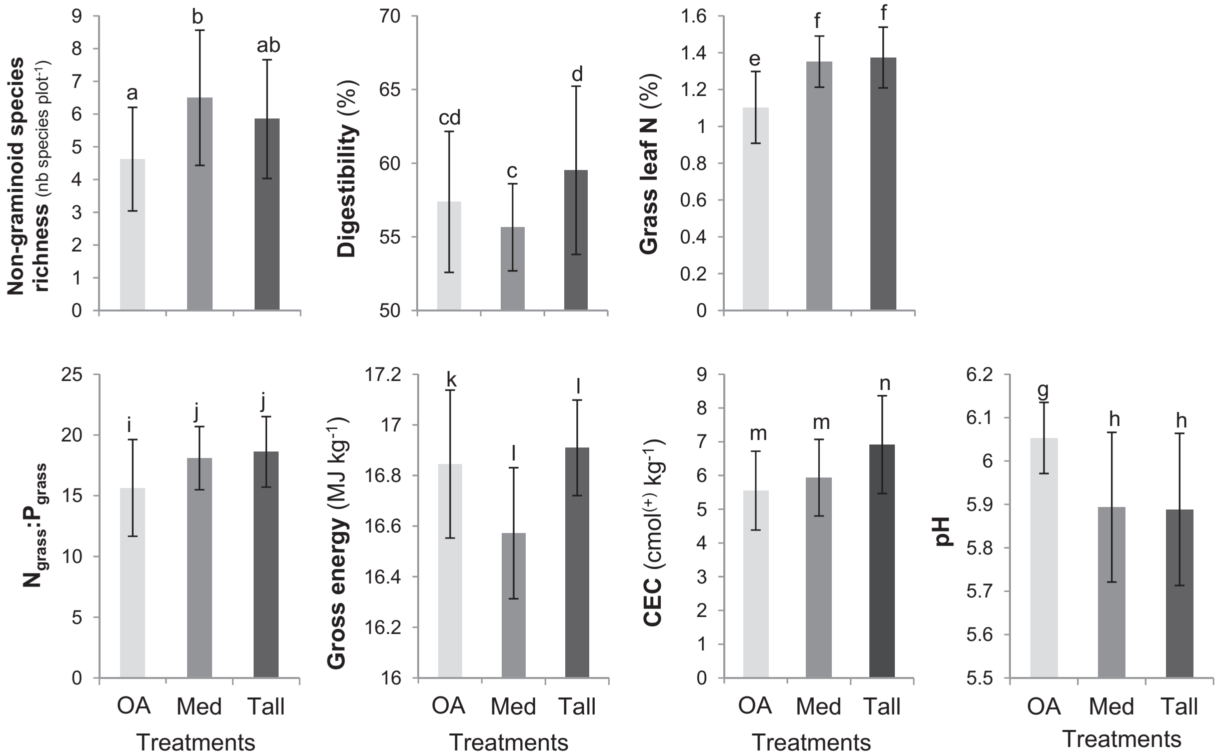

**Fig. 3.** Main significant effects of *Tree* on explanatory variables. Means and standard deviations are displayed. Letters indicate significant *p* values among treatments ($p < 0.05$). *OA*: open area; *Med*: medium *Acacia*; *Tall*: tall *Acacia*.

**Table 4**
Total biomass harvested and outputs from a three-way factorial analyses of deviance (deviance values) for the six most frequently encountered non-graminoid species with *Tree* (Tall *Acacia* = Tall, Medium *Acacia* = Med, Open Area = OA) and *Livestock* (Present, Absent). *Position* and all interactions were not significant and are thus omitted. Stars indicate significant *p* values (*<0.05, **<0.01, ***<0.001). Each model was simplified so some deviance values are not displayed.

| Non-graminoid species | Total biomass harvested (g) | Presence/absence | | | | Highest biomass | |
|---|---|---|---|---|---|---|---|
| | | Deviance values | % of plots where species was present for each tree size | | | Deviance values | |
| | | Tree | Tall | Med | OA | Tree | Livestock |
| *Richardia braziliensis* | 179.85 | – | 60 | 70 | 71 | 9.25* | – |
| *Sida dregei* | 68.35 | 12.74** | 50 | 10 | 8 | 18.28*** | – |
| *Vernonia natalensis* | 38.34 | – | 5 | 20 | 13 | – | – |
| *Senecio inaequidens* | 35.98 | 13.37** | 25 | 35 | 0 | 7.26* | – |
| *Centella asiatica* | 17.40 | – | 55 | 65 | 33 | – | 5.74* |
| *Hibiscus pedunculatus* | 12.02 | 9.90* | 20 | 0 | 0 | – | – |

significantly more frequent in the absence of livestock (28.1%) than in the presence of livestock (6.25%) (Table 4).

Both BD and pH increased significantly in the presence of livestock (bulk density: livestock presence 1.33 ± 0.06 g $cm^{-3}$, livestock absence 1.27 ± 0.06 g $cm^{-3}$; pH: livestock presence 5.99 ± 0.15, livestock absence 5.90 ± 0.16). The interaction *Tree* × *Livestock* was significant only for $C_{soil}$. In the presence of livestock, $C_{soil}$ was greater under tall *Acacia* than in open areas and *vice versa* in the absence of livestock (Table 5).

## 4. Discussion

### 4.1. Impact of trees on the sub-canopy vegetation and soil properties

We interpret the differences we found between soil and vegetation below *Acacia* and outside of their canopy as being due to the presence of *Acacia*. However, we acknowledge the fact that the reverse is also possible: the location of tree growth might be determined by some pre-existing heterogeneity (Robinson et al., 2010; Grellier et al., 2013). We believe that most of our results are better interpreted as impacts of *Acacia* on soil and sub-canopy vegetation because: (1) the sub-canopy plants could mainly impact the growth and survival of small *Acacia* but not of tall *Acacia* and (2) the differences between the effects of medium *Acacia* and tall *Acacia* suggest that the effect increases with their size and age, which supports the idea of a real effect of *Acacia*.

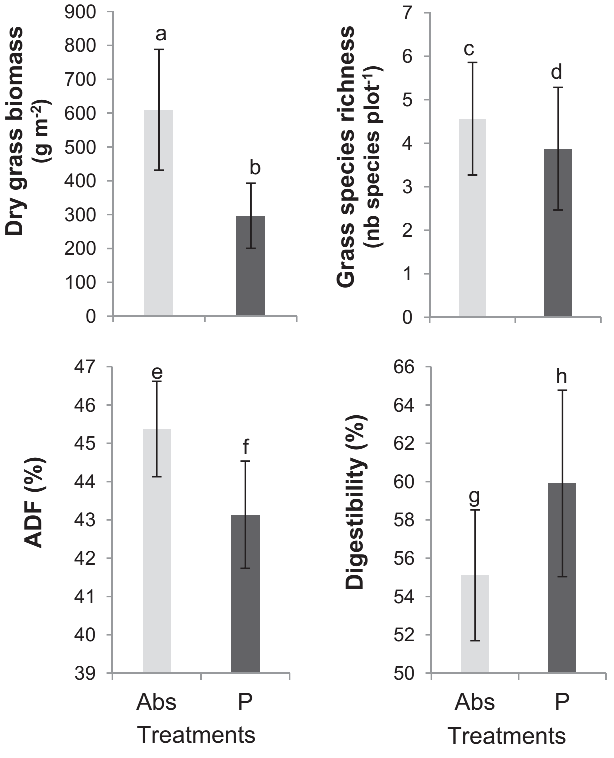

**Fig. 4.** Main significant effects of *Livestock* on explanatory variables. Means and standard deviations are displayed. Letters indicate significant *p* values among treatments. *P*: Present; *Abs*: Absent.

This study showed that *Acacia* trees have an effect on soil properties and sub-canopy vegetation, albeit not for all variables we measured. Nitrogen has been reported to accumulate in the soil following woody plant invasion (Wiegand et al., 2005; Liao et al., 2006) and total soil N is often higher under trees than in the open grassland (Abule et al., 2005), especially with leguminous trees (Wiegand et al., 2005; Treydte et al., 2007) due to their capacity for N-fixation. However, contrary to our first hypothesis, we did not measure such impacts, which may be linked to the increase in the grass leaf N content under *Acacia*. The uptake of mineral N from the soil and its storage in grass leaves (see e.g. Mbatha and Ward, 2010) or its immobilization by enhanced microbial activity under trees (Liao and Boutton, 2008; Creamer et al., 2013) are two of the processes that could explain this. Soil C and N were not affected by trees in this study. Similar results were reported in areas with similar mean annual precipitation (MAP) (Hughes et al., 2006).

The cations, $Mg^{2+}$ and $Ca^{2+}$ were higher under *Acacia*, as found in studies elsewhere in South Africa (Trinogga, 2010). This can possibly be explained by the base-pump function of trees and shrubs that reallocates nutrients from deeper soil layers to the surface by litter input to the top soil (Vejre and Hoppe, 1998; Vanlauwe et al., 2005). High concentrations of exchangeable cations are usually associated with an increase in pH (Hatton and Smart, 1984), which was not the case in this study. In this study, CEC was found to be higher under *Acacia*, as was also found by Trinogga (2010). The increase in CEC was likely due to litter input and decomposition which allows increases in $Mg^{2+}$ and $Ca^{2+}$ without a decrease in $H_3O^+$ (or an increase in pH).

In contradiction to our first hypothesis and several other studies (Belsky et al., 1993; Abule et al., 2005; Treydte et al., 2007; Ludwig et al., 2004, 2008) grass biomass did not differ between tall or medium *Acacia* and in open areas. This was also the case for total soil N content, which was similar under *Acacia* and in open areas.

Although the presence of *Acacia* did not alter the biomass of grass in our study, there was an increase in non-graminoid species richness, especially under medium *Acacia*. Ruthven (2001) found similar results. Other authors have related grass species richness to pH: lower pH increased species richness due to its effect on the availability of certain nutrients (Fynn et al., 2005; Tisdale et al., 1993). *S. dregei*, *S. inaequidens* and *H. pedunculatus* were found

**Table 5**
Means and standard deviations for the explanatory variables that presented significant effects of the interaction *Tree* × *Livestock*. Letters indicate significant *p* values among treatments. *OA*: open area; *Med*: medium *Acacia*; *Tall*: tall *Acacia*.

| Variables | Treatments | | Mean | ±SD | Significance |
|---|---|---|---|---|---|
| | Livestock | Tree | | | |
| $N_{grass}$ (%) | Absent | OA | 0.95 | ±0.07 | a |
| | | Med | 1.26 | ±0.08 | b |
| | | Tall | 1.35 | ±0.16 | bc |
| | Present | OA | 1.26 | ±0.14 | b |
| | | Med | 1.45 | ±0.12 | c |
| | | Tall | 1.40 | ±0.17 | c |
| $P_{grass}$ (%) | Absent | OA | 0.06 | ±0.01 | d |
| | | Med | 0.07 | ±0.02 | d |
| | | Tall | 0.07 | ±0.01 | de |
| | Present | OA | 0.09 | ±0.01 | e |
| | | Med | 0.09 | ±0.02 | e |
| | | Tall | 0.08 | ±0.01 | de |
| NDF (%) | Absent | OA | 75.82 | ±2.54 | f |
| | | Med | 73.22 | ±2.06 | g |
| | | Tall | 75.61 | ±1.38 | fg |
| | Present | OA | 73.82 | ±1.69 | fg |
| | | Med | 75.05 | ±2.08 | fg |
| | | Tall | 74.88 | ±1.91 | fg |
| Green grass leaf biomass (g $m^{-2}$) | Absent | OA | 106.47 | ±27.12 | hi |
| | | Med | 102.48 | ±19.01 | hi |
| | | Tall | 95.29 | ±31.58 | hi |
| | Present | OA | 89.93 | ±30.36 | hi |
| | | Med | 117.61 | ±21.55 | hi |
| | | Tall | 129.96 | ±22.59 | i |
| Root biomass (g $l^{-1}$) | Absent | OA | 16.65 | ±6.80 | jk |
| | | Med | 16.70 | ±7.28 | jk |
| | | Tall | 14.93 | ±6.24 | jk |
| | Present | OA | 19.97 | ±5.30 | jk |
| | | Med | 16.04 | ±5.50 | jk |
| | | Tall | 11.87 | ±3.28 | k |
| $C_{soil}$ (g $kg^{-1}$) | Absent | OA | 18.58 | ±3.51 | l |
| | | Med | 17.23 | ±3.53 | m |
| | | Tall | 17.23 | ±3.53 | m |
| | Present | OA | 17.25 | ±3.44 | m |
| | | Med | 16.65 | ±2.21 | m |
| | | Tall | 17.66 | ±3.32 | l |

mainly under *Acacia*. *S. inaequidens*, due to its toxicity (Dimande et al., 2007) for cattle and horses (Botha and Penrith, 2008) through the presence of pyrrolizidine alkaloids, could be very detrimental for livestock grazing. *S. inaequidens* was found more frequently and was larger under tall and medium *A. sieberiana* trees in this grassland and is likely to decrease the area available for grazing. This is one of the first occasions that this indigenous species has been recognized to be associated with sub-canopy areas in a grassland. However, other authors reported the association of trees and invasive toxic species such as *Lantana camara* (Rodger and Twine, 2002). In contrast, *R. braziliensis*, an invasive species, grew better in the open area, indicating their requirements for sun exposure and drier areas. To better understand the effect of trees on the vegetation beneath the canopy there is need for study of a wider range of species.

A well-known expression to describe isolated trees or tree clumps in grassland and savanna is ‘islands of fertility’ (Hibbard et al., 2001; Ludwig et al., 2008; Van Auken, 2009; Ravi et al., 2010), especially when leguminous trees are involved (Treydte et al., 2007; Wiegand et al., 2005). It has often been found that nutrient and protein content, gross energy and digestibility of grass leaves are higher and fibre content lower under trees than in the open grassland (Ludwig et al., 2008). In our study, leaf N of grasses and the ratio between N and P in grass leaves followed this tendency and is consistent with our first hypothesis. Typical values of $N_{grass}$:$P_{grass}$ ratio are about 10:1 (Cech et al., 2008). With values over 12 (Ludwig et al., 2001) or 15 (Koerselman and Meuleman, 1996) for tropical grassland, the $N_{grass}$:$P_{grass}$ ratio indicates that P availability in the soil of the study site was the limiting factor for grass growth (Cech et al., 2008).

### 4.2. *Effects of tree size*

The neutral effect of tall *Acacia* on grass quality could be the result of positive and negative effects occurring at the same time. Competition for water and nutrients between *Acacia* and grasses (Ludwig et al., 2004) may have been counteracted by benefits due to tree shade (Belsky, 1994), nitrogen fixing capacity (Belsky et al., 1989), hydraulic lift (Ludwig et al., 2001), and litter fall (Hudak et al., 2003).

In contrast, medium *Acacia* had a negative impact on gross energy and leaf digestibility of grasses. This resulting negative effect of medium *Acacia* indicates that benefits brought by medium *Acacia* were less important than competition for water and nutrients. This can be explained by the smaller size of *Acacia*, resulting in less shade, less nitrogen fixation, and less litter fall.

### 4.3. *Effects of tree location*

Even if soil properties presented a gradient along the catena from Upslope to Downslope (deeper, less acid, more organic matter and total carbon, lower bulk density and higher soil moisture), the location of trees in the landscape was not influential, which does not support our third hypothesis. Treydte et al. (2007) have shown that the positive effect of trees may be restricted to low rainfall grasslands (MAP ca. 450 mm) and degraded areas. Our study site, with a MAP of 750 mm, does not show clear resulting positive effects of *Acacia* on soil and vegetation properties which confirms Treydte findings. Moreover, the gradient of soil degradation between the upper part and the lower part of the catena may not be strong enough to measure differences. Other areas in the studied grassland are considered to be degraded but this is due to strong gully erosion (Grellier et al., 2012) and *Acacia* in these areas might have a more positive impact on soil and vegetation.

### 4.4. *Effects of livestock*

Livestock modified the impact of trees through several variables, consistent with our fourth hypothesis. Root biomass was higher in the open areas than under tall *Acacia* only when livestock were present. Grass shoot:root ratios can be modified depending on species-specific responses of grasses to grazing (Li et al., 2005). *S. inaequidens* is known to be toxic for cattle (Dimande et al., 2007) so that cattle is likely to avoid patches where *S. inaequidens* is abundant. Since this species is more frequent under *Acacia* canopy, *S. inaequidens* may decrease grazing under *Acacia*. Grazing of aboveground parts of the grass layer, mostly in open grassland, may favour grass root growth to compensate for aboveground biomass and nutrients removed by cattle (Li et al., 2005).

There was an increase in total soil C under trees, only when livestock were present. This increase may be due to dung deposition by cattle (Belsky et al., 1989). Indeed, cattle mainly defaecate where they rest (Hirata et al., 2009) and cattle often rest under trees in the shade. Another hypothesis can be proposed and is consistent with the finding of higher soil C content in the open area without cattle compared to open area with cattle. Grazing is associated with lower aboveground plant biomass (Kölbl et al., 2010; Mbatha and Ward, 2010) that decreases C input to the soil and thus reduces soil C in the presence of cattle. This phenomenon could be limited by a higher root biomass associated to grazing that may increase soil C.

### 4.5. Management strategies

This study demonstrates that *Acacia* affected sub-canopy vegetation and soil properties in a mesic grassland and that this impact differed according to tree size and presence of livestock but not tree position in the catena. The association of *Acacia* with indigenous toxic species, which is an indirect negative effect of woody plant encroachment for grazing, has rarely been reported. Adding to the fact that encroaching *A. sieberiana* may ultimately cover the entire grassland surface (Grellier et al., 2012) and thereby limit the access of cattle for grazing, the presence of *S. inaequidens* under the canopy of *A. sieberiana* suggests that it would be important to monitor both *A. sieberiana* encroachment and the population of *S. inaequidens*. To limit the development of *A. sieberiana*, we would recommend retaining tall *Acacia* trees and partially removing medium *Acacia* trees because the latter had negative effects on grass quality. Tall *Acacia* trees create shade for cattle and maintain a source of protein from pods for cattle (Or and Ward, 2003). Spatial heterogeneity at the landscape scale should be considered, such as keeping topographically flatter areas free of trees while areas less accessible to cattle could be maintained with trees.

Complex ecological relations are demonstrated in this ecosystem and should be considered in a broader context when monitoring tree encroachment in savannas. The results obtained in this study are valid for a low density of *Acacia* (28 *Acacia* ha$^{-1}$ or a canopy cover of 10% of the watershed area) and may change with *Acacia* density. Further studies should examine, along with sub-canopy vegetation and soil properties, how the population of toxic sub-canopy species responds to higher *Acacia* densities.

## Acknowledgements

We would like to thank the Institute of Research and Development (IRD) and NRF (to DW) for its financial support as well as the University of KwaZulu-Natal for its technical support. We also thank the community of Potshini where the work was done and especially Sibonelo Mabaso for his contribution in the field. We finally thank Lucas Janeau for his assistance in the study and all anonymous reviewers for improving this manuscript.

## References

Abule, E., Smit, G.N., Snyman, H.A., 2005. The influence of woody plants and livestock grazing on grass species composition, yield and soil nutrients in the Middle Awash Valley of Ethiopia. J. Arid Environ. 60, 343–358.

Archer, S., 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecosci. 2, 83–99.

Archer, S., Boutton, T.W., Hibbard, K.A., 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schulze, E.-D., Heimann, M., Harrison, S., Holland, E., Lloyd, J., Prentice, I.C., Schimel, D. (Eds.), Global Biogeochemical Cycles in the Climate System. Academic Press, San Diego, pp. 115–138.

Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E., Harris, A.T., 2004. Grazing systems, ecosystem responses, and global change. Annu. Rev. Env. Res. 29, 261–299.

Association Française de Normalisation, 1992. NF X 31-108: determination of cations Ca, Mg, K, Na extractible by ammonium acetate. In: Qualité des sols. AFNOR, Paris, pp. 59–65 [French].

Baize D., 1988. Guide des analyses courantes en pédologie, INRA, Paris.

Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Ali, A.R., Mwonga, S.M., 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. J. Appl. Ecol. 26, 1005–1024.

Belsky, A.J., Nwonga, S.M., Amundson, R.G., Duxbury, J.M., Ali, A.R., 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. J. Appl. Ecol. 30, 143–155.

Belsky, A.J., 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. Ecology 75, 922–932.

Bond, W.J., 2008. What limits trees in $C_4$ grasslands and savannas? Annu. Rev. Ecol. Evol. Syst. 39, 641–659.

Botha, C.J., Penrith, M.L., 2008. Poisonous plants of veterinary and human importance in southern Africa. J. Ethnopharmacol. 119, 549–558.

Cech, P.G., Kuster, T., Edwards, P.J., Venterink, H.O., 2008. Effects of herbivory, fire and $N_2$-fixation on nutrient limitation in a humid savanna. Ecosyst. 11, 991–1004.

Crawley, M.J., 2009. The R Book. Wiley, Chichester, England.

Creamer, C.A., Filley, T.R., Olk, D.C., Stott, D.E., Dooling, V., Boutton, T.W., 2013. Changes to soil organic N dynamics with leguminous woody plant encroachment into grasslands. Biogeochemistry 113, 307–321.

Dimande, A.F., Botha, C.J., Prozesky, L., Bekker, L., Rösemann, G.M., Labuschagne, L., Retief, E., 2007. The toxicity of *Senecio inaequidens* DC. J. S. Afr. Vet. Assoc. 78, 121–139.

Dunne, T., Western, D., Dietrich, W., 2011. Effects of cattle trampling on vegetation, infiltration, and erosion in a tropical rangeland. J. Arid Environ. 75, 58–69.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol. Lett. 14, 709–722.

Famiglietti, J.S., Rudnicki, J.W., Rodell, M., 1998. Variability in surface moisture content along a hillslope transect: Rattlesnake Hill, Texas. J. Hydrol. 210, 259–281.

Fynn, R.W.S., Morris, C.D., Edwards, T.J., 2005. Long-term compositional responses of a South African mesic grassland to burning and mowing. Appl. Veg. Sci. 8, 5–12.

Graz, F.P., 2008. The woody weed encroachment puzzle: gathering pieces. Ecohydrol. 1, 340–348.

Grellier, S., Kemp, J., Janeau, J.-L., Ward, D., Florsch, N., Barot, S., Podwojewski, P., Lorentz, S., Valentin, C., 2012. The indirect impact of encroaching trees on gully extension: a 64 year study in a sub-humid grassland of South Africa. Catena 98, 110–119.

Grellier, S., Florsch, N., Camerlynck, C., Janeau, J.-L., Podwojewski, P., Lorentz, S., 2013. The use of Slingram EM38 data for topsoil and subsoil geoelectrical characterization with a Bayesian inversion. Geoderma 200–201, 140–155.

Hatton, J.C., Smart, N.O.E., 1984. The effect of long-term exclusion of large herbivores on soil nutrient status in Murchison Falls National Park Uganda. Afr. J. Ecol. 22, 23–30.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity and productivity experiments in European grasslands. Science 286, 1123–1127.

Hibbard, K.A., Archer, S., Schimel, D.S., Valentine, D.W., 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. Ecology 82, 1999–2011.

Hirata, M., Hasegawa, N., Nomura, M., Ito, H., Nogami, K., Sonoda, T., 2009. Deposition and decomposition of cattle dung in forest grazing in southern Kyushu, Japan. Ecol. Res. 24, 119–125.

Holm, S., 1979. A simple sequentially rejective multiple test procedure, Scandinavian Journal of Statistics 6, 65–70.

Hudak, A.T., Wessman, C.A., Seastedt, T.R., 2003. Woody overstorey effects on soil carbon and nitrogen pools in a South African savanna. Austral Ecol. 28, 173–181.

Hughes, R.F., Archer, S.R., Asner, G.P., Wessmans, C.A., McMurtry, C., Nelson, J., Ansley, R.J., 2006. Changes in aboveground primary production and carbon and nitrogen pools accompanying woody plant encroachment in a temperate savanna. Global Change Biology 12, 1733–1747.

Kambatuku, J.R., Cramer, M.D., Ward, D., 2011. Savanna tree–grass competition is modified by substrate type and herbivory. J. Veg. Sci. 22, 225–237.

Kenneth, H., 1990. Official Method of Analysis of the Association of Official Analytical Chemists, 15th ed. Association of Official Analytical Chemists Inc., Arlington, Virginia, USA.

Koerselman, W., Meuleman, A.F.M., 1996. The vegetation N: P ratio: a new tool to detect the nature of nutrient limitation. J. Appl. Ecol. 33, 1441–1450.

Kölbl, A., Steffens, M., Wiesmeier, M., Hoffmann, C., Funk, R., Krümmelbein, J., Reszkowska, A., Zhao, Y., Peth, S., Horn, R., Giese, M., Kögel-Knabner, I., 2010. Grazing changes topography-controlled topsoil properties and their interaction on different spatial scales in a semi-arid grassland of Inner Mongolia, P.R. China. Plant Soil 340, 35–58.

Lett, M.S., Knapp, A.K., 2003. Consequences of shrub expansion in mesic grassland: resource alterations and graminoid responses. J. Veg. Sci. 14, 487–496.

Li, J.H., Li, Z.G., Ren, J.Z., 2005. Effect of grazing intensity on clonal morphological plasticity and biomass allocation patterns of *Artemisia frigida* and *Potentilla acaulis* in the Inner Mongolia steppe. New Zeal. J. Agr. Res. 48, 57–61.

Liao, J.D., Boutton, T.W., Jastrow, J.D., 2006. Organic matter turnover in soil physical fractions following woody plant invasion of grassland: evidence from natural $^{13}C$ and $^{15}N$. Soil Biol. Biochem. 38, 3197–3210.

Liao, J.D., Boutton, T.W., 2008. Soil microbial biomass response to woody plant invasion of grassland. Soil Biol. Biochem. 40, 1207–1216.

Ludwig, F., de Kroon, H., Prins, H.H.T., Berendse, F., 2001. Effects of nutrients and shade on tree–grass interactions in an East African savanna. J. Veg. Sci. 12, 579–588.

Ludwig, F., de Kroon, H., Berendse, F., Prins, H.H.T., 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. Plant Ecol. 170, 93–105.

Ludwig, F., de Kroon, H., Prins, H.H.T., 2008. Impacts of savanna trees on forage quality for a large African herbivore. Oecologia 155, 487–496.

Maestre, F.T., Bowker, M.A., Puche, M.D., Belén Hinojosa, M., Martìnez, I., García-Palacios, P., Castillo, A.P., Soliveres, S., Luzuriaga, A.L., Sánchez, A.M., Carriera, J.A., Gallardo, A., Ascudero, A., 2009. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. Ecol. Lett. 12, 930–941.

Matejovic, I., 1996. The application of Dumas method for determination of carbon, nitrogen, and sulphur in plant samples. Rost. Vyroba 42, 313–316.

Mbatha, K.R., Ward, D., 2010. The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa. J. Arid Environ. 74, 1294–1301.

Metson, A.J., 1956. Methods of Chemical Analysis for Soil Survey Samples. Rep No 12, DSIR Soil Bur. Bull., New Zealand.

Mucina, L., Rutherford, M.C., 2006. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria, South Africa.

Or, K., Ward, D., 2003. Three-way interactions between acacias, large mammalian herbivores and bruchid beetles – a review. Afr. J. Ecol. 41, 257–265.

Oztas, T., Koc, A., Comakli, B., 2003. Changes in vegetation and soil properties along a slope on overgrazed and eroded rangelands. J. Arid Environ. 55, 93–100.

Pfisterer, A., Diemer, M., Schmid, B., 2003. Dietary shift and lowered biomass gain of a generalist herbivore in species-poor experimental plant communities. Oecologia 135, 234–241.

Ravi, S., D'Odorico, P., Huxman, T.E., Collins, S.L., 2010. Interactions between soil erosion processes and fires: implications for the dynamics of fertility islands. Rangel. Ecol. Manag. 63, 267–274.

Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernandez, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B., 2007. Global desertification: building a science for dryland development. Science 316, 847–851.

Riginos, C., Grace, J.B., Augustine, D.J., Young, T.P., 2009. Local versus landscape-scale effects of savanna trees on grasses. J. Ecol. 97, 1337–1345.

Robinson, D.A., Lebron, I., Querejeta, J.I., 2010. Determining soil–tree–grass relationships in a California oak savanna using eco-geophysics. Vadose Zone J. 9, 1–8.

Rodger, J., Twine, W., 2002. Tree canopies facilitate invasion of communal savanna rangelands by Lantana camara. Afr. J. Range For. Sci. 19, 131–135.

Ruthven, D.C., 2001. Herbaceous vegetation diversity and abundance beneath honey mesquite (*Prosopis glandulosa*) in the South Texas plains. Tex. J. Sci. 53, 171–186.

Salako, F.K., Tian, G., Kirchhof, G., Akinbola, G.E., 2006. Soil particles in agricultural landscapes of a derived savanna in southwestern Nigeria and implications for selected soil properties. Geoderma 137, 90–99.

Scholes, R.J., Archer, S.R., 1997. Tree–grass interactions in savannas. Annu. Rev. Ecol. Syst. 28, 517–544.

Schmidtke, A., Rottstock, T., Gaedke, U., Fischer, M., 2010. Plant community diversity and composition affect individual plant performance. Oecologia 164, 665–677.

Tisdale, S.L., Nelson, W.L., Beaton, J.D., Havlin, J.L., 1993. Soil Fertility and Fertilizers, fifth ed. Macmillan Publishing Company, New York.

Treydte, A.C., Heitkonig, I.M.A., Prins, H.H.T., Ludwig, F., 2007. Trees improve grass quality for herbivores in African savannas. Perspect. Plant Ecol. Syst. 8, 197–205.

Treydte, A.C., Grant, C.C., Jeltsch, F., 2009. Tree size and herbivory determine below-canopy grass quality and species composition in savannahs. Biodivers. Conserv. 18, 3989–4002.

Trinogga, J., 2010. Arid Savanna Shrubs Affect Soil Chemistry and Vegetation Cover (Unpubl MSc thesis). Friedrich Schiller University, Jena, Germany.

Van Auken, O.W., 2009. Causes and consequences of woody plant encroachment into western North American grasslands. J. Environ. Manag. 90, 2931–2942.

Vanlauwe, B., Aihou, K., Tossah, B.K., Diels, J., Sanginga, N., Merckx, R., 2005. *Senna siamea* trees recycle Ca from a Ca-rich subsoil and increase the topsoil pH in agroforestry systems in the West African derived savanna zone. Plant Soil 269, 285–296.

Van Soest, P.J., Robertson, J.B., Lewis, B.G., 1991. Methods for dietary fibre and non-starch polysaccharides in relation to animal nutrition. J. Dairy Sci. 74, 3583–3597.

Vejre, H., Hoppe, C., 1998. Distribution of Ca, K, Mg, and P in acid forest soils in plantations of *Picea abies* – evidence of the base-pump effect. Scand. J. For. Res. 13, 265–273.

Ward, D., Olsvig-Whittaker, L., Lawes, M., 1993. Vegetation-environment relationships in a Negev Desert erosion cirque. J. Veg. Sci. 4, 83–94.

Ward, D., 2005. Do we understand the causes of bush encroachment in African savannas? Afr. J. Range For. Sci. 22, 101–105.

Ward, D., 2009. The Biology of Deserts. Oxford University Press, Oxford, UK.

Wiegand, K., Ward, D., Saltz, D., 2005. Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. J. Veg. Sci. 16, 311–320.

WRB, 1998. World Reference Base for Soil Resources. Rep No 84, World Soil Resources Reports. FAO, Rome.

Zacharias, P., 1986. The use of the cellulase digestion procedure for indexing the dry matter digestibility of forages. Afr. J. Range For. Sci. 3, 117–121.