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REGULAR PAPER

Soil chemical properties and plant species diversity along a rainfall gradient in semi-arid grassland of South Africa

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Background and aims – Plant diversity is affected by several biotic and abiotic influences that include the availability of soil nutrients and precipitation regimes. Our study investigated the relationship between soil chemical properties and plant diversity in semi-arid grasslands of South Africa.
Methods – We collected plant species data and determined soil chemical compositions in Kimberley, Bloemfontein and Bethlehem. The three locations lie along an increasing rainfall gradient from around 450 to 750 mm per annum. We conducted ANOVA to examine differences in diversity indicators [species richness (N_0), the inverse Simpson diversity index (N_2) and species evenness ($N_{20} = N_2/N_0$)] among the locations, and differences in soil chemical properties (Ca, K, Mg, Na, P, N, C and pH). We further performed correlation analysis between soil variables and diversity indicators.
Key results – The geographical gradients of N_0 and N_2 were positively associated with the rainfall gradient and correspondingly with N and C. However, N_0 and N_2 were negatively correlated with soil pH. N_{20} did not show any relationships with the geographical gradient and soil properties. Our results further revealed a hump-shaped model of N_0 with soil pH, characterised by an increase in N_0 with increasing soil pH in acidic grassland (Bethlehem) but a decrease and levelling-off in the lower rainfall, alkaline grasslands of Bloemfontein and Kimberley. The negative effect of soil pH on N_0 is presumably a result of less intense leaching of the base cations in the lower rainfall areas of Bloemfontein and Kimberley.
Conclusions – Our results indicate soil pH as the main variable determining plant species diversity in semi-arid grasslands.

Key words – Biodiversity, inverse Simpson index, soil carbon, soil nitrogen, soil pH, species richness, *Themeda triandra*.

INTRODUCTION

Highly productive grasslands globally are often associated with intensive agricultural production (Critchley et al. 2002a), which is one of the most important direct drivers responsible for biodiversity loss (Millennium Ecosystem Assessment 2005). In southern Africa, the grassland biome has had the greatest loss compared to other biomes, with plant diversity loss estimated at more than 25% by the year 2000. The loss mainly stemmed from the conversion of natural grassland to cultivated land, urban sprawl and plantation forestry (Scholes & Biggs 2005). Plant diversity in grasslands is determined by several biotic and abiotic effects at interplay, including soil characteristics and climate (Janssens et al. 1998, Roem & Berendse 2000, Adler & Levine 2007, Chytrý et al. 2007). In arid and semi-arid grasslands, plant diversity is regulated mainly by the availability of soil moisture and nutrients. Furthermore, anthropogenic influences such as grazing and prescribed burning affect plant community structure (Hoffman et al. 1994, Taddese et al. 2002, Harrison et al. 2003, Fynn et al. 2004, Rutherford & Powrie 2011).

Temporal variability in rainfall has been linked to changes in species composition (Anderson 2008) and is widely shown to influence plant diversity (Adler & Levine 2007, Hassler et al. 2010). In particular, climatically harsh periods, such as droughts, can lead to reductions in local species richness, mainly by increasing the rate of local extinction of rare species (Tilman & El Haddi 1992). Plant diversity is

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further influenced by spatial variability in rainfall. Sites distributed along a geographical gradient and receiving different amounts of mean annual rainfall display strong differences in species composition, and species richness shows significant increases with increasing mean annual rainfall (Hoffman et al. 1994, Adler & Levine 2007).

Conversely, plant diversity is known to decline with increasing soil nutrient availability (Critchley et al. 2002a, Cornwell & Grubb 2003). In grasslands, increasing nutrient availability favours a small number of competitive species capable of rapidly capturing resources and accumulating biomass (Critchley et al. 2002b). The increased productivity fosters intense competition for light, thus only a few tall, fast growing grasses replace the slower growing herbs or shrubs (Roem & Berendse 2000). Most importantly, available soil nitrogen (N), which depends on organic carbon (C) as an energy source for the activity of soil microorganisms in N mineralization/immobilization, has been established as the primary nutrient limiting terrestrial plant production, with the potential to reduce species richness under high N conditions. For example, N addition experiments show a decline in species richness with increased N amounts (Wedin & Tilman 1996, Baer et al. 2003, Clark & Tilman 2008), and similar trends have been reported for atmospherically deposited N (Stevens et al. 2004). In contrast, an increasing trend of species richness has been reported for relatively low levels of soil N in natural temperate European grasslands (Janssens et al. 1998). Other key nutrients such as phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sodium (Na) also have weak linear or humped-shaped relationships with species richness (Janssens et al. 1998, Roem & Berendse 2000, Rutherford et al. 2012).

The availability of soil nutrients to plants is determined by soil pH (Taiz & Zeiger 1991). Accordingly, soil pH often affects plant community composition and species richness because plants differ in their requirements for available nutrients as well as tolerance of soil acidity or basicity (alkalinity) (Laughlin & Abella 2007). The nature of the species richness-soil pH relationship varies and largely depends on vegetation type (Chytrý et al. 2003, Palmer et al. 2003, Schuster & Diekmann 2003). Studies in grassland show species richness to increase with increasing soil pH (Roem & Berendse 2000, Stevens et al. 2004, Weiher et al. 2004), some show a hump-shaped pattern (Schuster & Diekmann 2003, Tyler 2003), others show no clear relationship (Janssens et al. 1998, Chytrý et al. 2003) or even negative trends have also been reported (Palmer et al. 2003, Enright et al. 2005). Chytrý et al. (2007) highlight precipitation as another important variable in the species richness-soil pH relationship. Species richness increases with pH in areas with fairly high precipitation, where soils are generally acidic but in areas with low precipitation, the soils tend to be base-rich and the species richness-pH relationship is linear negative (Chytrý et al. 2007).

In our study we investigated the relationships of plant diversity with climatic and edaphic conditions in the central part of South Africa, a region where water is the most important factor limiting plant growth. In particular, we focused on the following questions: (1) how is plant diversity, especially species richness related to rainfall? and (2) which soil chemical properties are possible indicators of plant diversity in semi-arid grassland? Such studies are important because they provide a glimpse of how plant diversity is likely to respond to perturbations to the natural ecosystem, caused by human activities as well as the envisaged changes in climate regimes. According to the Millennium Ecosystem Assessment report (2005), land use change, changes in climate and nitrogen deposition are projected to be the most dominant drivers of terrestrial biodiversity loss. The main perturbation caused by human activities is agricultural expansion (i.e. land use change), and agricultural practices directly affect soil chemical properties through the use of fertilisers and animal grazing. Grazing is associated with changes in soil pH, organic carbon and soil nutrients such as N, P and K (Yates et al. 2000, Cui et al. 2005, Jeddi & Chaieb 2010, Tefera et al. 2010, Dingaan et al. 2013).

MATERIALS AND METHODS

Study area

The study was carried out mainly in the Free State Province of South Africa, lying between 26.6–30.7°S and 24.3–29.8°E (fig. 1). Approximately 15% of the total area of South Africa is arable or suitable for cultivation, about 70% is principally used for the livestock industry, and the rest is set aside for nature conservation and forestry (Tainton 1999, DAFF 2010). The Free State Province lies in the Grassland Biome, a biome which forms an important part of the limited arable land as the main region for maize and wheat production. The biome is also very important for dairy, beef, and wool production (Rutherford & Westfall 1994). The total area of the Free State Province is about 13 million ha, 91% of which is farm land consisting of potentially arable land (33%) and grazing land (58%) (DAFF 2010). The vegetation is described by Tainton (1999) as extremely productive climatic climax grassland, dominated by sweet grasses i.e. grasses with high nutritional value that remain palatable throughout the year (van Oudtshoorn 1999).

The altitude of the province increases from about 1,100 m a.s.l. in the west to over 3,000 m a.s.l. in the east, on the border of northern Lesotho. The higher lying areas of the east are characterised by a dry sub-humid climate with an annual rainfall of about 1,000 mm, and the rainfall decreases towards the lower lying semi-arid areas in the west, which receive about 400 mm of rainfall annually. The soil type varies across the province; according to the FAO soil classification, Luvisol and Lixisol are found mainly in the central part of the province, Vertisol in the northeast, Plinthosol in the east, Arensol in the northwest, and Cambisol in the west (FAO/IIASA/ISRIC/ISSCAS/JRC 2009). In general, Vertisol and Phinthosol have more clay and organic matter content than Arensol and Cambisol such that soil habitat conditions are more favourable for the grassland communities in the eastern than the western parts of the study area.

The present study focused on *Themeda triandra* Forssk. dominated grasslands in three locations: around Bethlehem and Bloemfontein, and included parts of Kimberley in the Northern Cape Province (fig. 1). According to long-term (1961–2010) rainfall data collected at the three study loca-

Table 1 – **Long-term mean monthly and annual rainfall (mm) in Kimberley, Bloemfontein and Bethlehem, South Africa.**
The data were averaged for the period from 1961 to 2010.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Annual
Kimberley	74	78	70	41	15	8	5	9	17	40	52	55	464
Bloemfontein	86	96	73	47	18	11	7	14	19	47	61	61	541
Bethlehem	124	100	84	48	23	11	7	20	28	78	98	98	719

tions by the Agricultural Research Council and the South African Weather Service, there is a west-east gradient of increasing mean annual rainfall from Kimberley to Bethlehem (table 1). The monthly rainfall pattern is similar between the locations, as rainy season starts in October and ends in March/April. The monthly mean temperature (2004–2010) is 24.2°C in January (maximum) and 10.3°C in July (minimum) in Kimberley, 23.4°C and 9.6°C in Bloemfontein, and 20.3°C and 7.7°C in Bethlehem. An aridity index, defined as the ratio of mean annual rainfall to mean annual potential evapotranspiration (Middleton & Thomas 1992), was calculated for the three locations, with the Hargreaves & Samani (1985) evapotranspiration equation modified by Moeletsi & Walker (2012). The aridity index for the period of 2004–2010 was 0.28, 0.29 and 0.46 for Kimberley, Bloemfontein and Bethlehem, respectively. This confirms that all three locations are semi-arid, but the first two have a relatively more arid climate.

Data collection

We carried out vegetation surveys around Kimberley, Bloemfontein and Bethlehem from late November to late December in 2010 and 2011. The annual rainfall in both the years was above normal (except for Bethlehem in 2011): 526 and 616 mm in 2010 and 2011, respectively, in Kimberley; 645 and 647 mm in Bloemfontein; and 863 and 589 mm in Bethlehem. In each location, the vegetation surveys were carried out in grasslands consisting of communal land and private farm land, and also in vast open grassland on Municipality land. Within each of the three locations, we selected roughly 1 km^2 portions of grassland, each of which shall be referred to as a site henceforth.

We surveyed five sites in each of the three study locations, and at each site we sampled 2 to 5 plots. A total of 44 sample plots were surveyed. The plots were 4 m × 4 m in size and in each, all vascular plant species present were recorded. The absolute cover of each species was estimated following the Braun-Blanquet phytosociological method (Mueller-Dombois & Ellenberg 1974, Kent & Coker 1995, van der Maarel 2005). Three soil samples were taken from 0 to 10 cm depth in each plot. The samples were analysed for Ca, K, Mg, Na, P (Olsen), total N, total C, and pH (H_2O). The three replicated soil data were then averaged for each plot. All analyses were done according to the methods compiled by the Non-Affiliated Soil Analysis Work Committee (1990), except for total N and total C which were analysed with a Carbon/Nitrogen Determinator (LECO Corporation, St. Joseph, MI, U.S.A.).

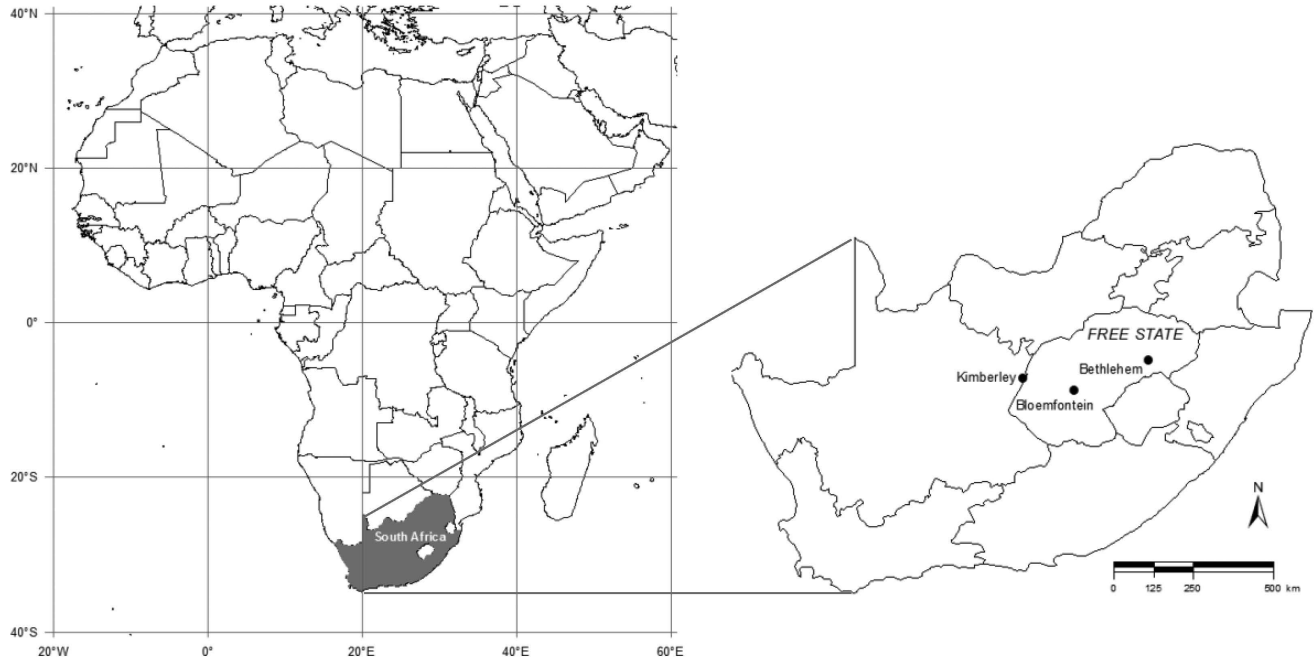

Figure 1 – The location of the study area in Free State Province, South Africa.

Calculation of biodiversity indices

Biodiversity is measured by species richness (N_0), or the number of species in a given area, and evenness, defined as the relative abundance of species in a community (Stirling & Wilsey 2001, Wilsey & Stirling 2007). A number of biodiversity indices have been proposed over the years (Hill 1973, Magurran 2004, Jost 2006, Chalcraft et al. 2009) and in the present study, the inverse Simpson diversity index (N_2) and species evenness based on N_0 and N_2 ($N_{20} = N_2/N_0$) were used to compare plant species diversity of grassland sites along a geographical gradient. N_2 was calculated as follows:

$$N_2 = \frac{1}{\sum_{i=1}^{N_0} p_i^2}$$

where p_i is the proportion of cover of the i-th species (species relative cover). The cover values used were based on median values (except Category r & +) of the cover categories derived from the Braun-Blanquet cover-abundance scale: 1% for Category r & + (cf. Ma 2005); 3 % for Category 1 (1–5%); 15% for Category 2 (6–25%); 38% for Category 3 (26–50%); 63% for Category 4 (51–75%); 88% for Category 5 (76–100%). The cover-abundance values follow the scales of Mueller-Dombois & Ellenberg (1974), Kent & Coker (1995), and van der Maarel (2005). In addition, the Rao (1982) quadratic entropy with the Jost (2007) correction was calculated to compare taxonomic diversity between the locations (using $d_{ij} = 1$ for every $i \neq j$ and $d_{ij} = 0$ otherwise, where d is dissimilarity between each pair of species i and j). The gamma (γ) diversity was partitioned into alpha (α) and beta (β) components (i.e. $\gamma = \alpha + \beta$), applying the weighted contribution of α diversities to the γ diversity (de Bello et al. 2010, Perronne et al. 2014, Gillet et al. 2016).

Data analysis

First, we performed canonical correspondence analysis (CCA), using the programme CANOCO for Windows (ter Braak & Šmilauer 2009), to elucidate geographical patterns of species compositions with soil variables. Data of the species relative cover in the sample plots were used as response variables for the CCA, and the explanatory variables were soil Ca, K, Mg, Na, P, N, C and pH. Second, we carried out a one-way ANOVA with a post-hoc test (Bonferroni correction) at $p \leq 0.05$ to examine differences in diversity indicators (N_0, N_2 and N_{20}) and the soil chemical properties. To perform the ANOVA, sample plot data collected for the biodiversity indices and soil properties was averaged for each site. The p-values were adjusted with the false discovery rate (FDR) method (Benjamini & Hochberg 1995). The Microsoft® Excel spreadsheet provided by Pike (2011) was used to calculate the FDR-adjusted p-values. Prior to the ANOVA, the Shapiro-Wilk normality test was conducted with the assumption of normally distributed datasets; the majority (29 of 33) datasets met the assumption at $p \leq 0.05$. We use the

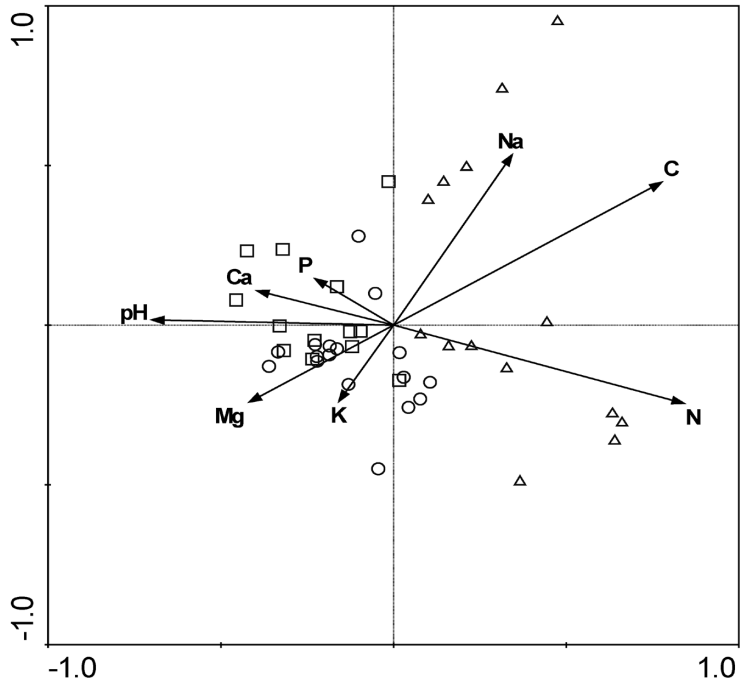

Figure 2 – A canonical correspondence analysis biplot of vegetation plots and soil variables of Kimberley (□), Bloemfontein (○) and Bethlehem (Δ) for the first two axes: Axis 1 (horizontal, eigenvalue 0.588) and Axis 2 (vertical, eigenvalue 0.458). The total inertia and the sum of all canonical eigenvalues were 8.182 and 2.108, respectively. Explanatory variables are soil characteristics (Ca, K, Mg, Na, P, N, C and pH).

Table 2 – **Plant species richness (N_0), inverse Simpson diversity (N_2), species evenness ($N_{20} = N_2/N_0$) and soil properties in Kimberley, Bloemfontein and Bethlehem, South Africa.**
Standard deviations are shown in brackets, and the same letters indicate not significant differences between locations at $p \leq 0.05$.

	Kimberley	Bloemfontein	Bethlehem
Number of sites	5	5	5
N_0	5.6 (1.1) a	5.6 (1.5) a	10.6 (3.9) b
N_2	1.65 (0.52) a	1.85 (0.61) a	2.98 (0.27) b
N_{20}	0.30 (0.04) a	0.34 (0.08) a	0.34 (0.16) a
Ca (mg kg^{-1})	2378 (906) a	1480 (1071) a	848 (233) a
K (mg kg^{-1})	242 (88) a	307 (124) a	206 (42) a
Mg (mg kg^{-1})	355 (203) a	425 (173) a	194 (42) a
Na (mg kg^{-1})	39 (27) a	27 (10) a	50 (18) a
P (Olsen) (mg kg^{-1})	3.3 (2.3) a	4.0 (2.6) a	2.7 (0.4) a
Total N (%)	0.08 (0.03) a	0.11 (0.04) ab	0.16 (0.04) b
Total C (%)	0.60 (0.23) a	0.69 (0.26) a	1.49 (0.52) b
pH (H_2O)	7.4 (0.4) a	6.6 (0.6) ab	5.8 (0.2) b

term datasets to refer to three diversity indices and eight soil variables for the three locations, which make a total of 33 datasets. Regarding the assumption of homogeneity (equity) of variance among the datasets, the Levene's test was used; only a few (3 of 11) variables did not meet the assumption at $p \leq 0.05$. Both the assumptions were by and large met for the ANOVA. Third, we determined Pearson correlations between the diversity indicators and the soil chemical properties. Fourth, we conducted partial correlation analysis for relationships of the diversity indicators with a specific soil variable to detect the effect of the other soil variables. This was carried out only for the soil chemical properties that showed significant Pearson correlations with the diversity indicators. In addition, Pearson correlation analysis was conducted to examine a geographical gradient of the diversity indicators with the long-term annual rainfall. Cook's distance (D) analysis, which detects outliers, indicated that all the data points for correlation analysis did not exceed the threshold (i.e. D < 1). All statistical analyses were conducted using SPSS® version 19 software.

RESULTS

Geographical (rainfall) gradient of plant diversity and soil properties

The CCA ordination model revealed a distinct geographical pattern of soil variables (fig. 2), with a clear discontinuity between sites sampled in Bethlehem from those in Bloemfontein and Kimberley. The total inertia was 8.182; axes 1 and 2 explained 7.2% and 5.6% of the variation of the species matrix, respectively. The sum of all canonical eigenvalues was 2.108; hence axes 1 and 2 explained 27.9% and 21.7% of the variance of the species-environment relation, respectively. The first two canonical axes were significant ($p = 0.002$ for axis 1 and $p = 0.046$ for axis 2). Vegetation plots for Kimberley and Bloemfontein lie on the left half of the diagram, in association with Ca, Mg and pH. The right half is mainly showing the distribution of sample plots from Bethlehem, associated with C and N. The ordination diagram further shows strong associations of pH, Ca, Mg, C and N with axis 1.

The ANOVA results indicate that there were significant increases in N_0 and N_2 from Kimberley to Bethlehem (table 2). The geographical gradients of N_0 and N_2 were therefore associated with the rainfall gradient (fig. 3) as it can be seen that N_0 and N_2 increased across the gradients with increasing rainfall from Kimberley to Bloemfontein to Bethlehem, but N_{20} did not ($p > 0.05$). When we tested the differences in soil chemical properties across the three locations, ANOVA results indicated that total N and total C increased

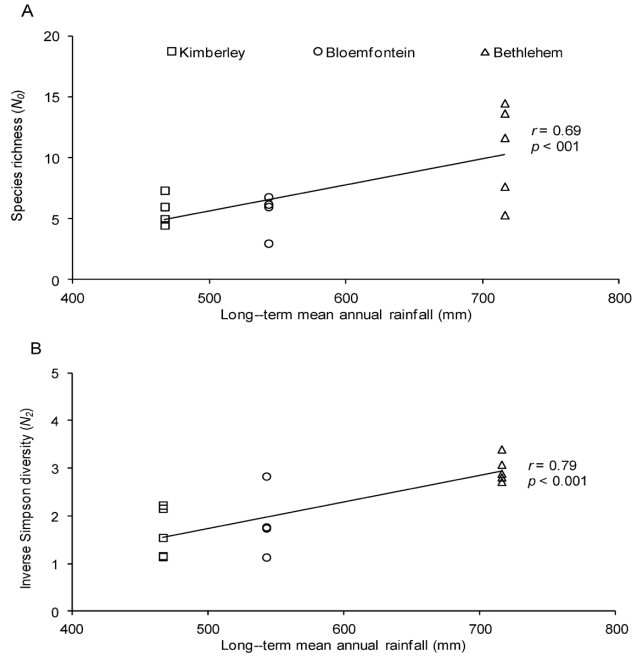

Figure 3 – Relationships of (A) plant species richness (N_0) and (B) inverse Simpson diversity (N_2) with long-term mean annual rainfall (1961–2010) in semi-arid grassland of South Africa.

Table 3 – **Correlation coefficients for relationships between diversity indicators and soil chemical properties in semi-arid grassland of South Africa.**
*, ** and *** indicate $p \leq 0.05$, 0.01 and 0.001, respectively, and ns indicates non-significant relationship ($p > 0.05$), and controlling variables for partial correlation are shown in brackets.

Variable	Species richness (N_0)		Inverse Simpson diversity (N_2)		Species evenness (N_{20})
	Pearson	Partial	Pearson	Partial	Pearson
Ca	ns	–	ns	–	ns
K	ns	–	ns	–	ns
Mg	ns	–	ns	–	ns
Na	0.54*	ns (N, C, pH)	ns	–	ns
P (Olsen)	ns	-	ns	–	ns
Total N	0.53*	ns (Na, C, pH)	0.57*	ns (C, pH)	ns
Total C	0.82***	ns (Na, N, pH)	0.63*	ns (N, pH)	ns
pH (H_2O)	-0.52*	ns (Na, N, C)	-0.70**	ns (N, C)	ns

with increasing rainfall, but pH decreased; Ca, K, Mg, Na and P did not differ across the locations (table 2). Regarding spatial diversity, β was higher in Bethlehem than Kimberley and Bloemfontein (fig. 4). The same was true for γ.

Relationships of plant diversity with soil properties

The diversity indicators and soil properties were significantly correlated within the study area (table 3). N_0 and N_2 decreased with increasing pH, but showed a positive association with N and C. N_0 also had a significant positive correlation with Na. N_{20}, on the other hand, did not show any relationships with the soil properties. In addition, soil pH had a strong positive association with Ca ($r = 0.86$, $p < 0.001$), and N with C ($r = 0.75$, $p < 0.001$). Partial correlation analysis shows that the relationships between diversity indicators and specific soil variables were in fact not significant when the effects of the other soil variables were controlled (table 3). This therefore indicates that the diversity-soil relationships were affected by the controlling variables.

Comparisons of the plant diversity-soil property relationships between locations

The aridity index for Bethlehem (0.46) is higher than that for Bloemfontein (0.29) and Kimberley (0.28), and is close to the threshold (0.5) dividing the semi-arid and dry sub-humid climates. This indicates that the relationships between the diversity indicators and the soil chemical properties for Bethlehem could be consistently distinguished from those of the relatively lower rainfall areas (Kimberley and Bloemfontein). Therefore when Bethlehem data was analysed separately, there was a linear positive relationship between N_0 and soil pH in the range of pH 5.5 to 6.0. Bloemfontein had a linear negative relationship in the range of pH 6.1 to 7.7 (fig. 5A), but no relationship was found for Kimberley. However, both Bethlehem and the lower rainfall areas did not display any significant relationships between N_0 and the other soil variables.

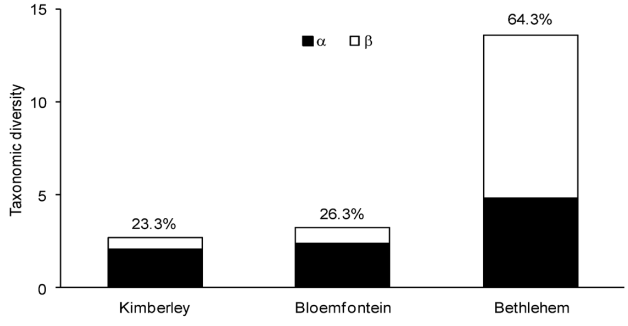

Figure 4 – Taxonomic alpha (α), beta (β) and gamma (γ) diversities in semi-arid grassland of South Africa. γ is the sum of α and β; percentages are proportions of β to γ.

Figure 5A can be interpreted as a generally hump-shaped N_0-pH relationship across the study area. A hump-shaped curve is often described using the gamma distribution. In this study, the dataset of N_0 and pH was fitted to a gamma probability density model by introducing three coefficients, i.e. minimum species richness selected from among the sampling plots (N_{0min}), minimum soil pH selected from among the sampling plots (pH_{min}) and a multiplier (k):

$$N_0 = N_{0\min} + \frac{k b^a (pH_{obs} - pH_{min})^{a-1} \exp\left[-b(pH_{obs} - pH_{min})\right]}{\Gamma(a)}$$

where a (> 0) and b (> 0) are shape and scale parameters of the gamma distribution, respectively, pH_{obs} is soil pH observed in the sites, and $\Gamma(a)$ is the gamma function. $N_{0min} = 2$ and $pH_{min} = 5.26$ were recorded in the total of 44 sampling plots. Figure 5B shows the best fitted gamma distribution curve with k = 11.809, $a = 2.265$, $b = 2.163$ and $\Gamma(a) = 1.128$ ($r^2 = 0.48$, $p < 0.01$).

DISCUSSION

Plant diversity is generally shown to be positively related to rainfall (Adler & Levine 2007). The spatial variation in rainfall in the subcontinent of southern Africa is typified by an increasing gradient of rainfall from west to east (Tyson & Preston-Whyte 2000), and this gradient is also characteristic of our study area. The geographical gradients of N_0 and N_2

were clearly detected in our study area (table 2) and shown to be positively associated with the rainfall gradient (fig. 3). Also, all the Rao α, β and γ diversities increased from Kimberley to Bethlehem (fig. 4). Hoffman et al. (1994) reported a similar biodiversity-rainfall relationship from South Africa, though their study area (west of 27°E) varied from arid to semi-arid regions and receives less rainfall than our study area (i.e. 100–500 mm/year). In regions where rainfall is the most limiting factor to plant growth, more phytomass (plant organic matter) is produced in relatively high rainfall areas (Bethlehem in this study) than low rainfall areas (Kimberley and Bloemfontein). This results in more decomposable organic matter, and subsequently more C together with N is deposited on the soil surface in the higher rainfall areas (table 2). Biomass production is further linked to plant diversity, and a number of experimental studies have reported a positive relationship between plant diversity and productivity in artificial grasslands (Tilman et al. 1996, Hector et al. 1999). For that reason, elevated soil C and N are positively related to higher species diversity in natural semi-arid grassland, as shown in the present study (table 3).

In semi-natural and intensively managed grasslands, however, increased N (beyond a certain threshold) is associated with a decline in plant diversity. For example, McCrea et al. (2004) reported a decline in species richness with more mineralisable N in humid semi-natural meadows. In addition, a number of studies have reported a similar observation that plant diversity decreases with increased N fertiliser (Wedin & Tilman 1996, Baer et al. 2003, Clark & Tilman 2008). In humid grasslands, which have relatively acidic soils, Janssens et al. (1998) showed the optimum total soil N for species richness to be 0.5% dry soil. This implies that in N poor soil, plant diversity is positively correlated with N. The soil N in the study area is relatively low (0.05–0.21%), so it might not reach the optimum for high plant diversity.

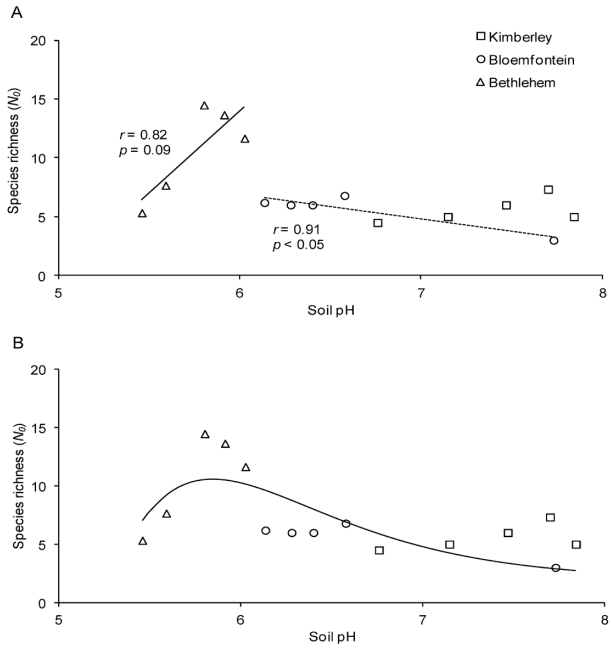

Figure 5 – Relationships of plant species richness (N_0) and soil pH in semi-arid grassland of South Africa. A, linear relationships for Bloemfontein (dotted line) and Bethlehem (solid line); B, a hump-shaped relationship indicating the gamma distribution function: $N_0 = N_{0\min} + kb^a \cdot (pH_{obs} - pH_{min})^{a-1} \cdot \exp[-b(pH_{obs} - pH_{min})] / \Gamma(a)$ where $N_{0\min} = 2$, $pH_{min} = 5.26$, $k = 11.809$, $a = 2.265$, $b = 2.163$ and $\Gamma(a) = 1.128$ ($r^2 = 0.48$, $p < 0.01$).

The soil pH in our study area ranges from 5.5 to 7.8 and there are two main drivers responsible for this variation. First, grasslands produce new phytomass annually and subsequently utilise bases, these with time are accumulated in the surface soil (Troeh & Thompson 1993). Second, in lower rainfall areas there is a lower intensity of leaching of the soil than in high precipitation areas (Chytrý et al. 2007). The lower rainfall areas in our study, Kimberley and Bloemfontein, have more base cations in the topsoil, resulting in increased pH (basicity) (table 2). Due to the low rainfall, not enough water leaches the cations from the soil allowing them to accumulate. In addition, more cations are kept in the soil as a result of high potential evaporation. Bethlehem, on the other hand, has higher rainfall and a relatively higher intensity of leaching, hence the lower pH in the soil.

The maximum availability of all soil nutrients to plant roots is attained at a slightly acidic soil pH (Taiz & Zeiger 1991), and several studies confirm that optimum pH, which maximises species richness in grasslands, is between 6 and 7 (Palmer et al. 2003, Chytrý et al. 2007). Fewer plant species can adapt to soils having pH higher or lower than the optimum because most species are restricted in absorbing certain nutrients at pH outside the optimum range (Schuster & Diekmann 2003, Tyler 2003). Our results show this clearly (fig. 5A). The correlation between soil pH and N_0 for Bethlehem was distinguishable from that for the relatively lower rainfall areas (Kimberley and Bloemfontein). N_0 in Bethlehem increased with increasing soil pH that ranged from 5.5 to 6.0. Similar results were reported from different grasslands; for example, Rutherford & Powrie (2011) in Eastern Cape Province of South Africa showed higher species richness with higher soil pH in slightly acidic grassland. In contrast, soil pH in the Kimberley-Bloemfontein area ranged between 6.1 and 7.8 and tended to have a negative correlation with N_0. Based on the results of our study, together with the observations in other grasslands, we can suggest that species richness of plant communities most likely assumes a hump-shaped model from acidic to alkaline soils, with a ceiling slightly below neutral where plant growth is optimal (fig. 5B). This is in accordance with Schuster & Diekmann (2003) and Chytrý et al. (2007). The hump-shaped model was also reported from other vegetation types in southern Africa, for example, across the succulent Karoo, Nama Karoo, savanna and woodland in south western Africa (Medinski et al. 2010).

CONCLUSION

Studies that enhance our understanding of the interactions between environmental variables and plant diversity are vital for the management and preservation of semi-arid grasslands. Our findings indicate that soil pH is the primary factor influencing variation in species richness in the study area, compared with soil N and C. However, because our study area extends over various soil types and rainfall zones, there

are potential confounding effects of the correlation between soil pH, rainfall and soil physical characteristics (Chytrý et al. 2010). According to Chytrý et al. (2007), in low rainfall areas such as Bloemfontein and Kimberley, low species richness may be due to climatic stress instead of (or in addition to) physiological intolerance of high pH. All in all, although soil pH does not ensure high species richness, it may act as one of the environmental filters that constrain plant diversity (Medinski et al. 2010). It is therefore plausible that soil pH can be an indicator of plant diversity and can thus be employed for monitoring the plant diversity of grassland communities in semi-arid regions.

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