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Parent material and fire as principle drivers of foliage quality in woody plants

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Abstract

Identification of the factors that determine the variation in browse quality, as determined by their chemical composition, is an important step towards understanding herbivore distribution patterns. Therefore, the variation in leaf chemical composition (digestibility lowering compounds: condensed tannin and total polyphenol concentration, and nutrients: nitrogen and phosphorous concentration) was related to geomorphology, vegetation structure, and fire history, in mopane (*Colophospermum mopane*) open woodland in Kruger National Park. The results show that the principle drivers of foliar nitrogen, condensed tannins and total polyphenols differ from those for foliar phosphorus. Nitrogen, condensed tannin and total polyphenol concentrations are mainly determined by the effect of fire. The foliar concentration of phosphorus is mainly determined by parent material. This difference may be related to differences in the mobility of nitrogen and phosphorous in the soil.

Keywords: Nitrogen; Phosphorus; Condensed tannin; Polyphenol; *Colophospermum mopane*; Fire; Savanna; Foliage; Ecosystem drivers

1. Introduction

The nutrient and energy intake of browsers directly depends on the chemical composition of the leaves and young twigs of trees and shrubs. Therefore, the identification of factors that determine the variation of browse quality is essential for understanding the distribution of herbivores.

Major drivers of unevenness in vegetation structure and chemical composition have been identified, many of which operate and interact at different spatial scales. Climatic variables, such as temperature and precipitation, are known to affect vegetation quality at a landscape level (Van Soest, 1987), and, except in areas with very erratic rainfall, are not expected to vary significantly over a few kilometres. On this kilometre scale, surface properties such as slope and aspect are dominant, affecting profile depth, water availability, and nutrient distribution (Buol et al., 1973; Young, 1976). The chemical and physical characteristics of the parent material of a soil, in combination with local climate and age of the soil, determine for a large part the soil properties, such as water retention capabilities, soil rootable depth and nutrient content (Jenny, 1941), which in turn affect vegetation height and chemical composition. Plants on nutrient-rich soils are expected to have a higher leaf nutrient content, and a lower concentration of non-structural carbohydrates, than plants on nutrient-poor soils (Coley et al., 1985; Kraus et al., 2004), but in contrast with (Ferwerda et al., 2005).

The effect of greater availability of nutrients on richer soils translates into a higher production of grass, which is the main source of fuel for fire in savanna landscapes (Langevelde et al., 2003). As a consequence of the increased grass production under the same rainfall conditions, fire frequency and intensity on nutrient-rich soils may be higher than on nutrient-poor soils (Fischer et al., 2003; Vigilante and Bowman, 2004). The expected effects of fire on plant chemical composition, plant growth and nutrient cycling are a reduction of aboveground biomass (Ben-Shahar, 1998), accelerated nitrogen mineralization (Giardina and Rhoades, 2001), increased post-fire growth

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(Rieske, 2002), and tree mortality (Vigilante and Bowman, 2004). Tree mortality results in a reduction of woody biomass height (Shackleton and Scholes, 2000), and a general rejuvenation of the vegetation, which is expressed in short term increments in vegetation nutrient content (Vijver et al., 1999; Bennet et al., 2002), and temporal decreases in non-structural carbohydrates (Rieske et al., 2002).

The Kruger National Park (KNP) in South Africa is a well-known African savanna reserve (Du Toit et al., 2003). Fire is an important tool for management, and both the date and extent of fire-events in KNP are registered in a geographical information system. The combination of a 'mosaic' burning policy together with unintentional fire events and natural fires, results in a patchy distribution of fire events in space and time. The woody component in the north of KNP is near mono-specific and consists of mopane (*Colophospermum mopane*, *J. Kirk* ex Benth.) trees and shrubs (Venter et al., 2003). This tree is an important browse species for elephants (Timberlake, 1995), but is avoided by many herbivores, except at the end of the dry season, when refoliation starts. Then the young foliage is well sought after, probably because of the reduced foliar concentration of herbivore deterring chemicals (deterrents) such as polyphenols (e.g., condensed tannins, CT) (Styles and Skinner, 1997). Crude protein digestibility of browse is thought to be reduced by CT, and browsers may avoid plants with a high CT content (McLeod, 1974; Provenza et al., 1990; Styles and Skinner, 1996). This change in foliage usage makes it a particularly interesting tree for studies on the factors that affect plant biochemistry.

Here we show that the factors that drive the local unevenness in concentration of foliar nitrogen, condensed tannin, and total polyphenol may be fundamentally different from the factors controlling foliar phosphorus concentration in woody plants.

2. Methods

The study area covered 240 km^2 (8 km × 30 km) in the north of KNP, stretching from west to east to cover the main north–south running geological formations. These are: (1) sandstone with quartzites and some andesite, (2) shales, and (3) basalts rich in olivine (Venter, 1990; Venter et al., 2003). The sandstone-derived soils are well-drained, medium and fine sands with some admixture of coarse sand. The shale-derived soils are fine loamy to clayey and may show an enrichment of clay and cations in the subsoil. The area underlain by basalt is poorly drained, vertic clays (Venter, 1990).

2.1. Data collection

Samples of mopane were collected and dried (48 h at 65 °C) for chemical analysis in the peak of the growing season (from mid-January to mid-March 2003). Plot locations were determined at random before entering the field. A plot of 15 m × 15 m to the north and east from each of the 59 plot-coordinates was laid out at each point. One foliar sample was collected of fully grown mopane leaves for each plot, from multiple trees and shrubs of median height, at the sunlit side of the plant, between 1.50 and 2.00 m, between 2 h before and after true midday.

At each plot the grass height was taken to be the average height of 10 random tufts. The percentage grass and bare soil cover within a 1 m × 1 m frame, randomly thrown into the plot (Kent and Coker, 1992), was estimated by two observers. The estimates of three repeats per plot were averaged into 5% interval classes. The cover of herbs was generally low (<5% of total cover) and the variation in this vegetation stratum was not analysed. Tree and shrub height were measured using a calibrated 'dimension meter' (Westfall and Panagos, 1984; Smith, 1996). The projected cover of trees ($DBH > 2$ cm) and shrubs ($DBH < 2$ cm) was visually estimated by two observers from each of the four plot corners, and averaged into 10% interval classes. For an estimated projected cover of less than 10%, classes of 0% (no trees), 1% (one tree/shrub present, with low cover), and 5% (a few trees/shrubs with low cover) were included.

Parent material was determined from the geological map by Venter (1990) (data source: KNP GIS database). Scale numbers (1 for sandstone and quartzite; 2 for shale; and 3 for basalt), were assigned based on typical weatherability and relative nutrient retention capabilities (Jenny, 1941; Buol et al., 1973). The elevation, slope, and aspect were calculated from a 90-m resolution digital elevation model. The digital KNP fire record from 1978 to 2003 was used to calculate the fire return frequency and the number of days since the last fire for each plot using ArcGIS (ESRI).

2.2. Chemical analysis

Condensed tannin (CT), total polyphenol (TP), nitrogen (N), and phosphorus (P) concentrations in ground, dried foliar samples were determined. CT and TP were extracted following Hagerman (1998, 2002) and the CT concentration was determined following Porter et al. (1986). TP concentration was measured following Graham (1992). CT and TP levels were standardized against a quebracho tannin calibration series (Waterman and Mole, 1994). After chemical destruction of dried samples following Novozamsky et al. (1983), N and P concentrations were measured with a Skalar San-Plus auto analyser.

2.3. Data analysis

The concentration of N, P, TP and CT was recorded as a fraction of the dry weight. Since these values are generally low (<10%), these concentrations were log-transformed to adjust for deviations of normality (Zar, 1999) for ANOVA's and *t*-tests, after which groups did not deviate from normality (Shapiro Wilks' W; $p > 0.05$).

The effect of fire was assessed as two individual factors: firstly the effect of individual fire events, measured through the time elapsed since the last fire event, and secondly the effect of re-occurrences of fire, measured through the fire frequency. Therefore, the data were split: plots with frequent fire (more than 6 fire events in 25 years, $n = 27$) and less frequent fire (less

Table 1
Effect of fire return frequency, and the time elapsed since the last fire event on the chemical composition of mopane tree leaves

	Fire return frequency		Time elapsed since the last fire event	
	High, $n = 27$	Low, $n = 32$	<1 wet season, $n = 34$	>1 wet season, $n = 25$
Condensed tannin	0.213	0.258^{***}	0.222	0.256^{*}
Total polyphenol	0.031	0.046^{***}	0.034	0.046^{***}
Nitrogen	2.21	1.91^{***}	2.14	1.93^{*}
Phosphorus	0.186	0.205^{ns}	0.178	0.226^{ns}

Given values: mean concentration in % (nitrogen and phosphorus), and quebracho tannin equivalents g/g (total polyphenols and condensed tannins) and levels of significance of differences ($^{*}p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$, $^{\mathrm{ns}}p$ = not significant) as a result of a Tukey t-test on log-transformed data.

than 6 fire events, $n = 32$). A t-test was used to test for differences in chemical content. The Spearman rank correlation coefficient between tree height and cover, and fire return frequency was calculated. Related to ‘fire frequency’ is the ‘time passed since last fire’. The sample set was split: plots that were burnt after the 2002 growing season ($n = 34$), and the rest ($n = 25$). Using a t-test, the difference in CT, TP, N and P was determined.

The effect of parent material on leaf chemical composition was tested with an ANOVA. We tested for the interaction between parent material (3 classes), and time elapsed since the last fire event (2 classes) and fire return frequency (2 classes).

The number of interacting variables was reduced with a principle component analysis. Principle component transformation on the reduced dataset (grass, shrub, and tree height and cover as active variables) revealed the main relations with the chemical composition of foliage. These were combined into a path-diagram for N, TP and CT, depicting the interaction between individual chemical components and the factors affecting them.

The correlation between foliar concentration of N, P, TP, and CT and the selected environmental factors was calculated. After transformation, several parameters (tree height, time since fire and fire frequency) deviated from normality (Shapiro Wilks’ W test: $p \leq 0.05$). Therefore, a Spearman rank correlation test was used.

3. Results

The effects of fire return frequency and the time elapsed since the last fire event are significant for all chemical components, except for P (see Table 1). Foliar CT and TP concentration was higher on sites where fire frequency is low than where fire frequency was high, and lower on sites with more recent fire events. For N this relation is inversed. The time elapsed since fire has a positive relation with grass, shrub, and tree height and cover, except for shrub cover (Table 2). For fire return frequency, this relationship is inversed (Table 2).

The effect of parent material, and the interaction with time since fire, are only significant for foliar P concentration (foliar P is higher on nutrient-rich (basalt) than on nutrient-poor (sandstone, shale) soils, ANOVA; $p \leq 0.05$; foliar P is lower in trees on nutrient-rich soils with recent fire than other trees on nutrient-rich soils, ANOVA; $p \leq 0.01$). The interaction between parent material and fire return frequency is biased (more samples on nutrient-rich sites with high fire frequency), and group differences were not calculated.

Most of the variation in vegetation structure is captured by the first two principle component axes (Fig. 1a). The first axis shows a strong relation to tree height, cover and bare soil. The second axis is mainly defined by differences in grass and shrub cover. The effect of slope, aspect, and elevation on the structure of vegetation is minimal (Fig. 1a).

Slope, elevation, or aspect do not explain much of the plot structural variation (Fig. 1a); grass height, tree cover and, shrub height are strongly related to grass-cover, tree height and shrub cover (Fig. 1a) and bare soil is a pseudo variable, related to grass, shrub and tree cover. These variables were removed from the analysis. A new set of principle component axes was defined with vegetation structure and environmental variables as active variables (Fig. 1b). Foliar N has a weak but positive relation to geology and fire return frequency. For CT and TP this relation is reversed. Foliar P shows a weak relation to parent material and time since fire.

The correlation with the time since fire is positive for CT, TP and P, and negative for N. The correlation between the fire return frequency, and all measured chemical components was significant (Table 2); negative for CT and TP, and positive for N and P. Tree height shows a significant correlation with CT, TP, and P content (Table 2): with increasing tree height, leaf CT

Table 2
Spearman rank correlation coefficients and, if significant, levels of significance ($^{*}p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$) between plot structural variables, continuous environmental variables and the concentration of nutrients and deterrents in mopane leaves

	Tree H	TSF	FRF
CT	0.31^{**}	0.38^{**}	-0.39^{**}
TP	0.37^{**}	0.46^{**}	-0.54^{***}
N	-0.16	-0.39^{**}	0.30^{*}
P	-0.47^{***}	-0.06	0.34^{**}
Grass	Height	0.43^{**}	-0.46^{***}
	Cover	0.46^{***}	-0.40^{**}
Shrub	Height	0.37^{**}	-0.36^{**}
	Cover	-0.13	-0.19
Tree	Height	0.37^{**}	-0.59^{***}
	Cover	0.42^{***}	-0.53^{***}
Bare	Soil	-0.59^{***}	0.49^{***}

CT, condensed tannin content; TP, total polyphenol content; TSF, time elapsed since the last fire event; FRF, fire return frequency; tree H, tree height.

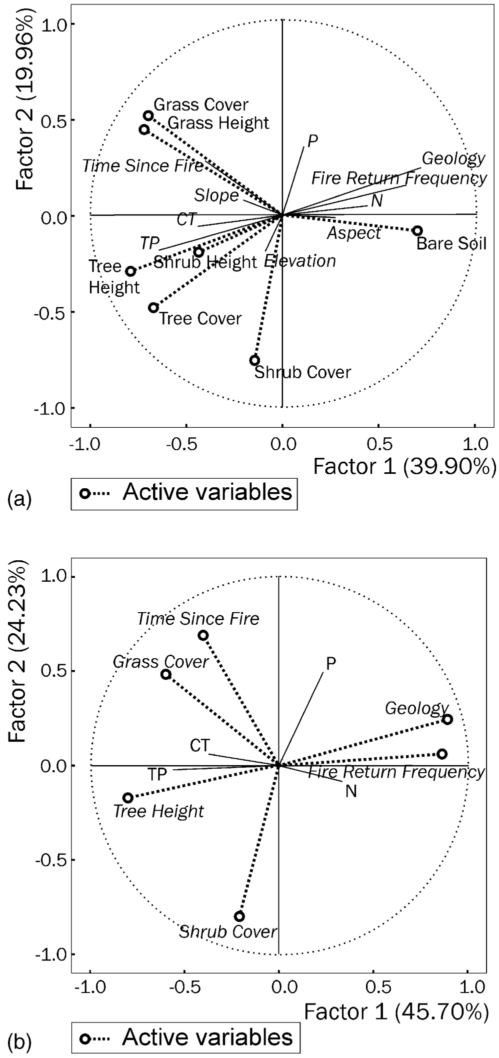

Fig. 1. (a) *X–Y* vector plot of factor loadings for the chemical composition of mopane samples, and each explanatory factor. Plot structure was used to define the principle component space (active factors). (b) *X–Y* vector plot of factor loadings for the chemical composition of mopane samples, after reducing the number of explanatory factors. Plot structure, fire history and parent material were used to define the principle component space (active factors). The *x*-axes display factor loadings (correlation) for each explanatory factor and the first principle component factor, the *y*-axes display the factor loadings for the explanatory factor and the second principle component factor.

content and leaf TP content increase, while leaf N and P content decrease.

4. Discussion

This study is based on a single observation of continuous processes, and agrees with studies that show, in response to fire events, a reduction of woody biomass (Shackleton and Scholes, 2000), increments of foliar nitrogen (Rieske, 2002) and decreases of non-structural carbohydrates (CT and TP) (Rieske, 2002). We found, in a PCA that linked the structure and environmental variation to foliar chemical concentration (Fig. 1b), that foliar P was not related to foliar N, CT and TP concentration. This indicates that variation in foliar P may be driven by factors other than those controlling foliar N, CT and TP.

Although individual fire events may result in a reduction of grass, shrub and tree height and cover, with increased foliar nutrient concentration, eventually causing a decrease in deterrent concentration in the season after a fire, in this study the effect of returning fire was stronger (Fig. 1b, Tables 1 and 2). An increase in fire frequency resulted in increased N concentration and decreased non-structural carbohydrate (TP and CT) concentrations (Tables 1 and 2). We think that this decrease is most likely related to an increased demand of carbon for biomass production as a result of increased N availability (Bryant et al., 1983; Coley et al., 1985; Coley, 1988). This may result in a reduction of available carbon to produce CT and TP (Jones and Hartley, 1999). With decreasing fire frequency and intensity trees can escape the so-called fire trap (Higgins et al., 2000). This allows trees to grow larger, affecting growth and physiology through size-mediated ageing (Moorby and Wareing, 1963): evapotranspriration is reduced, and as trees grow larger transport of water and nutrients to their leaves becomes less efficient (Magnani et al., 2000; Mencuccini et al., 2005). This effect seems to be inversed by grafting and reductions in above-ground biomass, and size in itself seems to be the main controlling factor (Mencuccini et al., 2005; Penuelas, 2005). This effect of tree size on chemical composition raises an interesting question regarding tree-usage by large herbivores. Elephants in an other South African semi-arid savannah ecosystem (the Venetia–Limpopo Nature Reserve) have been found to feed mainly on smaller trees (<4 m tall) and preferred to use branches of previously utilized trees (Smallie and O'Connor, 2000). The authors concluded that there is a preference for a certain branch size (0.9–1.7 cm in diameter). No chemical analysis of the branches or foliage was performed. Could it be that this preference is related to the effects of ageing, and rejuvenation after regrowth of pant material?

In an ANOVA, the effect of parent material was not significant on foliar CT, TP and N. However, fire frequency is related to geology (Fig. 1b). This may be the result of increased grass production on nutrient-rich soils, which results in increased fire frequencies (Fig. 2). Fig. 2 shows that, although fire reduced woody plant height, this did not affect N content. There was however a direct effect of fire on foliar N. This may be related to increased nitrogen mineralization in the soil or a general rejuvenation of plant material.

Foliar P showed a different relation to environmental factors compared to foliar N, and to keep Fig. 2 clear, the relation with foliar P was not included. In contrast to N, foliar P is affected by parent material but not by the time since the last fire event. This may reflect a difference in mobility of N and P in the soil. After mineralization of organic material, nitrogen mainly occurs in mobile NO_3^- or NH_4^+, which can be easily absorbed by plants (Sumner, 1999). Soil P however is quickly immobilized by Al, Fe, Mn and Ca in the soil, a process which is strongly affected by soil properties (Sumner, 1999).

The ratio between N and P is thought to be a good predictor for the limitation of plant growth by either N or P in savanna

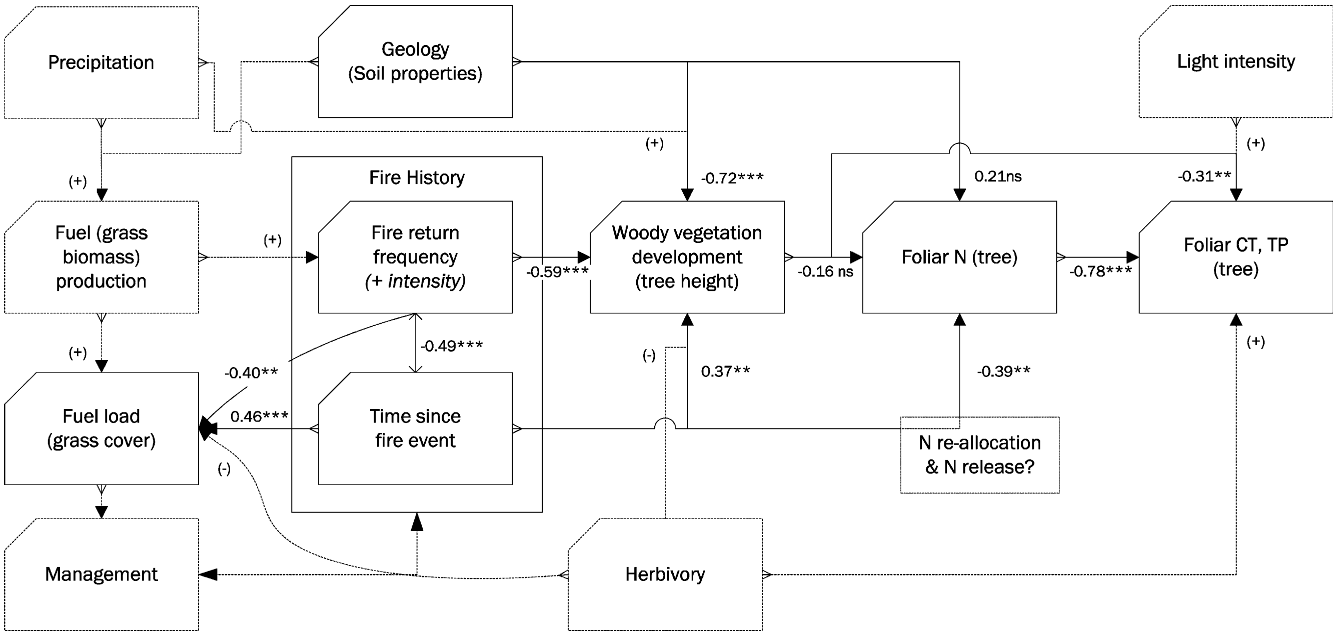

Fig. 2. Overview diagram of the interaction between environmental factors, vegetation structure and mopane (*Colophospermum mopane*) chemical composition. The strength of relations was calculated using a Spearman rank correlation test (levels of significance: $^{***}p \leq 0.001$; $^{**}p \leq 0.01$; $^{*}p \leq 0.05$; ns: not significant). Solid lines depict variables and relations which have been observed/calculated. Dashed lines depict other important factors affecting vegetation structure, fire or the chemical composition of mopane leaves, but have not been measured. Where possible the direction of the effect (positive: + or negative: −) has been included in the diagram.

ecosystems. A ratio of 12 or higher indicates a P limitation (Ludwig et al., 2001). For herbivores, N and P are important nutrients that are often available at sub-optimal concentration in forage (Van Soest, 1987), and the uptake of N from forage may be hindered by higher concentrations of CT and TP, causing herbivores to avoid forage with high concentration of TP and CT (Provenza et al., 1990). Our study therefore provides insight in how geology directly, and through differential effect of fire caused by the geological substrate indirectly, may affect resource quality, and therefore herbivore abundance.

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