Browsing intensity of herbaceous forbs across a semi-arid savanna catenal sequence

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ARTICLE INFO

ABSTRACT

Ecological models to explain savanna heterogeneity and functioning weakly represent herbaceous forbs, which inevitably created knowledge gaps regarding the diversity and ecology of forbs. Forbs constitute over 70% of semi-arid savanna species richness. The aim of this study was therefore to (i) identify forb species that potentially form part of herbivore diet, and (ii) determine forb browsing intensity across a granitic savanna catenal sequence. Localized contrasts between nutrient-poor dystrophic uplands and nutrient-rich eutrophic bottomlands led us to predict that bottomlands would host forb assemblages dominated by browsed species. Forbs contributed to 78% of the total herbaceous layer species richness, of which 43% were browsed at varying intensities along the catenal sequence. Each topographic zone hosted a unique assemblage of browsed forbs, although browsing intensity was highest in the sodic bottomlands. Some browsed forbs formed prostrate, stoloniferous covers on the bottomlands, creating a lawn type dominated by forbs. Results presented here are the first to identify browsed forb species and to illustrate the turnover in browsing intensity of forbs across a semi-arid savanna catenal sequence. Our results add weight to the need to include herbaceous forbs in savanna management models to better understand savanna resource ecology and heterogeneity.

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1. Introduction

African savannas are characterized by heterogeneous landscape types that provide a template upon which structural diversity and resource availability are shaped (Pickett et al., 2003). The general association of savanna types with soil fertility led to the concept of moist, nutrient-poor (i.e. dystrophic) savannas on highly leached, sandy soil versus arid, nutrient-rich (i.e. eutrophic) savannas on clayey substrates (Huntley, 1982). In arid and semi-arid savannas (<650 mm rainfall per annum), nutrient distribution can however be patchy. For instance, in a granitic savanna catenal sequence, there is a discernible turnover in nutrients and vegetation structure from uplands to bottomlands (Scholes, 1990), where uplands are associated with a nutrient-poor, broad-leaved savanna type (i.e. equivalent to dystrophic) and the clay-rich bottomlands with a nutrient-rich, fine-leaved savanna type (i.e. equivalent to eutrophic). This form of heterogeneity is however not attributed to abiotic variance in the landscape only, but is enhanced by the top-down effects of herbivory and fire, particularly so for the southern African savannas (Sankaran et al., 2005; Jacobs and Naiman, 2008; Smit et al., 2012). Despite of its variability, a defining feature of savannas is a continuous herbaceous layer and a discontinuous stratum of trees and shrubs within the same landscape (Knoop and Walker, 1985).

Understanding this ecologically important coexistence of trees and grasses is extremely valuable, particularly for savanna ecosystem management (O'Connor et al., 2014).

During the past two decades, savanna management has shifted its focus from causes of ecosystem change, habitat homogeneity, equilibrium and carrying capacity to responses to change, heterogeneity, dynamic equilibrium and ecosystem redundancy perspectives (Rogers, 2003; Grant et al., 2011). The understanding and application of these concepts to the herbaceous layer are however, largely based upon findings from rangeland science, a discipline driven by agriculture (i.e. herbivore productivity) rather than conservation in southern Africa (Tainton, 1999). For this reason, savanna management models exclusively used grass species, particularly due to their significant contribution to total standing biomass and their important role in forage for both ruminant and non-ruminant savanna grazers (Treydte et al., 2013). Herbaceous dicotyledonous species, non-graminoid monocots and geophytes (collectively termed 'forbs' hereafter) have been ignored or merely lumped into a 'non-grassy, Increaser II' category in management models (Scott-Shaw and Morris, 2014), although they constitute the largest component of herbaceous species richness in grasslands (Pokorny et al., 2004; Bond and Parr, 2010; Koerner et al., 2014; Scott-Shaw and Morris, 2014), temperate deciduous forests (Axmanová et al., 2012) and savanna ecosystems (Shackleton, 2000; Uys, 2006; Jacobs and Naiman, 2008; Pavlovic et al., 2011; Van Coller et al., 2013). In a study on savanna browser resource use, Du Toit

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(1988) reported that forbs constitute between 50% and 80% of the diet of three savanna mesoherbivores (measured in terms of feeding time allocation of kudu, impala and steenbok). Impala (*Aepyceros melampus*) feed mostly on palatable grass species and to a lesser extent on microphyllous woody species (e.g. *Acacia* spp. and *Dichrostachys* spp.), although forbs are also present in their diet and play an important role in the selection of feeding stations (Van der Merwe and Marshal, 2012). Forbs have also been recorded in the diet of two megaherbivores, i.e. African elephant (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*) (Malan et al., 2012; Landman et al., 2013). Further motivation for studies on forbs in diets of larger mammals was revealed through a DNA metabarcoding study of ancient DNA preserved in permafrost sediments (Willerslev et al., 2014). Contrary to earlier studies on Arctic vegetation, the study revealed that forbs, and not graminoids, dominated Arctic vegetation up until the Last Glacial Maximum (25–15 kyr before present), and that both graminoids and forbs featured in the diets of megafaunal mammals (Willerslev et al., 2014).

The Kruger National Park (KNP) in South Africa is a well-studied savanna ecosystem in which heterogeneity and complexity are acknowledged and applied in management practices. Landscape heterogeneity in KNP influences vegetation patterns and hence community assemblages and densities of large herbivores at different spatial scales (Du Toit, 2003). At the smaller scale, savanna catenas represent gradual or sometimes abrupt turnover in soil moisture, nutrients, species assemblages and vegetation structure (Scholes, 1990). This study expands on work showing the value of savanna forbs (Du Toit, 1988) and is specifically aimed at testing whether differences exist in the distribution and browsing intensity of savanna forbs between dystrophic uplands and eutrophic bottomlands (Scholes, 1990). Knowledge of herbivore preference among forb species and differences in browsing intensities across the catenal sequence should improve our understanding of the resource value of savanna forbs.

2. Materials and methods

2.1. Study area

The Nkuhlu study area (24°58′S, 31°46′E) is adjacent to the Sabie River in southern KNP. The climate is semi-arid subtropical with two broadly distinct seasons: a hot, occasionally wet, growing season and a warm, dry, dormant season (Williams et al., 2009). Mean annual rainfall at Skukuza, 30 km west of Nkuhlu, is ~550 mm (http://www.sanparks.org/parks/kruger/conservation/scientific/weather). Average daily temperatures at Skukuza are 15.7 °C in June and 26.6 °C in January. Average minimum temperature in June is 5.7 °C and average maximum temperature in January is 32.6 °C. The topography is an undulating landscape, 200–230 m above mean sea level, derived from granite and covering the sequence of terrain morphology from bottomlands to uplands. The uplands are characterized by shallow, sandy, coarse soil overlying rock, while the bottomlands (below the seepline) are characterized by deep, sodic, duplex soil, which is a typical pattern on catenas in granite-derived, semi-arid landscapes (Khomo and Rogers, 2005; Grant and Scholes, 2006). Sodic soils in the study area are composed of shallow (<15 cm) sand overlying impermeable clay and have high pH (>8.5) and reduced hydraulic conductivity (Khomo and Rogers, 2005; Grant and Scholes, 2006; Tarasoff et al., 2007). Sodic soils are therefore regarded as potentially stressful environments for vegetation, which is sparse, but regarded as more attractive than upland vegetation to large herbivores, especially grazers and mixed feeders (Tarasoff et al., 2007; Levick and Rogers, 2008). The attractiveness of sodic patches to herbivores is because the vegetation is inherently more nutritious (Bailey and Scholes, 1997) and because it offers other attractions such as predator vigilance, water, dietary salts or anti-acidosis minerals (Khomo and Rogers, 2005). Nevertheless, trampling, excretion and defoliation are thought to maintain the vegetation in a nutritious vegetative state (Grant and Scholes, 2006). Directly adjacent to the Sabie

River, the bottomlands are composed of deep alluvial soils underlying riparian vegetation that is dense for the most part. Vegetation of the study area was described by Siebert and Eckhardt (2008). Common mammal herbivores included impala (*Aepyceros melampus*), African elephant (*Loxodonta africana*), hippo (*Hippopotamus amphibius*), black rhino (*Diceros bicornis*), white rhino (*Ceratotherium simum*), blue wildebeest (*Connochaetes taurinus*), Cape buffalo (*Syncerus caffer*), plains zebra (*Equus quagga*), greater kudu (*Tragelaphus strepsiceros*), steenbok (*Raphicerus campestris*), giraffe (*Giraffa camelopardalis*) and scrub hare (*Lepus saxatilis*). Elephant density fluctuated around 0.5–2.0 km^{-2} (Grant et al., 2008). A breeding herd of 30–40 impala, several impala bachelors, two black rhino and an unknown number of steenbok were resident in the study area, while low numbers of giraffe and kudu were occasionally present.

2.2. Sampling design

Long-term monitoring transects were located perpendicular to the perennial Sabie River. These transects, which crossed the catenal sequence consisted of 10 m × 20 m fixed plots (long side parallel to the river channel) with two nested 1 m² plots in the eastern and western corners of each 200 m² plot respectively in which all rooted forb and grass species were identified and counted for species richness and density analyses (see Van Coller and Siebert (2015) for a detailed account on the experimental design and layout of the transects). A total of 156 1 m² plots provided data for calculating mean values per growth form. For browsing intensity, data were collected in 78 of the larger, fixed 200 m² plots along the transects. Sampling was done during the rainy season (November/December 2013) when plant cover was at its maximum and most plant species were present. Half of the plots were located in a fire treatment, although no effect of fire was expected since the last fire occurred in 2007 (6 years prior to sampling).

2.3. Browsing intensity

An index was designed to record the intensity of browsing signs on all individuals of potentially palatable forb species encountered in each 200 m² plot. A forb species was considered 'potentially palatable' if it showed any signs of browsing. The index (Table 1) was broadly based upon Walker's Palatability Index (Walker, 1980). Although this index is referred to as a palatability index, it is based upon browsing intensities of forb species and individuals. Since insects contribute substantially to herbivory patterns in savanna ecosystems, browsing signs by insects were included in the index for an overall view of herbivore selection of forbs. Browsed forb species were grouped according to plant family (Germishuizen and Meyer, 2003) to determine whether these taxa (i.e. browsed forbs) represented similar plant families. Habitat preference (fidelity to a topographic zone) was used to differentiate between diagnostic (i.e. species dominant in one topographic zone), unique or character (i.e. restricted to one topographic zone) and common (i.e. common across all topographic zones) browsed species.

The following were calculated for each plot: (i) the total number of browsed individuals for all species; (ii) the total number of browsed

Table 1
Index used to measure browsing intensity on herbaceous forbs (after Walker, 1980).

Index value	% leaf area removed	Description
0	0	Not browsed. No signs of herbivory
1	1–10%	Few holes in leaves
2	>10–50%	Lightly browsed. Few branches/branchlets/leaves removed. Most leaves remain on plant
3	>50–80%	Moderately browsed. Most branches/branchlets/leaves removed, leaving only a few leaves to remain on plant
4	>80–100%	Intensively browsed: Almost all branches/branchlets/leaves removed. Mostly only one or two leaves to remain on plant