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Herbaceous responses to herbivory, fire and rainfall variability differ between grasses and forbs

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ABSTRACT

Herbivory and fire are known to shape plant community structure and function in savanna ecosystems worldwide, yet these drivers are increasingly being altered in their behaviour, or completely excluded. Furthermore, herbaceous responses to rainfall in semi-arid and arid savannas may outweigh the effects of herbivory and fire, especially in nutrient-rich ecosystems. Despite considerable recognition of herbaceous responses to drivers in savanna systems, few studies consider grasses and forbs as distinct herbaceous functional entities. To address this shortcoming, we used long-term herbaceous vegetation data collected from herbivore and fire exclusion treatments in the Kruger National Park (KNP) in South Africa. We investigated response patterns in herbaceous abundances per functional group for three sampling years, which represented different rainfall conditions (i.e., average for 2010, above average for 2001, and below average for 2015. Dynamic shifts in forb versus grass dominance were revealed across treatments. Surprisingly, palatable annual forb communities seemed more resilient to herbivores, or their removal, dominating over palatable annual grass communities. Furthermore, unpalatable perennial forbs were revealed to be more resilient to herbivore presence than their absence. Palatable perennial grass abundances were consistently enhanced by above-average rainfall conditions, whereas equal dominance of palatable grasses and forbs was evident during the drought year. This highlights that palatable perennial functional groups (not grasses alone) provide important ecosystem functions, such as forage stability, and hence functional redundancy to absorb disturbances such as droughts. Moreover, rainfall variability and herbivory are considered the main drivers of palatable perennial functional groups in this nutrient-rich ecosystem. Palatable perennial grass abundances differed significantly from other alleged unfavourable herbaceous functional groups (e.g., unpalatable perennial grasses, annual grasses, and annual and perennial forbs) and, although they presented contrasting patterns for each sampling year, fire and herbivory treatments, palatable perennial grasses remained the dominant functional group in this ecosystem type. Therefore, this study did not support previous findings that conditions such as drought, fire and herbivory favour unfavourable functional groups at the expense of palatable perennial grasses. Observed patterns provide evidence of a dynamic and less predictable coexistence between grasses and forbs.

1. Introduction

Savanna herbaceous layers are co-dominated by two life-forms (forbs and mainly C_4 grasses), which are floristically, morphologically and physiologically distinct (Turner and Knapp, 1996). The grass component functions as the main source of forage that supports, not only the high diversity of African grazers, but also domestic livestock (Bell, 1971; McNaughton and Georgiadis, 1986; Murray and Illius, 1996; Smith et al., 2012). Palatable perennial grasses are an important source of forage stability to grazers in semi-arid savanna systems (O'Connor, 2015), and are considered important for livestock production (Uys, 2006; Trollope et al., 2014). Consequently, assessments of range condition in savanna systems are largely based on dominant palatable

Abbreviations: LMH, Large mammalian herbivores; HLM, Hierarchical linear modelling; F, Forbs; G, Grasses; PPF, Palatable perennial forbs; PPG, Palatable perennial grasses; PAF, Palatable annual forbs; PAG, Palatable annual grasses; UPF, Unpalatable perennial forbs; UPG, Unpalatable perennial grasses; UAF, Unpalatable annual forbs; UAG, Unpalatable annual grasses.

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perennial grass species (Uys 2006; Kioko et al. 2012; Treydte et al. 2013; Trollope et al. 2014). Increased abundances of alleged unfavourable functional groups (e.g. annual grasses and forbs) at the expense of taller, palatable perennial grass species are often used as an indication of land degradation (e.g. Savadogo et al., 2008; Buitenwerf et al., 2011; Tessema et al., 2011; Koerner and Collins, 2014). However, increases in these 'undesirable' functional groups may not necessarily be negative to the overall functioning of savanna ecosystems (Du Toit, 2003; Van Oudtshoorn, 2009; Siebert and Scogings, 2015), since the ecological functions of these plant groups are relatively unknown. For instance, forbs (herbaceous dicotyledonous species, non-graminoid monocots and geophytes) are a particularly nutritious and high-quality food class for browsers in South African savannas (Du Toit, 2003), and may constitute an important part of ungulate diets at certain times of the year (Scholes, 1987; Van Der Merwe and Marshal, 2012). Moreover, evidence of more intensely browsed herbaceous forbs on nutrient-rich patches compared to adjacent sites (Siebert and Scogings, 2015) confirms their functional plasticity along small-scale environmental gradients (Shackleton, 2002; Lettow et al., 2014). Forbs have largely been overlooked, or simply lumped into a 'non-grass', Increaser II category in range condition assessments (Scott-Shaw and Morris, 2015). For this reason, the ecological function of forbs and the way they respond to common drivers of herbaceous vegetation dynamics (i.e. herbivory, fire and rainfall variability) remain less explored (Lettow et al., 2014; Scott-Shaw and Morris, 2015; Siebert and Scogings, 2015).

Understanding the effects of various types of disturbances on all herbaceous life forms is essential for designing multiple-use management plans for semi-arid savanna systems (Savadogo et al., 2009), whether the disturbance represents an increased pressure or a release thereof (partial or total release). Despite an increasing awareness of the importance of understanding resilience in complex systems, there is limited information available on the underlying functions of herbaceous life forms, other than the supposed desirable ones. Although it is widely accepted that forbs and grasses co-dominate and often switch dominance in response to environmental changes (Illius and O'Connor, 1999; Koerner and Collins, 2014), the complete functional identity of these dominant life forms is less explored. In this study, we attempt to address some of these shortcomings by considering forbs and grasses as separate functional entities within the same structural layer of a nutrient-rich ecosystem. We used common drivers of savanna structure and function, such as herbivory, fire and rainfall variability, to assess forb-grass dominance shifts when nutrients are not limited. A further objective of the study was to determine which conditions favour dominance of the alleged undesirable functional groups (i.e. annual grasses and forbs) at the expense of palatable perennial grasses. Varying annual rainfall quantities for different sampling years allowed us to link herbaceous life form dominance to average, above-average and below-average rainfall. Anticipated variation in responses of herbaceous life forms was hypothesised to provide functional redundancy, i.e. when two or more life forms share similarities concerning a specific function in such a way that one life form can fully or partially compensate for another should it disappear or decline in abundance (Kotschy, 2013). It was predicted that combined effects of average rainfall, fire and herbivores will favour palatable perennial grasses, since indigenous African grasses are well-adapted to withstand severe grazing (Scholes and Walker, 1993; Owen-Smith, 2013). It was furthermore hypothesised that unpalatable grasses and forbs will be more abundant with higher grazing pressure and drought, whilst the exclusion of herbivores and fire will favour palatable perennial grasses at the expense of other functional groups as a result of competitive exclusion effects (Van Coller and Siebert, 2015). Herbivory was expected to be the primary driver of herbaceous vegetation dynamics under variable rainfall conditions in this system. Herbivores maintain low aboveground biomass, as opposed to their exclusion, which allows for increased biomass (Jacobs and Naiman, 2008; Van Coller et al., 2013; Van Coller and Siebert, 2015). Consequently, fire was not expected to have significant effects on herbaceous species dynamics when herbivores are present. However, fire effects were anticipated to become more distinct in herbivore absence and the consequent increase in aboveground biomass. Fire improves quality of grazing for wildlife by reducing competition and removing moribund and undesirable grass material (Garnier and Dajoz, 2001; Trollope, 2011). It was, therefore, expected that fire effects in the absence of herbivores would enhance dominance of palatable grass species.

2. Materials and methods

2.1. Study area

The study was conducted in the semi-arid Dry Sodic Savanna of the Nkuhlu exclosures a large-scale, long-term exclusion experiment situated on the northern bank of the perennial Sabie River (24°58′S, 31°46′ E), approximately 18 km downstream from Skukuza in the Kruger National Park (KNP), South Africa (Siebert and Eckhardt, 2008). The Nkuhlu exclosures research site is located within the Granite Lowveld vegetation unit (SVI 3) of the Savanna Biome (Mucina and Rutherford, 2006).

Sodic patches are generally associated with footslopes of undulating granitic landscapes and characterised by sodium-rich duplex soil (Dye and Walker, 1980; Venter, 1990; Alard, 2010), consisting of a shallow (<15 cm), coarsely textured sandy loam A–horizon, supporting most plant life, overlying a B–horizon of almost impervious calcium-rich heavy clay, often leading to vegetation mortality and the limitation of rooting of woody species (Khomo and Rogers, 2005; Grant and Scholes, 2006; Siebert and Eckhardt, 2008; Alard, 2010; Siebert and Scogings, 2015). The relatively continuous herbaceous layer is dominated by forb species such as *Abutilon austro-africanum*, *Portulaca kermesina* and *Ocimum americanum*, whilst dominant grasses include *Chloris virgata*, *Enteropogon monostachyus* and *Sporobolus nitens* (Siebert and Eckhardt, 2008). The discontinuous woody component is dominated by *Vachellia grandicornuta* (syn. *Acacia grandicornuta*), *Euclea divinorum*, *Spirostachys africana* and *Pappea capensis* (Grant and Scholes, 2006; Scogings, 2011).

Large mammalian herbivores (LMH) residing in the study site include browsers (giraffe, black rhino, bushbuck and greater kudu), grazers (Cape buffalo, hippopotamus, blue wildebeest, and plains zebra) and mixed- or intermediate feeders (impala, African elephant, grey duiker, and steenbok) (Scogings et al., 2012).

2.2. Experimental design and sampling

To determine responses of herbaceous vegetation to rainfall variability and combined effects of fire and herbivore presence or absence, life form abundance data were sampled in two exclusion treatments in the Nkuhlu exclosures. These treatments were designed to include a fire and no-fire treatment (Fig. 1). Fire treatment was dependent on the occurrence of fire in the surrounding fire management units, as part of a rotational burn every 5 years. Fire treatment in the exclosures was first established in 2002 (Govender, 2016), with prescribed fires having occurred in October 2002, August 2007 and June 2012. One exclusion treatment was specifically designed to exclude elephants (although giraffes were also excluded due to their body size), but not other LMH (O'Keefe and Alard, 2002) (Fig. 1). Since the African elephant is absent in many protected areas in savannas and, therefore, managed for grazers and meso-browsers only (Uys 2006; Buitenwerf et al., 2011), the herbivory exposure treatment ('with herbivores') in this study represents the area from which elephants (and giraffe) were excluded (Fig. 1). The experimental design of the Nkuhlu exclosures further allowed us to test the effects of total release of LMH pressure in a fully fenced area (i.e. 'without herbivores', Fig. 1). The total area of the experimental site relevant to this study was approximately 114 ha.