



Multiple nutrients control threatened grassland vegetation in eastern South Africa



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ABSTRACT

Grassland types associated with highly weathered upland soils derived from igneous dolerite and sedimentary sandstone in eastern South Africa are rich in restricted range plant species, and have been extensively destroyed for agriculture and other land uses. Anthropogenic increases in nutrient supply, including atmospheric N deposition, and changes in herbivore abundance may alter vegetation and threaten species in remaining fragments. We investigated the influence of multiple nutrient limitation and herbivory on the productivity, diversity, and composition of these distinctive grasslands, as part of the world-wide Nutrient Network. We examined nutrient limitation using three years of factorial additions of N, P + Ca, and K + micronutrients at two sites, one dolerite-derived and one sandstone-derived. Adding N and P + Ca increased aboveground productivity at both sites by 33–55%, indicating that these nutrients co-limited productivity. Adding N reduced species richness (by 11%) and effective species richness (by 24%) at the sandstone site; all nutrient additions also tended to reduce diversity at the dolerite site. At both sites, adding N increased the abundance of grasses at the expense of (N-fixing) legumes, which declined in relative abundance by 44–60%, whereas adding P + Ca tended to increase the abundance of legumes. At the dolerite site, a factorial fencing and nutrient addition experiment showed that large herbivores did not significantly influence vegetation during three years. Widely increasing atmospheric N deposition, and perhaps warming-induced increases in N mineralization at high elevation, will likely increase productivity, reduce diversity, and reduce legume abundance in these dolerite and sandstone grasslands, posing an additional challenge to conserving them.

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1. Introduction

Eastern South Africa holds mesic grasslands valued for their high biodiversity, as well as livestock grazing and other ecosystem services such as streamflow and medicinal plant production (Bond and Parr, 2010). Agriculture and urbanization have caused extensive habitat loss and fragmentation (Driver et al., 2005; Mucina and Rutherford, 2006; Zaloumis and Bond, 2011). Accordingly, many restricted range plant species associated with distinctive geomorphology and soils are threatened with extinction (Raimondo et al., 2009). Biodiversity in remaining grassland fragments may be threatened by anthropogenic environmental changes. Here we investigate how increasing nutrient supply rates, e.g., through N deposition, and changing grazer abundance influence grasslands of two types: Drakensberg Foothill Moist Grassland on igneous dolerite outcrops, and KwaZulu-Natal Sandstone Sourveld on sedimentary sandstone plateaus (Mucina and Rutherford, 2006).

The association of these vegetation types with particular soil types suggests that low nutrient supply rates or other soil properties may strongly influence their species composition and diversity; if this is so then they may be radically altered by anthropogenic increases in nutrient supply.

Nitrogen (N) commonly limits productivity and influences diversity and composition in grasslands, and is increasingly available to plants (Tilman, 1982; Tilman, 1988; Vitousek and Howarth, 1991; LeBauer and Treseder, 2008). Nitrogen supply rate is increasing with widespread increases in atmospheric deposition of inorganic N (Vitousek et al., 1997). The nearest measurements of wet N deposition, combined with models of dry deposition, indicate total deposition rates of 4.2–9.7 kg N/ha/yr from 2000 to 2007 in the South African Lowveld and Highveld to the north of the study region (Vet et al., 2014); wet deposition rates are increasing at these measurement stations (Conradie et al., 2016). A global model of N deposition estimated a similar mean of 5 kg N/ha/yr in the Maputaland–Pondoland–Albany biodiversity hotspot that encompasses the study sites in the 1990s, and predicted that this would triple to a mean of 14 kg N/ha/yr by 2050 (Phoenix et al., 2006). These rates of N deposition are comparable with rates that have caused species loss elsewhere (e.g., 5–25 kg/ha/yr

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in European grasslands (Bobbink et al., 2010)). Nitrogen availability to plants may increase with global warming in mountain grasslands that have high total soil N but low temperature-dependent N mineralization rates, including Drakensberg Foothill Moist Grasslands (Carbutt et al., 2013). Increased N supply commonly reduces diversity in N-limited grasslands (Clark and Tilman, 2008; Bobbink et al., 2010), by mechanisms including increased productivity and reduced light availability (Hautier et al., 2009). Increased N supply rates can also alter functional and species composition by increasing the abundance of grasses at the expense of forbs (Tilman, 1982; Stevens et al., 2006), reducing legumes' competitive advantage from fixing N (Tilman, 1982; Suding et al., 2005), and favoring species that compete better for light over those that compete better for N (Tilman, 1988; Gough et al., 2012). Increasing N supply may also affect biodiversity by acidifying soil and altering the availability of limiting or toxic cations (Clark et al., 2007; Stevens et al., 2010).

It is increasingly recognized that nutrients other than N also commonly limit productivity and influence diversity and composition in grasslands (Tilman, 1982; Tilman et al., 1994; Elser et al., 2007; Harpole et al., 2011; Fay et al., 2015). Phosphorus (P), potassium (K) and micronutrients are especially likely to be limiting on land surfaces that have been highly weathered through millions of years of exposure without major erosion or glaciation, such as parts of Australia, South America and the Cape of South Africa (Chadwick et al., 1999; Hopper, 2009). Also ancient but less well known are the quartzite plateaus underlying KwaZulu-Natal Sandstone Sourveld, which are geologically allied with the sandstones of the Cape (King, 1982). The igneous dolerite outcrops on which Drakensberg Foothill Moist Grassland occurs are more nutrient-rich than sandstone but, like quartzite, are resistant to erosion and highly weathered. If non-N nutrients limit productivity then increases in their supply rates due to agricultural or other impacts could alter grassland vegetation. Therefore, we ask whether and which nutrients limit productivity in these grasslands, and how they influence diversity and composition.

Another potential impact on these grasslands is changing abundance of large herbivores. Herbivores can influence plant diversity and composition by changing resource availability, as well as dispersing seeds, creating germination microsites, selectively consuming more palatable species, and favoring species more tolerant of frequent defoliation (Olff and Ritchie, 1998; Knops et al., 2000; Hempson et al., 2015). Whereas, on agricultural land, cattle are typically stocked at rates high enough to strongly reduce standing biomass, in many grassland fragments large herbivores have become uncommon due to fragmentation and hunting of wild animals (O'Connor, 2005). If herbivores maintain plant diversity then further loss of herbivores may reduce plant diversity. On the other hand, further loss of large herbivores could have little impact because grazer abundance in these grasslands has already been strongly reduced for over a century, perhaps to levels too low to be influential. Moreover, herbivory may not have been highly influential even pre-historically, given the low productivity of these grasslands (Proulx and Mazumder, 1998; Bakker et al., 2006), though this is unclear given that grazing has been found to be at least locally influential in a wide range of conditions (Hempson et al., 2015). Fire has also been important in this landscape over evolutionary timescales, indicated by many species requiring smoke to germinate or flower (Bond and Parr, 2010). Fire is widely used to manage grasslands – the sites we study are burned annually – and may serve some of the roles of lost grazers (Bond and Keeley, 2005). On balance, it seems unlikely that excluding already-sparse large herbivores from these fragmented, nutrient-poor, frequently-burned grasslands will strongly influence plant diversity and composition, but it remains an open question.

We investigated how nutrients and herbivory influence grassland productivity, diversity, and composition by experimentally manipulating nutrient supply rates and herbivore abundance at two sites, in the context of the globally distributed Nutrient Network experiment (Borer et al., 2014a). Some data from these experiments have been

used in global treatments (Borer et al., 2014b; Fay et al., 2015; Harpole et al., 2016); here, we report results in more detail.

Specifically, we asked (1) how adding N, P + Ca, and other nutrients influences (a) aboveground net primary productivity, (b) plant diversity, and (c) functional group and species composition of these grasslands. We investigated functional group and species composition responses both to understand which vegetation components drive overall productivity responses and to discover how the relative abundances of functional groups and species depend on nutrient supply. We also asked (2) how excluding large herbivores using fences influenced vegetation.

2. Methods

2.1. Study sites

We established comparable experiments at two sites in KwaZulu-Natal province, South Africa. The Gilboa experiment is on the summit plateau of a dolerite mountain at an elevation of 1748 m, on a gently (~2°) west-facing slope (29.28424S, 30.29174E; Fig. 1A). The soil is a sandy loam, with mean measured particle percentages of 60–31–9 (sand–silt–clay) and mean exposed rock cover of 6.3% (sampling methods below). This site is similar in elevation and biota to the Drakensberg mountain range 100 km to the west. This site is classified as Drakensberg Foothill Moist Grassland (Mucina and Rutherford, 2006), but also has species characteristic of Moist Midlands Mistbelt grasslands that surround it on lower slopes (Appendix A). It is in a private nature reserve. The Summerveld experiment is on a sandstone (quartzite) plateau at an elevation of 679 m, on a gently (~4°) south-facing slope (29.81161S, 30.71573E; Fig. 1B). The soil ranges from sandy loam to loam, with mean measured particle percentages of 57–23–20 (sand–silt–clay) and mean exposed rock cover of 0.1%. This site is in the KwaZulu-Natal Sandstone Sourveld vegetation type (Mucina and Rutherford, 2006), on private land in a powerline corridor.

The two sites had similar precipitation regimes, with modeled mean annual totals of 926 mm (Gilboa) and 939 mm (Summerveld), both strongly focused in summer (Table 1). At Gilboa, modeled temperatures were 0 °C to 22 °C (mean minimum in the coolest month to mean maximum in the warmest month), whereas at Summerveld temperatures were 7 °C to 26 °C (Table 1). Both sites were burned annually in winter (June–August). Burning every 1–3 years is common in these grasslands, especially where grazing is light; less frequent burning allows woody plants to encroach (Titshall et al., 2000). Both sites were lightly grazed by antelope, hares and other small mammals. Domestic livestock were absent but had been present in the past, at low abundance at Gilboa and moderate abundance (and at least a decade earlier) at Summerveld. Neither site had been plowed. Both sites were strongly dominated by indigenous perennial plants (Seabloom et al., 2013). Gilboa had two annual species, both rare (maximum cover 1%, in only a handful of plots); Summerveld had no annuals.

2.2. Experimental design

Experimental design and sampling followed the Nutrient Network protocol (Borer et al., 2014a), which we summarize with some site-specific details. At each site 30 plots, each 2 × 2 m, were established in September 2009 in a 6 × 5 grid with 1 m buffers between plots. Each grid was divided into three blocks of 10 plots. Within each block, eight randomly selected plots were randomly allocated the factorial combinations of N, P + Ca, and K + micronutrients. At Gilboa, there was also a partially overlapping fence experiment. To generate the four factorial combinations of fencing and adding all nutrients, the remaining two plots per block were randomly allocated to fenced but unfertilized, and fenced and fertilized treatments; the two unfenced treatments were shared with the nutrient experiment. At Summerveld, there were no fences; one of the remaining two plots in each block was

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