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Grass competition and the savanna-grassland 'treeline': A question of root gaps?

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ABSTRACT

Upland grasslands in South Africa occur in climates warm enough and wet enough for forests yet, unlike savannas, trees are absent. We hypothesize that the lack of trees in grasslands is due to the scarcity of gaps suitable for tree seedling establishment in the grass root layer. We assessed which demographic bottlenecks, seedling recruitment or sapling release, were limiting large tree populations of Acacia species in 229 sites on a gradient from lowland savannas to upland grasslands in eastern South Africa. We explored the frequency of 'root gaps' by quantifying grass root biomass in grids of 18 points at six sites distributed from lowland savannas to upland grasslands. Across the altitudinal gradient, sapling release was the most common bottleneck at low elevation sites switching to seedling recruitment in upland savannas and adjacent grasslands. Root studies showed grass root biomass at upland sites to be double than that of lowland sites. When grass root biomass of all 108 sample points was ranked, lowland savanna sites had the most frequent 'gaps' defined as the lowest percentiles of values (5, 15, 25, 35, 45). The number of 'gaps' decreased along the elevation gradient with none in the grassland site. Dense grass roots may prevent seedling establishment and 'root gaps' may be safe sites with reduced competition where seedlings can establish. We suggest that a lack of root gaps could explain the treeless nature of many upland grasslands.

1. Introduction

Treeless grasslands are common in upland regions around the world, often forming mosaics with closed forests (Fig. 1). Examples include extensive grasslands such as the campos in South America (Behling et al., 2007; Overbeck et al., 2007), tall grass prairies in North America (Knapp et al., 1999), Western Ghats in India, and upland grasslands throughout Africa (Acocks, 1953; White, 1983) and Madagascar (Bond et al., 2008); as well as balds, small grass patches in forested areas, in Poland, south eastern Australia (Webb, 1964; Fensham and Fairfax, 1996, 2006; Fairfax et al., 2009) and Oregon and the Appalachian mountains in the USA (Mark, 1958; Lindsay and Bratton, 1979; Weigl and Knowles, 2014). The climate of these grasslands has the potential to support forests (Bond et al., 2003, 2005, 2008; Bond, 2008; Bond and Parr, 2010) and indeed, forest patches are common (Fig. 1). While long thought to be of anthropogenic origin, most of these grasslands are now known to be ancient and much older than human deforestation activities (for reviews see, e.g., Bond and Parr, 2010; Parr et al., 2014; Weigl and Knowles, 2014). Given that many of these grasslands are similar to savannas as they are dominated by C_4 grasses and burn regularly (Acocks, 1953), it is puzzling that fire-tolerant savanna trees, such as *Acacia karroo* (Schutz et al., 2009), do not occur within them.

Savanna tree-grass coexistence has long been of interest to ecologists (Walter, 1971; Walker and Noy-Meir, 1982; Sarmiento, 1984; Scholes and Archer, 1997; Higgins et al., 2000; Jeltsch et al., 2000; Sankaran et al., 2004, 2005, 2008; Scheiter and Higgins, 2009), with explanations including demographic bottleneck (Higgins et al., 2000) and root niche separation hypotheses (Walter, 1971). Savanna tree populations experience two major demographic bottlenecks: the establishment of seedlings in the grass layer, the recruitment bottleneck, and the emergence of saplings above the grass layer into adult size classes inhibited by fire and browsing, the sapling release bottleneck (Higgins et al., 2000). Walter (1971) hypothesized that trees and grasses can coexist as their roots occupy different niches in the soil profile. It has since been shown that both adult trees (Riginos, 2009; February and Higgins, 2010) and tree seedlings (Knoop and Walker, 1985; Cramer et al., 2007, 2009; Riginos, 2009; Tedder et al., 2012, 2014) are forced to compete directly with grasses where they occupy the same soil layers below-ground.

In grassy biomes, below-ground competition with grass is intense and typically suppresses tree seedlings far more than above-ground competition (Wilson, 1988, 1993; McPherson, 1993; Partel and Wilson, 2002; Cramer et al., 2007; Bloor et al., 2008). This leads to the suggestion that, just as tree seedlings in a forest may require a light gap, seedlings in grasslands may require a volume of soil where grass roots are sparse, a 'root gap', to establish successfully. This idea was tested experimentally

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Fig. 1. Grassland–forest mosaics from around the world.

in North American savannas by creating root exclusion sites of varying depth or diameter and observing *Prosopis* seedling establishment (Jurena and Archer, 2003). Available soil volume, especially in the vertical dimension, was a major factor influencing growth and survival of the tree seedlings. We suggest that the absence of trees in upland grasslands could be explained by the lack of gaps in the grass root layer, which are required for seedling establishment. To test this we first explored if savanna tree populations experience seedling recruitment and/or sapling release bottlenecks along an altitudinal gradient from lowland savannas into upland grasslands. We then measured the amount and variation in grass root biomass along the same gradient and assessed the availability of gaps in the grass root layer for seedling establishment. We predict that root gaps will decrease in frequency from arid to mesic sites (~600 to 1050 mm per annum) with the fewest gaps in dense grass swards in montane grasslands. Seedling establishment bottlenecks should be prevalent not only at arid sites where chronic drought limits recruitment, but also in highly productive mesic sites where high and continuous grass root biomass, with few gaps, creates intense competition that prevents tree seedling establishment. At the arid end, recruitment will vary depending on inter-annual cycles of wet and dry periods. In mesic montane grasslands, recruitment should be consistently low.

2. Methods

To quantify which demographic stage was limiting adult tree populations, we censused *Acacia* tree populations at 29 sites along an altitudinal gradient from lowland savannas into upland grasslands in northern KwaZulu-Natal, South Africa, between Nov 2009 and Mar 2010 (Fig. 2). Mean annual precipitation values were extracted for each site from Schulze (1997) and covered a range from ~600 to 1050 mm per annum. Sites also varied in tree density from savanna through mixed savanna grassland to pure grassland. We assumed that dispersal was not limiting to our study sites. Savanna trees were present at each savanna site and within a kilometer of the grassland sites. *Acacia sieberiana* (= *Vachellia sieberiana*) is the most common tree in upland savannas and has indehiscent pods dispersed by bovids (including cattle). Previous studies have shown that mammal-dispersed acacias are well dispersed appearing, for example, in fire suppression plots in grasslands hundreds of meters from the nearest adults (Titshall et al., 2000; O'Connor et al., 2010). All sites were composed of C_4 grasses, including the high elevation grassland sites and were dominated by one or more of the following grass species: *Themeda triandra*, *Hyparrhenia filipendula* and *Sporobolus pyramidalis* (nomenclature follows http://posa.sanbi.org/).

Along the two independent 125 × 2 m transects per site all juvenile (<1.5 m) and adult (>1.5 m) *Acacia* trees were counted. These data were combined with similar population data for *Acacia* species in two hundred 40 × 10 m plots in savannas in Hluhluwe-iMfolozi Park (HiP) that varied in elevation, fire frequency and herbivore intensity, measured as number of dung piles (Staver et al., 2009). Mean annual precipitation was estimated for sites within HiP using the formula: Rainfall $= 1.164 * (\text{altitude}) + 462$ (Balfour and Howison, 2001).

To help determine if seedling recruitment or sapling release was the primary constraint on tree populations, a demographic bottleneck index, n/K, was calculated for each site. n is the number of juvenile plants per hectare and K is the carrying capacity (maximum potential density) of adult trees per hectare. The potential number of adult trees at a site is estimated as:

$$K\left(\text{trees} \cdot \text{ha}^{-1}\right) = 10\ 000/a$$

where a is the mean canopy area (m^2) of large trees. Canopy radius varied among species ranging from 1.9 m (*Acacia karroo*) to 8.5 m (*A. sieberiana*). The average canopy diameter at each site was used in calculating canopy area. Sites without measured canopy diameters (such as grasslands) were assigned the value $K = 250$ trees$\cdot$ha^{-1}. This was the K obtained for the overall average canopy diameters across all the sites, and was for trees with a mean canopy diameter of approximately 7 m. Where the demographic bottleneck index (n/K) is greater than one, there are sufficient