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Comparing the differential effects of canopy shading by *Dichrostachys cinerea* and *Terminalia sericea* on grass biomass

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ABSTRACT

Woody encroachment is occurring globally; however, the tropical grassy ecosystems, which dominate Africa, are particularly vulnerable to this phenomenon. Encroached ecosystems experience significant changes in biodiversity, ecosystem functioning and service provisioning. One such vital ecosystem service is the provisioning of grazing. As encroachment can reduce grass production through the shading out of shade-intolerant grasses, there is a need to better predict these impacts particularly, since multiple woody species act as encroachers and little is known on their differential effects. Encroacher species may affect grass production differently, depending on the architecture of their canopies. This study therefore aimed to compare the effects of two structurally different encroaching species (a shrub vs a tree) (*Dichrostachys cinerea* and *Terminalia sericea*) on grass biomass. We tested the effects of canopy architectural traits of these two species on grass biomass using field sampling in a savanna conservation area in southern Zimbabwe. Canopy cover was a strong predictor of grass biomass, where increasing canopy cover significantly reduced grass biomass under both species. However, the architecture of the shrub *D.cinerea*, typified by a large crown diameter and crown height and a small crown base-height, created more shade, which had a significantly greater negative effect on grass biomass than the canopies of *T.sericea* at the same stem density. Architectural traits are therefore considered useful in predicting impacts of encroaching species on grass biomass. The findings show that encroachment of *D.cinerea* holds the potential to cause a regime shift from an open system to a closed system as a result of its extensive canopy cover.

1. Introduction

Woody encroachment can be defined as an increase in the cover of woody species, and has been reported globally (D'Odorico etal., 2012; Myers-Smith et al., 2015; Naito and Cairns, 2011; O'Connor etal., 2014; Stevens etal., 2017). This phenomenon is common in C4-grassy ecosystems, which dominate in the warmer tropical and subtropical regions of the world (Edwards and Still, 2008; Lehmann & Parr, 2016; Stevens etal., 2017). While there is variation in the magnitude of encroachment of grassy ecosystems between continents, grassy African ecosystems appear to be highly susceptible (Stevens etal., 2017). One well-established impact of encroachment in African grassy ecosystem function is a decrease in shade-intolerant C4 grass biomass with increases in woody cover (e.g.,Angassa, 2005; Ratajczak etal., 2012; Scholes, 2003; Zarovali etal., 2007). C_4 grasses evolved under low atmospheric CO_2 levels (Christin etal., 2008) and frequent fires (Hoffmann, 1999), and are therefore restricted to high light intensity, open ecosystems and are shade-intolerant. This makes C4 grasses highly susceptible to competitive exclusion by woody cover increase (Sage and Kubien, 2003). As woody cover increases, canopy cover reduces photosynthetically-active radiation reaching the grass layer (Eldridge etal., 2011; Moleele etal., 2002; Mudzengi etal., 2014; Price and Morgan, 2008; Richter etal., 2001), until a threshold of canopy cover is reached where grass growth is limited by the extent of shading (Belay and Moe, 2015; Charles-Dominique etal., 2018;Sage and Kubien, 2003). A reduction in grass biomass lowers the grazing capacity of the land, which is considered the most important factor restricting sustainable livestock production in savanna systems (de Klerk, 2004).

The impact of encroachment on ecosystems is determined by not only tree density but also by the identity of encroaching species, as different functional traits associated with different tree species may result in differential ecosystem impacts (Osborne etal., 2018). Canopy architecture traits like shape, height and leaf orientation have been shown to influence canopy cover. Some studies indicate that shrubby plants with a small crown base-height (CBH) (Blaser etal., 2013) and a large crown diameter (CD) are more likely to reduce grass biomass than single stemmed trees of similar heights as a lower CBH (i.e.,the height from ground level to the bottom of the canopy) increases the length of time that the grass layer is shaded, whilst the size of the shaded area is influenced by CD (Belay and Moe, 2015). Alternatively, other studies suggest that taller trees have a greater shading effect on grass through increased

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leaf biomass (Eldridge etal., 2011). Either way, it is likely that traits of individual plants are better predictors of the impacts of encroachment on the growth of understory vegetation than plant density alone (Belay and Moe, 2015; Belay etal., 2013; McIntyre etal., 2006).

We therefore investigated how the canopy architecture traits of two encroaching species, each with different growth forms, impacted grass production across an encroachment gradient in a semi-arid savanna in Zimbabwe. We investigated how the relationship between grass biomass and canopy cover, of the shrub *Dichrostachys cinerea* and tall tree *Terminalia sericea*, changed across a gradient of canopy cover, whilst controlling for tree density. Grass biomass was analysed across a gradient of canopy cover to detect the threshold of canopy cover at which grass biomass becomes limited. Differences in canopy traits such as canopy height and diameter and CBH were used as a potential explanation for the differing impacts on grass biomass between the two species.

2. Methods and materials

2.1. Study site

The study site is located in a savanna system, in a private nature reserve known as Quiet Water's (20°12′23.73″S 28°58′22.89″E), in southern Zimbabwe. The site is ~1000 m above sea level and receives a mean annual precipitation (MAP) of ~625 mm. Rainfall is concentrated between October and March. Mean monthly summer temperatures (October–March) range between 14.8 and 29.1 °C, whilst monthly winter temperatures (April–September) range between 7.2 and 13.0 °C. Infrequent frosts (1–2 per season) are experienced during the dry and cool period. The study took place in a savannah system, on sandy, nutrient-poor granitic soils which is dominated by the trees *Pterocarpus rotundifolius*, *P.angolensis, Burkea Africana, Dichrostachys cinerea* and *Terminalia sericea*. The most dominant grass species are *Cynodon dactylon* (L.) Pers., *Eragrostis viscosa* (Retz.) Trin., *Heteropogon contortus* (L.) Roem & Schult., *Hyperthelia dissoluta* (Nees ex Steud.) Clayton, *Melinis repens* (Wild.) Zizka subsp. Repens and *Themeda triandra* Forssk.

The nature reserve was officially opened in 1985, prior to which it was managed as a cattle ranch. Encroachment by some woody plants has occurred since the reserve was established. Three plant species have spread extensively throughout the reserve over the last 30 years, one of them being the highly invasive scrambling shrub, *Lantana camara*. Two native encroachers, *Dichrostachys cinerea* and *Terminalia sericea*(Fig. 1) have proliferated within the reserve, with *T.sericea* preferring the sandveld areas and *D.cinerea* showing no preference for a specific soil type (*pers.comm*. Gordon MacDonald).

2.2. Encroaching species descriptions

Dichrostachys cinerea (L.) Wight & Arn. is a member of the Fabaceae family. It is a highly variable deciduous, small tree or large shrub (≤8 m tall) that is distributed in tropical and subtropical Africa, America, Australia, Arabia and tropical Asia(Coates Palgrave, 2012). It is a woody, thorny (lateral shoots up to 8 cm long) plant with bipinnate leaves (4–8 cm long with 2–11 pairs of pinnae, each with 12–22 pairs of leaflets) (Coates Palgrave, 2012). There are two subspecies of *D. cinerea* within this region; *Dichrostachys cinerea subsp. africana* was the subject of this study.

Dichrostachys cinerea is a renowned encroacher species globally, especially within southern Africa(Munyati etal., 2013; Moleele etal., 2002). It can form dense thickets that span as much as a few hundred meters wide (Mudzengi etal., 2014). The canopy cover of encroachers such as *D.cinerea* can reduce the abundance of shade-intolerant species through competition for light, nutrients and space (Mudzengi etal., 2014; Munyati etal., 2013). It can do this through prolific root suckering that provides persistence and resilience to disturbances such as fire (Wakeling and Bond, 2007). *Dichrostachys cinerea* is a nitrogen-fixing plant, which occurs in a large range of altitudes and has been found to rapidly spread into disturbed land through its high seed germination rates and rapid propagation (Mudzengi etal., 2014).

Terminalia sericea Burch. ex DC., is a broad-leaved, deciduous savanna plant occurring across central and southern Africa. Found within the Combretaceae family, *T.sericea* either grows as a single-stemmed tree (8 m) or as a multiple-stemmed shrub (4–6 m) (Moyo etal., 2015). *Terminalia sericea* grows slowly, has a layered canopy (flat or rounded) and horizontal branches (Coates Palgrave, 2012), and exhibits narrowly obovate-elliptic leaves (5.5–12 cm long, 1.5–4.5 cm wide), spirally arranged and clustered at the tips of branchlets. *Terminalia sericea* is adapted to drought and some frost and forms dense thickets when burnt or cut (Moyo etal., 2015). Like *Dichrostachys cinerea*, it has become

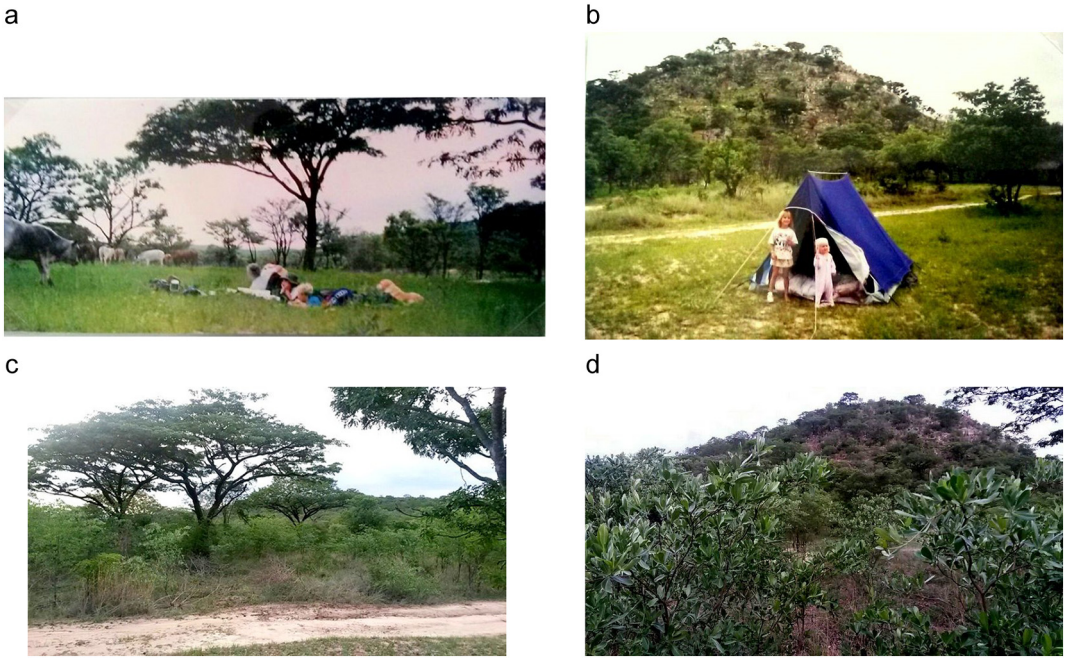

Fig. 1. A *Terminalia sericea* encroached area in Quiet Water's. (a) and (b) photographs were taken in 1999. (c) and (d) photographs were taken of the same area in 2016 (Photographs: B Randle).