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Patterns of granivory in *Acacia cyclops* stands under biological control at Langebaanweg, South Africa

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ABSTRACT

Low seed abundance associated with effect of biological control agents in an invasive shrub *Acacia cyclops* may limit its seed banks and further spread of the remaining seed crop in the South-western Cape, South Africa. However, there is a limited knowledge on how a reduced seed abundance, and vegetation cover which is positively correlated to seed bank size, affects patterns of granivory in *A. cyclops* stands. To fill this knowledge gap, granivory rates were measured using seed exclosure cages located both in closed and open *A. cyclops* tree canopy covers at Langebaanweg. Fresh seeds of *A. cyclops* were presented in tens per cage, and monitored in four-hour intervals of the day during the seeding season (December–July, 2013). Seed removal by rodents (74%) was not affected by vegetation cover suggesting an increased demand of the scarce seeds of A. cyclops. Conversely, seed removal by invertebrates (16%) was lowest among treatments, and was restricted in low tree canopy cover possibly due to competition for seeds under shady canopy. About 10% of the remaining seeds were consumed by vertebrates during the afternoon times associated with limited dispersal chances. In combination, biological control agents and rodents' seed predation may effectively reduce seed banks of *A. cyclops* and invasion of this species in South Africa.

Introduction

Invasive trees and shrubs represent a major threat to natural resources in South Africa (Richardson & van Wilgen, 2004; Gaertner et al., 2009), and their currently increasing numbers (Richardson & Rejmánek, 2011), suggest that their threat might intensify in future. Of the approximately 70 *Acacia* tree species that have been introduced into South Africa, predominantly during the 19th Century, at least 13 are currently recognised as invasive (Henderson, 2007; Richardson et al., 2011). Of these, *Acacia cyclops* commonly known as Rooikrans, was introduced into South Africa in 1835, primarily for stabilisation of sand dunes in the south-western Cape region (Shaughnessy, 1980). It has since become naturalised and has invaded coastal regions across the southern Cape (Henderson, 2007). The proliferation of *A. cyclops* in South Africa is ascribed to it having been widely propagated as a source of fuel wood for domestic

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and small-scale commercial purposes (Richardson et al., 2011), and to its prolific seed production (Milton and Hall, 1981; Impson et al., 2011) which increases chances of dispersal by vertebrates. Each seed has a nutritional and orange-reddish aril which attracts vertebrates, especially birds that consume and pass the indigestible seeds and thereby enhance the population dynamics of the plant (Glyphis et al., 1981; Underhill and Hofmeyr, 2007; Mokotjomela and Hoffmann, 2013). Indeed, recent study has shown that several bird species including selected ubiquitous dove species improve germination rates of ingested seeds (Mokotjomela et al., 2015). The seeds are also buried underground in accumulations by ants (Holmes, 1990) and possibly seed-hoarding rodents (Midgley and Anderson, 2005), and thus reducing impacts of predation and incineration of seeds during periodic fires. Holmes (1990) reported that *A. cyclops* seed banks tend to increase with vegetation cover and thus suggesting dense foliage and tree canopy limit predators' access for seeds.

Biological control agent species including *Melanterius servulus* (a seed-feeding weevil) and *Dasineura dielsi* (a flower-galling midge) have been released on *A. cyclops* in South Africa in 1991 and 2002, respectively. Both agents were imported from Australia (the native range of *A. cyclops*), and they are prolific, causing high levels of seed damage in *A. cyclops* which in turn is expected to limit the invasiveness of the species (Impson et al., 2011; Moran et al., 2013). For instance, *M. servulus* inflicts seed damaged of up to 97.5%, with an overall average reduction of seed production of 56% between 1998 and 2009 in the Southwestern Cape (Impson et al., 2011). An earlier study at Koeberg Nature Reserve during the 2012 seeding season showed that invertebrate (e.g. ants) removal of seeds was much lower under dense stands of *A. cyclops* (Mokotjomela and Hoffmann, 2013) than in the 1980s (Holmes, 1990). However, it is not known how seed reduction imparted by the biological control agents has affected patterns of granivory by other organisms that potentially influence recruitment processes in *A. cyclops*.

Foraging patterns in vertebrates, especially rodents and other organisms, are influenced by degree of food availability (Bartness and Albers, 2000) and environmental temperatures (Bartness and Albers, 2000; Feldhamer, 2007; Orrock and Danielson, 2009). Consistently, the frugivorous birds in the Mediterranean climate region in South Africa foraged on exotic species with abundant fruit resources (Mokotjomela et al., 2013). Also, foraging patterns of the murid rodent, Ice rat (*Otomys sloggetti*) in the Drakensberg Alps was restricted to warm parts of the day (Hinze, 2005) while the desert rodents in southern Africa choose to forage during cooler times to avoid thermal stress (Feldhamer, 2007). Because vegetation cover may change the habitat quality for seed predators by modifying, for example, the microclimate (e.g. light, temperature) and soil characteristics (e.g. plant litter), and the risk of predation (Manson and Stiles, 1998), granivory rates tend to be higher under cover than open areas (Meiss et al., 2010). In addition, seed removal and dispersal by ants tend to be more common in hot and semi-arid areas in South Africa than in mesic areas (Bond and Slingsby, 1983). Feeding times of the day on seeds (i.e. morning, midday and afternoons) have important influence on potential dispersal of the ingested seeds in birds (Bibby et al., 2000; Kays et al., 2011), with the seeds of the Panamanian nutmeg tree (*Virola nobilis*), for example, consumed in the mornings by birds standing a greater chance of dispersal than those consumed later in the day (Kays et al., 2011). Furthermore, feeding peak time in the afternoon have disadvantage since the ingested seeds are then deposited at the roosting sites where seed mortalities are high due to predators and competition between seedlings (Westcott et al., 2005; Kays et al., 2011; Mokotjomela et al., 2013).

Despite the knowledge that birds are important seed dispersers of the highly invasive *A. cyclops* in South Africa (Glyphis et al., 1981; Underhill and Hofmeyr, 2007; Mokotjomela and Hoffmann, 2013; Mokotjomela et al., 2015), there is a limited knowledge on the temporal patterns of granivory in *A. cyclops* stands that have seen seed reduction due to biological control agents, and how habitat characteristics such as vegetation cover may influence the patterns of granivory. Granivory of seeds of *A. cyclops* has important implications on seed banks dynamics which reportedly account for its invasion success, since a larger proportion of the seed crop falls on the ground when pods dry up (Holmes, 1990). The major aim of the present study was to determine how granivory rates in *A. cyclops* are affected by vegetation cover during different phases of seeding period associated with variable abundance of seeds, and different times of day, which have implications for seed dispersal probabilities. This study tested predictions that rodents' granivory might be higher in seed cages located under dense tree canopy cover, where predation risk is relatively lower than in those seed cages located in open and low vegetation cove, and that invertebrates' seed removal might predominate due to semi-arid to arid conditions of the study site.

Material and methods

Study site

The study area of Langebaanweg (32°57′52.52″ S, 18°7′4.51″ E) is located in the Cape Floristic Region (CFR) of south-west South Africa, recognised as one of the most biologically diverse regions on earth (Goldblatt and Manning, 2002), and thus there is a conservation concern as this region is threatened by invasive trees and shrubs. The predominant vegetation in CFR is a shrubland known as fynbos, which comes from an Afrikaans word meaning "fine bush". Fynbos primarily comprises four growth forms, namely proteoid, ericoid, restoid and geophyte (Cowling et al., 1996). Langebaanweg is located at the component of the fynbos dominated by dune thickets, although this has been heavily transformed by anthropogenic activities. The climate is Mediterranean with 75% of annual rain falling between April and September, although there is a sharp drop in the average rainfall towards the northwest coast, and thus Langebaanweg is classified as semi-arid (see daily temperature and rainfall variation; Fig. 1).

At Langebaanweg, plants grow in the old phosphate mine dumps where they were originally planted as part of rehabilitation programme for the disturbed landscape. The mean height of adult trees was 5.9 ± 0.3 m ($n = 28$) with the canopy cover of approximately 80% in the forest and less than 50% outside the forest. The tree canopy cover was estimated using a modified Braun-Blanquet scale taking into consideration tree