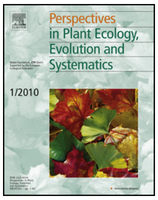
Perspectives in Plant Ecology, Evolution and Systematics 17 (2015) 405–411

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees



Research article

How does the seed fate of *Crotalaria podocarpa* DC, a highly competitive herbaceous legume in arid rangelands, contribute to its establishment probability?

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ARTICLE INFO

Article history:
Received 11 December 2014
Received in revised form 23 July 2015
Accepted 23 July 2015
Available online 29 July 2015

Keywords:
Encroachment
Invasion success
Pre-dispersal seed predation
Post-dispersal seed predation
Seed dispersal
Tree-grass coexistence

ABSTRACT

Plant recruitment can be constrained by processes shaping its seed fate, such as pre- and post-dispersal seed predation, while facilitated by higher seed production and more effective dispersal. These activities are controlled by specific predator and disperser guilds that respond to different microsite conditions such as vegetation density with varying predation and removal rates. In Namibia's arid rangelands, the native, annual herbaceous legume *Crotalaria podocarpa* has considerably increased after several years of elevated rainfall, thereby reducing density and vitality of economically important fodder grasses. To investigate whether this proliferation entails the risk of a permanent establishment, we studied pre- and post-dispersal seed predation, as well as primary and secondary seed dispersal of the legume and quantified the impact of different predator groups on post-dispersal seed removal. We experimentally excluded (i) neither vertebrates nor invertebrates, (ii) birds, (iii) vertebrates (birds and rodents), and (iv) vertebrates and large invertebrates on plots with different *C. podocarpa* density (0–35% cover). Seed predation was mainly caused by invertebrates, with 30% pre-dispersal seed predation in pods and up to 90% post-dispersal seed removal for free seeds on the ground which is the most persistent seed stage. *C. podocarpa* density did not affect post-dispersal seed removal or secondary seed dispersal. As main dispersal mode for the study species explosive dehiscence was identified, with seeds reaching dispersal distances of up to 4 m, while wind or rolling dispersal played a minor role. Subsequent secondary dispersal by animals accounted for dispersal distances up to 19 m. Our findings highlight the combined effects of pre- and post-dispersal seed predation to determine the total seed fate. With a contribution of about 370 seeds m^{-2} to the species persistent soil seed bank, seed numbers seems to be more important for *C. podocarpas* vagility than the species dispersal ability. Supplemented by seedling fate and adult mortality, this data can contribute to reliably predict the risk of a further spread of the species.

1. Introduction

Plant recruitment is a multiple-stage process which is determined by properties of the adult plant such as growth and seed production, but also by processes shaping its seed fate, such as seed dispersal characteristics, persistence of seeds in the soil seed bank, seed germination and growth rates (Nathan and Muller-Landau, 2000). The seed fate is thereby characterized by different pathways, where seeds are in different states, which either facilitate or reduce successful germination and seedling establishment (Forget et al., 2005). One state that can significantly reduce recruitment in many plant species is seed predation (Crawley, 1989; Kolb et al., 2007a; Kollmann, 1995). It can either affect seeds still on their mother plant ('pre-dispersal predation') or in fallen fruits or seeds on the ground or in the soil ('post-dispersal predation'; van Klinken and White, 2014). However, seed predation studies often focus on either pre- or post-dispersal predation (e.g. Kolb et al., 2007a; Mokotjomela and Hoffmann, 2013; but see van Klinken and White, 2014). In contrast, seed dispersal potentially facilitates plant recruitment, e.g. by increasing the probability of seeds reaching favourable microsites for germination (Cousens et al., 2008). Seeds can directly disperse from the mother plant to the ground ('primary dispersal') or can experience further movement after primary dispersal ('secondary dispersal'; Forget et al., 2005). To estimate total seed fate, seed predation as well as seed dispersal across all seed stages have to be taken into account (Vander Wall et al., 2005).

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http://dx.doi.org/10.1016/j.ppees.2015.07.002
1433-8319/

In arid ecosystems mainly specialized invertebrates, such as seed beetles (Coleoptera: Bruchidae), weevils (Coleoptera: Curculionidae), parasitic wasps (Hymenoptera: Pteromalidae) and their larvae are common pre-dispersal seed predators (Donnelly and Hoffmann, 2004; Fox et al., 2012). In contrast post-dispersal seed loss is mainly affected by larger, more generalist species, such as rodents, ground-foraging birds but also by invertebrates, such as weevils and ants (Hulme and Kollmann, 2005; Kuechly et al., 2011; Mokotjomela and Hoffmann, 2013). Besides their role as predator, these animals can also act as vectors for seed dispersal by ingestion and subsequent defaecation, by deliberate removal for later recovery or by epizoochorous transport (Cousens et al., 2008; Manzano et al., 2010; Stamp and Lucas, 1990), often increasing seed availability and recruitment success at the landscape level (Münzbergová and Herben, 2005; Vander Wall et al., 2005). Seed predation and removal are often influenced by biotic conditions, e.g. increasing predation rates with increasing vegetation density and height (Hulme, 1997; Walters et al., 2005; but see Kolb et al., 2007b), while seed dispersal patterns in arid regions are mainly shaped by abiotic conditions such as wind, water and sediment dynamics (Aguiar and Sala, 1999).

Seedling mortality and establishment have been discussed as important components within demographic bottleneck models with respect to plant encroachment (Joubert et al., 2013; O'Connor et al., 2014), the pronounced increase of indigenous (normally woody) plants in grasslands (Van Auken, 2000). This process is often associated with the decrease of economically important fodder grasses (D'Odorico et al., 2012; Eldridge et al., 2011; Wiegand et al., 2006), resulting in a lower productivity and reduced carrying capacity in terms of livestock production (de Klerk, 2004). Moreover, encroachment affects biodiversity, such as bird and plant species richness (Báez and Collins, 2008; Sirami et al., 2009) or leads to community shifts, like changes in arthropod assemblage composition (Blaum et al., 2009). However, encroachment is not restricted to woody species and similar processes have been described for annual or perennial forbs and grasses (DiTomaso, 2000; Grice, 2004). Just like woody encroachers, these forbs or grasses increase in population density, and, while themselves being unpalatable, reduce the pastures forage quality (DiTomaso, 2000). Similarly, after several years of increased rainfall, the native, annual herbaceous legume *Crotalaria podocarpa* DC (nomenclature according to Polhill, 1968) has considerably spread in Namibia's escarpment region (T.C. Wagner and F. van Biljon, pers. observ.), thereby reducing biomass production and vitality of perennial grasses and permanently damaging grass tussocks (T.C. Wagner and C. Fischer, unpubl. results). However, there is little knowledge about the invasion of annual plants in African savannahs and grasslands (Foxcroft et al., 2010), and the mechanisms and processes, which determine recruitment of herbaceous encroachers, such as *C. podocarpa*.

To elucidate theses mechanisms, to assess potential consequences for livestock production and to identify possible implications for long-term management of shifting legume-grass coexistence (Sheley et al., 2010), we studied the seed fate of *C. podocarpa* and its relevance for recruitment success. We investigated pre- and post-dispersal seed predation measured as removal under different *C. podocarpa* densities, as well as primary and secondary seed dispersal and determined the relative importance of seed predator species by exclusion treatments using cages with different mesh sizes to answer the following questions:

1. To what extent does pre- and post-dispersal seed predation limit seed availability and therefore establishment probability of *C. podocarpa*?
2. What is the main dispersal mode of *C. podocarpa* and the potential area of *C. podocarpa* recruitment due to seed-dispersion patterns?

2. Material and methods

2.1. Study area

The study was carried out during the rainy season from early March to mid-April 2014 on the farm Rooiklip (S 23°24′23.29″, E 016°03′37.35″). The farm comprises 7000 ha and is situated at 1000 m a.s.l. within the savannah-semi-desert transition zone of Namibia's great escarpment that links the semi-arid Nama-Karoo-Biome of the SW African Highveld with the hyper-arid Namib Desert in the west (de Pauw et al., 1998/99). Experiments were carried out in an area of 300 m × 300 m in the southern part of the farm, which serves as a 5000 ha private game reserve and is inhabited by large mammalian herbivores in low densities. Potential seed predators are invertebrates, such as ants (family Formicidae) and beetles (order Coleoptera), that abundantly occur all over the study area (S. Hane 2014, unpubl. data). Furthermore, rodents, such as *Micaelamys namaquensis*, *Rhabdomys pumilio*, *Petromyscus collinus* and *Aethomys chrysophilus* (Skinner & Smithers 1990) occur in low densities (ca. 1 rodent ha^{-1}; A. Battermann 2014, unpubl. data). The substrate is nutrient-poor calcisol, consisting of the weathering products of the underlying schist, with course gravel, stones and rock, and a high percentage of sand but no organic layer. Rainfall is erratic, often locally limited and seasonal, with a maximum between February and March. The mean annual precipitation between 2001 and 2013 was 192 ± 44 mm (mean ± SE) and 171 ± 42 mm during the rainy season from October to March (measured using a rain gauge at the Rooiklip farmhouse on a daily basis with 0.5 mm accuracy).

The vegetation is arid grassland, normally dominated by tussocks of perennial *Stipagrostis* spp. (nomenclature according to de Winter, 1962) with 1.5–2.0 tussocks m^{-2}. Within this matrix small shrubs, such as *Petalidium* spp., *Cryptolepis* spp. and *Orthanthera albida*, as well as sparse trees, mainly *Acacia reficiens*, *Commiphora glaucescens* or *Boscia foetida*, are loosely interspersed. During the rainy season various annual grasses and herbs occur, among them the native legume *C. podocarpa*.

2.2. Study species

The study was carried out with the legume *C. podocarpa* that is widespread in eastern and southern Africa (Polhill, 1968). It is part of the local grassland community in the study area, where it normally occurs as a pluvio-therophyte in moderate numbers after sufficient rainfall but has exhibited a significant and steady increase and spread since 2009 (T.C. Wagner and F. van Biljon, pers. observ.). This annual herbs appearance is shrub-like; its height, diameter, flowers and seed set vary considerable with water availability (T.C. Wagner and C. Fischer, pers. observ.). Due to its content of pyrrolizidine alkaloids and flavonoid glycosides of the aerial parts (Wanjala and Majinda, 1999) *C. podocarpa* is unpalatable and can even cause livestock poisoning (Botha and Penrith, 2008), while seeds of *C. podocarpa* do contain other alkaloids, which are not further described (Pilbeam et al., 1983) and therefore the impact on seed predators remains unclear.

During our study, fully grown plants ($n = 140$) randomly selected along a 500 m zigzag transect reached a height of 56.5 ± 2.0 cm, covered an average area of 0.19 m^2 (plant diameter 49.8 ± 2.5 cm) and produced 64.0 ± 5.8 pods $plant^{-1}$ (2–288 pods $plant^{-1}$). Average pod weight was 427.5 ± 9.0 mg (195–764 mg) and pods contained 14 seeds (10–17 seeds pod^{-1}) with a seed mass of 21.3 ± 0.3 mg.