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The role of pre- and post-dispersal seed predation in determining total seed loss

R.D. van Klinken*, A.J. White

CSIRO Biosecurity Flagship, EcoSciences Precinct, 41 Boggo Road, Dutton Park, PO Box 2583, Brisbane 4001, QLD, Australia

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Abstract

Most seed predation studies focus on either pre- or post-dispersal predation and may therefore underestimate the role of predation in regulating plant populations. We therefore estimated total seed predation of an invasive tree, mesquite (Leguminoseae: *Prosopis* spp.), by examining the entire seed pool from tree to seed bank. The spatio-temporal dynamics of total seed predation was examined by sampling across its Australian distribution and through time. The main predator was a host-specialist multivoltine beetle, *Algarobius prosopis* L. (Bruchidae), previously introduced as a biocontrol agent. Seed predation exceeded 20% in all seed stages (in pods on and off the tree, and seeds within woody endocarps (capsules) and free seeds on and in the ground) but was consistently highest in capsules on the ground (up to 90%). Pre-dispersal predation contributed little. Total seed predation rates were primarily determined by predation rates on the most persistent seed stage, in this case fallen pods if only pods are considered and seeds in capsules for the total seed pool. This pattern was consistent across the surveyed taxa, regions, years and seasonally. Predation rate was relatively unaffected by seed density, potentially because densities were always low (<150 seeds m^{-2}). Average total seed predation within a region reached 55%, but we conclude that any population regulation of mesquite by seed predation will principally be through reduced seed bank persistence. Our results highlight the need to consider the entire seed pool, especially the often cryptic and overlooked long-lived stages, when determining seed loss to predation and its likely population consequences.

Zusammenfassung

Die meisten Untersuchungen zu Samenprädation konzentrieren sich entweder auf Prädation vor oder auf die Prädation nach der Ausbreitung und unterschätzen deshalb möglicherweise die Bedeutung der Prädation bei der Regulation von Pflanzenpopulationen. Wir bestimmten deshalb die Gesamt-Samenprädation des invasiven Mesquitebaums (Leguminoseae: *Prosopis* spp.), indem wir den gesamten Samenpool vom Baum bis zur Samenbank erforschten. Die Raum-Zeit-Dynamik der Gesamt-Samenprädation wurde untersucht, indem wir Proben über sein australisches Verbreitungsgebiet und vier Jahre hinweg nahmen. Der Hauptprädator war ein spezialisierter, plurivoltiner Käfer, *Algarobius prosopis* L. (Bruchidae), der früher als biologischer Kontrollorganismus eingeführt worden war. Die Samenprädation übertraf 20% in allen Samenstadien (in den Hülsen auf dem Baum und nach dem Herunterfallen, Samen innerhalb des holzigen Endocarps (Kapseln) und freie Samen auf oder im Boden), war aber immer am höchsten in den Kapseln auf dem Boden (bis 90%). Die Prädation vor der Ausbreitung war gering. Die Gesamt-Samenprädationsraten wurden hauptsächlich bestimmt durch die Prädationsraten am langlebigsten Samenstadium, in

*Corresponding author. Tel.: +61 7 38335737; fax: +61 7 3833 5504.
E-mail address: rieks.vanklinken@csiro.au (R.D. van Klinken).

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diesem Fall herabgefallene Hülsen, wenn nur Hülsen betrachtet werden, bzw. den Samen in Kapseln für den gesamten Samenpool. Dies Muster war gültig für alle untersuchten Arten, Regionen, Jahre und Jahreszeiten. Die Prädationsrate blieb relativ unbeeinflusst durch die Samendichte, vermutlich weil die Dichten immer gering waren (<150 Samen m^{-2}). Die durchschnittliche Samenprädation innerhalb einer Region erreichte 55%, aber wir schließen, dass jedwede Populationsregulation des Mesquitebaumes durch Samenprädation prinzipiell durch reduzierte Langlebigkeit der Samenbank erfolgt. Unsere Ergebnisse belegen die Notwendigkeit, den gesamten Samenpool zu betrachten, insbesondere die oft kryptischen und übersehenen langlebigen Stadien, wenn Samenverluste durch Prädation und ihre Konsequenzen für die Populationsdynamik bestimmt werden sollen.

Keywords: Bruchidae; Invasive plants; Plant–insect interactions; Predator escape; Pre-dispersal seed predation; Post-dispersal seed predation; Seed bank

Introduction

Seed predation can be an important driver of plant population dynamics, and even community structuring (Crawley 1992; Hoffmann & Moran 1998; Kauffman & Maron 2006; Kolb, Ehrlén, & Eriksson 2007; Lewis & Gripenberg 2008; Ramírez & Traveset 2010). Seed predating insects are particularly diverse and widely studied, but their general importance is still disputed. Most studies of insect seed predators have focussed on seeds that are still on the plant (pre-dispersal predation) (Kolb et al. 2007). Univoltine insects, that pass through a single generation a year, can be well synchronised with typically observed seasonal peaks in seed production (Crawley 1992). In contrast, multivoltine insects, that pass through multiple generations a year, are less able to track sharp seasonal fluctuations in pre-dispersal host resources (Raghu, Wiltshire, & Dhileepan 2005; van Klinken et al. 2008). However, this can potentially be overcome if they continue exploiting more persistent post-dispersal seed stages (Johnson 1981; Lewis & Gripenberg 2008; van Klinken & Flack 2008; van Klinken & White 2011). Post-dispersal seeds are often cryptic and therefore overlooked in seed predation studies. As a consequence the role of multivoltine insects as a seed mortality factor, and ultimately in regulating host populations, may be underappreciated (Briese, 2000; Lewis & Gripenberg 2008).

Several closely-related *Prosopis* species (Leguminosae), together referred to as mesquite, are long-lived shrubs and trees that reproduce entirely by seed and are native to arid and semi-arid Americas. They have also been intentionally introduced around the world where they often become serious weeds (van Klinken, Hoffmann, Zimmermann, & Roberts 2009). Pods usually contain 10–20 seeds (c 0.024 g each, unpublished data) and remain closed at maturity (van Klinken & Campbell 2009). Mesquite seeds offer a particularly dynamic resource for seed predators. The pre-dispersal phase (Fig. 1) is typically brief, with pod maturation being relatively synchronised, and pods falling from the tree soon after maturation (van Klinken & Campbell 2009). Most pods are often consumed, either from the tree or ground, within days of maturation by a wide range of vertebrate herbivores. These herbivores are not seed predators, rather they derive nutrition from the pods and act as important seed dispersal vectors. Seeds are contained within a thin shell or endocarp (the seed capsule) which can remain intact even after the fleshy mesocarp has broken down during passage through the herbivore or through natural decay (van Klinken & White 2011) (Fig. 1). Mesquite seeds have hard-seeded (physical) dormancy imposed by the hard seed coat, from which most are released within 2–3 years under natural conditions (van Klinken et al. 2009).

Most seed predation reported on mesquite in its introduced range is by a multivoltine host-specialist, *Algorobius prosopis* Le Conte. (Bruchidae), sourced from the Americas in an attempt to regulate mesquite populations (van Klinken et al. 2009). Females lay eggs on mature pods, seed capsules and possibly free seeds, with each larva consuming and killing an individual seed before emerging as an adult (Impson, Moran, Hoffmann, Olckers, & Hill 1999; van Klinken and White 2011). Populations can pass through several generations a year, with development from egg hatch to eclosion taking *c* 33 days (Hoffmann, Impson, & Moran 1993). High seed predation levels can occur on long-lived seed stages. In South Africa it can kill over 90% of seeds in mature pods within 10–12 months provided vertebrate herbivores are prevented from consuming pods (Impson et al. 1999; van Klinken et al. 2009). In Australia predation rates by *A. prosopis* can be high

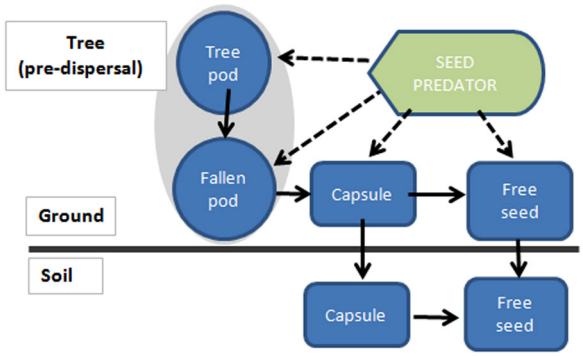

Fig. 1. A schematic of the mesquite seed lifecycle with the typically transient pod stages highlighted. It includes pre-dispersal seeds (tree-pods) and post-dispersal seed stages on and in the ground.