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Variation of predator satiation and seed abortion as seed defense mechanisms across an altitudinal range

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Abstract

Predator satiation and seed abortion have been reported as effective mechanisms reducing pre-dispersal seed predation, however, whether they may act simultaneously and whether their contribution to seed defense may spatially vary has been barely addressed. Across the altitudinal range of the dry tropical tree *Acacia pennatula* we investigated the importance of seed production and seed abortion as defense mechanisms against its pre-dispersal seed predators (*Mimosestes* spp.). Additionally, we measured the potential relationship between the number of seeds that escaped predation and plant recruitment. Predator satiation was effective since greater fruit production was associated with a lower proportion of predated seeds, while high seed abortion rates were related to increases in larval mortality. Although both mechanisms were present simultaneously, their relative contribution varied considerably across the altitudinal range: predator satiation was favored in the middle parts of the range, where seed production is much higher, whereas seed abortion was particularly relevant at the peripheral sites and especially high at the upper margin. The number of seeds that escaped predation was related to seedling density at plot level, indicating the demographic significance of these defense mechanisms against pre-dispersal seed predation. Overall, these results highlight the importance of considering spatial variability when analyzing seed defense traits and they also suggest considering predator satiation and seed abortion as two complementary mechanisms to reduce seed loss.

Zusammenfassung

Räubersättigung und Samenabort wurden als wirksame Mechanismen zur Reduzierung von Samenfraß vor der Samenausbreitung dargestellt. Indessen wurde kaum behandelt, ob sie gleichzeitig wirken und ob ihr Beitrag zur Verteidigung der Samen räumlich variieren kann. Entlang der Höhenstufen des tropischen Trockenwaldbaums *Acacia pennatula* untersuchten wir die Bedeutung von Samenproduktion und Samenabort als Abwehrmechanismen gegen zwei Samenkäferarten (*Mimosestes* spp.). Zusätzlich maßen wir den möglichen Zusammenhang zwischen der Anzahl der Samen, die nicht befallen wurden, und der Keimlingsetablierung. Die Räubersättigung erwies sich als effektiv, da eine höhere Fruchtproduktion mit einem geringeren Anteil befallener Samen einherging, während hohe Samenabortraten mit erhöhter Larvenmortalität in Verbindung gebracht werden konnten. Obwohl beide Mechanismen gleichzeitig auftraten, variierten ihre relativen Beiträge erheblich entlang der Höhenstufen: Räubersättigung trat bei den mittleren Stufen auf, wo die Samenproduktion wesentlich größer ist,

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während Samenabort in den Randbereichen des Gradienten größere Bedeutung hatte, insbesondere in den oberen Höhenstufen. Die Anzahl der intakten Samen, die den Samenfressern entgangen waren, korrelierte mit der Sämlingsdichte auf der Plot-Skala. Dies zeigt die demographische Bedeutung der beiden Abwehrmechanismen gegen Samenfraß vor der Ausbreitung. Zusammenfassend unterstreichen diese Ergebnisse, dass es wichtig ist, die räumliche Variabilität bei der Analyse von Verteidigungsstrategien zu berücksichtigen. Desweiteren legen sie nahe, dass Räubersättigung und Samenabort als komplementäre Verteidigungsmechanismen angesehen werden sollten.

Keywords: Acacia; Bruchinae; Neotropics; Seed predation; Tropical dry forests

Introduction

Seed predation by insects can have major impacts on the distribution and population dynamics of plants by reducing the seed output and hence seedling recruitment (Louda 1982; Crawley 2000; Kolb, Ehrlén, & Eriksson 2007). Consequently, plants have evolved resistance mechanisms such as physical and chemical barriers that reduce seed consumption and tolerance strategies like predator satiation (Hulme & Benkman 2002). This latter mechanism relies on spatially and temporarily irregular reproductive efforts which should result in lower predation rates with increasing seed production in a given site (Janzen 1971; Kelly & Sork 2002; Espelta, Cortés, Molowny-Horas, & Retana 2009). In addition, seed abortion may constrain the performance of insect seed predators directly by killing those larvae that infest aborted seeds and indirectly through increasing competition among predators for viable seeds (Ghazoul & Satake 2009; Holland, Bronstein, & DeAngelis 2004; Östergård, Hämback, & Ehrlén 2007; Stephenson 1981; Traveset 1993). Thus, independently of the causative factor (e.g. weather conditions, resource availability or insect damage) seed abortion may result in a density-dependent mechanism that controls the populations of insect seed predators and so offset the costs of the loss of aborted seeds (Holland & DeAngelis 2002).

However, whether different seed defense mechanisms can act simultaneously and whether their contribution may vary across the distribution range of a plant species has been barely addressed. Indeed, previous studies have suggested that local environmental conditions (e.g. drought) influence the amount of seeds produced and ultimately result in spatial differences in the success of predator satiation (Espelta, Cortés, Molowny-Horas, Sánchez-Humanes, & Retana 2008). Seed abortion typically rises at the boundaries of a plant distribution range owing to the increasingly adverse environmental conditions (García, Zamora, Gómez, Jordano, & Hódar 2000; Giménez-Benavides, Escudero, & Iriondo 2007; Jump & Woodward 2003). Hence, it could be hypothesized that across the distribution range of a plant species, predator satiation should be favored where environmental conditions are benign and more favorable to seed production, i.e. at the center of the range; whilst the relative contribution of seed abortion to seed defense should be greater in the harshest locations, i.e. at the periphery of the range.

The main aim of the present study is to investigate the variation of predator satiation and seed abortion across the altitudinal range of the dry-tropical tree *Acacia pennatula*. This species is an interesting study model for this purpose for two main reasons: (i) it is a common tree species from Mesoamerica down to Ecuador with a wide altitudinal range (Stevens, Ulloa, Pool, & Montiel 2001) and (ii) it produces large crops of multi-seeded fruits conspicuously predated by two bruchid species (*Mimosestes* spp., Janzen 1980). We hypothesize that the contributions of predator satiation and seed abortion to seed defense vary across the altitudinal range of *A. pennatula*. Specifically, massive seed production leading to predator satiation should be an important mechanism in the mid-parts of the range where climate is milder and reproduction costs should be lower. Conversely, the contribution of seed abortion to the reduction of the performance of seed predators should be higher at the edges of the distribution range. In order to test this hypothesis, we selected five elevations covering the altitudinal range of *A. pennatula* in Northwest Nicaragua (500–1400 m a.s.l.) and assessed: (i) the variability in fruit crop size, seed production, seed abortion and seed predation rates, (ii) the predator performance (i.e., the number of eggs laid per fruit and the proportion of adult emergences per egg laid), and (iii) the relationship between the number of seeds that escaped predation and seedling recruitment during the following wet season. The results of this study may be of interest to evaluate the potential interactions between different seed defense mechanisms resulting from the spatial variation of environmental conditions and seed predation pressures that plants must face.

Materials and methods

Study area and species

This study was conducted from the valley of the river Estelí to the Miraflor-Moropotente Protected Landscape covering the altitudinal distribution range of *A. pennatula*