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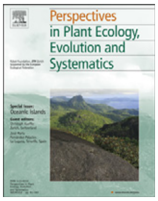

Research article

Predispersal seed-predation by insects in the Venezuelan Central Plain: Overall patterns and traits that influence its biology and taxonomic groups

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ABSTRACT

Predispersal seed predation (PSP) by insects was studied in a plant community of the Venezuelan Central Plain (VCP). The main goal was to examine to what extent vegetation structure and fruit–seed attributes determined the incidence of PSP by insects at the community level. We studied a total of 187 species from 59 families, in five habitat types. The proportion of seed-predated plant species ($N=89$; 47.6% of the total) was explained by different factors such as the abundance of legume families, plant species richness, fruit dehiscence, seed biomass, and starch content. Coleoptera was the most diverse taxonomic order of insect seed predators, with Bruchidae and Curculionidae showing the largest number of genera and species, followed by Lepidoptera (Pyralidae). Bruchidae and Pyralidae, but not Curculionidae, tended to be separated according to vegetation attributes, such as vegetation structure and flowering and fruiting phenology. In addition, Bruchidae was associated with dehiscent fruits, legumes, epizoochory, and granivory, whereas Curculionidae was more related with indehiscent fruits and endozoochory, and Pyralidae with abiotic seed dispersal. Bruchid larvae tended to prey upon single seeds, whereas larvae of Lycaenidae usually preyed upon more than one seed per fruit; Curculionidae did not show any clear pattern on this. One larva developing in a single seed (Type I) was the most common type of PSP, closely followed by one or more larvae developing outside seeds within the fruit (Type II). Type III (seed predation by adult insects inside the fruit) was the least common. Type I appears to occur most frequently in climbers, in the forest–savanna transition habitat, and in those cases in which insect adults emerged during the rainy season. By contrast, Types II and III tended to be associated with annual herbs, the lowest stratum (0.05–0.6 m), and disturbed areas. Moreover, Type I was usually found in samaras, drupes, and indehiscent fruits, whereas Type II and Type III were more commonly observed in capsules. Type I and Type II seeds differed in their nutritional composition, which in turn appears to affect seed predation specialization. The number of insect seed predator species and plant richness per habitat were positively correlated. The number of seed predator species was associated with the abundance of trees and climbers because more complex plant life forms offer a large variety of resources, woody species frequently had fruits and seeds larger than herbaceous species, and trees and climbers showed the lowest values of host specificity. To our knowledge, this study is the first one that characterizes the community of predispersal seed predators and simultaneously evaluates ecological, morphological, and nutritional factors determining the groups of seed predators and how PSP occurred.

Introduction

Predispersal seed predation (PSP, hereafter) by insects is one of the plant–animal antagonists relationships that have received less attention in community-level studies. Previous work has evaluated PSP by all insects (Raimúndez, 2000) or have limited to a specific group, such as coleopterans (Janzen, 1980). Other studies are restricted to a few numbers of plant species (Ernst et al., 1990), a few related plant species (Zwölfer and Brandl, 1989; Miller, 1996) or plant families on regional flora (Jermy and Szentesi, 2003). However, community characterization of predispersal seed predator species on the basis of major groups of insect seed predators, predation forms, and its relation with vegetation structure and richness have not been examined.

PSP can be studied both from the plants and the animals' viewpoints. From the plant's side, PSP may represent an important reduction on plant reproductive potential during the predispersal phase (e.g., Steffan-Dewenter et al., 2001; Ribas-Fernández et al., 2009; Kolb et al., 2007 and references therein). On the contrary, it may not be important for plant population

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dynamics (Szentesi and Jermy, 2003; Kolb et al., 2007; and references therein). In any case, the effect of PSP on plant reproductive success is highly variable in time and space (Moore, 1978; Ramírez and Arroyo, 1987a, b; Traveset, 1995; Wright, 1994; Kolb et al., 2007, and references therein). From the animal's perspective, seeds represent a resource to breed or feed upon directly. PSP is characterized by seed consumption frequently when seeds are not completely developed, and thus are not dispersed yet. The guild of predators that prey upon seeds at this time is usually different from that consuming the seeds once they have been dispersed.

In addition, there are different types of PSP depending on (1) the insect stage (larva or adult) consuming the seeds, (2) whether one or more larvae develop inside a fruit, and (3) whether a larva consumes one or more seeds within a fruit (Center and Johnson, 1974). In general, these particularities may influence the level of specialization of insect in the use of the resource. In this context, the evolution of herbivore guilds may strongly depend on the way that host resource is exploited: endophytic species which live as larvae within spatial compartments require more precise morphological adaptations to specific hosts than ectophytic species (Zwölfer and Brandl, 1989). By analogy, we might expect a lower specialization in those cases in which larvae consume several seeds from outside and when adult insects prey upon the seeds than when a single larva develops inside each seed. Therefore, endophytic guilds are considered more specialized than the external feeders (Novotny and Basset, 2005) or quasi-endophagous PSP (Szentesi and Jermy, 1995).

Evolutionary interactions between plant and their natural enemies are mediated by the ability of the plant enemy to attack its host, and the ability of the host plant to resist such attack (Marquis and Alexander, 1992). Those plant traits avoiding or ultimately allowing insect seed predation result from evolutionary interactions, and represent, in ecological terms, those factors structuring the community of seed predators and their host plants. These plant–insect interactions at the community level are constructed from plant and insect adaptations, which include ecological, morphological, chemical, and behavioral traits. Previous studies have pointed out that seed predation intensity may be affected by four major categories of attributes:

(a) *Vegetation traits*: Plant reproductive phenology (i.e. Janzen, 1977b, 1980; Forget et al., 1999), host plant population size (Östergård and Ehrlén, 2005; Arvanitis et al., 2007), spatial distribution of host plants (Bach, 1988; Turchin, 1991; Arvanitis et al., 2007), vegetation disturbance (Notman and Gorchov, 2001), and plant life form (Raimúndez, 2000).

(b) *Morphological and morphometrical traits of fruits and seeds*: Are the most widely recognized attributes influencing the degree of seed predation (Janzen, 1969, 1977a, b; Center and Johnson, 1974; Mitchell, 1977; Moore, 1978; Siemens et al., 1992; Miller, 1996; Raimúndez, 2000; Moles et al., 2003). Among morphological traits, seed size seems to play an important role, because preference of seed predators often is determined by size constraints (Honek et al., 2007) and host specificity may be related to seed size (Center and Johnson, 1974; Miller, 1996). In addition, morphological traits of fruits and seeds are in many cases intimately related with dispersal mode (Jordano, 1995), and therefore may have interactions and consequences different with PSP (Sallabanks and Courtney, 1992; Wang and Smith, 2002).

(c) *Chemical properties of seeds*: The relative immunity of seeds to insect attack may be due, at least partly, to the high concentrations of toxic secondary compounds (Bell and Janzen, 1971; Janzen, 1973, 1977a; Rehr et al., 1973a; Rosenthal et al., 1977; Bowers, 1988; Kestring et al., 2009). Moreover, toxic compound in seeds are very important because several larvae have become specialized on those substances (Bleiler et al., 1988) and, thus, are likely to be partly responsible for the extreme host-specificity shown by seed-eating insects (Janzen et al., 1977). In this sense, chemicals are probably effective against generalist predators but not against specialist that have evolved counter-adaptations (Sallabanks and Courtney, 1992). Specialized predation by insects on toxic seeds is accompanied by adaptation of degradation and detoxification of toxic products (Rehr et al., 1973b). By the contrary, high concentrations of toxic compounds may be induced in seeds from infested fruits, which may affect insect development (Kestring et al., 2009).

(d) *The nutritional composition of seeds*: This has been poorly examined in the context of PSP. However, Sallabanks and Courtney (1992) suggest that insect larvae depend on nutritional quality of fruit for survival. A previous study by Kelrick et al. (1986) had found that seed preferences by rodents (post-dispersal seed predators) were strongly influenced by their soluble carbohydrate content. A more recent study has also shown that seeds with high fat concentrations are harvested more quickly by rodents (Xiao et al., 2006).

Our general goal in this study is to identify the relative importance of different types of attributes that determine the incidence of PSP in a plant community in the Venezuelan Central Plain, and consequently determine the relation of predispersal seed predator species and plant richness. Our specific objectives are to answer the following questions, which we group into two groups of questions:

(1) What ecological, morphological and nutritional attributes of fruits and seeds influence (a) the incidence of PSP, (b) the major families of seed predators, and (c) the type of PSP depending on insect stage and number of developing larvae per seed?

(2) Do patterns of PSP differ across habitats with different species richness?

Methods

Study area

Field work was conducted in *Trachypogon* savannas at Estación Biológica de los Llanos (8°56′N, 67°25′W), located approximately 12 km southwest of Calabozo, Estado Guárico, in the Venezuelan Central Plain (VCP thereafter). The climate is markedly seasonal, with a rainy season from May to November and a dry season from December to April. Annual precipitation varies between 800 and 1839 mm, and the average annual temperature is 27 °C for 25 years of records (Sarmiento and Monasterio, 1968; Walter and Medina, 1971).

Differences in vegetation structure are produced by varying soil types or by anthropogenic activity. Five types of vegetation (habitats, hereafter) were distinguished in the 250-ha study area (Ramírez, 2003): (1) forest vegetation or groves, locally called "matas", composed of discontinuous patches with several trees and a typical understory layer of herbs and shrubs; large clusters of trees also interrupt the grassland; (2) forest–savanna transition or ecotone vegetation (transitional between forest and savanna); (3) savanna vegetation, consisting of scattered trees on a continuous grass stratum dominated by *Trachypogon* and *Axonopus* spp.; (4) secondary vegetation, consisting of herbaceous vegetation on disturbed areas, dominated by pioneer species; and