Olycella aff. junctolineella (Lepidoptera: Pyralidae) florivory on Opuntia microdasys, a Chihuahuan Desert endemic cactus

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ABSTRACT

The object of this study was to provide the first data on the natural history of the little known plant–florivore interaction between Opuntia microdasys and Olycella aff. junctolineella larvae and to study interindividual variability in the number of reproductive structures attacked as a function of plant resource availability.

Field observations of larval activity and a quantification of the damages produced were done at the Southern Chihuahuan Desert, Mexico. To quantify the interindividual variation of florivory damage as a function of resource availability (water and nutrients), a resource addition experiment was carried out.

Larvae caused 21% of buds and 7% of flowers to abort. Adding resources (water and nutrients) to plants had no effect on bud production, although more buds developed into flowers and fruits in fertilized plants, suggesting a selective abortion against ill-nourished reproductive structures. The number of buds and flowers attacked by larvae were higher for non-fertilized than for fertilized plants, indicating that reproductive structures of plants under abiotic stress become more suitable as food for florivores. The number of structures attacked was a non-linear function of the number of buds originally produced, suggesting a florivore satiation threshold.

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1. Introduction

Although the effect of tissue herbivory on plant fitness has been extensively studied, little research has focused on florivory (i.e., bud or flower consumption prior to the formation of the seed coat, Krupnick and Weis, 1999; Krupnick et al., 1999; McCall and Irwin, 2006) even though the evidence indicates that florivory is a very specialized (Fernández et al., 2008; Mann, 1969) and old interaction (Frame, 2003). In particular, Lepidoptera larvae have been recognized as major consumers of reproductive structures (i.e., flowers, fruits, or seeds) in certain families of plants (Ehlers and Olesen, 2003; Pratt and Pierce, 2001; Winotai et al., 2005). Mutualistic relationships have also been documented, in which larvae consume reproductive structures, either partially or entirely, and adults are pollinators (Addicott, 1986; Petterson, 1991; Udovic and Acker, 1981). The scarce literature on florivory is generally devoted to estimating either the direct or indirect trophic effects of florivory (McCall and Irwin, 2006). Direct effects occur because of a reduction in the amount of buds, flowers, fruits, or seeds produced by attacked plants (Oguro and Sakai, 2009). Indirect effects occur

because of changes in pollinator behavior due to a reduction in floral rewards or modification of floral structure and/or floral displays caused by florivory (Cascante-Marín et al., 2009; Krupnick et al., 1999; Malo et al., 2001) affecting male and/or female floral functions (Krupnick and Weis, 1999). Both direct and indirect effects have been shown to decrease population performance (Kelly and Dyer, 2002; Leege and Wolfe, 2002; Louda and Potvin, 1995).

The amount of resources available to a plant determines the energetic allocation toward the production of reproductive structures and floral rewards (Roach and Wulff, 1987; Stephenson, 1981) but can also indirectly influence herbivory (Bazzaz et al., 1987; Dempster and Pollard, 1981; Price, 1991; Tobler et al., 2006; Trumble et al., 1993). This is particularly important in environments such as deserts, with marked inter-annual fluctuations in resource availability (Noy-Meir, 1973; Schlesinger et al., 1990). Herbivore populations respond to an increase in plant resources in vastly different ways (Jones and Coleman, 1991). Traditionally it was thought that plants under abiotic stress become more suitable as food for herbivorous insects. However, the responses can be positive (concentrating attack on vigorous plants; Price, 1991), negative (concentrating attack on weak or stressed plants; White, 1984), or neutral (reviewed by Larsson, 1989, see also Lejeune et al., 2005 and Schowalter et al., 1999). However, there is no

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information on the response of florivores to the level of plant resource availability.

For Cactaceae, little research has been done to assess damage to reproductive structures caused by lepidopterans or insects in general (Badii and Flores, 2001; Pimienta-Barrios, 1990). Zimmerman and Granata (2002) report that 75% of the insects that affect cacti are "internal feeders," 3% "external feeders," 12% sap suckers, and 1% leaf miners; only 6% consume fruit, with no insects observed to consume flowers. Within the known community of insects that feed on cacti, the family Pyralidae (Lepidoptera) that mostly consume vegetative parts, is the most diverse, with 58 species (Longo and Rapisarda, 1995; Zimmerman and Granata, 2002). There are only a few reports of flower or fruit predation by their larvae (e.g. Pemberton and Cordo, 2001: Mann, 1969; McIntosh, 2002a,b), while mutualistic relationships have been reported for Lophocereus schotii and Upiga virescens (Pyralidae, Glaphyriinae; Holland and Fleming, 1999).

For the genus Opuntia (the prickly pears, with over 200 species), attacks by several phytophagous insects have been reported (Badii and Flores, 2001; Pimienta-Barrios, 1990). Two species of lepidopterans stand out as consumers of cladodes and stalks: Olycella nephelepsa Dyar (zebra worm, Pyralidae) and Lanifera cyclades Druce (white worm, Pyralidae, Badii and Flores, 2001; Lummus and Wanberg, 1981; Ueckert, 1998). Another lepidopteran, of South American origin, that affects the vegetative structures of Opuntia (29 known hosts) is Cactoblastis cactorum (Pyralidae), which is considered a threat to cacti populations in Mexico and the United States (Golubov et al., 2001; Pemberton and Cordo, 2001). To our knowledge, no studies of lepidopterans that consume only Opuntia flowers have been performed.

In this study we describe the natural history of the Opuntia-Olycella interaction, experimentally assess whether or not Olycella prefers to attack plants that receive additional resources, and measure the effect of Olycella on reproductive success. In particular, we studied interindividual variability in the production of flower buds and damage from florivory (in this case, causing the total destruction, or abortion, of reproductive structures) as a function of experimentally adding resources to plants. Given the marked limiting conditions of resources (water and nutrients) in desert settings, we expected that plants provided with additional resources would produce more flower buds than those given no such supplement. We also expected a positive response of florivores to changes in the quality and/or quantity of floral resources produced – i.e., plants receiving resource supplementation would be attacked more than those that did not.

2. Methods

2.1. Plant and study site

Research was conducted at the Mapimí Biosphere Reserve (Chihuahuan Desert, Mexico, 26°41′N, 103°45′W, 1150 m asl, 264 mm annual precipitation, 20.8 °C mean annual temperature; Montaña, 1990). This study was carried out in an area of approximately 3500 ha, in a "bajada" (gentle sloping terrain, slope: 3–16%, that connects piedmonts to the bottom of endorreic basins). Vegetation (Montaña, 1990) consists of scrubs growing in sandy-clayed soils and dominated by Larrea tridentata (DC.) Cov. (Zygophyllaceae), Opuntia rastrera (Weber) Britton and Rose, Opuntia microdasys, Jatropha dioica Cerv. (Euphorbiaceae), and Fouqueria splendens Engelm (Fouquieraceae). O. microdasys is a cactus endemic to the Chihuahuan Desert (commonly known as nopal cegador or bunny-ears prickly pear). It blooms from March to May more or less synchronously. Flowers produce abundant nectar (>30 μl/flower), last for a single day, and lose the perianth a few

days following anthesis (Piña et al., 2007). Flower production and fruit set are limited by nutrient availability (Piña et al., 2007). The main pollinator is the oligolectic bee, Diadasia sp., and the fruit and seed set has been shown to be limited by pollen (Piña et al., 2007). Seedling recruitment is very rare (Palleiro et al., 2006), but clonal propagation is more common and occurs through plantlets stemming from cladodes and roots produced in areoles from the pericarpel of aborted fruits (Palleiro et al., 2006; Mandujano, Montaña and Golubov, unpublished data). Opuntia spp. has a very shallow root system that allows water uptake even after very low rainfall spells. Moreover, a few hours after it has rained, they produce new fine roots ("rain roots," Gibson and Nobel, 1986) that enable a very efficient water uptake process (Nobel, 1995).

2.2. Larval activity

Detailed field observations of larval activity were done during the blooming period (April–May 2002). In order to provide a detailed description of the damage caused by larvae, we dissected 50 flower buds and 50 flowers from 15 plants that showed typical signs of florivory during the blooming peak (April 2002). On each structure, data on larval position and evidence of damage were recorded. Observations of parasitoids and predators of larvae were also made.

2.3. Quantification of damage to reproductive structures

We quantified the type of tissue damage (i.e., attacks at the perianth and ovarian level) on aborted flowers at the blooming peak (April 2002) by analyzing all aborted structures on 40 randomly selected plants. For that purpose, we visited the 40 selected plants every other day and collected all aborted structures. In order to determine if larvae also attack fruits, 20 recently aborted reproductive structures in each of 20 randomly selected plants were examined after the blooming season had ended (late May 2002).

2.4. Effect of resource availability on flower bud production and florivory

To quantify variation in flower bud production and the intensity of florivore damage (number of aborted structures) as a function of water and nutrient availability, a resource addition experiment was carried out during the 2002 blooming season. We used 60 randomly selected plants that had been given a combination of two treatments, also random (addition of 300 L of water per plant or no addition of water) and two types of fertilization (addition of a mixture of 350 g of ammonium sulfate, 300 g of simple calcium superphosphate, 200 g of potassium chloride, and no fertilizer addition). The amounts of fertilizer used met the reproductive needs of cultivated Opuntia spp. (Pimienta-Barrios, 1990). The addition of fertilizer was done on two occasions immediately prior to the watering dates, with 425 g delivered at a time. Watering was done in circular plots of 7 m^2 delimited by a soil border, so that upon watering, moisture was retained and could filter into the soil that surrounded the plant. This plot size was sufficient to water a surface larger than the area of influence for the root system of O. rastrera (6.61 m^2, Briones et al., 1998), a sister species of the same lifeform and very similar to O. microdasys in morphology and phenology. Watering was done on two occasions before flowering (September 2001 and March 2002,150 L each time, the equivalent to a 20 mm rain). These dates were chosen in order to ensure that the resources would be available to the plants before blooming (which starts in early March and ends in May, with the first rainfalls). De la Barrera et al. (2009) (see also Pimienta-Barrios, 1990) mention that floral differentiation for various species of Opuntia