



Contents lists available at ScienceDirect

Acta Oecologica

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

Ecological factors associated with pre-dispersal predation of fig seeds and wasps by fig-specialist lepidopteran larvae

Finn Piatscheck, Justin Van Goor, Derek D. Houston, John D. Nason*

Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, United States

ARTICLE INFO

Keywords:

Flowering phenology
Density effects
Ficus
Lepidoptera
Seed predation
Symbiosis

ABSTRACT

In brood pollination mutualisms, predation of developing fruit can have large negative repercussions for both plant and pollinator population dynamics. The Sonoran Desert rock fig *Ficus petiolaris* and its highly-coevolved wasp pollinator are subject to frequent attack by lepidopteran larvae that consume fig fruit and the developing seeds and larval pollinators they contain. We used generalized linear mixed models to investigate how the phenology, quantity, and spatial distribution of fig fruits is associated with variation in lepidopteran damage intensity on individual trees at nine geographic locations spanning a 741 km latitudinal transect along Mexico's Baja California Peninsula. We found lepidopteran damage to be strongly positively associated with more synchronous fig crops and larger trees, and only weakly associated with lower local host tree density. These results imply that fruit production that is asynchronous within trees and spread out over time, as observed in several fig species, benefits female and male components of fitness (pollen disperser and seed production, respectively) by reducing pre-dispersal predation by frugivores.

1. Introduction

The majority of flowering plants rely on animals for pollination services while pollinators, in turn, obtain valuable plant resources (Ollerton et al., 2011). The success of this mutualistic interaction depends on numerous ecological factors, as the plant-pollinator partners may be differentially affected by both biotic and abiotic environments. For example, numerous studies have investigated climate variation effects on plant phenology as well as temporal mismatches between plants and pollinators that their negatively impacts on mutualistic outcomes (Harrison, 2000; Wall et al., 2003; Memmott et al., 2007; Hegland et al., 2009; Burkle et al., 2013; Rafferty et al., 2013, 2015). Theoretical and empirical studies of optimal foraging also indicate plant density and per-plant production of floral resources to be positively associated with pollinator attraction, floral visitation and, ultimately, seed production (Platt et al., 1974; Silander, 1978; Klinkhamer and de Jong, 1990; Kunin, 1993, 1997), while decreases in both the density and spatial continuity of natural plant populations negatively impact pollinator visitation rates and plant reproductive success (Nason and Hamrick, 1997; Tschardt and Brandl, 2004; Aguilar et al., 2006; Potts et al., 2010). Such studies are of growing importance since the global-scale increase in average temperature is causing a temporal shift towards earlier flowering (Fitter and Fitter, 2002; Walther et al., 2002; Cleland et al., 2007; Franks et al., 2007; Cook et al., 2012) and human-

mediated landscape fragmentation is already advanced and increasing (Vitousek et al., 1997; Achard et al., 2002; Hansen et al., 2013), which together are driving concerns about both temporal and spatial mismatches in plant-pollinator interactions.

In addition to mutualistic interactions with insect pollinators, flowering plants are ubiquitously subject to antagonistic interactions from a diverse assemblage of phytophagous insects (including herbivores, florivores, seed predators, and frugivores), which may also be subject to environmentally-driven spatial and temporal mismatches with host plants (Thompson and Gilbert, 2015). A number of studies have investigated host plant density and frequency effects on insect herbivory (Root, 1973; Bach, 1980, 1988; Fagan et al., 2005) and phenological mismatches in plant-antagonist interactions (Augsburger, 1981; Brody, 1997; Visser and Holleman, 2001; Singer and Parmesan, 2010; Yang and Rudolf, 2010; Liu et al., 2011; Rafferty et al., 2013). Few studies, however, have jointly investigated spatial and phenological effects on plant-pollinator-herbivore interactions (but see Parsche et al., 2011). Concerning phenology, the theoretical study by Fabina et al. (2010) indicates that changes in phenological overlap in these interactions can alter the relative population densities and persistence of all three symbionts in ways not predicted solely from their pair-wise interactions. This suggests that temporal and spatial variation in climate may simultaneously affect the phenological overlap/mismatch of pollinators, phytophagous insects, and a shared host plant, and,

* Corresponding author.

E-mail addresses: finnp@iastate.edu (F. Piatscheck), jvangoor@iastate.edu (J. Van Goor), derek.d.houston@gmail.com (D.D. Houston), jnason@iastate.edu (J.D. Nason).

<https://doi.org/10.1016/j.actao.2018.03.001>

Received 6 February 2017; Received in revised form 15 February 2018; Accepted 6 March 2018
1146-609X/ Published by Elsevier Masson SAS.

consequently, the outcome of their species interactions.

Researchers considering the consequences of changes in flowering phenology have focused on the distribution of flowering time among individuals within and among populations. Virtually unstudied is the variance in flowering phenology *within* individual plants and, in turn, its effects on antagonistic interactions with phytophagous insects. While more asynchronous flowering may potentially ameliorate environmentally-driven phenological mismatches with pollinators, it may similarly benefit antagonists and, thus, have unappreciated costs for mutualism. Flowering phenology, resource availability (flower or fruit production), and plant density might thus be factors potentially affecting the plant-phytophagous insect dynamic. We expect that 1) within-plant asynchronous flowering will extend the phenological overlap between plant resources and insect antagonists leading to greater costs to the plant, 2) larger crops of resources will experience greater damage than smaller ones, and 3) fruit damage will increase with local host plant density. We tested these predictions by investigating interactions between a native fig and an associated pre-dispersal fruit-feeding insect in Baja California, Mexico.

Figs (*Ficus*, Moraceae) are diverse (750 + species) and widely distributed across tropical and subtropical environments worldwide (Berg, 1989). *Ficus* is typically one of the most speciose genera in tropical forests, with members functioning as keystone species because their aseasonal fruit production provides food vital to the survival of many vertebrate frugivores, especially during seasons when fruiting activity of other plant species is low (Terborgh, 1986; Lambert and Marshall, 1991; Shanahan et al., 2001; Serio-Silva et al., 2002; Harrison, 2005; Kissling et al., 2007). Contributing to reproductive isolation where they co-occur, each fig species typically has a species-specific relationship with a single pollinating chalcidoid wasp species (family Agaonidae; superfamily Chalcidoidea) that develops within galled fig seeds before mating within host inflorescences (syconia, commonly called fig fruits). The reproductive phenology of figs is unusual in that flowering is generally highly synchronized within trees and yet highly aseasonal at the population level. Moreover, the production of male and female flowers is separated by several weeks so that to interbreed trees must be phenologically out of phase with each other. In some species, however, trees exhibit substantial within-crown flowering asynchrony and may simultaneously bear syconia at various stages of development (Smith and Bronstein, 1996; Gates and Nason, 2012). This asynchrony may be of substantial benefit to the reproductive success of figs and pollinators by increasing overlap in flowering times and, hence, opportunities for pollinator and pollen transfer between trees (Gates and Nason, 2012). It is expected to be particularly beneficial where host populations are small and spatially isolated (Bronstein et al., 1990; Anstett et al., 1995, 1997; Gates and Nason, 2012).

In addition to providing an excellent model system for studying obligate mutualism, figs are exploited by a diversity of non-pollinating insects. The best known of these are non-pollinating fig wasps (multiple chalcidoid families) that reproduce within fig syconia (West et al., 1996; Weiblen, 2002; Borges, 2015). These non-pollinating wasps exploit the mutualism in various ways and are generally associated with a decrease in pollinator production, and to a lesser extent seed production (West and Herre, 1994; Kerdelhue et al., 2000). Less well studied are the myriad of other animals that are antagonist of the fig-pollinator mutualism, including moths. In the Sonoran Desert rock fig, *Ficus petiolaris*, an undescribed moth species (family Crambidae) lays eggs on or under the cuticle of the fig syconium, with later instar caterpillars boring into syconia and consuming developing seeds and wasps. Although few cases of fig boring lepidopteran caterpillars have been reported in the literature (New World: Janzen, 1979; Bronstein, 1988; Jandér, 2015; Old World: Sugiura and Yamazaki, 2004), we observed lepidopteran damage to the syconia of *F. petiolaris* to not only be common but to sometimes be drastically high, destroying all syconia with their developing seeds and pollinators within a tree. *Ficus petiolaris* thus provides a useful and interesting biological system to study the

effects of flowering phenology, crop size and plant density on levels of attack by a phytophagous insect that has significant consequences on host fitness.

For this study we first obtained samples of the moth antagonist of *F. petiolaris* from nine sites spanning its range in Baja California, Mexico, and employed mitochondrial sequences and phylogenetic tools to confirm its species delimitation and determine its taxonomic placement within the Crambidae. We then used generalized linear mixed models to test whether within- and among-site variation in fig damage caused by the moth larvae are related to measures of asynchronous flowering, crop size and/or local fig tree density. These models enabled us to test our *a priori* hypotheses, namely that each of the three predictor variables will be positively associated with levels of caterpillar damage and fruit loss.

2. Materials and methods

2.1. The biological system

Ficus petiolaris is an evergreen rock-strangling fig tree occurring within Mexico from Oaxaca in the south to the Sonoran Desert environments of Sonora and Baja California in the north. Because *F. petiolaris* grows on rocks, cliffs or canyon walls, it forms small natural population patches on rocky landscapes. Tree size varies greatly and can reach 20 + meters in height (Finn Piatscheck, pers. obs.). As a member of subgenus *Urostigma* (section *Americana*), this species is monoecious with syconia containing both female and male flowers. In contrast to most other *Americana* species, however, syconia production in *F. petiolaris* is often asynchronous within individual trees (Smith and Bronstein, 1996; Gates and Nason, 2012). *Ficus petiolaris* is pollinated by a single species of chalcid wasp (*Pegoscapus* sp., Agaonidae), with this mutualism being exploited by several obligately-associated insects, including eight species of non-pollinating chalcidoid wasps and one species of crambid moth. Extensive surveys of *F. petiolaris* trees and surrounding vegetation have located larvae of this moth only on fig trees (J. Nason, pers. obs.), consistent with it being a fig specialist. Moth larva typically bore into syconia near the peduncle and an individual late-instar caterpillar consumes the interior of several syconia - including seeds and wasp larvae - during its development. Indeed, after consuming the inside of one syconium, a caterpillar will move to another syconium (often the nearest one), chew its way inside, and use latex produced by the fig mixed with other material to then close the entry hole (F. Piatscheck, pers. obs.). In addition, a caterpillar will often feed within a pair of adjacent syconia connected via a tunnel it constructs from latex material, an unusual behavior further suggesting fig specialization. Oviposition by female moths and movement of larvae between syconia is exclusively nocturnal, and fifth instar caterpillars drop by night on silken threads from *F. petiolaris* trees to pupate in the soil. Any fig damaged by a caterpillar will abort with the loss of all remaining developing seeds and pollinators. The total damage to a tree can be substantial as we have in some cases observed fruit crops of *F. petiolaris* in which 100% of syconia were consumed by the caterpillars.

2.2. Site distribution and sampling

Field data were collected from nine sites distributed along a 741 km transect on Mexico's Baja California peninsula (Fig. 1, Table 1). At each site, we established a census population of geo-referenced *F. petiolaris* trees. Field data, including measures of reproductive activity and lepidopteran damage per tree, were obtained during three extended field trips: during the dry season in spring (May–June) 2013 and 2014, and during the wet season in fall (November–December) 2013. Southern sites were relatively mesic with more summer rainfall, whereas northern sites are climatically more extreme with less rainfall and greater seasonal temperature variation. Due to natural variation in reproductive activity, the number of flowering trees censused for

Download English Version:

<https://daneshyari.com/en/article/8846493>

Download Persian Version:

<https://daneshyari.com/article/8846493>

[Daneshyari.com](https://daneshyari.com)