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RESEARCH

Seasonal Dynamics of the Flower Head Infestation of *Smallanthus maculatus* by Two Nonfrugivorous Tephritids

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ABSTRACT. Seasonal dynamics of the capitula infested by *Dictyotrypeta* sp. and *Rhynencina spilogaster* (Steyskal) (Diptera: Tephritidae) was evaluated throughout the flowering cycle of their host plant the sunflower, *Smallanthus maculatus* (Cavanilles) Robinson (Asterales: Asteraceae). In central Veracruz, Mexico, along 16 consecutive weeks, a total of 1,017 mature capitula were collected, recording the presence and abundance of immature stages (larvae and pupae) and their related parasitoids. Both fly species were present throughout the entire season, with overall infestation of 51.5% of the capitula examined. However, *Dictyotrypeta* sp. infested 11.3%, representing about one-fifth of them, and *R. spilogaster* was most abundant infesting four times as many capitula (42.9%), whereas both species were found together in only 2.6% of the capitula examined. Based on the temporal occurrence of larvae and pupae into flower heads as well as their associated parasitoids and times of emergence, *Dictyotrypeta* sp. had two yearly generations, and it seems that the second generation could enter a seasonal diapause; in contrast, *R. spilogaster* was a univoltine species that entered diapause that lasted until the next year.

Key Words: Tephritinae, Asteraceae, trophic interaction, immature stage, parasitoid

Fruit flies of the subfamily Tephritinae (Diptera: Tephritidae) are widely distributed in temperate and subtropical regions of the world; however, most studies of their biology and ecology have been focused on Nearctic species inhabiting northern temperate regions (Headrick and Goeden 1998). On the contrary, few studies have documented the relationship between nonfrugivorous tephritids and their host plants in Neotropical species, in many cases, recording the first biological data and the findings of new taxa (Prado et al. 2002, 2004; Almeida et al. 2006; Norrbom and Prado 2006; Norrbom et al. 2010).

In the central region of Veracruz, Mexico, an undescribed species of *Dictyotrypeta* and *Rhynencina spilogaster* (Steyskal) (Diptera: Tephritidae) were found feeding on the capitula of *Smallanthus maculatus* (Cavanilles) Robinson (Asterales: Asteraceae) (V.H.O., unpublished data). The genus *Dictyotrypeta* comprises six species of exclusive Neotropical distribution stretching from Mexico to Argentina, with the recent inclusion of two further species, *Tetreuaresta crenulata* (Wulp) and *Baryplegma incisa* Wulp (Norrbom et al. 1998, 2010). The limited biological data available indicate that *Dictyotrypeta atacta* (Hendel) feeds on the capitula of *Lessingianthus*, *Proteopsis*, and *Trichogonia* (Asteraceae) in Brazil (Prado et al. 2002), whereas *Dictyotrypeta incisa* has been reared from the capitula of *S. maculatus* and *Smallanthus riparius* (Kunth) Harold Robinson in Mexico and Guatemala (Norrbom et al. 2010). The genus *Rhynencina* contains four Neotropical and one Nearctic species (Norrbom et al. 1998). The biology of these species is also poorly understood, as only the host plant of *Rhynencina emphanes* (Steyskal) is known, as these develop on *Espeletia* sp. flowers in Colombia (Freidberg and Norrbom 2000); likewise, *Rhynencina longirostris* Johnson feeds on *Smallanthus uvedalius* (L.) Mackenzie ex Small in North America, whose biology has already been studied (Steck and Sutton 2000, Steck et al. 2003).

The presence of Tephritinae species on their host plants is influenced by several characteristics, for instance, plant height, flowering time, and spatial host abundance (Walton et al. 1990, Rivero-Lynch and

Jones 1993, Fondriest and Price 1996, Williams et al. 2001, Walker et al. 2008), in addition to climatic features as precipitation and temperature (Solbreck and Sillén-Tullberg 1986, Milton 1995). Some authors have reported significant differences in the levels of parasitism under natural conditions, suggesting that parasitism rates may be associated with host range and the particular biology of each fly species involved (Duan and Messing 1998, Alyokhin and Messing 2003, Knio et al. 2007, Edwards et al. 2009). Especially, seasonal variation during flowering season and development time of capitula may influence their rates of infestation and life cycles (English-Loeb and Karban 1992, Alyokhin et al. 2002, Woods et al. 2008, Duguma et al. 2009). However, in most of the studies, flower head infestation throughout continuous seasonal cycle has not been assessed, which allows monitoring temporal changes on infestation patterns. The aim of this study was to assess the seasonal dynamics of infestation yielded by *Dictyotrypeta* sp. and *R. spilogaster* on the capitula of *S. maculatus*, as well as recording the occurrence of natural parasitism along its entire flowering season, in a coffee-growing region of central Mexico.

Materials and Methods

Study Area. The study sites were located in the montane cloud forest in the central region of Veracruz. Currently, this kind of vegetation occurs as a fragmented community, composed of natural forest patches and secondary growth species, particularly as a result of the presence of shaded coffee plantations and grasslands (Williams-Linera 2007). Field work was conducted from August to November 2008, in the neighboring towns of Coatepec (19° 27' N, 96° 06' W; 1,252 m altitude) and Teocelo (19° 23' N, 96° 58' W; 1,218 m altitude), both with similar climatic conditions. Highest rainfall occurred in June (571.5 mm), and the driest month was March (24.2 mm). The highest average temperature occurred in May (24.9°C), while the lowest was recorded in November (18.3°C) (CONAGUA 2008) (Fig. 1).

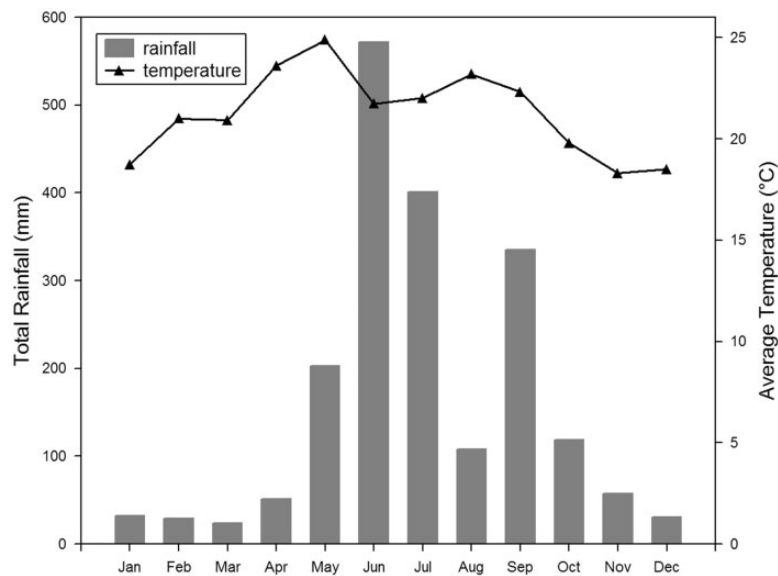


Fig. 1. Climatic conditions of monthly rainfall (mm) and average temperatures (°C) in the studied locality during the yearly cycle January–December 2008.

The Host Plant. *S. maculatus* is a Mesoamerican plant that occurs throughout extensive areas of Mexico, including the state of Veracruz, but its range goes as far as Panama. It is a herbaceous perennial, 1 to 2 m height (exceptionally reaching up to 5 m), with flower heads ranging from 1 to 2 cm in width, found growing in groups or panicles and rarely solitary (McVaugh 1984, Villaseñor and Espinosa 1998, Rzedowski 2001). Previous observations in the study area showed that *S. maculatus* grows in open disturbed areas, on roadsides, and coffee plantations, appearing in irregular groups from a few individuals up to several dozens of them, with a flowering cycle starting from July–August stretching to November–December (V.H.O., unpublished data).

Flower Head Sampling. During the flowering season of the host plant, 16 weekly collections of mature capitula were done, characterized by their ligulate and disc flowers dry, and by the presence of peripheral mature achenes. Assessing the extent of flower head infestation, collections were random among plants, and sample size was determined by the abundance and availability of mature capitula. Each time, the analyzed samples were obtained from different groups of plants, because *S. maculatus* is a weed periodically removed by coffee growers. Samples were placed in fine mesh bags and transported to the laboratory, where they were separated and placed in plastic chambers of 250 ml with adequate ventilation, and all information was recorded in a data matrix. Every week, each capitulum and its mature achenes were carefully dissected under the stereomicroscope, to detect and quantify the presence of immature stages. Part of the larvae and pupae sampled were kept in rearing chambers until emergence of adults. Identification of the specimens was done with reference to the characteristic damage into the achenes or receptacle, and by the size and color of pupae. Voucher adult specimens were pinned and deposited in the Entomological Collection of the Instituto de Ecología (IEXA), whereas botanical specimens were placed at the Herbarium of the Instituto de Ecología (XAL), both of these housing Instituto de Ecología A.C. (INECOL) institutional collections (Xalapa, Mexico).

Statistical Analysis. To evaluate the weekly proportion of infested capitula, linear regression of arcsine-transformed data ($\arcsin \sqrt{\text{proportion}}$) were performed; because flower head production exhibited a lot of variation along the sampling period, a correction factor was applied as follows: $CF = \sqrt{1 - n/N}$, where n is the weekly sample size and N the population size sampled (Zar 2010). Mean of individuals per sample within capitula was estimated by linear regression analysis (including polynomial of second and third order), and likelihood-ratio

tests were used for comparisons of these models (Crawley 2007). Possible relationships between some of the dependent variables along the seasonal cycle (e.g., density of individuals per capitulum and fly species, and number of individuals per fly species) were assessed using Spearman's rank correlations. All tests were performed using the R program (Development Core Team 2011).

Results

During the annual flowering cycle of *S. maculatus*, 16 weekly samples accounted for 1,017 of mature capitula. Infestations by two species occurred throughout the entire season, occupying 51.5% of the flower heads. However, *Dictyotrypeta* sp. infested 11.3%, representing about one-fifth of all infested capitula; whereas *R. spilogaster* resulted more abundant infesting four times as many capitula (42.8%), and both species were found together in only 2.6% of the capitula examined (Table 1).

Seasonality. The accumulated infestation by *Dictyotrypeta* sp. showed differences in terms of abundance, presenting low rates of infested capitula (13.9%) during the first half of the cycle (August–September), with a notable increase in the second half (October–November), occupying 86.1% of them. On the other hand, in *R. spilogaster*, the highest infestations occurred during the first half of the season (64.2%), decreasing in the second half to 35.8% (Fig. 2). The linear regression analysis showed that the capitula infested by *Dictyotrypeta* sp. increased significantly toward the end of the season ($R^2 = 0.28$, $F_{1,14} = 5.55$, $P = 0.033$), contrasting with a decrease in the infestation by *R. spilogaster*, which also proved to be significant ($R^2 = 0.34$, $F_{1,14} = 7.45$, $P = 0.016$) to the end of the flowering cycle (Fig. 3).

Average density of individuals per capitulum infested by *R. spilogaster* was 2.83 individuals per capitulum (± 1.8 SD), the most frequent ratio was 2–3 specimens observed in 41.5% of cases, a single specimen in 28.7%, 4–6 specimens in 25%, and 7–10 specimens in only 4.8% of the capitula. High densities of individuals (≥ 3 individuals per capitula) mainly occurred through September and early October. In contrast, lower densities were observed starting August and extending from late October to November. Comparisons of the rate of individuals observed throughout the flowering season, using the third-order polynomial regression analysis, showed significant differences ($R^2 = 0.55$, $F_{3,12} = 4.98$, $P = 0.017$; Fig. 4), and these infestation rates were positively correlated with increases in the capitula infested (Spearman's rank correlation, $\rho = 0.70$, $P = 0.001$).

Table 1. Capitula infested by two tephritid species throughout the flowering season of *S. maculatus*

Samples (weeks)	Sampling date (2008)	Capitula examined	Correction factor	Infestation by sample	Capitula infested (%)		
					<i>Dictyotrypeta</i> sp.	<i>Rhynencina spilogaster</i>	Both species
S1	8 Aug.	44	0.9781	57.80	11.12	53.35	6.67
S2	13 Aug.	75	0.9624	46.20	7.70	41.06	2.57
S3	23 Aug.	101	0.9490	56.38	1.88	55.44	0.94
S4	30 Aug.	35	0.9826	58.96	0.00	58.96	0.00
S5	5 Sept.	39	0.9806	67.89	2.51	67.89	2.51
S6	10 Sept.	37	0.9816	58.37	0.00	58.37	0.00
S7	17 Sept.	42	0.9791	55.95	0.00	55.95	0.00
S8	24 Sept.	92	0.9537	74.64	2.07	73.60	1.04
S9	1 Oct.	20	0.9901	94.06	14.85	84.16	4.95
S10	7 Oct.	83	0.9583	65.81	8.08	61.19	3.46
S11	22 Oct.	25	0.9876	51.36	35.55	27.65	11.85
S12	29 Oct.	76	0.9619	46.83	6.33	44.30	3.80
S13	5 Nov.	142	0.9276	20.90	15.68	6.53	1.31
S14	12 Nov.	36	0.9821	60.02	54.56	16.37	10.91
S15	19 Nov.	40	0.9801	41.66	4.90	36.76	0.00
S16	26 Nov.	130	0.9339	28.02	20.83	9.34	2.16
Total		1,017		524 (51.5%)	115 (11.3%)	436 (42.8%)	27 (2.6%)

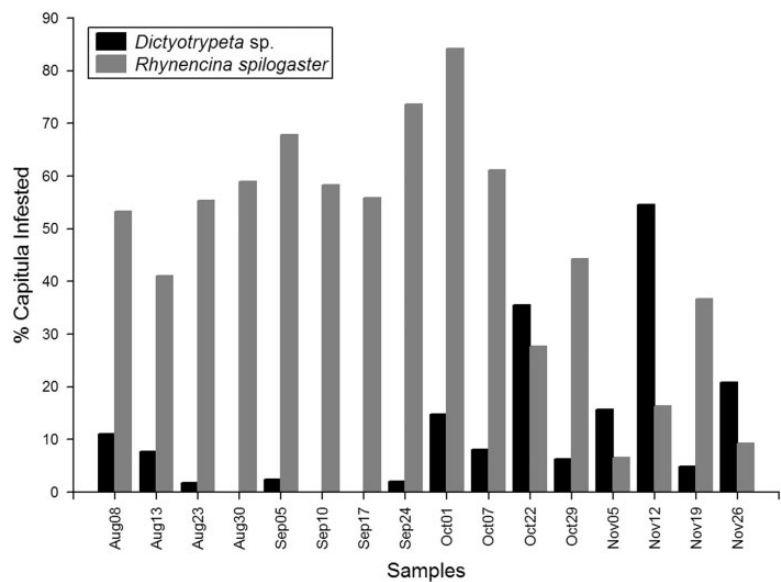


Fig. 2. Proportion of the capitula infested by *Dictyotrypeta* sp. and *Rhynencina spilogaster* along the flowering season of *S. maculatus*.

Meanwhile, the average density of *Dictyotrypeta* sp. individuals was 1.40 individuals per capitulum (± 0.7 SD); thus, most of the capitula was accounted to be infested by a single specimen in 68.7% of cases, two specimens in 23.5%, and 3–5 specimens in only 7.8% of the capitula. However, tested comparisons of the rate of individuals inside the capitula throughout the flowering season neither showed a correlation ($P > 0.1$; Fig. 4) nor was there a correlation between average of individuals and the number of capitula infested (Spearman’s rank correlation, $\rho = 0.31$, $P = 0.12$).

Immature Stages and Infestation. Total infestation by *Dictyotrypeta* sp. was represented by 162 specimens (larvae 15.4%, pupae 84.6%), and correlation analysis showed that individual abundance increased significantly toward the second half of the season (Spearman’s rank correlation, $\rho = 0.51$, $P = 0.019$). Larvae were absent from the initial two-thirds of the season, appearing later into this period; meanwhile, pupae were observed throughout the entire cycle, with the highest abundance focused in the second half (Fig. 5A). Both larvae and pupae were found mostly within the mature achenes (82.7%), but

they were also discovered inside the receptacle (17.3%). Achenes infested by larvae of this species showed a typical damage, indicated by an orifice covered with waste from feeding, while damage to the receptacle was recognized by the presence of galleries that lead toward an achene.

R. spilogaster was recorded by a total of 1,234 individuals, without significant variations along the entire season (Spearman’s rank correlation, $\rho = -0.41$, $P = 0.055$). In this case, most individuals recovered were larvae (80.2%) appearing throughout the flowering period, while pupae accounted for only 19.8% of the specimens, especially observed in the early weeks of the flowering season (Fig. 5B). Larvae and pupae were found exclusively within the mature achenes without apparent traces of infestation, so its presence was detected just dissecting each one of them.

Parasitism. To assess natural parasitism in *Dictyotrypeta* sp., 118 pupae were kept alive in emergence chambers. Here, 22 adult flies were obtained in a rate of emergence of 15.7 days (± 3.1 SD), while from remaining pupae 88 Hymenopteran parasitoids were recovered,

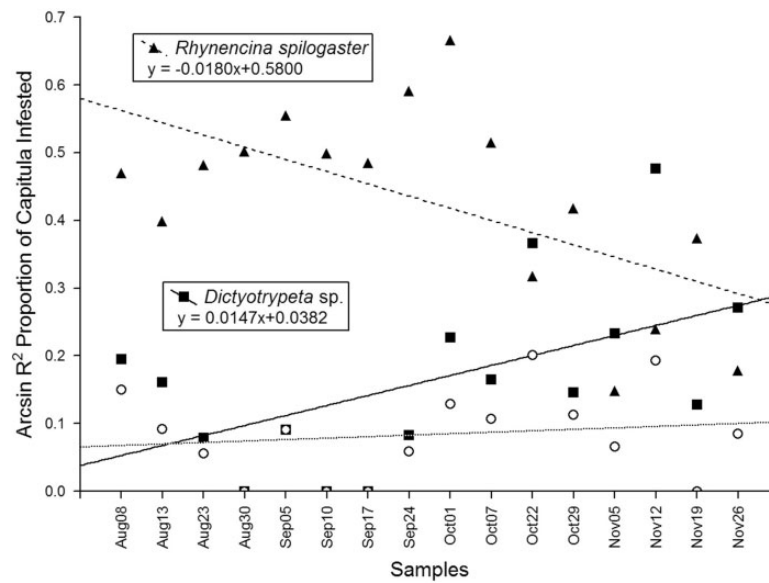


Fig. 3. Correlation analysis of the proportion of capitula infested by two Tephritinae species throughout the flowering cycle of *S. maculatus* (August–November 2008).

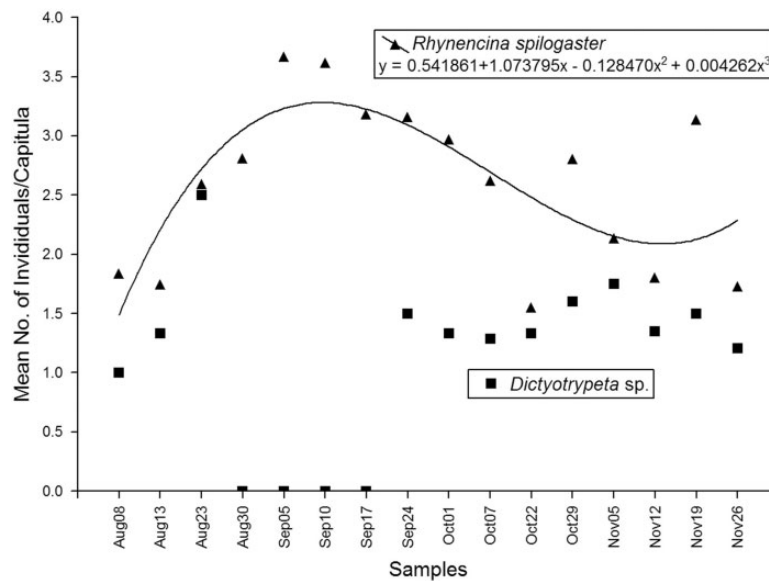


Fig. 4. Analysis of the density of tephritid individuals infesting the capitula of *S. maculatus* (August–November 2008): mean of individuals observed in *R. spilogaster* showed significant differences ($P < 0.05$).

representing 74.6% of parasitism in the sample. All parasitoid specimens belong to five species from the families Figitidae sp. 1 (48) and Pteromalidae sp. 1 (37), followed by three species of Eupelmidae (1), Eurytomidae (1), and Eulophidae (3), respectively. The average times of emergence were as follows: Figitidae sp. 1 = 79.7 days (± 35.4 SD) and Pteromalidae sp. 1 = 50.9 days (± 34.3 SD), while emergence times of the single specimens of Eulophidae, Eupelmidae, and Eurytomidae ranged from 15 to 19 days (Fig. 6A). All parasitoids were reared from a single puparium, excluding the three Eulophid specimens that showed a gregarious parasitism.

Likewise, 135 puparia of *R. spilogaster* were kept in the emergence chambers, and 69 of them remained alive for 303.9 days (± 71.2 SD), whereas 66 parasitoids of Pteromalidae sp. 2 emerged from the other puparia, which came into diapause because adults lasted for 303 days (± 134.2 SD) after collection, and accounted for 48.9% of parasitism in the sample (Fig. 6B).

Discussion

Insects that share food resources follow two survival strategies, either an avoidance strategy or maximizing their competitiveness (Zwölfer 1979). In Tephritinae infesting a single host, phenomena of interspecific competition have been reported, but there are also evidences of avoidance strategies during the seasonality of the host (Michaelis 1986, Straw 1989a, Knio et al. 2001, Story 2002, Holt and Zwölfer 2007). Results of this study showed differences in temporary patterns of infestation by *Dictyotrypeta* sp. and *R. spilogaster*, suggesting distinct strategies of resource exploitation, as only 2.6% of the capitula were simultaneously occupied by two species.

The flowering season of the host offered a constant resource supply for both tephritids; however, *R. spilogaster* presented populations approximately four times larger than *Dictyotrypeta* sp. These results can be related to the particular biology of each species, because the mature larvae of the former are small-size specimens, and each

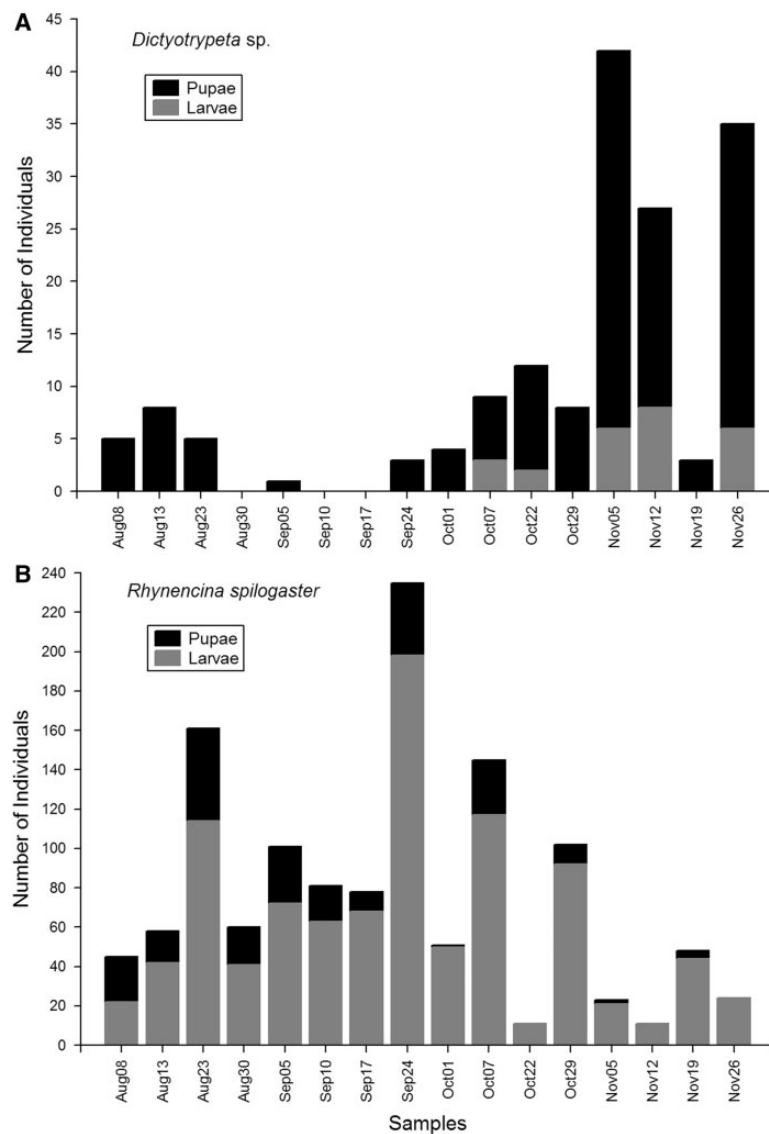


Fig. 5. Abundance of larvae and pupae recovered from 16 samples along flowering season of *S. maculatus* in central Veracruz, México: (A) *Dictyotrypeta* sp. and (B) *R. spilogaster*.

individual feeds exclusively on a single achene. Although the larvae of the latter are twice as large, their food requirements are greater, and therefore, it was found in the achenes and in the receptacle. The habit of feeding in the receptacle is a facultative mode of resource exploitation, and it may provide additional nutrients for continued development within the capitulum (Knio et al. 2001).

The average density of 1.4 individuals observed in *Dictyotrypeta* sp. suggests that females usually lay 1–2 eggs per capitulum and probably do so during its early development, because damage was always observed in the center of the receptacle, and in most of the cases, a later transferral took place to the achene. Low densities per capitulum indicated a small clutch size as a strategy to maximize the probability that offspring found enough food resources for development, but it may also indicate the existence of a marking pheromone after oviposition, which would be recognized by conspecific females (Straw 1989b; Pittara and Katsoyanos 1990; Lalonde and Roitberg 1992a,b). In the case of *R. spilogaster*, the average density of 2.8 individuals per capitulum suggests that females made multiple ovipositions, depositing a single egg in each achene, which provides enough resources for individual development, whereas an increase in the density of individuals per capitulum was correlated with population growth along the season.

In *Dictyotrypeta* sp., only pupae were found at the beginning of the season, suggesting that oviposition may occur during the early development of the capitula. However, to the end of the season (S10–S16), larvae also appeared, indicating a second generation of this species. From the start of the season, some adults emerged in an average time of 15 days (range 9–22), whereas during the second half of the season, the two most abundant parasitoid species emerged in an elapsed time of 50–79 days, suggesting that second generation could enter diapause. Contrastingly, *R. spilogaster* is clearly a univoltine species with a long life cycle that entered diapause, because larvae as pupae were present throughout the entire season, and larvae were represented by 80.2% of the specimens, while 19.8% were pupae remaining viable for up to 303 days on average. Nearly identical times of emerged parasitoids were also recorded. Similar observations were done in the North American sister species, *R. longirostris* that breeds in the capitula of *S. uvedalensis*, showing that flies and parasitoids exhibited a single annual generation (Steck et al. 2003).

Mature achenes per capitulum produced by *S. maculatus* were estimated in 13.03 (± 2.4 SD; $N = 276$), so the total number of damaged achenes by two tephritids was 20.6% (*Dictyotrypeta* sp. 2.02% and *R. spilogaster* 18.6%). It means that nearly one-fifth of the seeds were

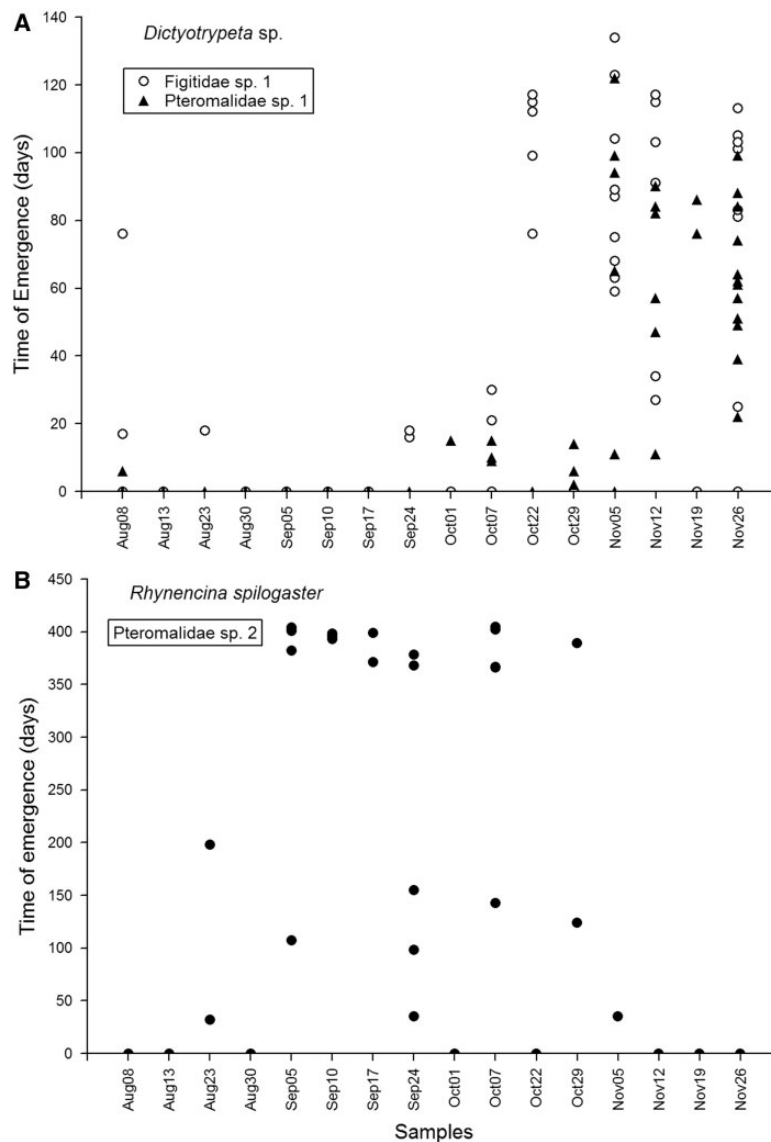


Fig. 6. Parasitoids recovered and times of emergence in two Tephritinae species: (A) Figitidae sp. 1 and Pteromalidae sp. 1, parasites of *Dictyotrypeta* sp. and (B) Pteromalidae sp. 2, parasite of *R. spilogaster*.

predated, which represents a relatively low impact on the reproductive success of the host plant. However, the damage to the receptacle by the former species may have an indirect effect on the seed production, because studies on other receptacle feeders, such as *Chaetostomella cylindrica* and *Terellia colon*, suggest that they may restrict the flow of nutrients, reducing the fitness and weight of healthy seeds (Kinkorová and Micková 2006, Koprdoval and Martinková 2006).

There are evidences of high spatial and temporal variability in predispersal seed predation by insect herbivores (Kolb et al. 2007, Abdala-Roberts et al. 2010). Moreover, the action of the natural parasitism found in some Tephritinae species used for control of weeds could also exert a reduction in their effectiveness, limiting their establishment and impact as agents for biological control (Marshall et al. 2004, Edwards et al. 2009).

Results of multiple interactions between these tephritids and their parasitoids were restricted to single-year sampling at a single locality. Further research on several cycles and localities are required to make generalizations of these assertions. Multiple interspecific interactions may also affect whether there is a reduction or an increase in seed predation (Lamp and McCarty 1982, Groenteman et al. 2007, Tonkel and Piper 2009). Moreover, species of Coleoptera and Lepidoptera were observed either in the achenes, the receptacle, or both, whose trophic

interactions are being assessed as a whole (V.H.O., unpublished data). This will provide a comprehensive view of the impact of these herbivores on the reproductive success of the host plant.

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References Cited

- Abdala-Roberts, L., V. Parra-Tabla, C. Díaz-Castelazo, L. Salinas-Peba, and G. H. Delfin. 2010. Spatial variation in the strength of a trophic cascade involving *Ruellia nudiflora* (Acanthaceae), an insect seed predator and associated parasitoid fauna in Mexico. *Biotropica* 42: 180–187.
- Almeida, A. M., C. R. Fonseca, P. I. Prado, M. Almeida-Neto, S. Diniz, U. Kubota, M. R. Braun, L. G. Raimundo, L. A. Anjos, T. G. Mendonça,

- et al. 2006. Assemblages of endophagous insects on Asteraceae in São Paulo Cerrados. *Neotrop. Entomol.* 35: 458–468.
- Alyokhin, A. V., and R. H. Messing. 2003. Parasitism of Hawaiian non-frugivorous fruit flies (Diptera: Tephritidae) by an exotic parasitoid, *Eurytoma tephritidis* Fullaway (Hymenoptera: Eurytomidae). *Proc. Hawaiian Entomol. Soc.* 36: 29–37.
- Alyokhin, A. V., R. H. Messing, and J. J. Duan. 2002. Infestation of *Elephantopus mollis* (Asteraceae) flowerheads by *Tetraulicaria obscuriventris* (Diptera: Tephritidae) on Kauai, Hawaiian islands. *Entomol. News* 113: 247–252.
- (CONAGUA) Comisión Nacional del Agua. 2008. Weather information provided by the National Water Commission. Organismo Cuenca Golfo-Centro, Xalapa, Veracruz, México.
- Crawley, M. J. 2007. *The R book*. John Wiley, West Sussex, England.
- Development Core Team. 2011. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria, (<http://www.R-project.org>) (accessed 22 June 2011, version 2.13.0).
- Duan, J. J., and R. H. Messing. 1998. Effect of *Tetrastichus giffardianus* (Hymenoptera: Eulophidae) on nontarget flowerhead-feeding tephritids (Diptera: Tephritidae). *Environ. Entomol.* 27: 1022–1028.
- Duguma, D., T. J. Kring, and R. N. Wiedenmann. 2009. Seasonal dynamics of *Urophora quadrifasciata* on spotted knapweed in the Arkansas Ozarks. *Can. Entomol.* 141: 70–79.
- Edwards, P. B., R. J. Adair, R. H. Holtkamp, W. J. Wanjura, A. S. Bruzese, and R. I. Forrester. 2009. Impact of the biological control agent *Mesoclanis polana* (Tephritidae) on bitou bush (*Chrysanthemoides monilifera* subsp. *rotundata*) in eastern Australia. *Bull. Entomol. Res.* 99: 51–63.
- English-Loeb, G. M., and R. Karban. 1992. Consequences of variation in flowering phenology for seed head herbivory and reproductive success in *Erigeron glaucus* (Compositae). *Oecologia* 89: 588–595.
- Fondriest, S. M., and P. W. Price. 1996. Oviposition site resource quantity and larval establishment for *Orellia occidentalis* (Diptera: Tephritidae) on *Cirsium wheeleri*. *Environ. Entomol.* 25: 321–326.
- Freidberg, A., and A. L. Norrbom. 2000. A generic reclassification and phylogeny of the tribe Myopitini (Tephritinae), pp. 581–627. In M. Aluja and A. L. Norrbom (eds.), *Fruit flies (tephritidae): phylogeny and evolution of behavior*. CRC Press, Boca Raton, Florida, U.S.A.
- Groenteman, R., D. Kelly, S. V. Fowler, and G. W. Bourdôt. 2007. Interactions between nodding thistle seed predators. *New Zeal. Plant Prot.* 60: 152–157.
- Headrick, D., and R. D. Goeden. 1998. The biology of nonfrugivorous tephritid fruit flies. *Ann. Rev. Entomol.* 43: 217–241.
- Holt, C., and H. Zwölfer. 2007. Life history and behaviour of *Terellia longicauda* (Meigen), a highly specialised tephritid of the woolly thistle, *Cirsium eriophorum*. *Stud. Dipterol.* 14: 331–340.
- Kinkorová, J., and M. Micková. 2006. Life history of the European tephritid fly *Chaetostomella cylindrica* (Diptera: Tephritidae) and its possible use as a biocontrol agent in the USA. *Proc. Entomol. Soc. Wash.* 108: 51–61.
- Knio, K. M., R. D. Goeden, and D. H. Headrick. 2001. Resource utilization in the sibling species *Trupanea nigricornis* (Coquillett), a polyphage, and the narrowly oligophagous *T. bisetosa* (Coquillett) (Diptera: Tephritidae) in Southern California. *Proc. Entomol. Soc. Wash.* 103: 946–961.
- Knio, K. M., D. Goeden, and D. H. Headrick. 2007. Natural enemies of the cryptic and sympatric species, *Trupanea nigricornis* (Coquillett), a polyphage, and the narrowly oligophagous *T. bisetosa* (Coquillett) (Diptera: Tephritidae). *Proc. Entomol. Soc. Wash.* 109: 187–197.
- Kolb, A., J. Ehrlén, and O. Eriksson. 2007. Ecological and evolutionary consequences of spatial and temporal variation in pre-dispersal seed predation. *Perspect. Plant Ecol. Evol. Syst.* 9: 79–100.
- Koprdoval, S., and Z. Martinková. 2006. Pre-dispersal predation and seed damage of *Centaurea scabiosa* L. (Asteraceae). *J. Plant Dis. Prot.* 20: 305–308.
- Lalonde, R. G., and B. D. Roitberg. 1992a. Field studies of seed predation in an introduced weedy thistle. *Oikos* 65: 363–370.
- Lalonde, R. G., and B. D. Roitberg. 1992b. Host selection behavior of a thistle-feeding fly: choices and consequences. *Oecologia* 90: 534–539.
- Lamp, W. O., and M. K. McCarty. 1982. Biology of predispersal seed predators of platte thistle, *Cirsium canescens*. *J. Kansas Entomol. Soc.* 55: 305–316.
- Marshall, J. M., R. A. Burks, and A. J. Storer. 2004. First host record for *Pteromalus cardui* (Hymenoptera: Pteromalidae) on *Urophora quadrifasciata* (Diptera: Tephritidae) in spotted knapweed (*Centaurea biebersteinii*, Asteraceae) in Michigan, U.S.A. *Entomol. News* 115: 273–278.
- McVaugh, R. 1984. *Polymnia*. Flora Novo-Galiciana: a descriptive account of the vascular plants of western Mexico. The University of Michigan Press, Ann Arbor, Michigan, U.S.A.
- Michaelis, H. 1986. Competition of *Urophora stylata* F. and *Terellia serratulae* L. (Dipt. Tephritidae) in the flowerheads of *Cirsium vulgare*, pp. 191–199. In M. Mangel (ed.), *Pest control: operations and systems analysis in fruit fly management*. Springer-Verlag, Berlin, Heidelberg, New York.
- Milton, S. J. 1995. Effects of rain, sheep and tephritid flies on seed production of two arid Karoo shrubs in South Africa. *J. Appl. Ecol.* 32: 137–144.
- Norrbom, A. L., and P. I. Prado. 2006. New genera and host plant records of Asteraceae-feeding Tephritidae (Diptera) from Brazil. *Zootaxa* 1139: 1–17.
- Norrbom, A. L., L. E. Carroll, F. C. Thompson, I. M. White, and A. Freidberg. 1998. Systematic database of names, pp. 65–251. In F. C. Thompson (ed.), *Fruit fly expert identification system and systematic information database*. Backhuys Publishers, Leiden, Netherlands.
- Norrbom, A. L., B. D. Sutton, G. J. Steck, and J. Monzón. 2010. New genera, species and host plant records of Nearctic and Neotropical Tephritidae (Diptera). *Zootaxa* 2398: 1–65.
- Pittara, I. S., and B. I. Katsoyannos. 1990. Evidence for a host-marking pheromone in *Chaetorellia australis*. *Entomol. Exp. Appl.* 54: 287–295.
- Prado, P. I., T. M. Lewinsohn, A. M. Almeida, A. L. Norrbom, B. D. Buys, A. C. Macedo, and M. B. Lopes. 2002. The fauna of Tephritidae (Diptera) from capitula of Asteraceae in Brazil. *Proc. Entomol. Soc. Wash.* 104: 1007–1028.
- Prado, P. I., A. L. Norrbom, and T. M. Lewinsohn. 2004. New species of *Tomoplagia* Coquillett (Diptera: Tephritidae) from capitula of Asteraceae in Brazil. *Neotrop. Entomol.* 33: 189–211.
- Rivero-Lynch, A. P., and T. H. Jones. 1993. The choice of oviposition site by *Terellia ruficauda* on *Cirsium palustre*. *Acta Oecol.* 14: 643–651.
- Rzedowski, J. 2001. Compositae, pp. 764–975. In G. Calderón and J. Rzedowski (eds.), *Flora fanerogámica del Valle de México*, segunda edición. Instituto de Ecología AC y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Pátzcuaro, México.
- Solbreck, C., and B. Sillén-Tullberg. 1986. Seed production and seed predation in a patchy and time-varying environment. Dynamics of a milkweed-tephritid fly system. *Oecologia* 71: 51–58.
- Steck, G. J., and B. D. Sutton. 2000. New records for Tephritidae (Diptera) in Great Smoky Mountains National Park. *Insecta Mundi* 14: 256.
- Steck, G. J., B. D. Sutton, and D. Defoe. 2003. Biology of *Rhynencina longirostris* Johnson (Diptera: Tephritidae). *Proc. Entomol. Soc. Wash.* 105: 542–547.
- Story, J. 2002. Spotted knapweed, pp. 169–180. In F. V. Driesche, B. Blossey, M. Hoodle, S. Lyon, and R. Reardon (eds.), *Biological control of invasive plants in the eastern United States*. United States Department of Agriculture, Forest Service Publication, Morgantown, West Virginia, U.S.A.
- Straw, N. A. 1989a. The timing of oviposition and larval growth by two tephritid fly species in relation to host-plant development. *Ecol. Entomol.* 14: 443–454.
- Straw, N. A. 1989b. Evidence for an oviposition-detering pheromone in *Tephritus bardanae* (Schränk) (Diptera: Tephritidae). *Oecologia* 78: 121–130.
- Tonkel, K. C., and G. L. Piper. 2009. Patterns in resource partitioning by insect biological control agents of yellow starthistle (*Centaurea solstitialis* L.) in Washington. *Northwest Sci.* 83: 16–24.
- Villaseñor, J. L., and F. J. Espinosa. 1998. *Catálogo de Malezas de México*. Universidad Nacional Autónoma de México and Fondo de Cultura Económica. México D.F., México.
- Walker, M., S. E. Hartley, and T. H. Jones. 2008. The relative importance of resource and natural enemies in determining herbivore abundance: thistles, tephritids and parasitoids. *J. Anim. Ecol.* 77: 1063–1071.
- Walton, R., A. E. Weis, and J. P. Lichter. 1990. Oviposition behavior and response to plant height by *Eurosta solidaginis* Fith (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 83: 509–514.
- Williams, I. S., T. H. Jones, and S. E. Hartley. 2001. The role of resources and natural enemies in determining the distribution of an insect herbivore population. *Ecol. Entomol.* 26: 204–211.
- Williams-Linera, G. 2007. El bosque de niebla del centro de Veracruz: ecología, historia y destino en tiempos de fragmentación y cambio climático. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad e Instituto de Ecología AC, Xalapa, México.
- Woods, D. M., M. J. Pitcairn, D. B. Joley, and C. E. Turner. 2008. Seasonal phenology and impact of *Urophora sirumaseva* on yellow starthistle seed production in California. *Biol. Control* 47: 172–179.
- Zar, J. H. 2010. *Biostatistical analysis*, 5th ed. Prentice Hall, Upper Saddle River, New Jersey, U.S.A.
- Zwölfer, H. 1979. Strategies and counter-strategies in insect population systems competing for space and food in flower heads and plant galls. *Fortschr. Zool.* 25: 331–353.

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