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IRRIGATION AND FERTILIZATION OF *CHRYSOTHAMNUS NAUSEOSUS* (ASTERACEAE) AFFECT THE ATTACK AND GALL GROWTH OF *RHOPALOMYIA CHRYSOTHAMNI* (CECIDOMYIIDAE)

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Abstract.

Environmental factors can affect the suitability of host plants for the survival and development of galling insects. The effect of nutrients and water availability on the development of galls induced by Rhopalomyia chrysothamni *(Diptera: Cecidomyiidae) on* Chrysothamnus nauseosus *subsp.* hololeucus *(Asteraceae) was tested. The study was conducted in a xeric area with no signs of disturbances in Coconino National Forest, Arizona, USA. Individuals of* C. nauseosus *randomly selected underwent three treatments of water and nutrients availability. At the end of the growing season, the number of attacked plants, abundance and the development of galls in each treatment were evaluated. The differences in habitat quality simulated by the fertility and humidity conditions influenced both the number of attacked plants and the growth of galls. Plants with lower hydric-nutritional quality were more attacked by the galling insect. Otherwise, when both water and nutritional stresses were relieved plants developed galls with higher dry biomass and density. Therefore, this field experimental study indicates that while galling females attacked plants more in xeric environments, the galls grew larger in relatively more mesic conditions. The results showed a trade-off between the quantity and quality of galls of* R. chrysothamni *depending on the nutritional quality of the host plants.*

Key words: *environmental stress; gall development; host plant quality; insect galls; resource availability.*

Introduction

During the larval stage gall-inducing insects cannot move on the host plant, having evolved a unique way of draining resources of distant plant organs for their maintenance (e.g. Kirst & Rapp 1974; Price et al. 1987; Larson & Whitham 1991; Silva et al. 1996; Fernandes et al. 1999; Tooker & Helms 2014). Probably, this evolutionary path led them to an extreme of the specialist-generalist gradient as they are extremely specific about the choice of the host (Mani 1964; Price et al. 1998; Carneiro et al. 2009). In general, adult females of galling insects oviposit in meristematic tissues of the host plant and induce gall development, where their offspring grow. The galls provide the larvae with high quality food and protection from the adverse external environment and natural enemies (Price et al. 1986, 1987; Fernandes & Price 1991). The incapacity to move in order to explore the mosaic of nutrients of different qualities and degree of availability on the host plant were probably key factors in the evolution of the ability to divert plant resources and use them for its own development.

Galling insects may cause variable impacts on host plant performance depending on the drain strength and gall abundance (Fay et al. 1996; Gonçalves-Alvim et al. 1999, 2001; Fernandes et al. 2012; Xiang et al. 2020). But despite the efficiency of these herbivores in obtaining resources, the quality and amount of resources offered by the host plant play a crucial role in the choice made by females and subsequent development of their larvae (Price et al. 1990; Fernandes & Price 1992; Araújo et al. 2003; Fonseca & Fleck 2007; Santos et al. 2007; Miller & Raman 2019; reviewed by Cornelissen et al. 2008).

The interactions of host plant quality and success of galling insects are influenced by the habitat (Fernandes & Price 1988; Cuevas-Reyes et al. 2004; 2011). Several studies have indicated the existence of a greater richness and abundance of galling insects in xeric habitats as opposed to mesic habitats.

The greatest success of galling insects in xeric habitats is conditioned by hydric-nutritional stress of the environment and the host plant (Fernandes & Price 1988, 1992). Under conditions of nutrient deficiency, particularly phosphorus (Fernandes & Price 1991), plants become more sclerophyllous with leathery leaves, which reduce the likelihood of abscission (Fernandes & Price 1991; Gonçalves-Alvim & Fernandes 2001; Fagundes et al. 2001). Besides that, they have higher concentration of tannins and other defense compounds which apparently protect galling insects against pathogens and predators (Fernandes & Price 1988, 1992; Fernandes et al. 1994; Mithöfer & Boland 2012; Hall et al. 2017). Thus, the host plant tissues in xeric environments become large nutritive reserves and even provide shelter and protection to the larvae of galling insects, indicating that soil fertility is of considerable importance in the relationship between environmental quality, richness and performance of galling insects (Fernandes & Price 1991; Blanche & Westoby 1995; Gonçalves-Alvim & Fernandes 2001; Cuevas-Reyes et al. 2004, 2011).

Plants in fertilized soils grow better and larger. The additional nutrients can be diverted away from growth and reproduction and used to produce larger galls (e.g. Rossi & Stiling 1998; Cuevas-Reyes et al. 2004). Therefore, there are good indications that both the distribution of galls per plant and growth of galls are related to the distinct hydric-nutritional status of plant communities and habitats. In this context, the present study aimed to evaluate the effect of increasing water and nutrient availability in the host plant *Chrysothmanus nauseosus* subsp. *hololeucus* (A. Gray) H. M. Hall & Clem. (Asteraceae) on the oviposition by females of *Rhopalomyia chrysothamni* Felt (Diptera: Cecidomyiidae) and gall growth in the Sonoran Desert, USA. Galls of this cecidomyiid species are found in high abundance and are easily seen year-round, hence providing a good model for the study on the role of plant and habitat quality on insect gall numbers per plant and gall growth. In this study we tested the hypothesis that plants in habitats characterized by higher nutritional and water stresses have higher number of galls per plant and increased growth of galls.

Materials and Methods

Study area and selected species

The study was conducted in Schultz Pass (U.S. Forest Service Road 420, 2.4 km away from I-89 highway), north of Flagstaff , Arizona , USA , at an altitude of 2.400 meters in 1988. This area is characterized as a xeric environment with completely preserved vegetation and is located within the Coconino National Forest (35° 11' 15.6" N, 111° 40' 29.6" W).

Chrysothamnus nauseosus subsp. *hololeucus* (Asteraceae), from now on just *C. nauseosus* (Fig. 1a), is a morphologically diverse and abundant shrub species in the study area, distributed from southwestern Canada to northern Mexico (Anderson 1966; Toft & Fraizer 2003). This species is erect, thin and flexible with branches covered by a dense layer of white or greenish-gray trichomes. It has narrow leaves and it flowers late in summer (Anderson 1966). *Chrysothamnus nauseosus* is a host of a large number of galling insects (Floate et al. 1996; Fernandes et al. 2000b). This study focused on galls induced by *Rhopalomyia chrysothamni* (Cecidomyiidae: Diptera). The stem galls are conical in shape, a light green color, and with bunched white short trichomes (Fig. 1b) (Gagné 1989; Fernandes et al. 2001).

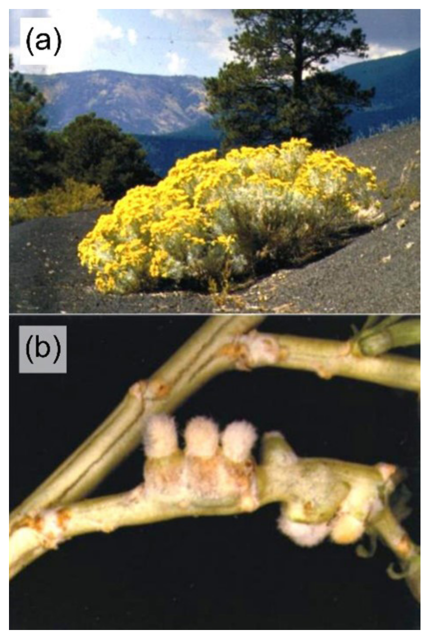

Figure 1. Studied host plant – galling insect system. a) Host plant *Chrysothamnus nauseosus* subsp. *hololeucus* (Asteraceae) in Schultz Pass, Arizona, USA. b) Stem galls induced by *Rhopalomyia chrysothamni* (Diptera: Cecidomyiidae).

Preparation of the Experiment

Sixty individuals of *C. nauseosus* were randomly marked in the field and randomly divided into three groups of 20 individuals per group. Before the experimental intervention, all branches containing stem galls of *R. chrysothamni* or any other types of galls were removed with the aid of pruning clippers. After this thinning of galled branches, the selected individuals had similar heights and numbers of branches. Each treatment group of plants was submitted to a nutrient and/or water application. The control treatment consisted of individuals that received neither irrigation nor fertilization, representing the xeric condition of the natural environment. Plants in the irrigated treatment received 3.8 L of water per week, while plants in the fertilized treatment (fertilizer + water) received 13g of NPK (20:20:20) applied weekly diluted in 3.8 L of water. These treatments simulated mesic environmental conditions considering that the soils had better water (irrigated) or hydric-nutritional (fertilizer + water) quality (see Fernandes & Price 1991). Fertilization and irrigation were conducted during the year 1988 from April 1 to September 15, which is approximately the growing season in the region. The irrigation process was equivalent to an increase of 129.6 mm of monthly rainfall, totaling an increase of 777.6 mm in annual precipitation.

Evaluation of the female galling insect attack

At the end of growing season (October / November) the number of attacked plants was recorded. All galls induced by *R. chrysothamni* found on the host plants were collected, placed in labeled plastic bags (one per individual) and brought to the laboratory where they were frozen for later analysis. All galls were thawed, had their diameter measured with a digital caliper (0.01 mm precision) for determination of basal area (considering the circular shape). After this stage the galls were separated from the stem with the aid of a dissecting needle and stereo microscope and their dry mass was measured with an analytical balance (precision 0.1 mg) after drying at 70°C to constant weight. A gall density index was calculated, which corresponded to the ratio between dry mass and gall basal area ($mg.mm^{-2}$). In total 35 plant individuals that had 698 galls (537 living galls) were sampled. To calculate the abundance, basal area and dry mass of galls only galls with live larva were considered.

Statistical analyses

Each plant individual (n = 10 to 15 individuals per treatment) was considered as a sampling unit in the analysis, according to the number of plants attacked in each treatment. To evaluate the effect of irrigation and fertilization on gall size of *R. chrysothamni*, the Kruskal-Wallis test followed by multiple comparisons between treatments (α = 0.05; Zar 1996) was used.

Results

The infestation of galls induced by *R. chrysothamni* was lower on irrigated and fertilized plant individuals. The rate of gall infestation in the more xeric treatment (i.e. control plants) was 75% (15 out of the 20 individuals), while only 50% of irrigated and fertilized plants (both; ten out of the 20 individuals) contained galls (Fig. 2a). On the other hand, the abundance of galls per plant was not significantly different among the treatments ($p > 0.05$), although there was a slight trend towards greater abundance of galls on plants in the irrigated and fertilized treatments (Fig. 2b).

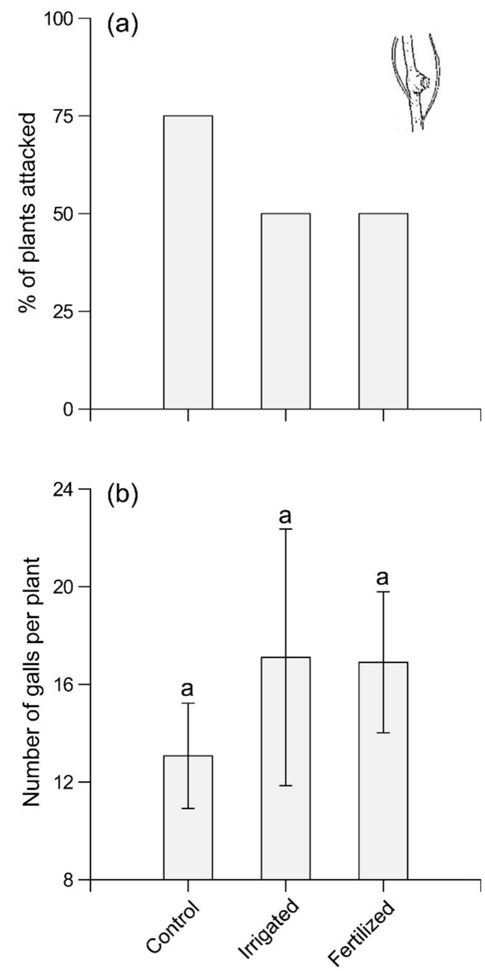

Figure 2. Effect of the host plant quality on % of plants attacked and number of galls per plant. a) % of host plants attacked by *Rhopalomyia chrysothamni* gall (n = 20 plants per treatment); b) Number of *R. chrysothamni* galls per individual of *Chrysothamnus nauseosus*.

Regarding to the growth of *R. chrysothamni* galls, fertilized plants had galls with higher dry mass compared to galls on control and irrigated plants (38% more tissue biomass; $p < 0.05$; Fig 3a). The average total biomass of galls per plant was 262.8 mg for control treatment, 367.4 mg for irrigated treatment, and 453.2 mg for fertilizer + water treatment. The gall density index on the fertilized plants was also 21% higher than on the control plants, and 31% greater than on the irrigated plants ($p < 0.05$; Fig. 3b). On the other hand, the basal area of the galls was not significantly different among the treatments ($p > 0.05$; Fig. 3c).

Discussion

The differences in habitat quality simulated by fertilizer and water treatments influenced both the number of galls per plant plant and the growth of the *R. chrysothamni* galls on *C. nauseosus*. The highest number of infected plants was found in the control treatment which represented the more xeric habitat condition that prevailed in the study area, hence supporting the hypothesis of water and nutritional stress that predicts a larger infestation rate by gall-inducing insects on plants under stressed or xeric environments. These results are similar to those found by Fernandes and Price (1992) analyzing different communities of galling insects in *C. nauseosus* in the southwest of the USA. The authors reported higher populations of 6 species of galling insects and larger number of attacked plants in xeric environments as opposed to mesic. On the other hand, Cuevas-Reyes et al. (2011) using nitrogen and phosphorus as indicators of soil fertility in populations of *Eremanthus glomerulatus* (Asteraceae) reported idiosyncratic patterns in the rate of galling insect infestation, depending on the species of Cecidomyiidae.

The present study did not corroborate the hypothesis of a greater abundance of galls on plants under more intense environmental stress. This result contradicts the trend observed in other studies that have shown that hosts in more stressed habitats (both in tropical and in temperate environments) harbor a greater abundance of galls (Fernandes & Price 1992; Ribeiro-Mendes et al. 2002; Jesus et al. 2012; Fagundes et al. 2020). Due to the fact that we were able to conduct such experiment only during one growing season, we argue that perhaps the time was not long enough to obtain a numerical response of the population by the galling species. While long-term study would likely represent an ideal scenario to test such

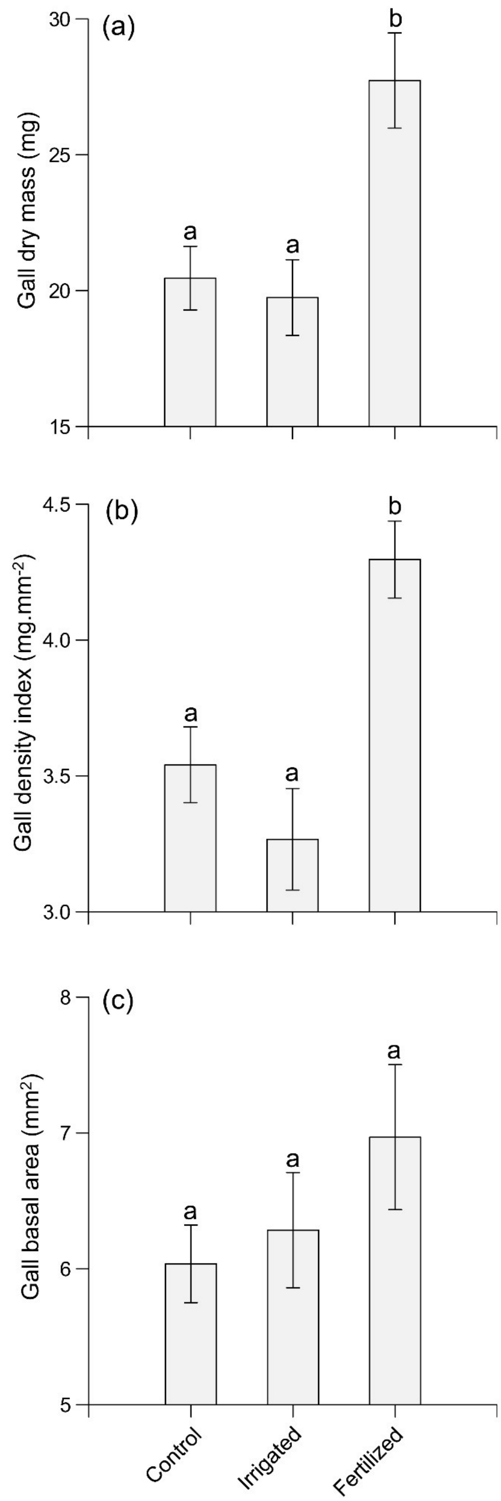

Figure 3. Effect of the host plant quality on the development performance of galls. a) Average gall dry mass (mg); b) Average gall density index (ratio of dry mass per basal area of each gall; $mg.mm^{-2}$); c) Average gall basal area (considering the cylindrical shape; mm^2).

hypotheses, the chances of conducting studies in the field would require different logistical arrangements.

Regarding gall growth, only in the situation where both water and nutritional stresses were relieved (fertilizer + water treatment) plants developed galls with greater dry mass. The fact that increased availability of water resulted in no increase in dry mass, density and size of galls, may suggest that the main factor of environmental stress on the system *Chrysothamnus - Rhopalomyia* is related to soil fertility. Rossi and Stiling (1998) showed that plants subjected to nitrogen fertilization harbored galls with a diameter 17.3% larger than the galls on plants in the control treatment. However, Fernandes et al. (2000a) analyzing the effect of NPK availability on galls induced by *Aciurina trixa* (Tephritidae) in the same population as in the current study of *C. nauseosus* found no significant differences between the diameter of galls on plants in fertilized and control treatments.

The results obtained in this study point to a paradox: although females of galling insects preferentially selected more stressed plants (i.e. less water and nutritional quality), *Rhopalomyia* galls that develop on less stressed plants reached a higher biomass, (which may theoretically results in larger larvae and fitter adults) (Abrahamson & Weis 1987; Weis et al. 1988; Santos et al. 2007). In other words, although females of galling insects preferentially select more xeric environments, the development of the galls was better in relatively more mesic environments. The results of the current study indicated that there is a trade-off between quantity and quality of galls of *R. chrysothamni* and that it is influenced by the nutritional quality of the host plant. Future studies related to mortality factors and performance of larval and adult stages of galling insects in the long term may help in better understanding of the mechanisms involved.

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