ECOLOGY, BEHAVIOR AND BIONOMICS

Response of the Galling Insect *Aciurina trixa* Curran (Diptera: Tephritidae) to Host Plant Quality

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Resposta do Inseto Galhador *Aciurina trixa* Curran (Diptera: Tephritidae)
à Qualidade da Planta Hospedeira

RESUMO - A seleção da planta hospedeira pela fêmea, o comportamento de oviposição e o desempenho da prole do tefritídeo galhador *Aciurina trixa* Curran (Diptera: Tephritidae) em plantas de *Chrysothamnus nauseosus hololeucus* Pall. (Britton) (Asteraceae), fertilizadas com NPK e em um grupo controle, foram estudados no Norte do Arizona, EUA. Não houve diferença na proporção de fêmeas que selecionaram o grupo controle e as que selecionaram as plantas fertilizadas nem entre o tempo de aceite da planta hospedeira no grupo controle e o tempo de aceite das plantas fertilizadas. As fêmeas ovipositaram menor número de ovos e levaram mais tempo durante a oviposição em plantas do grupo controle do que em plantas que receberam tratamento. O desempenho larval (medido como o período do início do desenvolvimento da galha na planta, diâmetro da galha e peso larval) não apresentou diferenças estatisticamente significantes entre plantas fertilizadas e do grupo controle ($P > 0,05$).

PALAVRAS-CHAVE: Insecta, *Chrysothamnus nauseosus*, galhas de inseto, comportamento do inseto, preferência alimentar.

ABSTRACT - Female host plant selection, oviposition behavior, and offspring performance of the gall-forming tephritid *Aciurina trixa* Curran (Diptera: Tephritidae) on NPK-fertilized and control plants of *Chrysothamnus nauseosus hololeucus* Pall. (Britton) (Asteraceae) were studied in northern Arizona, USA. There was no statistically significant difference in the proportion of females that selected control versus fertilized plants, and between the time to accept control versus treatment plants. Females laid fewer eggs and spent a longer time ovipositing on control plants than on treatment plants. Larval performance (measured as time of first gall appearance on plant, gall diameter, and larval weight) was not statistically different between fertilized and control plants ($P > 0.05$).

KEY WORDS: Insecta, *Chrysothamnus nauseosus*, insect galls, insect behavior, feeding preference.

The relationship between the oviposition preference of a female and the growth, survival, and reproduction of its offspring is vital in understanding host associations between herbivore insects and plants (Thompson 1988, Stein & Price 1995). Studies on preference and performance in phytophagous insects have contributed to the testing and generation of hypothesis about the evolution of host specificity (Bush & Diehl 1982), selection for enemy-free space (Price *et al.* 1980), host shifts (Bush 1975, Jaenike 1981), and how insects are distributed among plant species over evolutionary time (Jaenike & Holt 1991).

Host plant nutritional status affects the preference and performance of galling insects. Fernandes & Price (1988, 1991) have shown that the number of galling insect species increases with increasing habitat hygrothermal and nutritional stress in tropical and temperate regions. The mechanisms producing the patterns were the differential mortality of immatures in xeric and mesic habitats (Fernandes & Price 1992). Because plants living in xeric habitats may have a lower availability of water and nutrients it was argued that unfavorable habitat condition negatively influences hormone balance, expression of induced defenses, and the energetic balance between defense and plant growth (Herms & Mattson 1992); thus reducing plant resistance to galling insects.

Anderson *et al.* (1989) indicated two important components of plant resistance to galling herbivores: host acceptability and host suitability. The acceptability of a host involves chemical and/or physical characteristics of the plant that are used by herbivores to determine whether or not oviposition will occur. Host suitability is a measurement of offspring survival, growth or reproduction after attack.

This paper reports on a behavioral study of the response of a galling insect to plant quality. We studied female host selection, oviposition behavior, and offspring performance of the gall-forming tephritid, *Aciurina trixa* Curran (Diptera: Tephritidae) on *Chrysothamnus nauseosus hololeucus* Pall. (Britton) (Asteraceae) in northern Arizona, USA. *A. trixa* induces galls on five *C. nauseosus* subspecies (Dodson 1987, Fernandes & Price 1994). Eggs are laid on axillary buds of stems that grew in the previous year, and only one larva is found per gall. After hatching, the larva induces a spheroidal bud gall. *A. trixa* has three larval instars, and is multivoltine. More detailed life history parameters, courtship, and mating behavior of *A. trixa* can be found in Fernandes & Price (1994) and references therein.

This study aimed to answer the followings questions: 1. Does plant quality, i.e. nutritional status, influence female oviposition choice? 2. Does plant nutritional status influence the length of time spent by a female during oviposition? 3. Is developmental time of the gall influenced by host plant quality? 4. Is larval performance (e.g., gall diameter and larval weight) influenced by host plant quality?

Material and Methods

Experimental Plants. Oviposition preference and larval performance were measured using potted plants. In March of 1989, sixty plants (all of which had at least one gall from the previous year) were dug from a population at Schultz Pass (2.4 km from highway I-89), north of Flagstaff, Arizona at elevation of 2,400 m. Plants were matched for approximate size (range, 50-70 cm). Dug plants were placed in the center of 18.9 l pots which were filled until the roots were covered with soil from the site where plants were growing. Each potted plant received 7.6 l of water containing 20 drops of a root hormone (Superthrive). All galls were removed from the plants so they would not influence female behavior during the experiments nor change the pattern of plant growth.

Plants were numbered from 1 to 60. Thirty plants, hereafter called "treatment plants" were selected at random to receive water and fertilizer (Peters fertilizer, NPK at a ratio of 1:1:1 available elements). The other thirty plants, hereafter called "control plants", received only water. Fertilizer was applied at a concentration of 3.4 g/l of water to the treatment plants every second week from 30 March to 31 August 1989. Each control and treatment plant received 3.8 l of water weekly. Stem length and internode length of galled and nearest ungalled stems were measured to the nearest millimeter for control and treatment plants.

Behavioral Observations. Adult behavior was observed in cages at Northern Arizona University (Flagstaff, Arizona), and in the field at Schultz Pass, between 5 and 23 June 1989. Cylindrical nylon-mesh field cages (allowing penetration of > 80% of incident sun light) measuring 1.0 m diameter by 1.3 m height were used. Adult flies released into the field cage have been reared in the laboratory from galls collected in the field from 15 May to 30 May 1989. Flies were kept in the laboratory at environment temperature (25°C), and photoperiod of 12 hours. Trials were restricted to sunny days and appropriate times of day for oviposition (between 9:00 am and 5:00 pm; G. W. Fernandes pers. observation). The time a female took to accept the host plant, and the time from insertion to retraction of the ovipositor, observed by eye, were recorded to the nearest second.

Each oviposition may be preceded by a series of encounters and acceptance as the insect proceeds through a sequence of behaviors (Kennedy 1965). Thus, each time a decision is made to accept or reject a plant, or plant part, preference can be measured (see Singer 1986). We used sequential choice trials where the insects were allowed contact with more than one plant of *C. nauseosus hololeucus*, but only one plant was present at any given time. This was a realistic protocol because many insects encounter plants sequentially in their natural host-searching behavior (see Singer 1986).

Flies mated 12 h before the experiment were chosen for the preference experiment. Control and treatment plants were selected randomly and offered, individually, to a given fly. Each pair of control and treatment plants offered represented a trial. Up to three pairs of plants (three control and three treatment plants) were tested for each female. Flies were placed on the randomly assigned plant in sequence (the order also assigned randomly) until acceptance of one, both, or no plants was demonstrated. Flies were allowed to stay on a plant up to 10 min. After 10 min passed, the next plant was offered. Under field natural condition ovipositing females generally do not stay longer than 10 min on a plant if it is not suitable for oviposition (G. W. Fernandes pers. observation). Acceptance of a plant was recorded when the fly attempted to oviposit by curling its abdomen and extruding its ovipositor (see Anderson *et al.* 1989 for details).

The order in which a plant is accepted reflects oviposition preference (see Singer 1986). For example, a female that accepted a control plant, and subsequently rejected a treatment plant, was recorded as preferring the control over the treatment plant. Flies that accepted a control plant or a treatment plant for the first time, and then accepted the other plant in the same trial, were assigned to the non-preference (non-discriminating), or neutral group. The use of this technique for measuring preference assumes that an encounter with a particular plant at a particular time (without oviposition) does not influence an insect's response to the same or other plants encountered subsequently (for detailed discussion see Jaenike 1982, Singer 1986).

After the preference experiment, females were returned to their first-choice plants and allowed to lay eggs for a period of 30 min. Then, females were allowed to lay eggs on the plant offered second for 30 min. The egg laying period, time elapsed to next oviposition, the sites and number of eggs laid, and the sizes of selected and nearest neighbor non-selected stems were recorded. The number of eggs laid is here given by the number of times when the females' extruded ovipositor was inserted into the plant tissue attacked. Unfortunately, eggs could not be seen passing through the ovipositor nor we could open the lacerated tissue as we could have destroyed the future gall. Gall diameter (mm), larval weight (mg), and survivorship were also recorded after the period of larval development.

The proportion of neutral females versus females that selected control or treatment plants was tested by Chi-square analysis. Differences in preference and performance were analyzed by paired t-tests, or Wilcoxon signed rank tests (Zar 1996). Means are given with standard errors.

Results

Host Plant Quality. Plants responded to application of fertilizer that influenced the growth of treatment plants. At the end of the treatment period, the total length of the stems of treatment plants averaged 218.5 ± 16.7 mm ($\bar{x}$ ± SE) while the stems of control plants averaged 156.9 ± 17.9 mm (t test = 2.499, n = 60, $P < 0.02$). The mean distance between internodes was also larger on treatment (28.3 ± 1.2 mm) compared to control plants (21.1 ± 1.2 mm) (t test = 4.131, n = 60, $P < 0.0001$).

Female Behavior. Soon after landing on a plant, females started to walk up and down the stems in search of an oviposition site - with their wings frequently moving in several distinctive ways (see Jenkins 1990, Fernandes & Price 1994). They concentrated the search on the distal third of the stem. When a stem was rejected, the female flew to another stem, or if the whole plant was rejected, the female flew to the cage walls, or to another plant when in the field. Females were frequently seen to touch the substrate with their mouthparts. The ovipositor was sometimes half-extruded to touch the stem during a walk. The fully expanded leaf of the chosen axillary bud was also inspected a few times. A female stopped to search the stem when it accepted an axillary bud as site of oviposition. We considered a site as "accepted" when the female curled its abdomen and extruded its ovipositor.

During oviposition, the female may vigorously move its ovipositor up and down, and some females moved their whole body back and forth and sideways during oviposition. Females' mouthparts were frequently seen touching the substrate during oviposition. Females generally were positioned facing the proximal end of the shoot during oviposition. Eggs were laid within leaf axillary buds on internodes 2 to 6 only. The ovipositor was vigorously cleaned with the female's posterior legs and no apparent scar was left after oviposition.

Some females searched for another oviposition site in the same stem or flew to another stem. When they flew to an unacceptable stem, they often returned to the stem previously used for oviposition. Although not measured, winds did not seem to bother females during oviposition. However, ant activity near the oviposition site disrupted the process, causing the female to search for another site or to fly to a different stem. Ants (*Formica* spp.) were seen frequently cutting open axillary buds as well as young galls to prey upon the galling larvae in the field. Other arthropods caused the female to interrupt site selection but not egg laying.

Host Acceptability. Females were more likely to accept host plants in the first trial compared to the second and third trials [first trial: 82.1% (n = 23); second trial: 7.2% (n = 2); and third trial: 0%]. Only 10.7% (n = 3) of the tested females did not select any of the plants offered. When both plants were accepted (no preference = non-discriminating behavior), there was no difference between the elapsed time (time since placed on the plant) to select the first offered host and the elapsed time to select the second host offered (= 195 ± 26 $\bar{x}$sec, n = 25; and = 248 ± 43$\bar{x}$sec, n = 10, respectively; t test, P > 0.05).

The proportion of females that selected control (n = 5) over treatment (n = 10) plants, the number of females that showed no preference (n = 10), and the number of females that did not select any of the plants offered (n = 3) did not differ significantly ($\chi^2 = 0.70$, n = 28, P > 0.05). In addition, there was no difference between the time to accept control ($\bar{x}$= 177 sec ± 51, n = 5) and treatment plants ($\bar{x}$= 150 ± 51 sec, n = 10) by ovipositing females (P > 0.05).

Females selected the longest shoots for oviposition on both control and treatment plants. On control plants, attacked shoots averaged 195.5 ± 21.8 mm whereas nearest neighbor ungalled shoots averaged 118.4 ± 24 mm (paired t test = 2.341, n = 13, P < 0.02). On treatment plants, attacked shoots averaged 245.4 ± 7.8 mm whereas nearest ungalled stems averaged 169.9 ± 27.6 mm (paired t test = 2.707, n = 17, P < 0.05). Nevertheless, internode length did not differ between galled and nearest neighbor ungalled shoots of both control and treatment plants (P > 0.05, both).

All females laid fewer eggs on control than on treatment plants (control: $\bar{x}$= 3.5 ± 0.7; treatment:$\bar{x}$= 5.7 ± 0.7; P < 0.05). There was also a difference in the time of oviposition (log base 10 transformed). The females spent a longer time ovipositing on control plants than on treatment plants (control: $\bar{x}$= 155 ± 2 seconds, n = 79; treatment: $\bar{x}$= 146 ± 3 seconds, n = 124, t test = 3.721, P < 0.0001).

Larval Performance. More eggs were laid on treatment plants, but only 14% of the eggs produced galls (n =10), while on control plants, 24% developed galls (n = 9). There was no significant difference between the time to initiate a gall (time between egg deposition in plant tissue and first appearance of the gall), gall diameter, and larval weight on control versus treatment plants (Table 1).

Discussion

The discriminatory ability, female preference, and oviposition behavior have been studied in many fruit flies (Prokopy & Papaj 1988, Anderson *et al.* 1989, Fernandes-da-Silva & Zucoloto 1993, Chen *et al.* 1996, Fondriest & Price 1996). Chemoreceptors on the tarsi, labella, and ovipositor were found to be used in the differentiation among host species for oviposition in some tephritid species (Zacharuk *et al.* 1986, Stoffolano & Yin 1987), and host plant chemicals, pH, and possibly water content can be distinguished by the sensilla of tephritid flies (Ritter & Vasey 1989).

Variation in host plant quality may exert

Table 1. Average time (days) spent for gall initiation, gall diameter (mm), and larval weight (mg) for *A. trixa* on control and treatment plants in laboratory (t test, P > 0.05 in all).

Plants offered	Galler performance Gall initiation (days ± SE)	Gall diameter (mm ± SE)	Larval weight (mg ± SE)
Control	38.3 ± 2.3	5.89 ± 0.44	0.960 ± 0.33
(n)	7	7	7
Treatment	35.7 ± 1.0	6.97 ± 0.63	1.795 ± 0.17
(n)	10	8	6

strong selection pressure on oviposition behavior, particularly on galling insects in which the newly hatched larvae are relatively immobile and must feed on the plant or host plant organ on which eggs were laid (see Thompson 1988, Price *et al.* 1990). In this case females are frequently very selective in choosing the best possible host plants or plant parts for larval survival (e.g., Craig *et al.* 1986, 1989, Price *et al.* 1990, Stein & Price 1996). Oviposition site preferences determine the microhabitats used by their offspring (Jaenike & Holt 1991), hence females will benefit from being able to sense microhabitat characteristics that enhance offspring performance. However, although females tephritds have the ability to select oviposition sites nonrandomly, *A. trixa* have not any preference for control or treatment plants.

Response to increase nutrients concentrations varies among insect species (Waring & Cobb 1992). Most herbivore insects benefit from higher nutrients levels in fertilizer plants (Slansky & Feeny 1977, Price *et al.* 1987, Craig *et al.* 1989, Feller 1995, Fondriest & Price 1996). In contrast, fertilization of some plants may exert negative impact on insects (Leigh *et al.* 1974, Singh & Agarwal 1983, Cobb *et al.* 1997) or have no effect on herbivore insect population dynamics (Israel & Rao 1967, Prezler & Price 1995). Although fertilized plants had faster growth rates when compared with control plants, our results show that *A. trixa* female preference and galler performance were not affected by host plant quality. These differences in behavior among insects may reflect from the variable forms in while plants store and metabolize nitrogen and the interactions between insect nutrients and other chemical in the plants (Auerbach & Strong 1981). Furthermore, resource quantity, host plant geographic distribution, plant phenology, seasons of plant growth, climate, parasites, and predators are other factors which can exert strong selective pressure on herbivore insects (Auerbach & Strong 1981, Fondriest & Price 1996, Mayhew 1997).

A larger proportion of larvae produced galls on control plants than on treatment plants, but time to initiate the gall, gall diameter, and larval weight for control versus fertilized plants did not differ. These findings are corroborated by field experimental studies (Fernandes 1992). Larval weight and gall diameter were similar across plant treatment groups within a habitat (Fernandes & Price, in preparation). However, natural enemies and plant resistance were strong mortality factors on galls that developed on better quality plants. Differential mortality and survivorship of larvae caused by plant resistance and natural enemies, rather than larval weight, and gall diameter, may explain the higher *A. trixa* galling population size in dry habitats (Fernandes & Price 1988).

Females took a longer time laying eggs on control plants than on treatment plants. Nevertheless, females have deposited more eggs in longer shoots within a plant. This fact may indicate that *A. trixa* has not become physiologically specialized for vigorous host plants as galler performance did not vary among plant groups (Prezler & Price 1995). Thus, further detailed studies on the physiology, the genetics and the phylogeny are needed to better understanding the host selection by *A. trixa* females, and its role on the offspring fitness.

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