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Tree Size and Habitat Effects on Stem Gall Abundance in Conostegia oerstediana (Melastomataceae)

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ABSTRACT

The moth *Mompha sp.* (Coleophoridae, Lepidoptera) is known to induce a stem gall on the tree *Conostegia oerstediana* (Melastomataceae). There is little known about the distribution and abundance of galls. This study tested the difference in stem gall abundance between varying tree sizes and between two different habitats- pasture and secondary forest. Trees from each habitat were sampled and measured for diameter at breast height (DBH), height, number of branches, and number of galls. A significant difference was found between pasture and forested areas (unpaired t-test, p < 0.0001), with pasture trees having more galls. No relation was found relating tree size (DBH, height, number of branches) to gall abundance. I conclude from these results that tree size is not directly related to stem gall abundance. Instead, differences in habitats, such as predator and parasite abundance and host density, may be important factors that influence gall abundance.

RESUMEN

La polilla *Mompha sp.* (Coleophoridae, Lepidoptera) induce una agalla de tallo en el árbol *Conostegia oerstediana* (Melastomataceae). Poco es conocido de la distribución y abundancia de agallas. En este estudio se examinó la diferencia en la abundancia de agallas de tallo entre árboles de tamaños diferentes y entre dos ambientes- el pasto y el bosque secundario. Arboles de cada hábitat fueron medidos por DBH, altura, cantidad de ramas y cantidad de agallas. Una diferencia significante fue encontrado entre el pasto y el bosque (prueba de t unpariada, p < 0.0001), con el pasto poseyendo más agallas. No se encontró una relación entre el tamaño del árbol (DBH, altura, cantidad de ramas) y la abundancia de agallas. De estes resultos concluyo que el tamaño de árbol no es relacionado directamente a la abundancia de agallas de tallo. En vez de eso, diferencias entre hábitats, como la abundancia de predators y parásitos y la densidad de árboles, podrían ser factores importantes que influyen la abundancia de agallas.

INTRODUCTION

A great number of plant taxa harbor growth abnormalities know as galls. A gall is a mass of swollen plant tissue that develops in response to the parasitic attack of certain species of insects, bacteria, fungi, spiders, and mites (Mani, 1992). These gall-formers live inside the structure using if for nutrition and protection against parasites, predators, disease, and

harsh environmental conditions (Price *et al.*, 1987). Gall tissue is an excellent food source, being highly nutritive, even more so than the rest of the plant. Galls also contain a decreased amount of chemical defenses (Price *et al.*, 1987). Effects on the plant are quite detrimental. There is evidence that gall production prevents pollen and seed development (Graham, 1995) and may even cause shoot and branch death (Price et al., 1987). Galls occur on all plant organs, from roots to ovaries to leaves, and have a wide range of shapes and sizes (Mani, 1992). The appearance of a gall and where it is located on the plant is determined by the gall-forming species. This host-specific relationship is obligatory for the development of the galler.

The formation of insect-induced galls is initiated by oviposition or the feeding of the first instar larva. The mechanism of gall formation is not well known, but it has been hypothesized that either the mother, larva, or both inject or secrete a chemical that redirects and promotes growth of undifferentiated plant tissue (Borror *et al.*, 1989; Evans, 1984; Hogue, 1993).

Five orders of insects contain gall-making species; Diptera, Homoptera, Hymenoptera, Coleoptera, and Lepidoptera. Of the approximately 2000 species of gallers in North America, 1500 are gall wasps (Hymenoptera, Cynipidae) or gall midges (Diptera, Cecidomyidae) (Evans, 1984). Lepidoptera are not known to be common gallers, especially in Costa Rica, where galling insects are generally uncommon. However, Lepidopterans of the genus *Mompha* (Coloephoridae, Momphinae) are observed to make at least four different gall structures in the Neotropics; three on *Cuphea* (Lythraceae) and another on *Conostegia oerstediana* (Melastomataceae). *Mompha* are microlepidopterans with long, narrow wings. The larvae are herbivores that typically feed on leaves, buds, and flowers (Graham, 1995).

Conostegia oerstediana is a dominant secondary forest tree species in Monteverde, Costa Rica that is also typical in old pastures and forest edges (Haber *et al.*, 2000). This tree has been observed to be infested with galls on both its leaves and stems, the spherical stem galls being induced by *Mompha sp*. In this study I will examine the relationship between *C. oerstediana* and *Mompha sp*. to determine the effect of tree size and habitat on the abundance of galls.

There are two hypotheses that explain why galls may occur more often in one place than another. One is the spatial heterogeneity hypothesis (Akimoto, 1994), which predicts that gallers would choose plants with larger leaves and shoots, as this shows higher nutrition availability. The other is the synchronization hypothesis (Akimoto, 1994), which predicts that gallers choose and are most successful when they attack plants at a certain time, specifically bud burst. I hypothesize that there are many factors that vary between habitats that are likely to have an effect on gall abundance, such as availability of nutrients, presence of parasites and predators, and host density. I also hypothesize that tree size and number of galls per tree will have a positive relation. A larger tree provides a larger area for gallers to oviposit, and therefore they should be directly related. The purpose of this study is to determine whether tree size and habitat effects between pasture and secondary forest change the abundance of the *C. oerstediana* stem gall.

MATERIALS AND METHODS

Sample Site

This study was conducted in Monteverde, Puntarenas, Costa Rica (W 85 10', N 10 20') at elevations ranging from 1400-1700 m during April 10, 2003 – May 10, 2003. Measurements and collections of *C. oerstediana* were made at two secondary forest sites and two pasture sites. The two secondary forest sites were located in the surrounding forest of the Estación Biológica de Monteverde (EBM). The pasture sites were located north of the EBM and at the farm of Federico Muñoz in Las Nubes.

Data collection

Secondary forest trees were sampled by using every other *C. oerstediana* encountered along a 50 m transect. In pasture areas, each isolated *C. oerstediana* tree encountered was sampled. Diameter at breast height (DBH) and tree height were measured. Number of branches was counted, defining a branch as the extension of the tree that usually bore the gall (typically the quaternary branch). Number of galls per branch was counted with the aid of binoculars. In secondary forest distance to nearest neighbor was also measured. A total sample size of 55 trees, 30 from secondary growth and 25 from pasture, was obtained.

A maximum of 20 galls that were lower than six meters was collected per tree, using a tree pruner if necessary, and labeled by tree number. In the lab, the gall was cut open using a pocketknife and examined for presence of larvae, pupae, and adults. If larvae were found, the width of the base of the head was measured with a dissecting scope and an ocular micrometer to determine larval instar.

Statistical Analysis

Unpaired t-tests between DBH, tree height, number of branches, and gall abundance in pastures and secondary growth were performed. A simple regression analysis related DBH, tree height, and number of branches (and for secondary growth distance to nearest neighbor) to gall abundance for each habitat. Additionally, larval head sizes were plotted in a histogram. The histogram was divided into seven intervals to show the typical seven instars of a moth larva.

RESULTS

In secondary growth a total of 30 trees were sampled. The mean DBH was 11.7 ± 11.6 cm. The mean tree height was 6.6 ± 3.2 m. The mean number of branches was 381.2 ± 831.9 . Pasture trees were generally larger than secondary forest ones and had a small range of sizes. The mean DBH was 53.1 ± 30.8 cm. The mean tree height was 8.5 ± 2.8 m. The mean number of branches was 2133 ± 1699.5 . Number of galls per tree was also

higher in pasture. Pasture trees had a mean of 115.3 ± 97.6 galls per tree whereas secondary growth trees had a mean of 4.1 ± 4.9 galls per tree (Table 1).

A significantly greater abundance of galls was found in pasture trees than in secondary growth trees (unpaired t-test, p < 0.0001) (Fig. 1). Significant differences were also found between DBH (unpaired t-test, p < 0.0001) (Fig. 2), tree height (unpaired t-test, p = 0.0282) (Fig. 3), and number of branches (unpaired t-test, p < 0.0001) (Fig. 4) between the two habitats, with pasture trees being bigger in all cases. There was no relation between number of galls in the pasture versus DBH (simple regression, p = 0.595, $r^2 = 0.013$) (Fig. 5), tree height (simple regression, p = 0.716, $r^2 = 0.006$) (Fig. 6), or number of branches (simple regression, p = 0.392, $r^2 = 0.032$) (Fig. 7). A positive relationship was found between DBH versus number of galls in secondary growth (simple regression, p = 0.008, $r^2 = 0.227$) (Fig. 10), but there was no relationship between height (simple regression, p = 0.269, $r^2 = 0.043$) (Fig. 9) or nearest neighbor (simple regression, p = 0.094, $r^2 = 0.097$) (Fig. 11).

Head sizes of larvae found in pasture were also plotted in a histogram, which revealed that many of the larvae sampled (77 out of 174) were in their sixth instar (head size between 12.3 - 14.3 mm) (Fig. 12).

DISCUSSION

This study showed that there was a significant difference in tree size between pasture and secondary growth sites. Pasture trees were found to be significantly larger in terms of DBH (unpaired t-test, p < 0.0001) (Fig. 2), tree height (unpaired t-test, p = 0.0282) (Fig. 3), and number of branches (unpaired t-test, p < 0.0001) (Fig. 4). Because *C. oerstediana* is a dominant tree in the secondary forest of Monteverde and often develops nearly single species stands (Haber *et al.*, 2000), there is intense competition for resources, such as light, space, and nutrients. This strong intraspecific competition in secondary growth may be what causes the trees in that habitat to grow skinnier, shorter, and with fewer branches than pasture trees (Fig. 2, 3, 4). Pasture trees do not have to live in such conditions of high competition because they are isolated, and therefore can utilize resources to a greater extent, consequently forming larger, more robust individuals (Aldrich & Hamrick, 1998).

There was no significant relation found between number of galls per tree and tree size in terms of DBH (Simple regression, p = 0.595, $r^2 = 0.013$), tree height (simple regression, p = 0.716, $r^2 = 0.006$), and number of branches (simple regression, p = 0.392, $r^2 = 0.032$) in pasture trees (Fig. 5, 6, 7). Larger trees do not necessarily have more galls because there may be other factors that influence host selection by gall-formers. One, as suggested by the synchronization hypothesis (Akimoto, 1994), may be the developmental stage of the plant host organ. Other factors related to habitat differences may also influence gall abundance.

A significant difference was found in stem gall abundance between pasture and secondary growth sites (unpaired t-test, p < 0.0001) (Fig. 1). Pasture trees were found to have a greater number of galls per tree than secondary forest trees (Table 1). Abiotic

conditions in pasture sites are notably different than in secondary growth sites. Pasture sites are more exposed to wind and sunlight, have higher temperatures, and have lower humidity. These desiccating conditions are inhospitable to many species of arthropods. A study done by Lori Olson (1994) in Monteverde, Costa Rica found that species diversity of arthropods is lower in open habitats than in forested ones. Gall-making species, however, should not be affected by these abiotic conditions, as gall formation begins at the time oviposition, or soon thereafter, thereby protecting the egg from desiccation. Pasture habitat, therefore, may be preferred by gallers, as numbers of arthropod predators and parasitoids are lower there than in secondary forest.

Parasitoid abundance may also decrease in pasture areas because of the way they detect their host's location. Parasitoids are attracted to their hosts in large part by chemical stimuli released by the plant its host feeds on (Gauld & Hanson, 1995). Therefore, parasitoids of *Mompha sp.* would be more attracted to secondary growth where more chemical stimuli are released because *C. oerstediana* is the dominant tree species there. Parasitoids are known to, after attack, have the ability to change the structure of the gall (Hanson, 1995). If this indeed happened, I would not have been able to record the presence of an attacked gall. With the assumption that parasitoid presence is greater in forest sites, this would contribute to a lower observed abundance of stem galls in secondary growth.

For any given host there has been found to be an optimum carrying capacity, which is usually perceived by parasites (the gall-makers) as directly related to the host' physical size (Gauld & Hanson, 1995). The greater size of pasture trees (Fig. 2, 3, 4) may indicate a higher carrying capacity and therefore account for the difference in gall abundance between habitats.

Another possible explanation for the greater abundance of galls in isolated trees may be the surrounding distribution of conspecifics. Pasture trees are harder to find because they are isolated. However, once they are found, the galling insect will most likely oviposit many of its eggs there because there is nowhere else to lay them. In secondary growth however, there are many C. oerstediana available for oviposition, so the egg laying may be more diffuse. Studies have shown that hosts packed in groups are allocated fewer eggs because they have less exposed surfaces (Gauld & Hanson, 1995). Diffuse oviposition is also known to be preferable because it can help to avoid parasitoid attack. Once a parasitoid locates a host site, it remains in that area for a period of time, searching it for potential hosts (Gauld & Hanson, 1995). Therefore, it would be advantageous to the galling insect to spread out its eggs to many host sites, deterring the chance that all of them would be parasitized. Diffuse oviposition is also advantageous to gallers because galls on leaves unoccupied by other galls have been found to have a lower rate of abortion than those that reside on a leaf with one or more galls (Price, 1984). These results contradict information found in Begon et al. (1990), which states that gall-formers increase with the abundance of host plants. One may postulate that gallmakers would be able to find a clump of trees occurring together more easily than an individual isolated one, and so the clump would be more susceptible to attack. However,

experiments have shown that plants grown at high densities had the same probability of having eggs laid on them as did plants grown at low densities (Rausher & Feeny, 1980).

Many of the larvae in the galls sampled from the pasture (77 out of 174) were in their sixth instar (Fig. 12). This result most likely indicates that the galls were created at approximately the same time. It is generally known that Lepidopterans do indeed have a specific reproducing season. It is also possible that the sixth instar is somehow less susceptible to mortality than other instars. Developmental stage and size are known to be important factors in host identification for parasitoids (Gauld & Hanson, 1995). These larval stages are reaching a more mature stage that can resist abortion or predator attack.

In conclusion, this study supports the hypothesis that differences in habitats, such as predator and parasite abundance and host density, would influence stem gall abundance. The tree size hypothesis, however, was not supported by the study, showing that DBH, tree height, and number of branches are not directly related to stem gall abundance. Pasture trees are found to be larger, possibly due to reduced competition for resources as compared to secondary growth trees. This study gives insight into gallmaker behavior as well as plant-herbivore interactions. It implies complex interactions between trophic levels, such as the effect on distribution and abundance of a parasitic relationship due to the effect of parasitoids and predators on that parasite. This study also shows that there are more factors than just abiotic conditions that vary between open and forested habitats, and that significantly affect the species within these habitats. This study may have been enhanced if an improved means of viewing the galls was used. Gall presence was hard to observe on trees that were very tall, especially the tops of the trees. For further study, it would be interesting to study the abundance of another type of gall between pasture and secondary forest to determine whether different species interactions would give different results. Another interesting study would be to examine other habitats, such as primary and riparian areas, and the abundances of galls in those sites.

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		PASTURE	SECONDARY GROWTH
DBH (cm)			
	Mean	53.2 ± 30.8	11.7 ± 11.6
	Range	11.4-123.2	2.8-47.7
TREE			
HEIGHT (m)	Mean	8.5 ± 2.8	6.6 ± 3.2
	Range	3.9-16.3	3.3-18.3
NUMBER			
OF	Mean	2133 ± 1699.5	381.2 ± 831.9
BRANCHES	Range	90-6000	9-3250
NUMBER			
OF	Mean	115.3 ± 97.6	4.1 ± 4.9
GALLS	Range	4-381	0-18

TABLE 1. Means and ranges of pasture and secondary growth DBH's, tree heights, numbers of branches, and number of galls. N=25 for pasture, N=30 for secondary growth.



FIGURE 1. Difference in gall abundance between secondary forest and pasture sites. Pasture has a significantly greater amount of galls per tree than forest (unpaired t-test, p < .0001). Mean galls per tree in pasture is 115.3 ± 97.6 , while mean galls per tree in secondary forest is 4.1 ± 4.9 .



FIGURE 2. Difference in diameter at breast height between secondary forest and pasture sites. Pasture DBH is significantly larger than secondary forest trees (unpaired t – test, p < 0.0001). Mean pasture DBH = 53.1 ± 30.8 cm, while mean forest DBH = 11.7 ± 11.6 cm.



FIGURE 3. Difference in tree height between secondary forest and pasture sites. Pasture trees are significantly taller than secondary forest trees (unpaired t-test, p = 0.0282). Mean pasture tree height = 8.5 \pm 2.8 m, while mean secondary forest height = 6.6 \pm 3.2 m.



FIGURE 4. Difference in number of branches per tree between secondary forest and pasture sites. Pasture trees have a significantly greater number of branches per tree (unpaired t-test, p < 0.0001). Mean number of branches for pasture = 2133 ± 1699.5 , while mean number of branches for forest = 381.2 ± 831.9 .



FIGURE 5. Relationship between gall abundance and diameter at breast height in pasture sites. There is no significant relation between number of galls per tree and DBH (p = 0.595, $r^2 = 0.013$).



FIGURE 6. Relationship between gall abundance and tree height in pasture sites. There is no significant relation between number of galls per tree and tree height (p = 0.716, $r^2 = 0.006$).



FIGURE 7. Relationship between gall abundance and number of branches per tree in pasture sites. There is no significant relation between number of galls per tree and number of branches per tree (p = 0.392, r = 0.032).



FIGURE 8. Relationship between gall abundance and diameter at breast height in secondary growth sites. There is a significant positive relation between number of galls and DBH (p = 0.004, $r^2 = 0.265$).



FIGURE 9. Relationship between gall abundance and tree height in secondary growth sites. There is no significant relation between number of galls per tree and tree height (p = 0.269, $r^2 = 0.043$).



FIGURE 10. Relationship between gall abundance and number of branches per tree in secondary growth. There is a significant positive relation between number of galls per tree and number of branches per tree (p = 0.008, $r^2 = 0.227$).



FIGURE 11. Relationship between gall abundance and distance to nearest neighbor in secondary growth. There is no significant relation between number of galls per tree and nearest neighbor (p = 0.094, $r^2 = 0.097$).



FIGURE 12. Frequency distribution of head widths of larvae found in pasture galls. The sixth interval is disproportionately frequent, which shows that many pasture larvae are in their sixth instar of development.