DEVELOPMENT OF THE INSECT COMMUNITY CENTERED ON A LEAF-BUD GALL FORMED BY A WEEVIL (COLEOPTERA, CURCULIONIDAE) ON XYLOPIA AROMATICA (ANNONACEAE)

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ABSTRACT. We studied the development of the community of insects utilizing the leaf bud-gall formed by a weevil on Xylopia aromatica. Galled shoots were significantly longer than ungalled shoots indicating that the weevil had a preference for long shoots or induced shoot elongation. The probability of larval survival was not related to shoot length. Gall size was a good predictor of occupants: weevils were predominantly found in large galls, galls with no occupants were of an intermediate diameter, galls with a braconid parasitoid were smaller than average. Ants occupied and modified 48.6% of galls after weevil emergence. We found 18 ant species of 9 genera occupying galls, at least 11 of these had not previously reported using this gall. Ants predominantly occupied large galls still on the tree and were rarely found in galls on the ground. Ants were found in equal numbers in older and younger galls as indicated by gall color.

KEYWORDS. ANTS, BRACONIDAE, CURCULIONIDAE, INSECT GALLS, XYLOPIA AROMATICA.

INTRODUCTION

Galls are frequently occupied by other species in addition to the gall-maker. Gall-makers are “resource manipulators” (CRAIG et al., 1988) and can alter plant resources in a manner that benefits both the gall-makers and other gall occupants. The gall is a discrete resource that undergoes an ecological succession as it is used by a series of occupants (MANI, 1964). The gall-maker is often attacked by predators, parasitoids and inquilines. In addition galls are occupied by species termed “successors” (MANI, 1964; YUKAWA, 1983; see also NEW, 1982) after the emergence of the gall-maker parasitoids and inquilines. The development of this community has rarely been studied. Such communities offer excellent opportunities to understand how variation in discrete resource, a gall, can influence community development.

We studied the development of the community centered on galls of a weevil (Curculionidae) on Xylopia aromatica (Annonaceae). The community was initially described by FERNANDES et al. (1989). They found galls were occupied by 11 different ant species that partitioned gall resources on the basis of size. They found gall size was positively related to the size of ant colonies. They also found that unoccupied galls were smaller than occupied galls. Our first goal was to test
the generality of these results by collecting larger samples from additional trees. A second goal was to study the development of the community through time by answering the following questions. 1) What plant resources do the gall-makers most frequently attack? 2) Do ants act as predators, inquilines or successors? do the ants attack galls before or after weevil emergence? 3) Do ants occupy galls of particular ages? 4) Do ants prefer galls on the tree or on the ground?

METHODS

Galls were collected from the Ecological Station of Parapitinga, Três Marias, Minas Gerais, Brazil on 8 and 9 March 1988. The station is located on an island in a man-made lake, Três Marias Lake, for further information on the location see FERNANDES et al. (1989). We collected 577 galls from shoots on 9 trees and from the forest floor beneath the trees. Galls were collected that were still attached to shoots on the tree, and an approximately equal sample was collected from the ground immediately under the tree. In the sample from the tree we measured the galled shoot lengths and the nearest ungalled shoot to determine gall-maker preference for shoot lengths. Each gall was classified and ranked from green (younger galls = zero) to brown (older galls = 1).

Galls were dissected and the occupants identified. Ants were identified by L.M. Araújo using the following keys: WHEELER (1922); ENZMANN (1944); KUSNEZOV (1956); and KEMPF (1958, 1960, 1961, 1964, 1972, 1973). The presence of emergence holes made by the gall maker was recorded. The number of ant adults, eggs and larvae were counted and preserved for identification. The degree of ant modification was classified on a scale of 1 = unmodified, to 4 = completely hollowed out (Fig. 1). Modification is defined as any internal architectural departure, such as tunnel and gall wall holes, from the usual spheroid larval chamber (see FERNANDES et al. 1989 for further details). The gall diameter was measured with dial calipers.

![Fig. 1. Cross-sectional views of the four categories used to classify galls](image)

RESULTS

Plant-herbivore interaction

Galled shoots were significantly longer than ungalled shoots when compared with a two-sample t-test (X galled shoot length $\pm SE = 224.7 \pm 6.42$ mm, X
ungalled shoots $\pm SE = 142.0 \pm 5.68$ mm, $t = 9.65, P < .0001$, D.F. = 374). Thus, gall-formers either had a preference for vigorously growing shoots or induced accelerated shoot growth. There was no significant difference in the lengths of galled shoots with and without gall exit holes ($F_{1,374} = 0.54, P > .05$).

Gall diameter

The gall diameter of different groups of occupants differed significantly (Fig. 2). Galls from which weevils emerged were significantly larger than galls without emergence holes (Fig. 2) gall diameter with emergence holes (Ants, Weev galls in Fig. 2) $\pm SE 14.3 \pm .42$ mm, gall diameter without emergence holes (Zero, Para galls in Fig. 2) $\pm SE 12.3 \pm .16$ mm, $F_{1,35} = 4.09, P < .001$). Hence, larger galls were better resources for weevil survival. Galls containing parasitoids (Allorhogas sp., Braconidae) were smaller than average. Galls with ants or that had been modified by ants were the largest. Because the high diversity of ant species and low numbers of each species trends in diameter preference were difficult to assess. We did not find a positive relationship between gall size and the logarithm of ant number ($v = 0.44 + .115x, r^2 = 5.1\%, P > .05$) as reported by FERNANDES et al. (1989).

![Fig. 2. The mean gall diameter (± SE) of galls containing each of the following occupants: no gall occupant (ZERO), all species of ants (ANT), weevil larvae (WEEV), and braconid parasitoid (PARA). "Weev" and "Ants" galls had exit holes whereas "Zero" and "Para" galls did not.](image-url)

Ants

Ants only invaded galls after the weevil had emerged. We sampled 100 galls without exit holes and found no evidence of ant occupation. All galls with ants had an exit hole formed by the weevil, parasitoid or an inquiline. Ants occupied 48.6% of all galls. We found no cases of ant species co-occurring in galls. A high diversity of ant species (18) occupied the galls including several species recorded for the first time occupying these galls (Tab. I). We found ant adults, eggs and larvae in the galls.
TABLE I. Ant species associated with weevil leaf-bud galls on *Xylopia aromatica*. The species marked with an * were also found in the study done by FERNANDES et al. (1989).

<table>
<thead>
<tr>
<th>ANTSPECIES</th>
<th>NUMBER OF COLONIES</th>
<th>TOTAL</th>
<th>MEAN NUMBER OF</th>
<th>GALL MEAN DIAMETER</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>ADULTS</td>
<td>LABRAE</td>
</tr>
<tr>
<td>Azteca bicolor*</td>
<td>4</td>
<td>18.50</td>
<td>12.00</td>
<td>6.50</td>
</tr>
<tr>
<td>Brachymyrmex spp. 1</td>
<td>1</td>
<td>15.00</td>
<td>6.00</td>
<td>5.00</td>
</tr>
<tr>
<td>Brachymyrmex spp. 2</td>
<td>2</td>
<td>8.00</td>
<td>4.50</td>
<td>3.50</td>
</tr>
<tr>
<td>Camponotus crassus</td>
<td>3</td>
<td>15.60</td>
<td>8.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Crematogaster europaea</td>
<td>-</td>
<td>18.60</td>
<td>4.66</td>
<td>1.33</td>
</tr>
<tr>
<td>Dolichoderus spp. 1</td>
<td>6</td>
<td>38.16</td>
<td>8.33</td>
<td>15.16</td>
</tr>
<tr>
<td>Dolichoderus spp. 2</td>
<td>3</td>
<td>38.60</td>
<td>9.67</td>
<td>7.00</td>
</tr>
<tr>
<td>Dolichoderus spp. 3</td>
<td>1</td>
<td>4.00</td>
<td>4.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Mymelachilus nodigena</td>
<td>3</td>
<td>34.00</td>
<td>15.66</td>
<td>4.67</td>
</tr>
<tr>
<td>Mystacomyrmex spp. 1</td>
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<td>16.00</td>
<td>7.33</td>
<td>6.00</td>
</tr>
<tr>
<td>Pseudomyrmex spp. 2</td>
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<td>25.00</td>
<td>13.00</td>
<td>3.00</td>
</tr>
<tr>
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<td>5</td>
<td>9.40</td>
<td>2.00</td>
<td>5.40</td>
</tr>
<tr>
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<td>3</td>
<td>14.00</td>
<td>4.00</td>
<td>7.33</td>
</tr>
<tr>
<td>Pseudomyrmex spp.</td>
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<td>5.00</td>
<td>1.00</td>
<td>2.00</td>
</tr>
<tr>
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<td>1.00</td>
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<tr>
<td>Zephyropoecus paonii</td>
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<td>24.00</td>
<td>19.50</td>
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<tr>
<td>Zephyropoecus pusillus*</td>
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<td>19.00</td>
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<tr>
<td>Zephyropoecus spp. 4</td>
<td>43.00</td>
<td>20.00</td>
<td>9.00</td>
<td>14.00</td>
</tr>
</tbody>
</table>

Comparison of galls on the tree and on the ground

All gall occupants were found more frequently in galls on the tree than in galls on the ground (Fig. 3). Galls that had been modified but that were no longer occupied by ants were found predominantly on the ground. Ants were more frequently found in galls in the tree than in galls on the ground. Of the 18 species of ants identified, 14 were found only on galls in trees and 4 were found both in the

![Fig. 3. The percent of galls in the following categories that were found on shoots in the tree, the remainder were in galls on the forest floor. The abbreviations are as follows: no gall occupant (ZERO), weevil larva (WEEV), Braconid parasitoid (PARA), all ant species (ANT), galls with low modification without ants (LM), galls with moderate modification without ants (MM) and galls with high modification without ants (HM).](image)
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A total of 56 ant colonies were identified with 46 in trees and 6 in galls on the ground. This distribution differed significantly from what would have been expected if ants were occupying galls at random when tested with a chi-square goodness of fit test (\(c^2 = 22.52, P < .001, \text{D.F.} = 1\)).

Gall age

Galls of different age as classified by color had different occupants (Fig. 4). Galls with the gall-maker or the parasitoid were the youngest galls as indicated by their color. Galls with ants were nearly evenly split among brown and green galls. The number of ants did not differ significantly between green and brown galls (One-way ANOVA, \(F_{1,50} = 0.02, P > .05\)). While modified galls that were no longer occupied were predominantly brown galls.

The development of the community centered around the coleopteran leaf-bud gall-former can now be outlined. The gall is initiated on rapidly growing shoots, or it increases shoot growth. There is increasing evidence that many gall forming insects select rapidly growing plant parts (see PRICE et al. 1990 for a review). Nevertheless, studies would need to be conducted at the time of oviposition to test for shoot length preference. A parasitoid attacks the beetle larva before emergence. It either has a higher success rate in attacking small galls as has been found in other studies of parasitoids on gall-formers (WIEBES-RIJKS, 1982; WEIS & ABRAHAMSON, 1985: PRICE & CLANCY, 1986) or parasitism limits develop-
ment of the gall. Ants do not enter the gall until the weevil emerges leaving an exit hole through which the ants attack. Ants predominantly choose large galls to occupy. Ants occupy galls on the tree and evidently most species abandon the galls when they fall to the forest floor.

Galls are a resource that evidently decline in quality as they age and fall to the forest floor. At least two hypotheses could account for differences in the suitability of galls of different ages and location. If galls are primarily a food resource then as a gall ages food quality could decline as it desiccates and decays. If galls are primarily a shelter then the quality of the gall environment may decrease as the relative humidity in the gall declines. Habitat quality may further decline when the gall falls to the forest floor. Galls on the forest floor may have a different micro-environment than galls in trees (temperature, humidity, light) and may be vulnerable to a new suite of natural enemies. We did not find any group of ants that seemed to specialize on galls on the forest floor. It is also possible that most suitable galls are exploited while still on the tree and that few suitable galls remain unexploited by the time they reach the forest floor. The lack of a significant difference in ant numbers in brown and green galls in conjunction with the significant differences between ant numbers in galls on the forest floor and galls in the trees suggests that ant are more influenced by gall location than gall age.

Our study and that of FERNANDES et al. (1989) demonstrate how an insect that utilizes “resource modification” (CRAIG et al., 1988) can influence an entire component community. The community of ants and parasitoids could not exit if the gall-maker had not modified plant resources. By improving food resources and creating new structures, new habitats are created on the plant. The occupants of these habitats are also determined to some degree by the variation in gall characteristics such as size.

The community had a very high species diversity with a low frequency of any one species. The most common ant species occupied only 11.53% of the galls occupied by ants. It is unlikely that the surveys in this study and in FERNANDES et al. (1989) have identified all of the ant species that occupy this gall. FERNANDES et al. (1989) found 11 different ant species in 114 galls. We found 18 ant species in 578 galls. Only 3 of these species were definitely found in both studies, and a maximum of 7 could overlap. So at a minimum we report 11 new species and 6 new genera of ants utilizing the gall.

Unlike FERNANDES et al. (1989) we did not find ant species co-occurring in the galls. The samples were taken at different times of year and different ants were present in the community. As a result ants that co-occur may not have been found in this study. In addition we did not find a significant relationship between gall diameter, although the largest colonies occurred in large galls. Again this may relate to sampling at different times of year when ant densities differed. Additional studies are needed that follow the development of the community through the seasons to completely understand how succession takes place in this community.
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