

# GALL DISTRIBUTION ACROSS LEAVES AND PLANTS AND IMPLICATIONS FOR OVIPOSITING PREFERENCES IN GALL-FORMING PSYLLIDS

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**Abstract.** This study examined distribution of galls across individual leaves and plants on Mo'orea, French Polynesia. This study examined patterns of gall formation of the psyllid, *Megatrioza vitiensis*, which forms galls on the plant *Syzygium malaccense*. Specifically this study examined the distribution of galls across leaves of different relative ages and different sizes and the distribution of gall across individual leaves. Across individual leaves the distribution pattern of galls (clumped, random or uniform) was determined, in addition to the distribution of galls relative to the midrib. From the distribution of galls across leaves and plants oviposition preferences were examined. Results indicate that *Megatrioza vitiensis* prefers to oviposit on both smaller and relatively younger leaves. The distribution of galls across individual leaves tends to be clumped and galls tend to be closer to the midrib than would be expected with a random distribution, suggesting preferential ovipositing near the midrib. This study examined several factors that play a role in gall distribution and what determines where psyllids oviposit on host plants.

**Keywords:** *Gall-Forming Psyllids, Megatrioza vitiensis, Syzygium malaccense, quantitative biology, ovipositing preferences, Mo'orea, French Polynesia*

## INTRODUCTION

Plant-insect interactions present interesting examples of co-evolution, especially interactions where development of one organism is dependent on another organism. Plant-insect interactions can be symbiotic, but are often parasitic with the development of the insect having detrimental effects on the plant (Mello 2002). Detrimental plant-insect interactions are often of great interest when food crops are involved (Mello 2002; Macior 1971). Deeper understanding of plant-insect interactions that are detrimental to crop plants can allow for the development of methods to control or decrease the negative impacts insects have on food crops. In plant-insect interactions that are detrimental to the plant the insect will often depend on use of parts of a host plant to complete their development. The development of an insect frequently requires the utilization of a particular plant at a specific point in the development or growth of the plant. This pattern is seen very explicitly in temperate environments where seasonality affects plant growth and consequently affects the formation and maturation of the insect. In tropical environments, where there is significantly less seasonality, plants grow more continuously throughout the year, often exhibiting spurts of growth in response to small variation in conditions such as temperature and rainfall. Because of this insects in tropical environments often reproduce more regularly and grow on a more continuous basis than temperate insects as well.

Galls are abnormal plant growths caused by an organism other than the plant, where the gall-causing organism receives shelter and nutrition

from the host plant. Many insects, fungi, viruses, and other invertebrates can cause galls. Galls can be found on many plant parts, including leaves, stems, and flowers, depending on the plant and gall-former involved. Insect galls are outgrowths of plant material in which the insect larvae develop until some maturational state; the insect then bursts out of the gall (Hodkinson 2009; Fay, Hartnett, and Knapp 1996). There are a variety of terrestrial invertebrates that form galls, including many psyllids, aphids, and mites. Gall-forming psyllids tend to be extremely host specific, with very little to no reproductive success for individuals who oviposit on plants other than the host plant specific to that psyllid species (van Klinken 2000). In addition to the close relationship between a host plant and a particular psyllid species in oviposition, a psyllids' fecundity is also highly dependent on very close synchrony with their host plant (Hodkinson 2009; Sutton 1984). Gall-forming psyllids in temperate environments must oviposit so that the emergence of individuals corresponds with a particular developmental point in the plant's growth, often the emergence of new leaves or buds at the beginning of spring, and typically experience a diapause during winter (Hodkinson 2009). Furthermore small differences in weather and shade cover can have large effects on fecundity in temperate gall-forming psyllids (Leege 2005; Hodkinson, Bird, and Baxter 2001). Tropical gall-forming psyllids, because of the absence of large seasonal changes, oviposit throughout the year, although it has been suggested that tropical psyllids still vary ovipositing in response to plant growth and environmental conditions (Hodkinson 2009).

*Syzygium malaccense* (L.) Merr. & L. M. Perry, more commonly known as the Malay apple or

Mountain apple, is found throughout the Pacific, the Indo-Malaysian region, and Southeast Asia more broadly. It has been observed that *Syzygium malaccense* is associated with the psyllid *Megatrioza vitiensis* (G.W.) Kirkaldy throughout the Pacific. *Megatrioza vitiensis* oviposits on the leaves of *Syzygium malaccense* signaling the formation of galls around the eggs (Whistler and Elevitch 2006; Tuthill 1964; PestNet 2008). *Megatrioza vitiensis* has not been documented on Mo'orea before, but in preliminary work done for this project *Megatrioza vitiensis* was identified from individuals reared out from galls on *Syzygium malaccense* leaves. Furthermore although *Megatrioza vitiensis* has not been previously been documented on Mo'orea, *Megatrioza vitiensis* has been documented in locations throughout the Pacific, including the Solomon Islands, Fiji, the Hawaiian Islands, and New Zealand, so it is not surprising that *Megatrioza vitiensis* has been found on Mo'orea (Tuthill 1964; PestNet 2008). Although *Syzygium malaccense* is widespread and the appearance of galls on *Syzygium malaccense* has been noted, little is known about patterns of oviposition, such as oviposition location on a host and timing of oviposition, and gall formation of *Megatrioza vitiensis*. Additionally little is known about how interactions between *Syzygium malaccense* and *Megatrioza vitiensis* affect ovipositing, gall formation, or life cycle of *Megatrioza vitiensis*.

This study described the formation of galls from the initial appearance of galls through the emergence of individuals from the galls. In addition to the description of the development of galls this study also examined patterns of ovipositing across plants to determine if there exists preferential ovipositing on leaves of relatively younger or older leaves. This study also examined if patterns exist in spatial distribution of ovipositing on leaves, looking specifically at whether galls are clumped, uniformly distributed, or randomly spaced. It is hypothesized that there is preferential ovipositing on relatively younger leaves because younger leaves may provide a better nutrition source and may be less likely to fall off before the gall finishes development and the developing psyllid emerges. It is also hypothesized that galls will be clustered together. This could be because certain sections of the leaf provides a better nutrition source for developing psyllids or because a female oviposits eggs relatively close together on the leaf in each ovipositing event.

## METHODS

### *Study Organisms*

*Syzygium malaccense* (L.) Merr. & L. M. Perry, more commonly known as the Malay apple or Mountain apple, is found throughout the Pacific, the Indo-Malaysian region, and Southeast Asia more broadly. It has been observed that *Syzygium malaccense* is associated with the Psyllid *Megatrioza vitiensis* (G.W.) Kirkaldy throughout the Pacific. *Megatrioza vitiensis* oviposits on the leaves of *Syzygium malaccense* signaling the formation of galls around the eggs (Whistler and Elevitch 2006, Tuthill 1964, PestNet 2008). For this study branches of *Syzygium malaccense* with leaves that had galls were collected from individuals off of the Three Pines trail and the Three Coconuts trail on Mo'orea, French Polynesia. *Megatrioza vitiensis* has not been documented on Mo'orea before, but in preliminary work done for this project *Megatrioza vitiensis* was identified from individuals reared out from galls on *Syzygium malaccense* leaves. Furthermore although *Megatrioza vitiensis* has not been previously been documented on Mo'orea, *Megatrioza vitiensis* has been documented in locations throughout the Pacific, including the Solomon Islands, Fiji, the Hawaiian Islands, and New Zealand, so it is not surprising that *Megatrioza vitiensis* has been found on Mo'orea (Tuthill 1964, PestNet 2008).

### *Relative Leaf Age and Gall Abundance*

To examine the effect of leaf age on gall abundance, the number of galls was counted on each leaf and compared to the leaf's relative age. Relative leaf age was determined by measuring each leaf's relative distance to the meristem of the branch it is on. *Syzygium malaccense* leaves are organized along branches in pairs. Leaves closest to the meristem are the youngest with leaf age increasing with distance from the meristem. Since leaves of *Syzygium malaccense* are paired, each pair of leaves was given a number for relative age based on number of leaf pairs from the meristem it is. The leaves closest to the meristem were recorded as being the youngest and therefore given the smallest age number. The leaves farther down the branch were recorded as increasing in relative age as number of leaf pairs from the meristem increased. The number of galls per leaf in each age group was compared with the relative age of the leaf and a regression line was added to determine if leaf age and gall abundance are correlated. An Analysis of Variance test was also

performed to determine if there was a statistically significant relationship between relative leaf age and gall abundance.

### *Leaf Size and Gall Density*

To determine the effect that leaf size has on the abundance of galls the density of galls per unit area was compared with leaf size. The number of galls was counted on each leaf and the area of each leaf was recorded. To determine the density of galls on each leaf, the number of galls was divided by the area of the leaf. The number of galls per square cm was then compared with the area of the leaf and a regression line was added to the data to determine if leaf size and gall density per unit area are correlated. A Pearson's r test was performed to determine if a statistically significant relationship existed between leaf size and gall density.

### *Distribution of Galls*

The distribution of galls across individual leaves was studied to determine if there exists a pattern to the spatial distribution of galls across leaves. The *Clark-Evans Nearest Neighbor Method* was used to determine if galls are clumped, uniformly, or randomly distributed (Clark and Evans 1954). In *Clark-Evans Nearest Neighbor Method* the distance between the each individual point's nearest neighbor ( $r$ ) is measured and recorded, these distances are then averaged and the average nearest neighbor ( $r_A$ ) distance is compared to the distance to a nearest neighbor expected in an infinitely large random density ( $r_E$ ) (Clark and Evans 1954). This study used the program *Image J* to map galls on photos taken of the leaves. The X-Y coordinates for each point were recorded using *Image J* and then the distances between these points was then determined for use in the *Clark-Evans Nearest Neighbor Method*.

### *Clark-Evans Nearest Neighbor Formulas*

$$r_A = \Sigma r / N$$

$$r_E = 1 / 2 \sqrt{Q}$$

$$R = r_A / r_E$$

$Q = \text{density (the number of individuals per unit area)}$   
 $N = \text{number of galls}$   
 $r = \text{distance between galls}$   
 $c = (r_A - r_E) / \sigma r_E$   
 $c = \text{z-value}$   
 $\sigma r_E = 0.26136 / \sqrt{NQ}$

If the expected nearest neighbor distance is close to the actual average nearest neighbor

distance, then the population is randomly distributed (Clark and Evans 1954). If the actual average nearest neighbor distance is significantly greater than the expected distance then the population is uniformly distributed (Clark and Evans 1954). If the actual average nearest neighbor distance is significantly less than the expected nearest neighbor distance then the distribution is clumped (Clark and Evans 1954). Once the R value for the distribution of galls on each leaf was determined the z-value was determined and converted to a p-value to determine which leaves had distributions that statistically significantly uniform or clumped distributions.

### *Distribution of Galls and Relative Leaf Age*

The distribution pattern of each leaf (clumped, uniform or random), as described by its Clark-Evans Nearest Neighbor Index of Aggregation value, was compared to the leaf's relative age to determine if a relationship existed between these two variables. An Analysis of Variance test was performed to determine if there was a statistically significant difference in average index of aggregation values for the different relative ages.

### *Distribution of Galls and Leaf Size*

The distribution pattern of each leaf (clumped, random, or uniform), as described by its Clark-Evans Nearest Neighbor Index of Aggregation value, was compared to the leaf's relative age to determine if a relationship existed between these two variables. A Pearson's r test was performed to determine if the relationship between leaf size and index of aggregation value was statistically significant.

### *Distribution of Galls Relative to the Midrib*

The distribution of galls relative to the midrib of each leaf was studied to determine if gall distribution is correlated to resource distribution in leaves. To study whether galls are on average relatively closer to the midrib than would be expected randomly the galls on each side of the midrib for each leaf were plotted on photographs of the leaves using *J Image* and the average distance from each gall to the midrib ( $w_M$ ) on each leaf were compared to the average distance to the midrib expected for a random distribution ( $w_B$ ) for a leaf of the same size and shape as the actual leaf. The expected average distance to the midrib was determined by plotting points randomly on each side of every leaf, using *J Image*, and then

measuring the distance between those points and the midrib and averaging those distances. The actual average distance from galls to the midrib was then divided by the expected distance for the distribution of galls on each half of each leaf ( $W$ ).

$$W = w_M / w_B$$

The deviation of  $W$  from 1 indicates the deviation of the actual distribution from a random distribution.  $W$  values significantly greater than one indicate the galls are distributed on average farther away from the midrib than would be expected in a random distribution and  $W$  values significantly less than one indicate the galls are distributed closer to the midrib on average than would be expected with a random distribution. To test whether the  $W$  values obtained were statistically significant an analysis of variance test was used.

## RESULTS

### Leaf Age and Gall Abundance

The actual number of galls is correlated with the relative age of the leaf. Figure 1 indicates that leaves relatively closer to the meristem had a higher average number of galls. Relative distance from the meristem was used to indicate the relative age of each leaf, so as distance from the meristem increased relative age of the leaf increased.

The average number of galls per leaf decreased exponentially. A trendline with the equation,  $y = 35x^{-2.2}$  was added to the graph. The  $R^2$  value for this trendline is 0.94.

An Analysis of Variance (ANOVA) test was performed to determine if there existed a

statistically significant difference between the average number of galls and each leaf's relative age. The ANOVA test indicated that there was a statistically significant difference between relative leaf age and gall abundance ( $p < 0.0001$ , d.f. = 173).

### Leaf Size and Gall Abundance

The density of galls per square cm is correlated with leaf size. Figure 2 shows how at smaller leaf sizes the density of galls per square cm tends to be greater than at larger leaf sizes.

A trendline with the equation  $y = 16.5x^{-0.98}$  was fitted to the data. The trendline has a  $R^2$  value of 0.52.

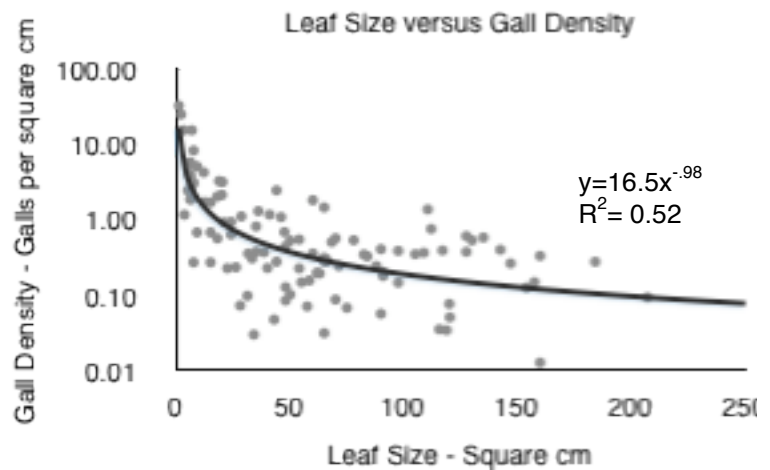


FIG. 2. Leaf size in square cm versus gall density in galls per square cm.

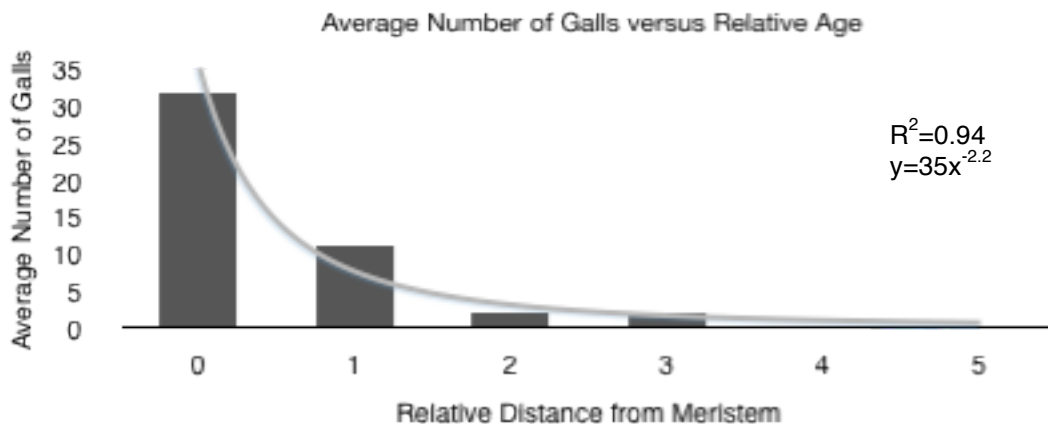


FIG. 1. Average number of galls for each relative distance from meristem. A relative distance of zero represents leaves closest to the meristem. Distance from meristem was used as an indicator of relative age.

average leaf size and gall density ( $p < 0.002478$ , d.f.=173).

#### Relative Leaf Age and Leaf Size

The average leaf size for each relative age group was graphed in Figure 3 to determine if the relationship between leaf size and gall density was simply the result of a relationship between leaf age and leaf size. It does not appear that leaf age and leaf size are strongly correlated, so relative leaf age and leaf size seem to effect the number of galls per leaf independently.

An Analysis of Variance (ANOVA) test was performed to examine if there existed a statistically significant difference in leaf size for each age group. The ANOVA test indicated that there was not a statistically significant relationship between relative leaf age and leaf size.

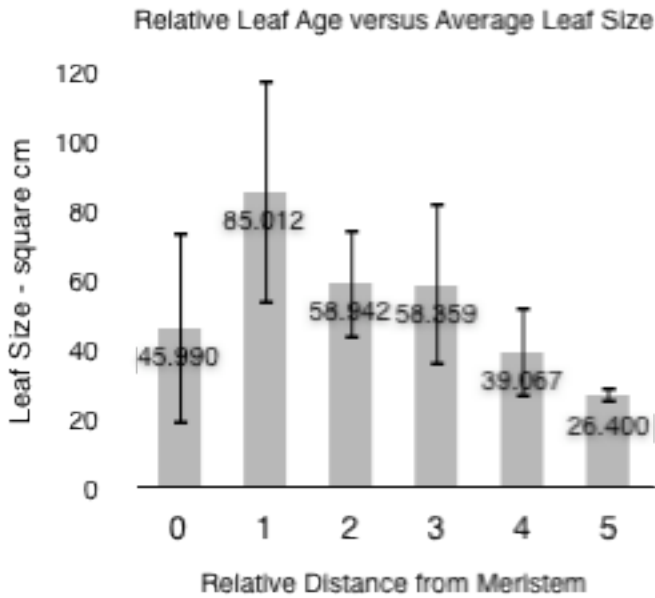


FIG. 3. Shows the average leaf size in square cm for each relative age group.

#### Distribution of Galls

The distribution of galls across leaves was studied to determine if galls have a clumped distribution, uniform distribution, or a random distribution. Using the Clark-Evans Nearest Neighbor method, it was determined that 50% of leaves had galls that were statistically significantly clumped ( $p < 0.05$ ) (Clark Evans 1954). Figure 4 shows a photograph of a representative leaf with a clumped distribution of galls.

Three percent of leaves had distribution of galls that were statistically significantly uniform ( $p < 0.05$ ) (Clark-Evans 1954).

The remaining 47% of leaves showed distributions of galls that were not statistically significantly clumped or uniform ( $p > 0.05$ ) (Clark-Evans 1954). These leaves had random distributions of galls.

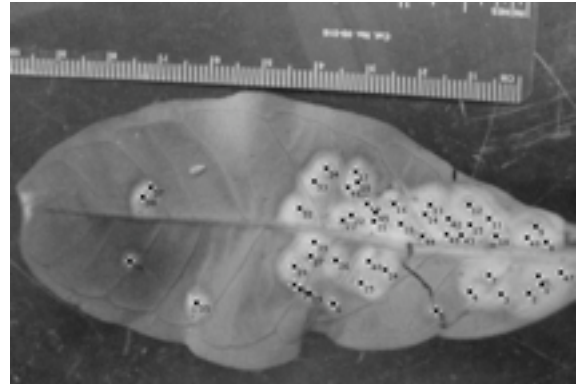


FIG. 4. Shows a representative leaf with a statistically significantly clumped distribution of galls.

#### Distribution of Galls and Relative Leaf Age

The distribution of galls across individual leaves was compared with relative leaf age to determine if leaf age affected gall distribution. As Figure 5 shows relatively younger leaves had

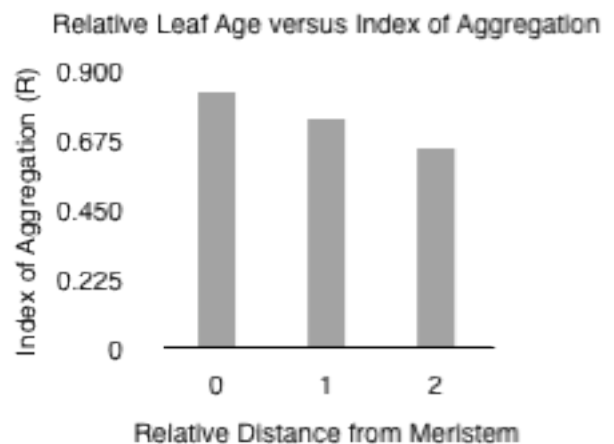


FIG. 5. Shows the average index of aggregation (R) versus relative leaf age. The relative distance of a leaf from the meristem was used to indicate the relative age of each leaf.

higher average index of aggregation values. Relatively older leaves have on average lower index of aggregation values, so relatively older leaves are more likely to display a clumped distribution of galls.

An Analysis of Variance (ANOVA) test was performed to determine if there was a statistically significant relationship between relative leaf age and index of aggregation. The ANOVA test indicated that there was not a statistically significant difference between average index of aggregation values for the three relative age groups.

*Distribution of Galls and Leaf Size*

The distribution of galls across individual

indicating the trendline accurately describes the relationship displayed by the graph.

A Pearson's r test was performed to determine if a statistically significant relationship existed between average leaf size and index of aggregation. The Pearson's r test indicated that there is a statistically significant relationship between leaf size and index of aggregation ( $p < 0.0010777$ ,  $d.f. = 173$ ).

*Distribution of Galls Relative to the Midrib*

The distribution of galls relative to the midrib was examined to determine if galls are closer or farther from the midrib than would be expected with a random distribution of galls. On the 93% of

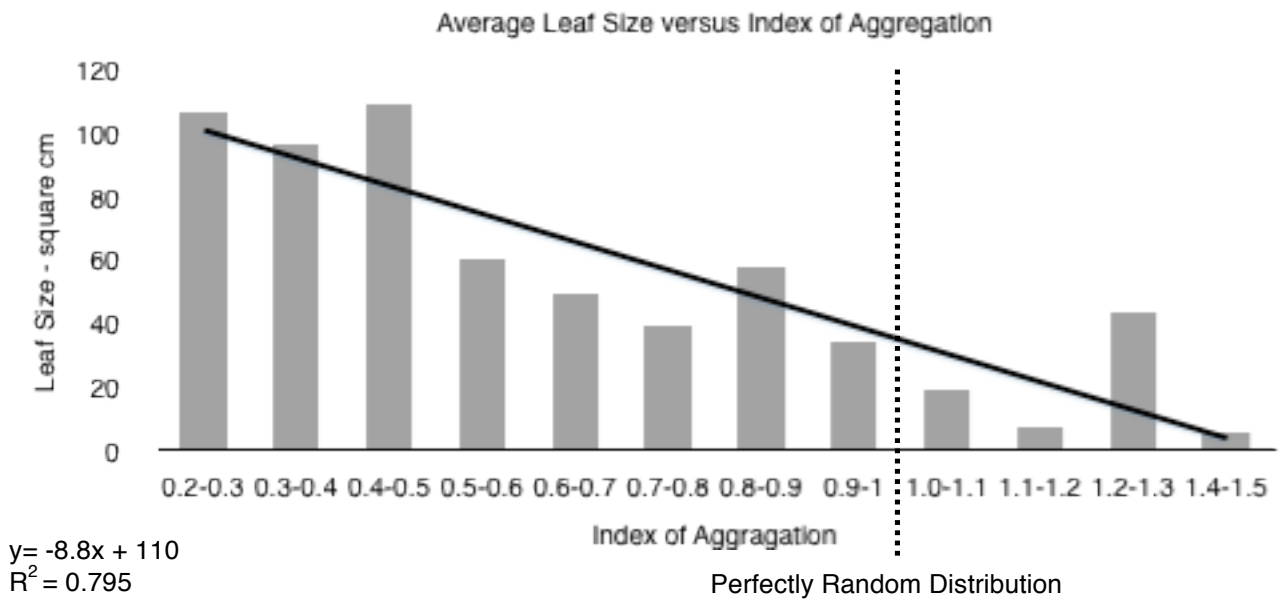


FIG. 6. Average leaf size for various index of aggregation values. An index of aggregation value of zero indicates a perfectly random distribution. Index of aggregation values less than 1 represent populations with clumped distributions and index of aggregation values greater than 1 represent populations with uniform distributions.

leaves was compared with the leaf size to determine if leaf size affects whether galls display a clumped, uniform, or clumped distribution. Figure 6 shows how at low index of aggregation values leaf size tends to be large and that with increasing index of aggregation values leaves tend to become larger.

The relationship between leaf size and index of aggregation showed a linear relationship. A trendline with the equation,  $y = -8.8x + 110$  was fitted to the data and had an  $R^2$  value of 0.795,

leaf halves galls were closer to the midrib than would be expected with a random distribution of galls. The remaining 7% of leaves did not have galls closer or farther from the midrib than would be expected by random chance.

## DISCUSSION

### *Relative Leaf Age and Gall Abundance*

As the results indicate there is a statistically significant relationship between relative leaf age and gall abundance, suggesting preferential ovipositing. There are significantly more galls on younger leaves indicating that *Megatrioza vitiensis* preferentially oviposits on younger leaves. *Megatrioza vitiensis* may prefer younger leaves because they offer superior nutrition for psyllids' developing within galls or for psyllids immediately after emergence from galls. *Megatrioza vitiensis* may also preferentially oviposit on younger leaves because younger leaves are less likely to fall off of the plant before the psyllid finishes development and emerges from the gall. There also could be fewer barriers or protections against gall formation in younger leaves, so ovipositing on younger leaves may successfully lead to gall formation more often than ovipositing on older leaves.

### *Leaf Size and Gall Density*

The results suggest there is a relationship between leaf size and gall density, suggesting preferential ovipositing on smaller leaves. *Megatrioza vitiensis* may preferentially oviposit on smaller leaves because galls may more often successfully develop on smaller leaves than larger leaves because of physical differences between leaves of different sizes. There could also be a feedback mechanism that affects growth with increasing gall density.

Many of the leaves with extremely high gall densities had very distorted shapes. Leaves with low gall densities showing very little distortion of shape and leaves with very high gall densities are often entirely curled over with the tip of the leaf touching the leaf's petiole. As the number of eggs oviposited on an egg increases, the leaf appears to have an increasingly distorted shape and as the shape of the leaf becomes increasingly distorted with higher gall density, leaf growth may be inhibited.

### *Relative Leaf Age and Leaf Size*

As the results show there is no statistically significant correlation between relative leaf age and leaf size, suggesting that the effect of relative leaf age and leaf size on ovipositing are independent. If there was a strong correlation between leaf size and relative leaf age in the sample of leaves collected for this study then it would be impossible to describe relative leaf age

and leaf size as independent factors affecting oviposition preferences.

### *Distribution of Galls*

Galls were statistically significantly clumped on the majority of leaves and a small group of leaves galls had a statistically significant uniform distribution suggesting that galls tend to be clumped, but that under some circumstances psyllids will oviposit on a leaf until what was once a clumped distribution of galls increases in density until it is uniform. The distribution of galls across leaves may tend to be clumped because females strongly prefer certain sections of leaves or because galls may be more successful in close proximity to other galls. If females have strong preferences for certain sections of the leaf or if female prefer to oviposit near other galls because galls are more successful in close proximity to other galls, one would expect that the developing psyllids in galls in close proximity to one another would be genetically different and would not all be at the same developmental stage.

Conversely, galls could tend to exhibit a clumped distribution if a single female oviposited many eggs in close proximity in a single event. If the clumped distribution of galls seen on the majority of leaves were due to mass oviposition events, one would expect galls in close proximity to be the same age and very closely related. Further studies would be required to determine the mechanism of oviposition that leads most leaves to have a statistically significantly clumped distribution of galls.

### *Distribution of Galls and Relative Leaf Age*

Although the distribution of galls appears to be increasingly clumped with older relative leaf age, there was no statistically significant difference between the average index of aggregation for the three age groups suggesting that relative age has no effect on the distribution pattern of galls or that the effect of relative age on index of aggregation was too small to be detected with this study.

### *Distribution of Galls and Leaf Size*

As the results show as the index of aggregation increases the average leaf size decreases indicating that larger leaves tend to have distributions of galls that are more often significantly clumped and tend to have distributions that are more clumped than distribution of galls on smaller leaves. The difference in the degree of clumping with larger

leaves is tied to the fact that females preferentially oviposit on smaller leaves. Because females preferentially oviposit on smaller leaves the density of galls is much greater on smaller leaves, so smaller leaves are less likely to display a clumped distribution, than larger leaves with lower gall densities.

There appears to be a minimum amount of space required for successful gall development, so as gall density increases the distribution goes from clumped to uniform. On smaller leaves, which tend to have higher gall densities, distribution is more likely to be uniform or random than on large leaves with low gall densities.

#### *Distribution of Galls Relative to Leaf Midrib*

The distribution of galls on the majority of leaves is closer to the midrib than would be expected by random chance, suggesting that females preferentially oviposit near the midrib. If females oviposited on all areas of the leaf in equal proportion, one would not expect such a large majority of the leaves to have the galls significantly closer to the midrib than expected with a random distribution of galls. Females may preferentially oviposit near the midrib so that galls are closer to the midrib which is a large source of vascular tissue. By preferentially ovipositing near the midrib, developing galls are closer to nutrients and water which may improve the chance that an egg develops successfully and emerge from its gall.

#### CONCLUSIONS

The results indicate that preferential ovipositing does exist in *Megatrioza vitiensis*. Higher gall abundances were found on relatively younger, smaller leaves and gall distributions tended to be clumped and closer to the midrib than would be expected randomly. These results suggest that *Megatrioza vitiensis* and *Syzygium malaccense* have exerted evolutionary influence on one another which has led to co-evolution and their current relationship.

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