

Galling Insects (Diptera: Cecidomyiidae) Survive Inundation during Host Plant Flooding in Central Amazonia¹

ABSTRACT

The effect of host plant inundation on survivorship of *Symmeria paniculata*'s galling herbivores was investigated in Central Amazonian floodplain forest. The majority of submerged galls were alive (62% of morphospecies 1 and 70% of morphospecies 2). Survivorship was similar between submerged leaves and new leaves that were never submerged. Some submerged galls were eaten by fish. To the best of our knowledge, this is the first report of galling insect survivorship under severe flooding.

RESUMO

O efeito da inundação da planta hospedeira na sobrevivência dos herbívoros galhadores de *Symmeria paniculata* foi investigado numa floresta inundável da Amazônia Central. A maioria dos insetos galhadores submersos estava viva (62% para morfoespécie 1 e 70% para morfoespécie 2). A sobrevivência foi semelhante entre folhas submersas e folhas que nunca foram submersas. Algumas galhas submersas foram predadas por peixe. Este é o primeiro estudo que relata sobrevivência de insetos galhadores à rigorosa inundação.

SEASONAL WATER LEVEL FLUCTUATIONS in Central Amazonian floodplain forest can be up to 14 m, and the period of inundation can last from 50 to 270 days (Junk 1989). The transition from terrestrial to aquatic habitat throughout the year creates considerable stress for resident plants and animals and has resulted in various adaptations for survival during long periods of total or partial submersion (Adis *et al.* 1988, Junk 1989, Ferreira 2000). Arthropods that inhabit the floodplain forest have also evolved strategies to compensate for the periodic loss of their terrestrial habitat, such as (1) staying near the waterline and moving in advance of the ascending flood; (2) moving to non-flooded trunks and canopy areas; (3) flying to adjacent dryland biotopes; and (4) evolving adaptations for remaining in flooded terrestrial areas (Adis 1986, Adis *et al.* 1988).

One group of arthropods that would suffer from the seasonal inundation in floodplain forests are galling herbivores. Galling insect larvae spend most of their lifetime embedded within the plant tissue, making them truly sessile herbivores (Fernandes 1990). Once inside the host tissue, larvae must adapt to variation in plant quality (hormones, nutrients, basic metabolism) and environmental stresses. Alternatively, gallers have evolved the ability to manipulate host plants' growth and development (Mani 1964, Rohfritsch & Shorthouse 1982, Fernandes 1990) and receive some protection against harsh environmental conditions (Price *et al.* 1987). These finely tuned adaptations may have led gallers to become the most abundant insect herbivores in these harsher habitats (Fernandes & Price 1988, Lara & Fernandes 1996, Price *et al.* 1998, Gonçalves-Alvim & Fernandes 2001). Although population studies of galling insects have been performed on host plants under several environmental conditions (*e.g.*, flooding [Ribeiro *et al.* 1998], salinity [Gonçalves-Alvim *et al.* 2001], and dryness [Waring & Price 1990, Fernandes & Price 1992]), only one study in a temperate region has addressed the direct influence of flooding on larval survivorship (Craig *et al.* 1989). Therefore, the goal of this study was to determine the effect of host plant inundation on galling herbivore survivorship.

Symmeria paniculata Benth. (Polygonaceae) is a shrub commonly found in inundated forest of Central Amazonia and considered to be highly flood-tolerant (Ferreira & Stohlgren 1999). Galls from two as yet undescribed Cecidomyiidae (Diptera, new genera; V. C. Maia, pers. comm.) were found at high densities on *S. paniculata* leaves. Gall morphospecies 1 induces spheroid galls on both leaf laminae near the margin. The galls are green, glabrous, single-chambered, have one larva per chamber, and can occur in clusters or as isolated entities. Gall morphospecies 2 induces cylindrical galls primarily on the adaxial leaf surface.

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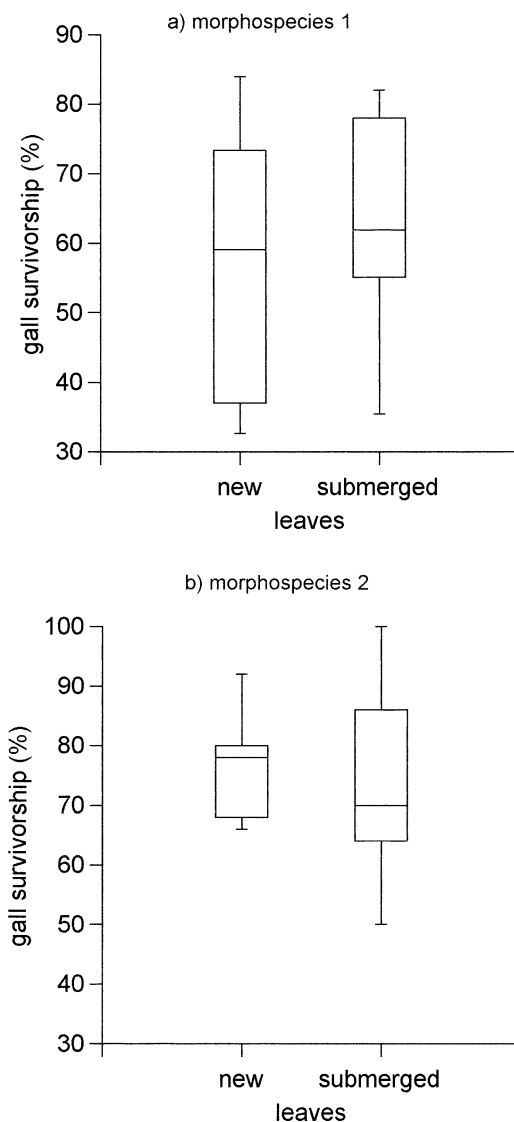


FIGURE 1. Box plots demonstrating gall survivorship (percentage) of (a) morphospecies 1 and (b) morphospecies 2 from submerged leaves and new leaves on *Symmeria paniculata* in a floodplain forest of Central Amazonia, Brazil. The center line represents the median, the box represents the 25th and 75th percentiles, and the whiskers represent the range.

The galls are brown, glabrous, single-chambered, and have an operculum through which the adult cecydomyiid emerges.

Fieldwork was carried out in the Arquipélago de Anavilhanas, an island system 80 km from Manaus, Brazil (3°5'S, 59°59'W). This site is part of the Rio Negro basin, a blackwater river with minor sedimentation (Goulding *et al.* 1988). Fieldwork was undertaken at the Lago do Prato, a lake permanently connected to the main river by a narrow channel. Data were collected during August 2001, when water level was receding. Ten *S. paniculata* shrubs at least 15 m apart were randomly selected. On each shrub, leaves with galls from two strata were collected: (1) submerged leaves corresponding to leaves found at the receding waterline that were continuously submerged (during 114 d) until two days prior and (2) new leaves corresponding to freshly expanded leaves that were never submerged. At each stratum, on

each shrub, ten leaves galled by morphospecies 1 and another ten leaves galled by morphospecies 2 were randomly collected. Five galls per leaf were randomly chosen for dissection to observe larval survivorship. Live larvae can be easily distinguished from dead larvae (Fernandes & Price 1992). For each morphospecies, the percentage of galling insect survivorship per plant was compared between the two strata by the Wilcoxon signed rank test.

The majority of cecidomyiid larvae encountered on both species were alive. The median percentage of submerged galls that survived was 62 percent for morphospecies 1 and 70 percent for morphospecies 2. The percentage of galling insect survivorship was similar in both strata for the two species (morphospecies 1: Wilcoxon test $Z = 0.76$, $N = 10$, $P = 0.44$; morphospecies 2: Wilcoxon test $Z = 0.66$, $N = 10$, $P = 0.50$; Fig. 1). Mortality was caused by several factors, including parasitism by unidentified microhymenopteran parasitoids, grasshopper predation on gall walls, plant-induced defenses (hypersensitivity), direct inundation of the gall chamber with water, and most interestingly, predation by fish. The latter was particularly clear on gall morphospecies 2, in which most of the mortality was caused by fish predation. The well defined, chisel-like biting marks left on gall walls indicated that one or more anostomid fish species (Ostariophysi: Characiformes) may have been responsible for the predation.

To our knowledge, this is the first report on galling insect survivorship under severe flooding. In contrast to these results, Craig *et al.* (1989) have shown that any gall of a shoot-galling sawfly that falls to the ground after shoot abscission and becomes waterlogged, survives. This temperate example clearly does not agree with the survivorship reported in Central Amazonia. Additionally, the ability of both galling species sampled to resist flooding would indicate that this may be a common phenomenon in Amazon floodplain forest. Unfortunately, no quantitative study of galling insect abundance has yet been undertaken in the floodplain forests of the Amazon. This is in contrast to the information available for many other vegetation types around the world (Fernandes & Price 1991, Price *et al.* 1998).

Many plants subjected to periodic flooding have evolved a series of adaptations to survive, including changes in ethanol, oxygen, and auxin concentrations, as well as changes in photosynthetic rates (Hook & Scholtens 1978). These changes likely affect galling insect larvae, which are known to be finely tuned to their host plants' physiological status (Mani 1964, Ribeiro *et al.* 1998). The possibility that galling insects may have developed adaptations to survive severe seasonal flooding is a promising topic that warrants future study.

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- ADIS, J. 1986. An "aquatic" millipede from a Central Amazonian inundation forest. *Oecologia* 68: 347–349.
- , V. MAHNERT, J. W. MORAIS, AND J. M. G. RODRIGUES. 1988. Adaptation of an Amazonian pseudoscorpion (Arachnida) from dryland forest to inundation forests. *Ecology* 69: 287–291.
- CRAIG, T. P., J. K. ITAMI, AND P. W. PRICE. 1989. A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. *Ecology* 70: 1691–1699.
- FERNANDES, G. W. 1990. Hypersensitivity: a neglected plant resistance mechanism against insect herbivores. *Environ. Entomol.* 19: 1173–1182.
- , AND P. W. PRICE. 1988. Biogeographical gradients in galling species richness: tests of hypotheses. *Oecologia* 76: 161–167.
- , AND ———. 1991. Comparison of tropical and temperate galling species richness: the roles of environmental harshness and plant nutrient status. *In* P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson (Eds.). *Plant–animal interactions: Evolutionary ecology in tropical and temperate regions*, pp. 91–115. John Wiley and Sons, New York.
- , AND ———. 1992. The adaptive significance of insect gall distribution: survivorship of species in xeric and mesic habitats. *Oecologia* 90: 14–20.
- FERREIRA, L. V. 2000. Effects of flooding duration on species richness, floristic composition and forest structure in river margin habitat in Amazonian blackwater floodplain forest: implications for future design of protected areas. *Biodiv. Conserv.* 9: 1–14.
- , AND T. J. STOHLGREN. 1999. Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia* 120: 582–587.
- GONÇALVES-ALVIM, S. J., AND G. W. FERNANDES. 2001. Biodiversity of galling insects: historical, community and habitat effects in the Neotropical savannas. *Biodiv. Conserv.* 10: 79–98.

- , M. C. F. V. SANTOS, AND G. W. FERNANDES. 2001. Leaf gall abundance on *Avicenia germinans* (Avicenniaceae) along an interstitial salinity gradient. *Biotropica* 33: 69–77.
- GOULDING, M., M. L. CARVALHO, AND E. G. FERREIRA. 1988. Rio Negro, rich life in poor water. SPB Academic, The Hague, The Netherlands.
- HOOKE, D. D., AND J. R. SCHOLTNS. 1978. Adaptation and flood tolerance of tree species. In D. D. Hook and R. M. M. Crawford (Eds.). *Plant life in anaerobic environments*, pp. 299–331. Ann Arbor Science, Ann Arbor, Michigan.
- JUNK, W. J. 1989. Flood tolerance and tree distribution in Central Amazonia. In L. B. Holm-Nielsen, I. C. Nielsen, and H. Balslev (Eds.). *Tropical forest botanical dynamics. Speciation and diversity*, pp. 47–64. Academic Press, London, England.
- LARA, A. C. F., AND G. W. FERNANDES. 1996. The highest diversity of galling insects: Serra do Cipó, Brazil. *Biodiv. Lett.* 3: 111–114.
- MANI, M. S. 1964. *Ecology of plants galls*. Dr W. Junk Publishers, The Hague, The Netherlands.
- PRICE, P. W., G. W. FERNANDES, A. C. F. LARA, J. BRAWN, H. BARRIOS, M. G. WRIGHT, S. P. RIBEIRO, AND N. ROTHCLIFF. 1998. Global patterns in local number of insect galling species. *J. Biogeogr.* 25: 581–591.
- , ———, AND G. L. WARING. 1987. Adaptive nature of insect galls. *Environ. Entomol.* 16: 15–24.
- RIBEIRO, K. T., J. A. MADEIRA, AND R. F. MONTEIRO. 1998. Does flooding favour galling insects? *Ecol. Entomol.* 23: 491–494.
- ROHERITSCH, O., AND J. D. SHORTHOUSE. 1982. Insect galls. In G. Kahl and J. Schell (Eds.). *Molecular biology of plant tumors*, pp. 131–152. Academic Press, New York, New York.
- WARING, G. L., AND P. W. PRICE. 1990. Plant water stress and gall formation (Cecidomyiidae: *Asphondylia* spp.) on creosote bush. *Ecol. Entomol.* 15: 87–95.

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Tropical Bees (*Trigona hockingsi*) Show No Preference for Nectar with Amino Acids¹

ABSTRACT

We offered Australian tropical stingless bees (*Trigona hockingsi*) artificial nectar (30% sucrose w/v) either with or without added amino acids (3.30 mM). Bees showed no preference for nectar type, suggesting that sugars, rather than amino acids, play a greater role in nectar choice by this species.

Key words: amino acid; feeding choice; nectar; Queensland, Australia; Trigona.

NECTAR IS AN IMPORTANT BIOLOGICAL RESOURCE that is utilized by a wide variety of animals. Insects are the most abundant floral visitors, but some vertebrates also regularly take nectar. These include flying animals such as birds and bats as well as nonflying animals (*e.g.*, primates, marsupials, and reptiles). Along with pollen, nectar can be regarded as a reward to the floral visitor in return for the pollinating service. Although composition of nectar is dominated by sugars, being in the range of 10 to 40 percent w/v, amino acids form a ubiquitous and substantial component of floral nectar, occurring at millimolar concentrations (Baker & Baker 1973). This discovery initiated a series of investigations into the concentration and composition of amino acids in nectar, and provoked debate concerning their ecological role as a resource (Baker & Baker 1975, 1982, 1983, 1986; Baker 1977; Gottsberger *et al.* 1984, 1989).

To date the role of nectar amino acids as a resource for pollinators has not been satisfactorily resolved, but the consensus view is that plants that are adapted to pollination by butterflies show high concentrations of amino acids. Plants pollinated by birds exhibit low concentrations of amino acids. The ecological rationale behind this is that butterflies are specialized liquid feeders as adults and nectar is their only source of nitrogen. Birds, however, are able to capture insects and so gain nitrogen in the form of protein (Brice & Grau 1991, Brice 1992). Bees are able to eat and digest pollen; plants that they pollinate form an intermediate group.

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