SECRETARIA
DE
PÓS-GRADUAÇÃO
I. B.

UNIVERSIDADE ESTADUAL DE CAMPINAS
INSTITUTO DE BIOLOGIA

ASSOCIAÇÃO CONDICIONAL ENTRE O HOMÓPTERO GUAYAQUILA XIPHIAS (MEMBRACIDAE) E SUAS FORMIGAS ATENDENTES: O EFEITO DA FENOLOGIA DA PLANTA HOSPEDEIRA NO RESULTADO DA INTERAÇÃO

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Este exemplar corresponde à redação final
da tese defendida pelo(a) candidato (a)
Tiago Bosisio Quental
e aprovada pela Comissão Julgadora.

Dissertação apresentada ao
Instituto de Biologia da
Universidade Estadual de
Campinas para obtenção do
título de Mestre em Ecologia

Orientador: Prof. Paulo Sérgio Moreira Carvalho de Oliveira

Campinas
2002

FICHA CATALOGRÁFICA ELABORADA PELA BIBLIOTECA DO INSTITUTO DE BIOLOGIA - UNICAMP

Quental, Tiago Bosisio

Q34a Associação condicional entre o homóptero *Guayaquila xiphias* (membracidae) e suas formigas atendentes: o efeito da fenologia da planta hospedeira no resultado da interação/Tiago Bosisio Quental. --
Campinas, SP:[s.n.], 2002

Orientador: Paulo Sérgio Moreira Carvalho de Oliveira

Dissertação (mestrado) – Universidade Estadual de Campinas.

Instituto de Biologia

1. Mutualismo. 2. Cerrado. 3. *Guayaquila xiphias*. I. Oliveira, Paulo Sérgio Moreira Carvalho de. II. Universidade Estadual de Campinas. Instituto de Biologia. III. Título.

Data da Defesa: 29/04/2002

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AGRADECIMENTOS

Inicialmente gostaria de agradecer ao meu orientador Paulo S. Oliveira pela orientação, incentivo, apoio, e amizade durante os dois anos do mestrado. Sem sua orientação esse trabalho não seria concretizado. Muito mais do que simplesmente me orientar na minha pesquisa de mestrado, o Paulo me mostrou que é possível fazer pesquisa de alta qualidade no nosso país. Seu exemplo como ótimo profissional foi extremamente importante na minha formação.

Ao prof. Dr José Roberto Trigo por me orientar nas análises químicas.

A todos do laboratório de Ecologia Química do Departamento de Zoologia da Unicamp pela enorme ajuda durante as análises químicas. Agradeço especialmente ao Paiva, à Eunice e à Breila. Sem vocês eu já teria me dissolvido em ácido sulfúrico ou me intoxicado com alguma outra coisa no laboratório.

Ao Kléber Del-Claro, José Roberto Trigo e André Victor Lucci Freitas pelas sugestões em versões anteriores deste trabalho.

Ao Dr. Arício Xavier Linhares e ao Dr. Carlos Roberto Fonseca por sugestões relacionadas a estatística envolvida na minha tese de mestrado.

Aos amigos Carlos Roberto Fonseca e Gislene Ganade por me incentivarem muito nesses últimos anos e pelas sugestões relacionadas a minha pesquisa de mestrado.

Aos meus amigos de laboratório Xaxá, Humberto, Rodrigo, Luciana, Glauco e Jarbas por terem me recebido tão bem no laboratório e me ajudado nesses dois anos.

Aos amigos André Tavares e Xaxá por terem me ajudado em algumas viagens de campo e ao amigo Adam por pelas sugestões no trabalho e pela revisão do inglês.

A todos do Museu de História Natural da Unicamp, em especial à Fátima, por me permitirem utilizar o "scanner" de slides.

Ao Instituto Botânico, em particular ao Marcos Mecca, pela autorização para trabalhar na Reserva Experimental de Mogi-Guaçu e utilizar o alojamento durante as viagens de campo.

A todos os funcionários da Reserva Experimental de Mogi-Guaçu, em especial a Marcos Mecca, João, Mara, Adão, Seu João (Abacaxi) e Paulo por terem tornado minha estadia na Fazenda Campininha mais prazerosa. Ao Paulo da Fazenda Campininha, também sou muito grato pela ajuda no campo.

Aos funcionários do Departamento de Zoologia, em especial a Eliana, por me ajudarem em alguns aspectos relacionados a apresentação da tese.

A minha esposa Luciana por todo seu amor, compreensão e companheirismo. Lu sem você tudo seria muito mais difícil, algumas coisas impossíveis! Muito obrigado pela sua enorme ajuda durante todos esses anos.

Aos meus pais, Angela e Francisco, que sempre me encorajaram em trilhar este caminho. Seu incentivo, interesse e seus conselhos foram fundamentais para que eu pudesse seguir estudando Biologia. Muito obrigado por sempre acreditarem em mim e por se mostrarem pais maravilhosos!

A todos os meus familiares, em especial a minha irmã Irene, à Tia Riza, à Tia Cecy e à Belita por terem me incentivado a fazer o mestrado na Unicamp, e me ajudado, direta ou indiretamente, em aspectos relacionados a minha mudança para Campinas.

A todos os amigos que fiz em Campinas por terem tornado esses dois anos momentos a serem lembrados para sempre.

A CAPES pela bolsa de mestrado concedida durante dois anos.

ÍNDICE

INTRODUÇÃO GERAL

O mutualismo é definido como qualquer relação mutuamente benéfica entre duas espécies, podendo variar de obrigatório a facultativo (Pianka, 1994). Geralmente, numa interação mutualística, uma espécie fornece algum tipo de "serviço" (ex: polinização, proteção, dispersão) e em troca recebe algum tipo de "recompensa" (usualmente comida e/ou abrigo) (Boucher, 1985). Apesar de sua importância, apenas recentemente o mutualismo vem recebendo uma maior atenção por parte dos ecólogos. Numa revisão sobre mutualismo, Bronstein (1994a) chama a atenção que, apesar do grande acúmulo de dados referentes a interações mutualísticas, somente 5% dos trabalhos analisam os benefícios em ambos os lados da interação. Isto mostra que grande parte destes estudos não analisa o mutualismo como uma forma de interação, e sim limita-se a descrever a história natural de uma das espécies envolvidas. Devido a este caráter descritivo (que de forma alguma deixa de ser importante), o estudo do mutualismo produziu poucas generalizações (Bronstein 1994a). Uma delas é que o mutualismo obrigatório é certamente menos comum que o mutualismo facultativo devido a restrições no processo co-evolutivo entre duas espécies (Howe, 1984). De qualquer modo as interações mutualísticas são freqüentes e importantes nas comunidades naturais (Bronstein, 1998).

A maior parte dos estudos de mutualismo envolve interações entre plantas e animais (Bronstein, 1994a) e o interesse por este assunto é bastante antigo. Já no final do século XIX, Belt (1874) sugeriu que havia uma relação mutuamente benéfica entre formigas e as plantas por estas visitadas. Janzen (1966) mostrou que a interação entre algumas espécies de formigas do gênero *Pseudomyrmex* e algumas espécies de plantas do gênero *Acacia* era fundamental para a sobrevivência das espécies participantes. Vários outros estudos mais recentes (Schemske 1980; Horvitz & Schemske, 1984; Fonseca, 1994; Freitas & Oliveira, 1996; Del-Claro et al., 1996; Oliveira, 1997; Oliveira et al., 1999; Heil et al., 2001) vêm demonstrando a importância de formigas na proteção de plantas contra a herbivoria. Esta relação mutualística entre formigas e plantas consiste na defesa oferecida pelas formigas contra o ataque de herbívoros em "troca" de alimento e, em alguns casos, também de abrigo (Beattie, 1985; Hölldobler & Wilson, 1990).

Price et al. (1980) argumentam que, para realmente entender a relação entre herbívoros e plantas, é necessário considerar um terceiro nível trófico: o dos inimigos naturais dos herbívoros. Esta abordagem enfatiza a relação mutualística entre formigas e plantas, já que as formigas são encaradas como parte do "arsenal" de defesa das plantas contra os herbívoros (Price et al., 1980).

As formigas nem sempre apresentam uma relação antagônica com herbívoros. Em alguns casos, formigas e insetos herbívoros interagem de forma mutualística. Neste caso, os herbívoros oferecem alimento e em troca recebem proteção contra predadores e parasitóides. Os herbívoros mutualistas mais comuns são: 1- Homópteros (adultos e ninfas) (em geral Aphididae, Membracidae, Coccidae e Pseudococcidae); 2- Larvas de Lepidoptera (Lycaenidae).

Os homópteros excretam um exsudato, rico em carboidratos (Auclair, 1963; Way, 1963; Buckley, 1987). As larvas de Lepidoptera (Lycaenidae) possuem um órgão especializado para secretar uma solução com açucares e aminoácidos (DeVries & Baker, 1989; Hölldobler & Wilson, 1990; Cushman et al., 1994;). Para estes herbívoros as vantagens são: maior sobrevivência (Pierce & Mead, 1981; Cushman & Whitham, 1989; Morales, 2000; Del-Claro & Oliveira, 2001); aumento da fecundidade (Bristow, 1983); aumento da massa e redução do tempo de geração (Cushman et al., 1994).

Em geral assume-se que a vantagem para as formigas é a obtenção de alimento. De fato, Fiedler & Saam (1995) demostraram experimentalmente que a interação entre formigas e larvas de borboletas da família Lycaenidae realmente afeta de forma positiva a sobrevivência das formigas. Cushman et al. (1994) demostraram que colônias que mantinham este tipo de interação produziam formigas maiores e reduzam o tempo de desenvolvimento das pupas.

Tradicionalmente as interações entre duas espécies apresentam uma classificação estática, ou seja, se encaixam em uma única categoria (e.g., predação, competição, mutualismo). Recentemente, mais atenção vem sendo dada à natureza dinâmica das interações entre duas espécies (Boucher, 1982; Cushman & Whitham, 1989; Cushman & Addicott, 1991; Bronstein, 1994b). Os custos e benefícios numa interação podem e devem variar de acordo com o cenário ecológico. Estas variações vêm sendo chamadas de interações condicionais (Cushman & Whitham, 1989; Cushman & Addicott, 1991). Apesar da natureza condicional das interações ser conhecida há cerca de três décadas (e.g. Paine, 1966), apenas mais recentemente tem se dado uma maior ênfase em se investigar como as condições ecológicas modificam o resultado dessas interações no tempo e no espaço. Isto permite um melhor entendimento da dinâmica ecológica e evolutiva destas interações (Cushman & Addicott, 1991).

Cushman & Addicott (1991) discutem a condicionalidade do ponto de vista do mutualismo. Segundo estes autores poderíamos considerar três maneiras distintas de condicionalidade variando no tempo e no espaço: 1- variações nos "problemas" ecológicos vivenciados por um organismo numa interação mutualística; 2- variação nas possíveis "soluções" que os parceiros mutualistas podem fornecer para estes "problemas"; 3- variação na disponibilidade de mutualistas.

Como exemplo do primeiro tipo de condicionalidade podemos citar o trabalho de Cushman & Whitham (1989), que verificou que a interação entre homópteros e formigas só é realmente benéfica para o homóptero nos anos em que a abundância do seu predador é alta. Um exemplo do segundo tipo de condicionalidade seria a capacidade distinta de diferentes espécies de formigas defenderem uma espécie de homóptero encontrada por Messina (1981). O número de formigas cuidando dos homópteros em sua planta hospedeira pode variar tanto com a densidade de homópteros em cada planta, quanto com a densidade de plantas infestadas com homópteros (Cushman & Whitham, 1991), caracterizando um exemplo do terceiro tipo de condicionalidade apresentado no parágrafo anterior.

Um sistema interessante para analisar a natureza condicional do mutualismo é a interação entre formigas e homópteros. Buckley (1987), em sua revisão sobre as interações envolvendo plantas, homópteros e formigas, apresenta uma série de exemplos onde a interação mutualística entre homópteros e formigas pode variar de obrigatória a facultativa, além de casos de predação de homópteros por algumas espécies de formigas. Algumas formigas "cultivam" determinadas espécies de homópteros dentro do seu ninho, e algumas fêmeas carregam homópteros imaturos no vôo nupcial antes de formarem uma nova colônia. As formigas normalmente atendem aos homópteros que estão sobre a planta hospedeira (e.g. Messina, 1981; Cushman & Addicott, 1991), mas às vezes podem também construir um ninho satélite na planta, que serve de abrigo para os homópteros (Cushman & Whitham, 1989; Del-Claro & Oliveira, 1999; observação pessoal). A interação entre formigas e homópteros pode apresentar um caráter bastante sofisticado, como o encontrado por Bristow (1983) para o membracídeo *Publilia reticulata*. Esta autora demonstrou que as formigas são capazes de assumir o cuidado parental dos homópteros imaturos, garantindo sua defesa contra inimigos naturais melhor do que a própria mãe. Além disto, as fêmeas de

P. reticulata que transferem o cuidado à prole para as formigas são capazes de produzir uma segunda prole.

O presente estudo teve como objetivo examinar alguns aspectos da condicionalidade da interação entre os homópteros da espécie *Guayaquila xiphias* (Membracidae) e suas formigas atendentes. Mais especificamente, este trabalho examinou como a fenologia da planta hospedeira poderia alterar o resultado da interação entre homópteros e formigas. Para investigar uma possível mediação da fenologia da planta hospedeira testei a seguinte hipótese: agregações de membracídeos localizadas em plantas com inflorescência se alimentariam de um floema mais nutritivo, resultando em um exsudato mais rico e atraindo um maior número de formigas atendentes. Com isso, estas agregações de homópteros seriam melhor protegidas contra seus inimigos naturais do que as localizadas em plantas sem inflorescência.

O capítulo único da tese foi escrito em inglês para facilitar a posterior publicação em revista especializada.

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CAPÍTULO 1: CAN HOST-PLANT PHENOLOGY MEDIATE THE OUTCOME OF ANT-HOMOPTERAN INTERACTION?

RESUMO

Estudei o efeito da fenologia da planta hospedeira (*Didymopanax vinosum*) na interação entre o homóptero *Guayaquila xiphias* e suas formigas atendentes. Os resultados mostraram que o floema de plantas com inflorescência apresenta uma concentração mais elevada de açúcar do que o floema de plantas sem inflorescência. Já o exsudato produzido pelos homópteros que se alimentam de plantas com inflorescência possui a mesma concentração de açúcar e é produzido na mesma quantidade do que o exsudato de homópteros que se alimentam em plantas sem inflorescência. Os dados também mostram que as agregações situadas em plantas com e sem inflorescência foram atendidas pelo mesmo número relativo de formigas. Os experimentos de campo mostraram que a presença de formigas aumentou a sobrevivência dos homópteros e reduziu abundância de seus inimigos naturais, porém a fenologia da planta hospedeira não mudou o resultado desta interação. Alem disso, a fenologia da planta hospedeira afetou a abundância dos inimigos naturais. Plantas com inflorescência acumularam mais inimigos naturais do que plantas sem inflorescência. Este é o primeiro estudo a examinar todos mecanismos envolvidos na mediação da planta hospedeira na interação entre formigas e homópteros, e o primeiro estudo experimental a testar na natureza o efeito da fenologia da planta no resultado desta interação.

ABSTRACT

We studied the effect of host plant phenology (*Didymopanax vinosum*) on the interaction between the honeydew-producing membracid *Guayaquila xiphias* and its tending ants in the 'cerrado' savanna of Brazil. Results showed that the phloem of plants with inflorescence had a higher sugar concentration compared to the phloem of plants without inflorescence. However, the honeydew produced by treehoppers feeding on flowering plants had the same sugar concentration and was produced in equal quantities compared to the honeydew from treehoppers feeding on plants without inflorescence. Moreover, membracid aggregations were tended by the same relative number of ants on plants with or without inflorescence. Controlled field experiments showed that ant presence reduced the abundance of *Guayaquila*'s natural enemies on the host plant and increased homopteran survival. Although plant phenology had no significant effect on ant-derived benefits to membracids, it did affect the abundance of natural enemies on the host plant. Plants with inflorescence accumulated more natural enemies through time than plants without inflorescence. This is the first study to experimentally investigate the effect of plant phenology on the outcome of an ant-homopteran system under natural conditions.

INTRODUCTION

The outcome of species interactions is strongly dependent on the ecological settings in which they occur (Boucher et al., 1982; Thompson, 1988; Bronstein, 1994). In order to get a realistic picture of ecological and evolutionary dynamics of species interactions we need to understand the full range of potential outcomes (Cushman, 1991; Cushman & Addicott, 1991; Bronstein, 1994). Although mutualism has been traditionally regarded as a static interaction, in the past few years it has been investigated under a cost/benefit perspective (Bronstein, 1994). Studies with several different taxa have shown that the association outcomes are conditioned in predictable ways by biotic and abiotic factors that change the costs and benefits for each species involved in the interaction (Cushman & Whitham 1989; Zamora 1999; Ommeren & Whitham 2002). The conditional nature of species interactions has been well documented in ant-homopterans systems. Manipulative studies have revealed that the outcome of such mutualistic interactions depend on biotic and abiotic conditions such as the age, identity and/or density of the species involved, as well as the type and abundance of natural enemies (Cushman & Whitham, 1989; Bretton &Addicot, 1992; Morales, 2000; Del-Claro & Oliveira, 2000).

Although interactions between ants and honeydew-producing homopterans have been traditionally regarded as mutualistic (Way, 1963), recent data have shown that the outcome of such associations depends upon the ecological scenario in which they occur (Cushman & Whitham, 1989; Cushman & Addicott, 1991). The honeydew produced by homopterans is rich in sugars (Auclair 1963; Völkl et al 1999) and for many ant species this secretions represents an important food resource (Hölldobler & Wilson, 1990; Rico-Gray 1993). Tending ants harvest the honeydew produced by the homopterans and, in turn, provide a wide range of benefits, including protection from natural enemies (Bristow 1984; Cushman & Whitham, 1989; Del-Claro & Oliveira, 2001) and increased fecundity (Bristow, 1983). Occasionally, ant-tended homopterans may also benefit from ant-constructed protective shelters (Del-Claro & Oliveira, 1999), increased feeding rates (Buckley, 1987), and reduced fungal infections (Queiroz & Oliveira, 2001). For a review of ant-homopteran interactions see Buckley (1987) and Hölldobler & Wilson (1990).

Plant characteristics can directly affect the survival and reproduction of insect herbivores such as phloem-feeding homopterans (Auclair, 1963; Mattson, 1980). Particularly interesting are the indirect effects of plant traits on the survival and reproduction of ant-tended herbivores. Cushman (1991) suggested that host-plant quality could mediate the outcome of the interactions between ants and ant-tended herbivores, and presented a potential mechanism for this mediation. First, the attractiveness of herbivores to ants (due to chemical composition and/or quantity of ant attractants produced by herbivores) should vary with host-plant quality. Second, ants should preferably tend those herbivores that produce the most nutritious rewarding attractants. Finally, the number and/or attentiveness of ants should have a significant effect on the fitness of herbivores.

Studies with ant-tended herbivores have shown that plant and herbivore characteristics can affect the myrmecophilous quality of the tended herbivore. Fiedler (1990) observed the attractiveness and secretory capabilities of caterpillars *Polyommatus icarus* were affected by diet type. Völkl et al. (1999) demonstrated that honeydew production and sugar composition affected ant preferences for different aphid species. Fertilization experiments performed by Baylis & Pierce (1991) demonstrated that fifth instar lycaenid butterfly larvae feeding on nitrogen-fertilized plants attracted a larger number of ants compared to those feeding on unfertilized plants, and that higher levels of ant-tending resulted in augmented cartepillar survival on fertilized compared to unfertilized plants.

The present study investigates the interaction between tending ants and the honeydew-producing treehopper *Guayaquila xiphias* (Membracidae) on the plant *Didymopanax vinosum* (Araliaceae) . Usually the phenological phase of the host-plant will determine the location of membracid aggregation. The membracids usually aggregate at the apical meristem of non-reproductive plants (hereafter plants without inflorescence). If the plant is flowering, the membracids are found on the main axis of the inflorescence (here after plants with inflorescence) (Del-Claro & Oliveira 1999). In general, when entering the reproductive phase, plants allocate most of their resources to the reproductive stem, resulting in increased local phloem quality (Salisburg & Ross 1992). This observations raises the question as to whether the feeding location of the membracids, as related to plant phenology (plants with inflorescence vs plants without inflorescence), could affect the benefits provided by honeydew-gathering ants.

The objective of this study is to test the hypothesis proposed by Cushman (1991) that host-plant could mediate the interaction outcome between ants and herbivores. We tested the hypothesis that membracid aggregations located on plants with inflorescence consume a higher quality food source, which would translate into a higher quality honeydew for the ants and, finally, lead to a increased ant attendance and better protection in comparison to membracids located at plants without inflorescence. To test this hypothesis the following specific questions were addressed:

1 Within a given time period, does phloem quality (sugar and nitrogen concentration) vary between plants with and without inflorescence?

2. Does plant phenology (and thus membracid feeding location) affect honeydew quality and/or quantity and membracid attractiveness to ants?
3. Does plant phenology (and thus membracid feeding location) affect ant-derived benefits to membracids?

THE STUDY SYSTEM

The ant-homopteran system studied is well described, occurs year-round in the Brazilian cerrado (sub-tropical savannah) and involves a wide assemblage of honeydew-gathering ants on the membracid's host plant, *Didymopanax vinosum* (Araliaceae) (Del-Claro & Oliveira, 1999). Although tending ants effectively defend the membracids against their natural enemies, the degree of protection varies both year to year and with the species of tending ant (Del-Claro & Oliveira, 2000). Moreover, the ants increase membracid fecundity because ant-tended females transfer parental care to the ants and can produce an additional brood (Del-Claro & Oliveira, 2000). If not tended by ants, the treehoppers flick the accumulating honeydew beneath the host-plant, effectively attracting ground-dwelling ants which climb onto the plant and begin tending activities (Del-Claro & Oliveira 1993, 1996).

The host-plant of *G. xiphias* (*D. vinosun*) does not possess any source of ant attractants, such as extrafloral nectaries. Therefore ant presence on the plant is solely due to their tending activities at the membracids. Del-Claro & Oliveira (2000) showed that ant spatial distribution and patrolling activity on the plant is determined by the presence and location of membracid aggregation, and this, in turn, affects the spatial distribution of one of their natural enemies, the parasitoid wasp *Gonatocerus*. This appears to be an very important association for the ants since other sugar sources do not distract ants, and virtually all aggregations are ant-tended (Del-Claro & Oliveira 1993, 1999). The fact that some ants tend the membracids both day and night and even construct a shelter as satellite nest to house the homopterans on the host-plant, also reinforces the idea that membracid honeydew might be a very important food source for some ant species in the cerrado (Del-Claro & Oliveira 1999).

MATERIAL AND METHODS

Fieldwork was carried out in the cerrado reserve of the Estação Experimental de Mogi-Guaçu, São Paulo State in southeastern Brazil. The vegetation consists of a dense scrub of shrubs and trees, defined by Goodland (1971) as cerrado *sensu stricto* (see picture 1). Observations and experiments were performed during 16 consecutive days in February and March 2001 between 0800 and 1600 hours.

A total of 56 *D. vinosum* plants of approximately the same height (1 to 2 m) were individually tagged and randomly assigned as control (ants present) or treatment (ants excluded). Ants were excluded from treatment plants by applying a sticky barrier of tanglefoot (Tanglefoot® Co., Grand Rapids, MI, USA) to the base of the plant. Vegetation bridges allowing ant access to the plants were regularly pruned. In addition, two major groups of plants where used: plants without inflorescence, and plants with inflorescence. This resulted in four experimental groups: (1) with inflorescence/with ants (n= 14), (2) with inflorescence/without ants (n= 13), (3) without inflorescence/with ants (n= 15) and (4) without inflorescence/without ants (n= 14). The plants in both phenological state used in the experiment were randomly spaced in the same track. During the experiment the number of treehoppers and their natural enemies (spiders, syrphid flies and parasitic wasps; see pictures 2, 3, 4 and 5), as well as tending ants of control groups, were recorded on the first, ninth, and final days of the experiment. Initial treehopper densities did not differ between treatments (with or without ants) in both plant groups (df= 3; MS effect= 1.7708; df error= 53 ; MS error= 9.2201 ; F= 0.1921 ; p= 0.9014). The species composition of the ant attendants at aggregations of control plant groups (with or without inflorescence) was roughly the same (see table 1). These 5 species were all of the *Camponotus* genus.

Three repeated-measures ANOVAs were performed: (1) to compare ant-tending levels through time between aggregations infesting either phenological plant group, (2) to investigate whether plant phenology and ant treatment would affect the abundance of *G. xiphias* and (3) to investigate whether plant phenology and ant treatment would affect the abundance of their natural enemies. Whereas square-root transformations were performed on the data to stabilize treatment variances for the statistical analyses the untransformed data are presented in the figures to facilitate viewing and interpretation. The transformed data displayed a normal distribution and homogeneity of variances.

Chemical analyses of the phloem of *Dydimopanax vinosum* were performed on material collected from additional 14 plants without inflorescence and 12 plants with inflorescence (plant groups were the same height; t= 0.413; p = 0.683; df= 24) not infested by *G. xiphias*. Phloem was collected by cutting the principal stem of tagged, and placing it in a tube with a solution of 20mM EDTA (after King & Zeevaart, 1974). The stems were oven dried for posterior weighing and comparisons. Total sugar and nitrogen content for each sample were calculated and normalized for the dry weight of the respective stem. Stems from either plant group had the same weight (t= -0.520; p-level= 0.608; df= 24). We performed square-root transformations on the data to stabilize treatment variances for the statistical analyses. Results were compared with t-tests.

Honeydew production by treehoppers was estimated for aggregations (13 to 201 individuals) infesting similar-sized *D. vinosum* plants without inflorescence (n= 8), and with inflorescence (n= 7). Only aggregations on plants where ants had been artificially excluded were used in the analyses because different tending levels could affect honeydew production (Del-Claro & Oliveira 1993). To quantify the honeydew produced by an aggregation, a plastic sheet (20 x 20 cm) was placed beneath the infested stem. The number of drops falling on the sheet within a 3-min period were counted and divided by the number of individuals in the aggregation. Each sheet containing the honeydew was then stored in a freezer. For chemical analysis, the honeydew from other untended aggregations were also collected, ending up with 10 samples of different aggregations feeding on plants with inflorescence and 13 samples of honeydew from different aggregations feeding on plants without inflorescence. The chemical analysis of the honeydew consisted in estimating the total sugar content per drop of honeydew. Square-root transformations were performed on the data to stabilize treatment variances for the statistical analyses. Students' t-tests were used to compare the flux of honeydew, as well as the sugar concentration in the honeydew produced by treehoppers on plants with and without inflorescence.

RESULTS

Ant-exclusion experiments: benefits to treehoppers on plants with and without inflorescence

The number of membracids through time in each experimental group is presented in figure 1A. In both plant groups, the size of ant-tended aggregations increased while untended aggregations decreased through time (ant treatment x time interaction; table 2A). We did not detect a significant interaction between plant phenology and ant treatment, nor between plant phenology, ant treatment, and time.

Abundance of natural enemies

The exclusion of ants resulted in a significant increase in the number of natural enemies both on plants with and without inflorescence (ant treatment effect, table 2B). The overall number of natural enemies increased during the course of the experiment (time effect in table 2B). We detected a statistically significant interaction between time and plant phenology: plants with inflorescence accumulated more natural enemies through time compared to plants without inflorescence, irrespective of the ant treatment (plant phenology x time interaction in table 2B, figure 1B).

Phloem quality in plants with and without inflorescence

We found a significant difference in the concentration of soluble sugar between the phloem of plants with and without inflorescence (df=24 ; t= 2.882; p-level= 0.008). The phloem of plants with inflorescence had 475.04 (± 108.12 SE) µg of sugar/g of dry plant material, whereas the phloem of plants without inflorescence had 192.01 (± 28.55 SE) µg of sugar/g of dry plant material.

No difference was detected in the concentration of nitrogen between the phloem of plants with and without inflorescence (df= 24; t= -0.066; p= 0.948). The phloem of the flowering plants had 0.009323 (± 0.001 SE) g of nitrogen/g of dry plant material, while the phloem of plants without inflorescence had 0.009499 (± 0.001 SE) g of nitrogen/g of dry plant material.

Honeydew quality and production, and ant visitation

No difference was detected in the concentration of soluble sugar in the honeydew produced by aggregations on plants with inflorescence (10.198 ± 2.038 SE μg of sugar/drop of honeydew) versus plants without inflorescence (7.415 ± 1.503 SE μg of sugar/drop of honeydew) (df= 21 ; t= 1.234 ; p=0.231).

No difference was detected in the number of honeydew drops produced by aggregations feeding on plants with and without inflorescence (df= 13; t= 1.696; p= 0.114). Over a 3 minute-period, aggregations on plants with inflorescence produced 0.811 (± 0.307 SE) drops per individual whereas aggregations on plants without inflorescence produced 0.467 (± 0.165 SE) drops per individual.

The number of ants per membracid did not differ significantly between aggregations on plants with and without inflorescence (table 3A; figure 2A). However, the absolute number of ants visiting aggregations increased significantly with time at aggregations on both plants with and without inflorescence (figure 2B, table 3B). This trend towards an increasing number of ants through time was similar for aggregations with and without inflorescence, as indicated by the absence of plant phenology x time interaction (table 3B). The absolute number of tending ants did not differ for aggregations on plants with and without inflorescence (phenology effect table 3B).

DISCUSSION

As predicted, plant phenology did affect the food quality gathered by the membracids. Phloem from plants with inflorescence was significantly richer in sugars comparted to phloem of plants without inflorescence. Contrary to expactation, this difference in phloem quality did not translate into richer or more copious honeydew for the ants. The honeydew produced by membracid aggregations feeding on plants with or without inflorescence had the same amount of soluble sugar and was produced in equal quantities. Therefore, host-plant phenology did not affect the outcome of ant-membracid interaction. Membracid aggregations survived better when tented by ants but plant phenology did not affect their survival or attractiveness to ants. This study is the first to investigate under field conditions the effect of plant phenology (and phloem quality) on an ant-herbivore system occurring on a single host-plant species.

Fiedler (1991) demonstrated that host-plant characteristics affected the quantity of ant reward (in this case secretions of the dorsal nectary glands) produced by the larvae of the lycaenid butterfly *Polyommatus icarus*. This differential production can potentially be explained by the fact that the experiment was performed on different host-plant species. We suspect that other plants characteristics not related to the nutritional value of the plant may also play an important role in determining the ant reward production and quality.

The idea that host-plant characteristics might affect the nutrient concentration of homopteran honeydew was confirmed by Douglas (1993). He found that the amino acid concentration in the honeydew of one aphid species varied with season (autumn vs. summer) and age of the leaf (newly emerged vs. mature leaves). Despite the fact that ants do not tend the aphid studied and that the nutrient analyzed was not sugar (the most common ant attractant), these results demonstrated that honeydew nutrient concentration might indeed vary with host-plant quality.

Although ants may assimilate amino acids while collecting homopteran honeydew, sugar concentration and composition are presumably the most important factors mediating the interaction between ants and homopterans (Kiss, 1982; Völkl et al., 1999; Fischer & Shingleton, 2001). Some authors have demonstrated that host-plant characteristics or species identity affect honeydew composition of homopterans (Hendrix et al., 1992; Fischer & Shingleton, 2001). Völkl et al. (1999) showed that sugar composition of aphid honeydew can affect the level of ant-tending. We have not looked at honeydew composition of membracids from plants at different phenological stages, but we suspect that there is no differences because ant attendance was similar for plants with or without inflorescence. Anyhow the honeydew composition of aggregations feeding on plants with different phenological phases remains to be studied.

Nitrogen is known to be an important limiting nutrient for herbivores (Mattson 1980; Strong et al 1984). In our study nitrogen concentration was the same for the phloem of plants with or without inflorescence. There is no reason to believe that membracid honeydew from aggregations feeding on plants with or without inflorescence would vary in the concentration of nitrogen, and there is no indication that nitrogen is involved in the attraction of ants in ant-homopteran interactions. We did not measure the nitrogen content of the honeydew but we believe that sugar concentration is probably more important in mediating this membracid-ant interaction for two reasons. First, it has been shown that the sugar concentration and composition are the primary attractants for ants (Völkl et al., 1999; Fischer & Shingleton, 2001). Second, the source of protein for most ant species involved in these interactions comes from prey species (Buckley, 1987; Hölldobler & Wilson, 1990).

Correlation between host-plant quality and the attractiveness of the myrmecophilous herbivore would characterize a tritrofic interaction involving the host-plant and two mutualistic species (Price et al 1980). The work of Bristow (1991) was the first study to suggest that ant-aphid interaction might be a tritrophic interaction. Although Bristow did not conduct experiments to test if the feeding location on host-plant and ant attendance would affect the survival of the aphids, her work comprised the first evidence demonstrating that host-plant quality can mediate an ant-aphid interaction. Aphids feeding on floral tips attracted more ants and were more vulnerable to generalist predators than aphids feeding on leaf tips. Although Bristow (1991) did not directly measure phloem and honeydew quality, her results suggest that host-plant quality does affect the quality of the honeydew produced by ant-tended herbivores. In contrast, Bretton & Addicott (1992) did not find any evidence of host-plant mediation of aphid-ant interaction. To determine wheter host-plant quality affects the outcome of an ant-lycaenid butterfly interaction, Bayles & Pierce (1991) manipulated plant nutritional quality. The authors have found that host-plant quality could indeed affect the outcome of ant-lycaenid interaction. It was observed that caterpillars feeding on fertilized host-plants attracted a bigger ant guard and survived better than individuals feeding on unfertilized plants (Baylis & Pierce, 1991).

In our study the treehoppers attractiveness to ants was the same independently of the plant phenology where the treehoppers were feeding on. In fact, our results show that both the sugar concentration and the rate of production of the honeydew is the same for aggregations located on plants with or without inflorescence. This may partially account for the lack of evidence towards host-plant mediation of the interaction outcome (see table 2A). It is possible, however, that ant presence could change the effect of plant phenology on honeydew characteristics. Although we did not measure honeydew quality and rate of production in aggregations tended by ants because we suspected that different levels of tending could affect the honeydew production, we suspect that there would be no difference because we did not find any difference in ant attendance between aggregations on both plant phenologies. Correspondly, Yao & Akimoto (2001) did not observe a difference in total sugar concentration and total volume produced between the honeydew of ant-tended and ant-excluded aphids feeding on one *Quercus* species in the same phenological phase. On the other hand, these authors found that the ant presence augmented the honeydew rate of production and affected its composition. Fischer & Shingleton (2001) also observed that ant presence could affect the honeydew composition.

Although no difference in ant attendance or honeydew characteristics was observed in the present study, plant phenology had a significantly effect on the abundance of natural enemies through time: as time goes by, membracids located on plants with inflorescence were subject to a higher predation and parasitism risk compared to membracids located on plants without inflorescence. Two non-exclusive explanations for the accumulation of natural enemies on plants with inflorescence can be put forth. First membracids located on plants with inflorescence may be more nutritious for the natural enemies, especially salticid spiders and dipterans larvae (Del-Claro & Oliveira, 2000) and second, plants with inflorescence may have a wider range of prey species than plants without inflorescence.

Bristow (1991) found that a generalist predator preferred aphids reared on floral tips than those reared on leaf tips. Although she did not make any chemical analysis, she suggested that this preference could be explained by different concentrations of cardenolides (a secondary chemical compound) in aphids feeding on different plant locations. The pattern observed by Bristow (1991) is also compatible with the hypothesis that predators respond to differences in the nutritional value (e.g. concentration of sugars or amino acids) of their prey and not only to the concentration of defensive chemicals.

The idea that membracids feeding on a high-quality host-plant compromise a high-quality prey for their natural enemies suggests another potential mechanism for host-plant mediation of ant-homopteran interactions. Improved host-plant quality could augment not only the attractiveness of ant-tended herbivores to ants, but also the attractiveness of these herbivores to their natural enemies. Hacker & Bertness (1995) have demosntrated that host-plant quality can have a cascading consequence in the population dynamics of an aphid specie by affecting the abundance of its predators. There again, plants of higher quality, for some reason not yet clarified, attracted more predators than plants of inferior quality. In our case and in that of Hacker & Bertness (1995) it is difficult to discern the effect of host-plant quality itself from other plant traits not related to nutritional value.

The presence of inflorescence certainly increases the complexity of plant architecture and this could be a possible explanation of why plants with inflorescence may have a wider range of prey species than plants without inflorescence. Additionally, the inflorescence itself compromises a different food resource not present in plants without inflorescence, and this could also be playing an important role in attracting additional prey species.

We found salticid spiders preying on species other than *G. xiphias* on plants with inflorescence, and we believe that both mechanisms (alternate prey species and more nutritious prey) could be responsible for the accumulation of natural enemies on plants with inflorescence. The presence of additional prey species near the inflorescence could create a dilution of predation risk analogous to that discussed by Krebs & Davies (1993) for con-specifics living in groups. This would be especially advantageous for membracids feeding on flowering plants, whom would not need to produce a more nutritious reward to attract a bigger ant guard and could suffice with average ant attendance despite occuring in a high predator niche. Additionally, by feeding on plants with inflorescence the membracids can also acquire more nutritional food for their own growth, in which case one would expect to find bigger adults and/or a faster development of this homopterans.

Our results revealed that plants with inflorescence provide a resource richer in sugars for the homopterans and host more natural enemies through time. Membracid survival, however, is affected by ant presence but not by plant phenology. This scenario suggests a trade-off between feeding on a better phloem and being at a more risky plant location. The fact that aggregations located at plants with and without inflorescence had the same numbers of tending ants and similar survival rates suggests that the membracids are very efficient at attracting tending ants (Del-Claro & Oliveira, 1996) and/or that a dilution of predation risk on plants with inflorescence may in fact occur.

To our knowledge this is the first study to simultaneously test all the steps proposed by Cushman (1991) to investigate the hypothesis of host-plant mediation in ant-homopteran interactions in the field, as well as the first to experimentally test the effect of plant phenology on this interaction outcome in the wild. Our results clearly show that host-plant quality, here assessed by the phloem sugar and nitrogen amount, did not affect the outcome of the interaction between ants and membracids. Although membracid aggregations located on plants with inflorescence fed on a phloem richer in sugars, this did not translate into a richer or more copious honeydew for the ants, or into a higher survival rate as compared to membracids feeding on plants without inflorescence. Future investigation of this plant-homopteran-ant system should examine the effect of phloem quality on homopteran growth and development, as well as the foraging performance of *G. xiphias*'s natural enemies on host-plants at different phenological phases. The current study illustrates the complexity of the *Didymopanax-Guayaquila*-ant system, and shows that only by considering the full range of selective pressures that potentially operates within the system we can get a better understanding of the ecology and evolution of interspecific associations (Thompson 1988).

Table 1: Composition of ant species tending *Guayaquila xiphias* membracids feeding on plants with and without inflorescence.

Ant species active in daytime	Ant species active at night	No. of treehopper aggregations
Plants with inflorescence		
Camponotus crassus	*Camponotus renggeri*	5
Camponotus aff. *blandus*	*Camponotus abdominalis*	1
Camponotus aff. *blandus*	*Camponotus renggeri*	6
Camponotus rufipes	*Camponotus rufipes*	2
Total no. of aggregations		14
Plants without inflorescence		
Camponotus crassus	*Camponotus renggeri*	7
Camponotus aff. *blandus*	*Camponotus abdominalis*	1
Camponotus aff. *blandus*	*Camponotus renggeri*	3
Camponotus rufipes	*Camponotus rufipes*	3
Camponotus renggeri	*Camponotus renggeri*	1
Total no. of aggregations		15

Table 2: Results of the two-way repeated-measures ANOVA on the effect of plant phenology and ant attendance on the number of treehoppers (A) and of their natural enemies (B) per plant through time (Plants without inflorescence: with ants N= 15 and without ants N= 14; Plants with inflorescence: with ants N= 14 and without ants N= 13). Calculations were performed on square-root transformed data.

	df effect	MS effect	df error	MS error	F	p-level
A- Treehoppers						
Plant phenology	1	0.80081	52	20.69347	0.038699	0.844814
Ant treatment	1	25.3616	52	20.69347	1.225584	0.273362
Time	2	1.33949	104	3.54243	0.378129	0.686080
Plant phenology x Ant treatment	1	3.61242	52	20.69347	0.174568	0.677804
Plant phenologyt x Time	2	3.27568	104	3.54243	0.924699	0.399887
Ant treatment x time	2	14.05266	104	3.54243	3.966959	**0.021864**
Plant phenology x Ant treatment x Time	2	1.27851	104	3.54243	0.360914	0.697909
B- Natural Enemies						
Plant phenology	1	0.156929	52	0.138217	1.13538	0.291553
Ant treatment	1	1.483015	52	0.138217	10.72962	**0.001880**
Time	2	0.381929	104	0.099804	3.82680	**0.024909**
Plant phenology x Ant treatment	1	0.331320	52	0.138217	2.39710	0.127625
Plant phenology x Time	2	0.527841	104	0.099804	5.28879	**0.006495**
Ant treatment x time	2	0.127730	104	0.099804	1.27981	0.282432
Plant phenology x Ant treatment x Time	2	0.134969	104	0.099804	1.35234	0.263143

Table 3: Repeated-measures ANOVA performed on the number of ant per treehopper (A) and the absolute number of ants (B) per aggregation through time on plants with inflorescence (N= 13) and without inflorescence (N= 15). Calculations were performed on square-root transformed data.

	df effect	MS effect	df error	MS error	F	p-level
A-number of ants/treehoppers						
Plant phenology	1	0.0357	26	0.4493	0.0730	0.7801
Time	2	0.2057	52	0.1661	1.4113	0.2981
Phenology x time	2	0.0861	52	0.1661	0.5904	0.5986
B- number of ants						
Plant phenology	1	24.85	26	16.316	1.523	0.2282
Time	2	9.367	52	2.177	4.3018	**0.0187**
Phenology x time	2	0.825	52	2.177	0.3789	0.6865

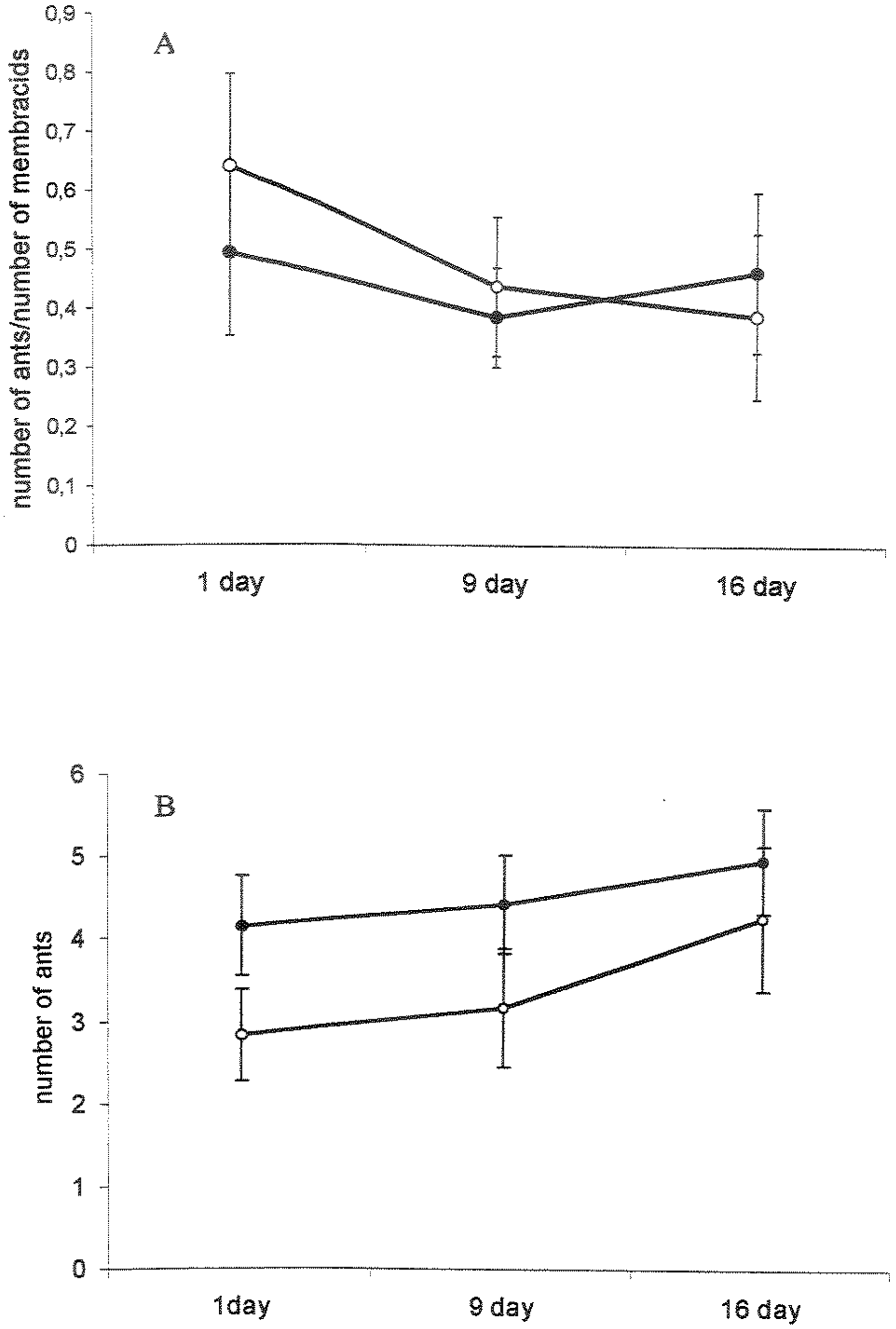

figure 2: Relative (**A**) and absolute number of tending ants (**B**) through time. Open circles (O) represent ants tending aggregations on plants without inflorescence, filled circles (●) represent ants tending aggregations on plants with inflorescence. Values are means and vertical bars illustrate ± 1 SE.

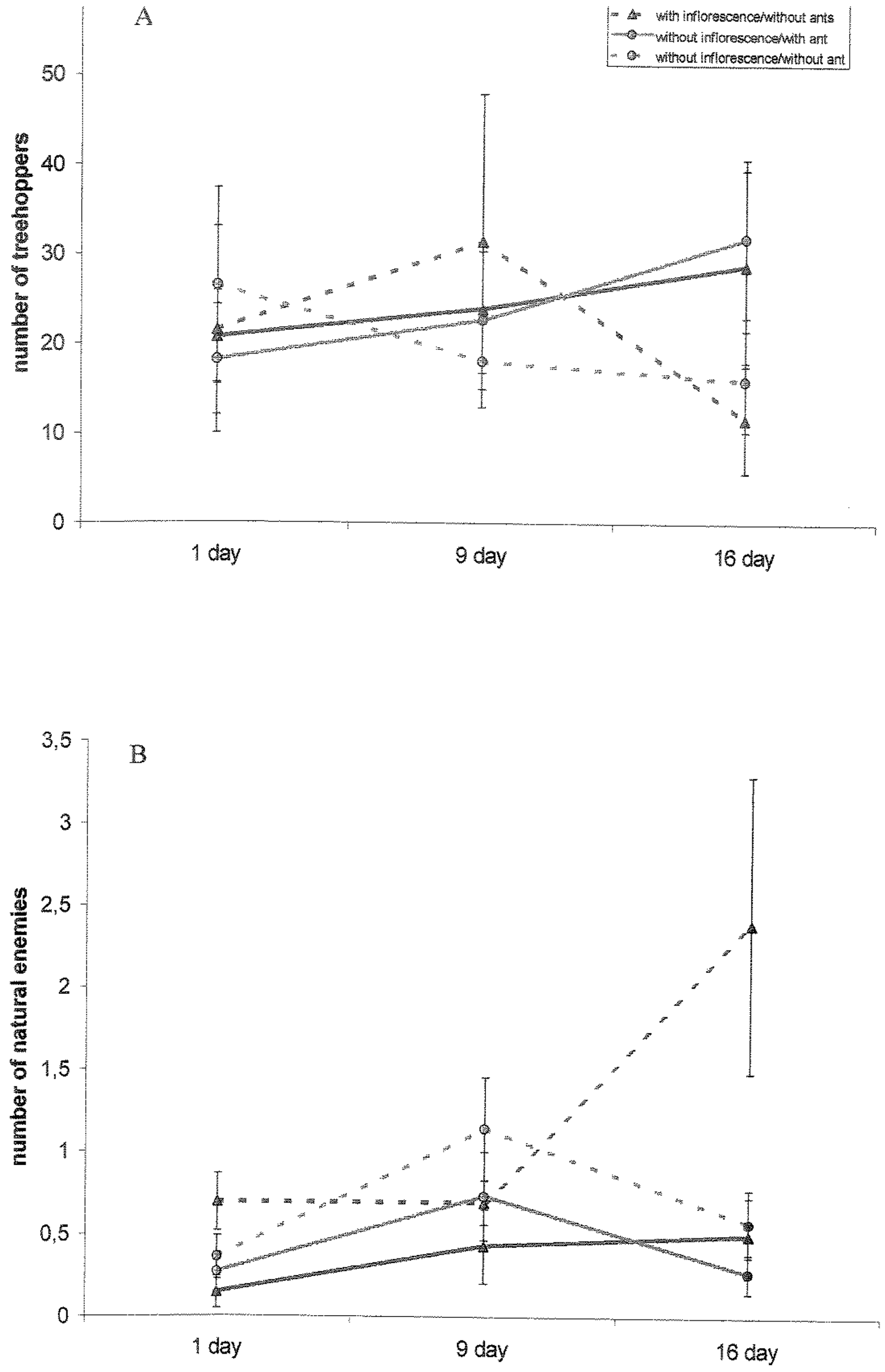

Figure 1: **A** - Number of membracids per plant through time; **B**- Number of natural enemies per plant through time. Values are means and vertical bars illustrate ± 1 SE.

Picture 1: study area view.

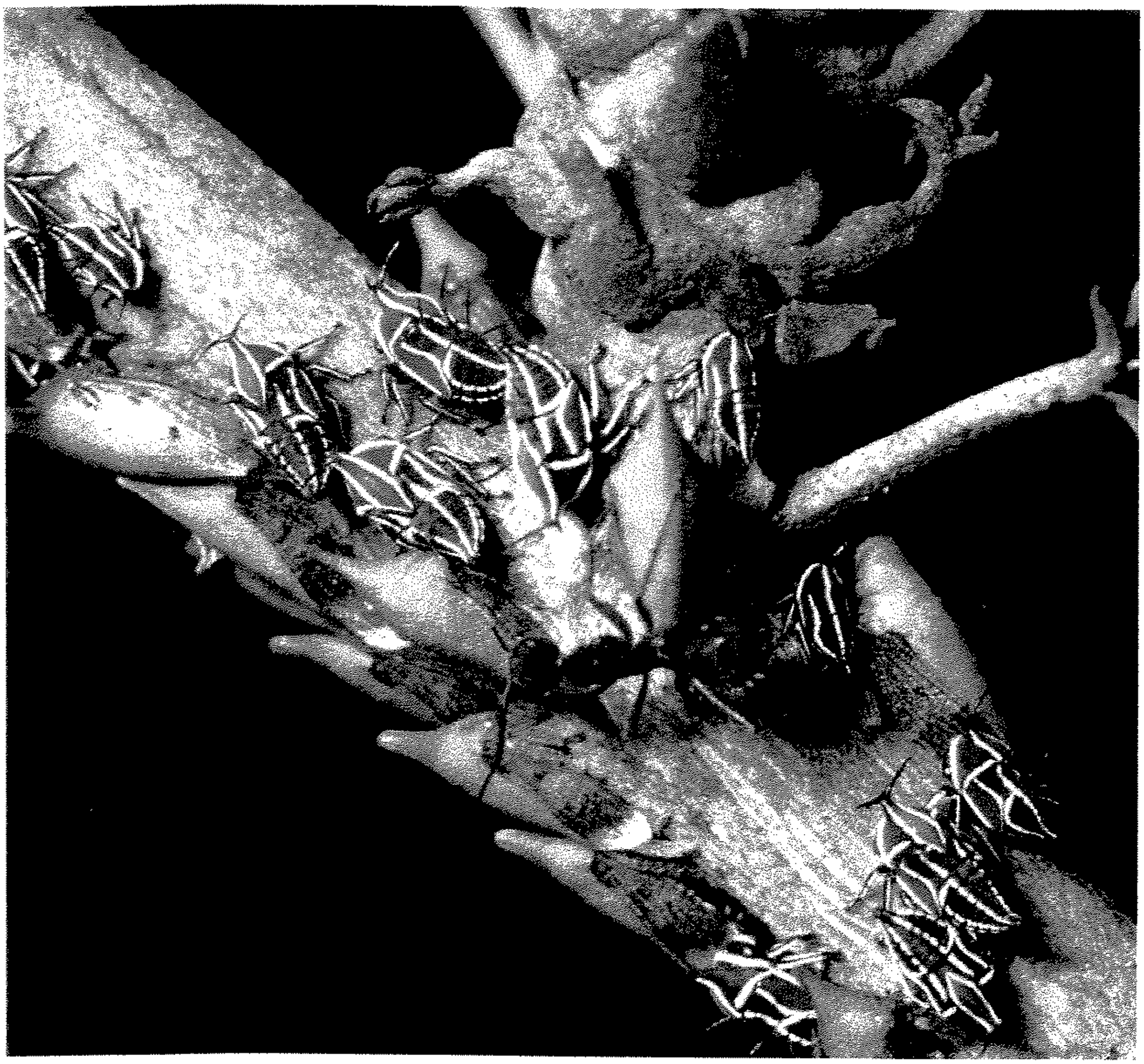

Foto de Paulo S. Oliveira

Picture 2: membracid aggregation tended by the ant *Camponotus rufipes*.

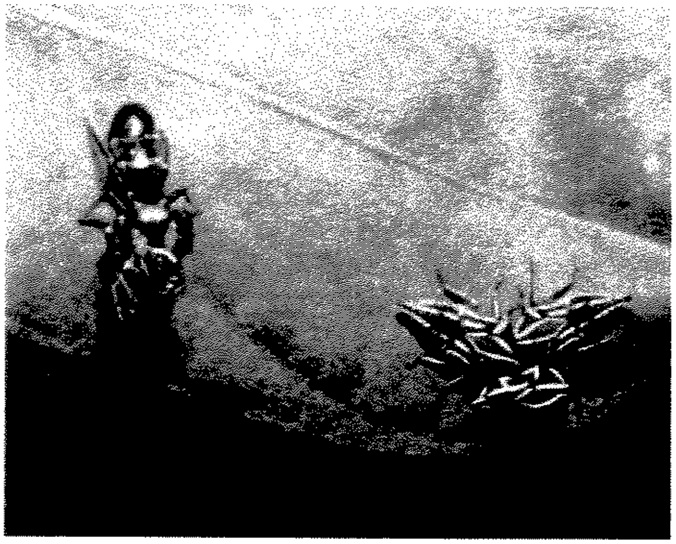

Foto de Kleber Del-Claro

Picture 3: Salticid spider preying in nimphs of *Guayaquila xiphias*

Foto de Kleber Del-Claro

Picture 4: Syphrid parasitic wasp near the egg mass of *Guayaquila xhipias*

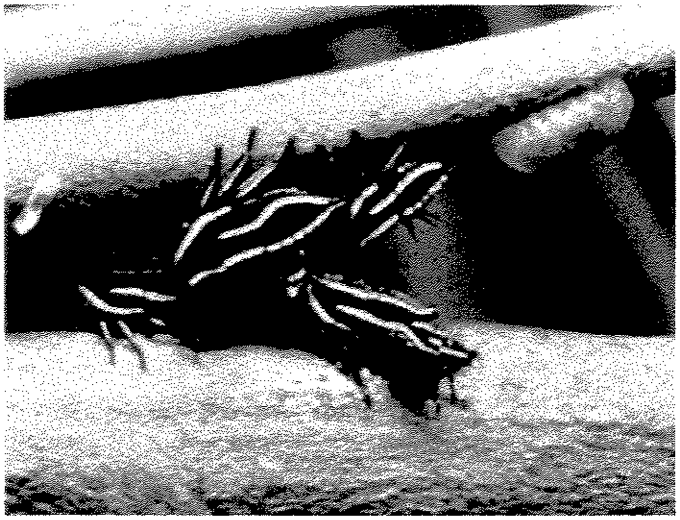

Foto de Kleber Del-Claro

Picture 5: fly larvae near a mebracid aggregation

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CONCLUSÃO GERAL

Como previsto, a fenologia da planta afetou a qualidade do alimento obtido pelos membracídeos. O floema de plantas com inflorescência é significativamente mais rico em açúcares do que o floema de plantas sem inflorescência. O interessante foi que esta diferença na qualidade do floema da planta hospedeira não se traduziu em um exsudato mais rico para as formigas. O exsudato produzido por agregações situadas em plantas com e sem inflorescência apresentou a mesma quantidade de açúcar e foi produzido em quantidades iguais. Os homópteros que se alimentam de plantas com inflorescência estão provavelmente retendo este alimento mais rico, e provavelmente se tornam adultos maiores ou apresentam um tempo de desenvolvimento menor do que os homópteros que se alimentam do floema de plantas sem inflorescência.

Os resultados também mostram que as formigas são muito eficazes em proteger os membracídeos e que a associação com as formigas reduz a abundância de seus inimigos naturais. Este é o primeiro estudo a investigar simultaneamente, no campo, os mecanismos de como a qualidade da planta hospedeira (aqui a concentração de açúcar e nitrogênio no floema) poderia afetar o resultado da interação entre formigas e homópteros, e também o primeiro estudo a testar experimentalmente o efeito da fenologia da planta hospedeira no resultado da interação entre formigas e homópteros na natureza. Nossos resultados mostram claramente que a fenologia, e consequentemente, a qualidade da planta hospedeira não afetaram o resultado da interação entre formigas e membracídeos.