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BIODIVERSIDADE EM Baccharis (Asteraceae):
INTERFACE DO STATUS NUTRICIONAL, STRESS, RADIAÇÃO
ULTRAVIOLETA E MICROORGANISMOS

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O PROJETO

“Biodiversidade em *Baccharis* (Asteraceae): interface do status nutricional, stress, radiação ultravioleta e microorganismos”

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INFLUÊNCIA DO SEXO E FENOLOGIA DE *BACCHARIS DRACUNCULIFOLIA* D. C. (ASTERACEAE) SOBRE INSETOS HERBÍVOROS

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ABSTRACT The influence of sex and phenology of *Baccharis dracunculifolia* D. C. (Asteraceae) on insect herbivores. The dioecious plant *Baccharis dracunculifolia* (Asteraceae) is attacked by a diverse array of insect herbivores. In this study we found 90 different species of herbivorous insects associated with the plant, of which 29 female and 43 male plants at the Campus of the Universidade Federal de Minas Gerais, Belo Horizonte, MG, during the plant's reproductive and vegetative phenological periods. Crown height, length and area correlated positively with the weight of the plant. Nevertheless, these traits did not vary between male and female plants. The total abundance of insect herbivores was higher in the reproductive period than in the vegetative period, but did not vary between plants. Plant phenology and sex did not influence the richness of insect herbivores, excepting gall-forming insects. Most galling species were found on male plants (7 species) compared to female plants (4 species). On both male and female plants, galls caused by the psyllid *Neopeltis baccharidis* (Homoptera) were the most common.

KEYWORDS: *Baccharis dracunculifolia*, Biological control, Insect galls, Herbivory on Plant Phenology, Sex-related Herbivory.

INTRODUÇÃO

Diversos insetos herbívoros atacam espécies do gênero *Baccharis* DC (Asteraceae). Vários estudos sobre os insetos associados a *Baccharis* spp. têm sido realizados, principalmente na América do Norte, devido à crescente necessidade de se conhecer potenciais herbívoros para o seu controle biológico (e.g., TILDEN, 1951; KRAFT & DUNN, 1982; BOLDT & ROBBINS, 1987; PALMER, 1987; PALMER & BENNETT, 1988; BOLDT et al., 1988; BOLDT & ROBBINS, 1990; LARA & FERNANDES, 1993).

As comunidades de insetos herbívoros são influenciadas por diversos fatores, dentre eles o sexo, fenologia e arquitetura das plantas hospedeiras (STRONG et al., 1984). LARA & FERNANDES (1993) registram uma grande variabilidade no número de espécies de galhas de *Neopeltis baccharidis* Buckhardt, 1888 (Homoptera: Psyllidae) em plantas de *B. dracunculifolia* DC. Provavelmente, esta variabilidade estaria relacionada ao sexo e fenologia da planta hospedeira. DANNEL et al. (1985) e BORCKLE & PRICE (1989) observaram uma maior taxa de herbivoria em clones masculinos de plantas do gênero *Salix*, corroborando assim a hipótese de herbivoria diferencial em plantas dioicas. De forma análoga, a ocorrência de fungos exclusivamente em plantas femininas deste gênero (JARVIS et al., 1991), aponta para a possibilidade de existência de proteção diferenciada em relação ao sexo.

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O presente trabalho visou obter dados sobre a fauna de insetos herbívoros associados à *B. dracunculifolia*, observando sua distribuição quanto ao: a) sexo da planta b) tamanho da planta (altura da planta, área basal e área da copa) c) fenologia (período reprodutivo e vegetativo); e finalmente, investigar a possibilidade de existência de diferenças na riqueza e abundância de galhos de insetos quanto ao sexo da planta.

**Planta Hospedeira**


Algumas espécies de *Baccharis* são de grande importância devido à sua toxicidade. Plantas e insetos citotóxicos, pertencentes ao complexo de antibióticos conhecidos como introduzidos (importante grupo de mesotóxicos), ocorrem naturalmente em espécies brasileiras (Kutt et al., 1990). A pesar de destes agentes serem responsáveis por vários casos de intoxicações humanas e animais de gado (veja Tokarnia & Dobriner, 1975; Jarvis et al., 1991), eles são também agentes antineoplasias (Kupchan et al., 1977), e portanto de interesse médico e farmacêutico.

*Baccharis dracunculifolia* é um arbusto dióico, lenhoso, de até quatro metros de altura, nativo do Brasil, comum em áreas de cerrado, pastagens abandonadas e áreas em processo de sucesso. A floração nessa espécie, como em outras espécies do gênero, ocorre após o período de chuvas (Boldt et al., 1988). Apenas de *B. dracunculifolia* ser uma espécie de ampla distribuição no Brasil, pouco se sabe sobre a fauna de insetos herbívoros associada a estes fatores que estruturam as comunidades no tempo e espaço. O conhecimento dos insetos herbívoros de *B. dracunculifolia* é de grande importância para implementação de programas de controle populacional das várias espécies das pragas pertencentes ao gênero *Baccharis* e de grande relevância em estudos ecológicos de interações inseto-plantas por ser um excelente sistema para o estudo da influência do sexo, químico e habitat na dinâmica de populações e diversidade de espécies.

**MATERIAL E MÉTODOS**

Local de estudos

O trabalho foi realizado entre abril e outubro de 1991 nas adjacências do estacionamento do Instituto de Ciências Biológicas, Campus da Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brasil. A área de estudo, com cerca de 2 ha, caracteriza-se por ser uma área em sucesso, onde predominam três espécies de

**Baccharis.** A altitude local é de 835 m, e a estação chuvosa ocorre entre os meses de dezembro e março.

Cinco quadrados de 5 x 5 m foram demarcados na área do estudo. Em cada um deles, todos os indivíduos de *B. dracunculifolia* foram contados e marcados com etiquetas numeradas. Posteriormente, o sexo de cada planta adulta foi identificado através de análise de morfologia floral externa. De cada indivíduo foram medidas a altura da planta, largura e comprimento da copa e área basal (calculada com base na medida da circunferência do caule a um centímetro do solo). A área total da copa foi calculada multiplicando-se os parâmetros largura e comprimento da copa. Para análise destes dados utilizaram-se regressões lineares e teste t de Student (Zar, 1984).

Insetos foram coletados mensalmente, no período da manhã, durante os meses de maio e junho (período reprodutivo) e julho, agosto e outubro de 1991 (período vegetativo) em cada planta. Para a coleta dos insetos, dez ramos de cada planta foram envolvidos em sacos plásticos de 30 x 50 cm e foi feito uma separação por 20 minutos. Foram ainda coletados insetos através do uso de rede entomológica, dando-se 10 batidas aleatórias ao redor da planta. Os insetos foram separados em morfogrupos e por hábito alimentar: galhadores, mastigadores e sugadores, pulinizadores, parasitóides e predadores. Todavia, para os propósitos deste trabalho apenas os galhadores, mastigadores e sugadores foram utilizados. Para se confirmar o "status" de insetos herbívoros, observaram-se 20 min por planta (n=70) foram efetuadas no ano de 1993 e 1994 em Belo Horizonte (G. Julião & G. W. Fernandes, em preparação). Além disso, foram realizadas várias análises dos dados com menos de 5 registros de ocorrência.

*Baccharis dracunculifolia* apresenta a mais alta riqueza de espécies de insetos galhadores do gênero *Baccharis* (Javine et al., 1995). Todos os tipos de galhas encontrados foram registrados, e para os três tipos mais frequentes foram calculadas a abundância de galhas em função do sexo e parâmetros de arquitetura da planta hospedeira. As galhas utilizadas neste estudo foram causadas por *Neopelma bacchardi* Buckh. & Fisch., 1988 (Psalididae: Homoptera), uma espécie ainda não descrita de Cecidomyiidae (Diptera) e *Rhaphochilus frugiperda* (L.) (Cecidomyiidae: Diptera) (veja Fernandes et al., 1995). As galhas de *Neopelma bacchardi* são clítoris, ovais, verdes, glabras, unicoculares e formadas pelo entumescimento da borda do fruto. As formas pelo cecidomyioide não identificado são nos frutos apicais do caule, verdes, glabras, unicoculares e em forma de roseta enquanto aquelas formadas por *Rhaphochilus frugiperda* são em brotos, esferóides, verdes, glabras e unicoculares. Para análise da abundância de indivíduos e morfogrupos de insetos em função do sexo e da fenologia da planta hospedeira, as galhas não foram consideradas por terem sido contadas em um único período de coleta.

Para se verificar as relações entre a altura, comprimento, largura, área da copa e área basal da planta foram utilizadas regressões, para comparar os parâmetros da arquitetura das plantas femininas e masculinas foi utilizado o teste t de Student (Zar, 1984).

**RESULTADOS**

Área da planta hospedeira

Segundo dois indivíduos de *B. dracunculifolia* foram encontrados e amostrados nos quadrados, sendo 43 plantas masculinas e 29 femininas. A altura, comprimento,
Insetos herbívoros: sexo e fenologia da planta

Foi registrado um total de 90 morfo-especies de insetos herbívoros (com mais de cinco registos de ocorrência durante os estudos) em B. dracunculifolia os quais pertencem a 9 ordens e 23 famílias diferentes. O número total de insetos herbívoros por planta difere estatisticamente entre o período reprodutivo e o período vegetativo em ambos os sexos de B. dracunculifolia (Masculinos: período reprodutivo=127,8 ± 31,9; período vegetativo= 32,1 ± 23,5; período reprodutivo= 30,6 ± 8,7; teste t, p=0,05). Por outro lado, o número total de insetos herbívoros por planta não difere significativamente em relação ao sexo da planta (t=0,920, p=0,05).

A riqueza de insetos herbívoros não variou em função do sexo e fenologia da planta. No período reprodutivo, plantas femininas (n=29) apresentaram média de 6,1 ± 0,8 espécies de insetos herbívoros e as plantas masculinas (n=43) uma média de 6,2 ± 0,4 (t=0,05). No período vegetativo, estas médias foram de 5,5 ± 0,8 e 6,6 ± 0,6 espécies de insetos herbívoros em plantas femininas (n=29) e masculinas (n=43), respectivamente (t=0,05).

Uma maior riqueza de galhas foi encontrada em plantas masculinas, tendo sido registradas cerca de 5% dos indivíduos. Em plantas femininas, galhas de N. baccharidis e Cecidomyiidae do gênero Makena ocorrem em 41,4% dos indivíduos. Em plantas masculinas, as porcentagens de ataque por galhas de N. baccharidis, Cecidomyiidae e R. friburgensis foram de 79,1%, 67,4% e 60,5%, respectivamente.

Dos três tipos de galhas mais numerosos nas 29 plantas femininas, a mais abundante foi aquela causada por N. baccharidis (412±70%, x=14,2 ± 5,4 por planta). O oecidídeo sp. 1 foi o segundo galhador mais abundante em plantas femininas (100±17%, x=3,5 ± 2,1), seguido por R. friburgensis (76±13%, x=2,6 ± 0,9). Nas 43 plantas masculinas, a galha causada por N. baccharidis representou 90% do total (1741, x=40,5 ± 9,8). O oecidídeo sp. 1 e R. friburgensis tiveram a mesma abundância, 5% cada (97, x=2,2 ± 1,6). A abundância de galhas de N. baccharidis foi significativamente maior em plantas femininas do que em femininas (t=15,347, p<0,05), enquanto que houve diferenças significativas entre a abundância das outras duas espécies (p<0,05).

A abundância de galhas de N. baccharidis mostrou-se positivamente correlacionada com a área da copa em indivíduos do sexo masculino (r=0,45, p=0,01), mas não se correlacionou em relação aos indivíduos femininos (p>0,05). Não foi encontrada correlação entre a abundância das outras espécies de galhas e os índices de tamanho da planta (p>0,05).

DISCUSSÃO

A complexidade estrutural das plantas (tamanho e forma de crescimento) é um dos principais fatores determinantes da riqueza de espécies de insetos herbívoros (Strong et al., 1984). Maior complexidade estrutural representa maior disponibilidade de recursos alimentares e de microhabitat, contribuindo para uma fauna mais abundante e diversificada (Lawton, 1983). Entretanto, estes parâmetros (altura, comprimento, largura e área) não diferem estatisticamente entre os sexos de B. dracunculifolia.

Apesar de não serem estatisticamente diferentes, houve uma tendência a maior riqueza e abundância total de insetos herbívoros em plantas masculinas em ambos os períodos fenológicos de B. dracunculifolia. Este fato pode ser devido à similaridade no tamanho das plantas masculinas e femininas observada neste estudo. Corrobora-se um possível efeito de complexidade estrutural, maior abundância total de insetos herbívoros foi observada durante o período reprodutivo da planta do que no período vegetativo em ambos os sexos de B. dracunculifolia. Durante o período reprodutivo há uma maior oferta de recursos alimentares devido ao aumento na biomassa, número de itens e qualidade dos recursos. Durante o período reprodutivo houve um aumento da biomassa (A.M. Araujo, dados não publ.) Após este período, grande parte das folhas foram perdidas, dando aos arbuscos um aspecto ressecado. O crescimento de novas folhas se inicia após o período de chuvas, quando ocorre nova floração. Essas observações mostram a relevância da fenologia e da qualidade e quantidade de recursos da planta como fator importante determinando a abundância de insetos herbívoros. Por outro lado, não foram registradas variações na riqueza de espécies de insetos herbívoros em função do sexo ou fenologia da planta hospedera.

Galhas de N. baccharidis foram mais abundantes em plantas masculinas, onde mostraram-se positivamente correlacionadas com a área da copa. Fatores como uma menor resistência de plantas masculinas ao ataque dos galhadores, taxa de mortalidade mais elevada para galhas de plantas femininas, ou preferência por parte das fêmeas de galhadores com relação às plantas masculinas, podem ser os determinantes de tais diferenças (Fernandes, 1992).}


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ASPECTOS BIOLÓGICOS DAS GALHAS DE
TONOPLAGIA RUDOLPHI (DIPTERA: TEPHIRITIDAE)
EM VERNONIA POLYANTHES (ASTERACEAE)

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(Com 4 figuras)

RESUMO

Galhas causadas por insetos são importantes devido à sua relação parasitária com as plantas hospedeiras e ao seu habitat sésil, facilitando estudos populacionais e ecológicos. A musca de frutas, Tonoiplagia rudolphi (Diptera: Tephritidae) forma galhas casulares em asta-peixe, Vernonias polygonanthex (Asteraceae). Estudou-se a biologia e a história natural do inseto galhador e da galha, observando-se ainda o impacto da galha na planta hospedeira.

As galhas são fusiformes, verdes, glabras e unicelulares. A média do número de galhas por planta foi de 2,8 e o número de larvas e pupas por galha variou de 1 a 12. Aspectos anatômicos mostraram uma desorganização dos tecidos vasculares, além da hiperтроfia das células do parenquima medular. Testes histoquímicos indicaram a presença de uma maior concentração de substâncias fenólicas e lipídios nos tecidos da galha quando comparados aos tecidos do caule não galhado.

O ciclo biológico de T. rudolphi foi aproximadamente de 45 a 60 dias. Inimagens naturais causaram 33,7% de mortalidade da galha. Organismos sucessores (principalmente formigas) representaram 7,88% dos inacessos associados à galha. T. rudolphi apresentou comportamento de corte comum a outras espécies de tephritídeos.

O número de galhas por planta não variou em função do tamanho das plantas hospedeiras. Outros fatores devem ser mais relevantes na seleção de plantas hospedeiras pela fêmea do galhador ou as galhas não sofrem mortalidade diferencial em plantas com tamanhos variados.

Palavras-chave: galhas de insetos, comportamento de corte, anatômia de galhas, Tonoiplagia rudolphi, Vernonias polygonanthex.

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ABSTRACT

Life history of Galls of Tolypelecia rudolphii (Diptera: Tephritidae) on Vernonia polyantha (Asteraceae).

Insect galls are excellent study objects due to the parasitic relationships with their host plants, and to their sporadic nature which facilitates population and biogeographical studies. The fruit flies, Tolypelecia rudolphii (Diptera: Tephritidae) induces galls on the stems of Vernonia polyantha (Asteraceae). We studied the biology and natural history of the galling fly and gall, and the impact of the gall on the host plant.

The galls developed are fusiform, green, glabrous, and one-chambered. The average number of galls per plant was 2.8 and the number of larvae and pupae per gall varied between 1 and 12. Anatomical aspects of the galls indicated the existence of hypertrophied cells of the medulla parenchyma and disorganization of the vascular bundles. Histological tests showed higher phenolic substances and concentration of lipids in galled tissues compared to healthy tissues.

The life cycle of T. rudolphii varied between 45 to 60 days. Natural enemies caused 33.75% of the galls mortality. After the emergence of T. rudolphii, the gall was occupied by several invertebrates (but primarily was) which represented 7.89% of the gall associated organisms. T. rudolphii mating behavior was similar to other tephritid flies.

The number of galls did not vary with host plant height. Other factors may be more relevant in host plant selection by the galling female and galling larvae may be under different levels of mortality on plants of different sizes.

Key words: courtship behavior, insect galls, gall anatomy, Tolypelecia rudolphii, Vernonia polyantha.

INTRODUÇÃO

Do ponto de vista morfológico as gálias caracterizam-se pela hiperplasia e/ou hiperтроfia de células, tecidos ou órgãos de plantas, resultantes da ação de vários organismos, principalmente insetos. São encontradas em todas as 250 000 plantas, desde a extremitade da raiz até as gemas apiciais do caule, nos órgãos vegetativos e reprodutivos (Marti, 1964; Fernandes, 1988). Estão presentes em quase todos os grupos de plantas, sendo as fereências, especialmente as dicotiledóneas, notáveis pela abundância e grande diversidade de espécies galo-hederas (Marti, 1964). Entre as plantas hospedeiras da região tropical destacam-se as Fabaceae, Asteraceae e Myrtaceae, famílias de ampla distribuição geográfica (Fernandes, et al., 1988, Fernandes, 1992a). Como dípteros galo-hederas mais comuns, destacam-se os Cecidomyiidae e Tephritidae. Praticamente todas as gálias de Tephritidae são formadas em espécies de Asteraceae, a maioria ocorrendo nos caules da planta hospedeira (Freidberg, 1984).

A maioria dos estudos sobre gálias de insetos da região neotropical se enquadram em diferentes tipos, com ênfase na história natural dos insetos galo-hederas (e.g., Fernandes, et al., 1987; Fernaia, et al., 1989; Lara e Fernandes, 1991), aquelas que enfocam os aspectos anatômicos (e.g., Andújar, et al., 1991) e aquelas que apresentam apenas listas de espécies (e.g., Fernandes, et al., 1988). Raros estudos foram desenvolvidos sobre a ecologia, evolução e biogeografia desses insetos. As contribuições neste sentido vêm de estudos realizados por Fernandes e Price (1988, 1991, 1992), onde os autores apresentam a importância de variáveis biológicas e abióticas na riqueza de espécies galo-hederas, além da comparação entre riqueza de espécies nas regiões tropicais e temperadas. Sendo assim, a falta de conhecimentos básicos da história natural e biologia de insetos galo-hederas tropicais é um problema comum, dificultando alguns estudos em ecologia.


O trabalho tem por objetivo descrever a biologia das gálias de T. rudolphii, abrangendo aspectos morfológicos, de comportamento, bem como, os fatores que influenciam as taxas de sobrevivência e mortalidade do inseto galo-hederas. Procuramos com isso, contribuir para maior conhecimento da interação galo-hederas/planta hospedeira.

MATERIAL E MÉTODOS

Os estudos de campo foram realizados no campus Pampulha da Universidade Federal de Minas Gerais (UFMG), em Belo Horizonte e em Lagoa Santa, MG. O campo da UFMG possui uma vegetação heterogênea composta de plantas nativas e introduzidas, ornamentais e frutíferas e situa-se a 80m de altitude (Fernandes et al., 1988). Em Lagoa Santa, as coletas foram realizadas ao bairro Bela Vista e ao redor da lagoa. Lagoa Santa situa-se a 42 km ao norte de Belo Horizonte e a uma altitude de 833m. A vegetação é composta por formações de mata, campos limpos, cerrados, brejos e formação invernais geralmente alteradas devido às intervenções humanas (Fernandes, 1954, Warneking e Fernandes, 1973).

Duas coletas foram realizadas entre os meses de junho e dezembro de 1991. As gálias foram coletadas e numeradas de acordo com a planta da qual haviam sido retiradas, acondicionadas em sacos plásticos e levadas ao laboratório para os diferentes estudos.

Para o estudo da morfologia externa foram feita observações e anotações sobre a forma e coloração da gália durante o seu desenvolvimento.

As medidas da largura e comprimento foram realizadas com o auxílio de paquímetro. As gálias foram abertas para verificar a presença espacial dos galo-hederas, bem como a presença de insetos nativos e inócuos.

Para o estudo anatômico foram feitas práticas nas mais temporárias com secções transversais ao eixo do caule da planta galo-hederas e não galo-hederas de alguns ramos. Foram utilizados apenas ramos com galo-hederas jovens para facilitar os cortes. As secções foram coradas com fusina e azul de astra (Roeser, 1972) e posteriormente imediatas em glicerina 50%. Os testes histológicos foram realizados com Sudan III para evidenciar a presença de materais grasos (freidberg) em meio ácido para paredes lignificadas, e coloração para substâncias fenólicas e lignina para amido (Fernandes, 1962). Os aspectos morfológicos mais relevantes foram registrados com estereoscópio e fotomicroscópio.

Visando a biologia do galho de galo-hederas gastos coletadas dentro de vides para obtenção de insetos associados (insetos naturais e organismos insetívoros). As gálias foram utebtes para obtenção de larvas do in-}

Para análise do comportamento e conhecimento de alguma gálias foram trazidas ao laboratório e coletadas em vides cobertos com folha osuv permaneceram até o momento da emergência dos insetos adultos, que após foram separados e coletados em vides cobertos com gálias. Nos vides foram colocados: 1) água fresca e pipo de envaso com armazém, 2) aliments de água como alimento água, água, água e aliments de envaso como substrato para o desenvolvimento de insetos. As observações de comportamento de insetos foram realizadas para mais e menos, nos períodos da manhã e da tarde.

Para se testar a influência do tamanho de ramos e preferência de espécies galo-hederas pelas fêmeas foram comparados o tamanho de ramos galhos e não galhos (Fernandes, 1992b) por meio de teste de paredes (Zar, 1984). A relação entre o tamanho da planta e o número total de gálias.
RESULTADOS

Aspectos Morfológicos Externos

Foram coletadas 279 galhas em 101 plantas com uma média de 2,8 ± 1,2 galhas por planta. As galhas são cadáveres e falsosformes (Fig. 1), com diâmetro variando de 6,6 a 33,2 mm ($\bar{X} = 19,8 \pm 0,78$) e comprimento variando de 11,6 a 34,9 mm ($\bar{X} = 24,0 \pm 0,75$). Fora encontrada, na maioria dos casos, apenas uma galha por ramo. As galhas jovens são maiores, glabras, de coloração verde-clara.

Aspectos Morfológicos Internos

A secção transversal da porção apical do casca não galhado apresenta epiderme constituída de uma única camada de células retangulares, com cutícula delgada (Fig. 2A). Em toda sua extensão ocorrem tricomas (T) glandulares e não glandulares. As canais mais externos do córtex (Pc) são constituídos de segmentos alternados de coloração
diferente. Quando maduros tornam-se fibrosas e de tonalidade marrom. São umbículares, com até doze seções ($\bar{X} = 4,2 \pm 0,6$ indivíduos/gálha, Fig. 1B). A escavação das paredes internas da galha pelas larvas resulta no seu preenchimento por excrementos em forma de grãos pretos. Na fase de pupa estes seco restousem-se endurecidos e formam seções, separando uma pupa da outra.

Fig. 1 — Ciclo biológico de T. rudolphii. A: Disposição em meristemas apicais; B: Aspecto externo da galha e em cortes transversais. C: Aspecto geral da fêmea adulta.

Biólogia e História Natural

Descrição dos diversos estágios de crescimento

Larvas — As larvas de T. rudolphii são branças, cilíndricas e alargadas, com segmentos transversais e intensamente dobrados. Possuem a região mediana e posterior mais largas; a extremidade anterior é mais estreita e côncica (Figs. 3A, B, C). O segmento pseudocefaelôide SI apresenta bastante retrusão e rugosidade no porção anterior (Fig. 3C). Ganchos labiais (GL), biselados, trevo escuro e esclerotizados são facilmente visíveis na porção anterior do primeiro segmento (Figs. 3B, C). O segmento prótorácico (S2) apresenta filárias de espinhos em sua porção posterior (ponto escuro nas figuras) e dois espiráculos antrópicos (EA) dispostos dorsalmente. Estes possuem uma coloração amarelada e numerosas papilas.

As superfícies posteriores dorsal e ventral dos demais segmentos apresentam filárias de pequenos espinhos marrons (Figs. 3A, 4A). O segmento caudal apresenta disco espiropterol posterior apical, com dois espiráculos e região anal em porção ventral (Figs. 4A, B). O segmento espiropterol da parte escuro são dispostos irregularmente por toda a região do disco. Cada placa espiropterol (PE) com coloração amarelada apresenta três funções espiráculares (FE), ovais, esclerotizadas. O tronco traqueal (TT) possui coloração amarelo-ôliva. A cabeça espiropterol (CE) situa-se no lado oposto às funções espiráculares (TE) (Fig. 4B). A região anal é aproximadamente suboval, com fenda anal (FA) estreita e mediana (Fig. 4B). Há ausência de processos intersegmentares na região da placa espiropterol.


Adulados — T. rudolphii é uma mosca grande, de aproximadamente 6,5 mm, robusta, de cor amarelo-oliváceo e verdes-claras. As asas são longas e tipicamente desenhadas. Apresentam certas costas que aparecem como pequenas pontuações no dorso. As fêmeas possuem a bainha do ovipositor côncica e o ovipositor em forma de agulha.

Ciclo Biológico

O ciclo de larva a adulto do galhador é de 45-60 dias. A fêmea ovipõe no meristema apical dos botões vegetativos (Fig. 1A) Após a eclosão, as larvas desenvolvem-se às custas do conteúdo das células do parênquima medular. Embora não tenha sido possível distinguir os estágios de desenvolvimento larval, a sua duração total é de 35 a 40 dias.

Com a eclosão das larvas, ocorre uma expansão dos tecidos do casca ao seu redor, originando uma galha fusiforme (Fig. 1B). No último estágio de desenvolvimento, as larvas escavam um orifício e, em seguida, empuram a fase de pupa dura de 15 a 20 dias. Após esse período, os adultos emergem, caíndo pelo orifício anteriormente preparado e reiniciam o ciclo (Fig. 1C). Não foram observados adultos no campo.


Inimigos Naturais

Inimigos naturais (parasitas, fungos e predadores) causaram uma taxa de 33,7% de mortalidade. Dos organismos considerados parasitóides, dois gêneros de bracuñídeos (Hymenoptera: Braconidae): Bracon e Apanteles sp. e um curtirolídeo (Hymenoptera: Eucharitidae) foram obtidos das galhas (Tab. I). Apesar de comum, a frequência de Bracon sp. foi subestimada devido ao fato de serem parasitóides larvais, com desenvolvimento total culminando no puparium do inseto galhador. Um inseto não identificado da família Scirtidae (Diptera) foi muito freqüente (16,49%) nas coletas. Dois lepidópteros foram também encontrados com certa frequência (Tab. I).

Os sucessores, que geralmente aparecem por último no processo de desenvolvimento da comunidade de organismos associados à galha, representam um total de 8,96% dos insetos associados à galha. Neste estágio destacaram-se as formigas (Tab. II).

Comportamento de Encontro

O comportamento de encontro de T. rudolfii consistiu de exploração das asas e ambulatórias. Após o contato visual com a fêmea, os machos movem uma das asas para frente, em posição perpendicular ao tórax, e mantêm a outra parcialmente caída, obliqua ao corpo. Enquanto realizam esse movimento alternadamente, deslocam-se de um lado para o outro. Essa exploração é mantida até a fêmea corresponde, estendendo suas asas perpendicularmente ao corpo. Para aproximar-se da fêmea o macho caminha vagarosamente em sua direção e permanece a uma distância de aproximadamente um centímetro, com as asas abertas. A fêmea geralmente fica imóvel de frente para o macho, podendo, às vezes, realizar movimentos semelhantes aos dos machos.

Antes e durante o encontro, machos e fêmeas esfregam suas patas posteriores na região abdominal e, em seguida, friccionam suas asas entre si. Outros movimentos de asa como tremulação e ondulação também foram observados. Os machos também movem suas asas quando aproximam-se dos outros. Foram observadas pulsações constantes dos pares bucais em ambos os sexos. Não foi possível observar a cópula devido ao número reduzido de casais obtidos neste experimento.

Preferência

A altura da planta hospedadora não influenciou o número de galhas por planta ($r^2 = 0,0, n = 101, p = ns$). Não houve diferença entre o tamanho de ramos galhados ($X = 60,23 \pm 4,38$) e não galhados ($X = 55,82 \pm 5,37$) ($t = 0,751, n = 84, p = ns$). A localização das galhas se deu preferencialmente na posição apical do caule.

DISCUSSÃO

As galhas de T. rudolfii em V. polyanthes enquadram-se na forma irregular e fusiforme descrita para galhas caulinares de tetrápteros (Mani, 1964). São chamadas galhas comunitárias, por conterem vários indivíduos na mesma cavidade (Foedelberg, 1984). O preenchimento da cavidade larval por fezes em forma de granulações sólidas ocorre com freqüência nas galhas de tetrápteros (Göeden, 1960b), característica também verificada para T. rudolfii.

A degeneração de tecidos do xilema e do floema e a hipertrofia de células do parênquima modular detectadas na galha caulinar de T. rudolfii segue o padrão comum de galhas descrito por Mani (1964). As galhas são estruturas que, geralmente, apresentam grande acúmulo de substâncias fenólicas (Mani, 1964; Fernandes e Martins, 1985). A presença destas substâncias ao redor do sítio de alimentação das larvas pode representar um mecanismo de defesa da planta contra o inseto galhador. Nas porções periféricas da galha, a presença de substâncias fenólicas pode, por outro lado, ser interpretada como mecanismo de defesa contra inimigos naturais do inseto galhador, como sugerido por Mani (1964).

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Fig. 2 — Secções transversais do caule de V. polyanthes: a) região caulinar (galha jovem) e b) galhada. A) Aspecto geral do caule não galhado; B) Detalhe do parênquima modular com células hipertrofiadas; C) Desorganização dos tecidos vasculares; D) Distribuição de substâncias fenólicas nos raios parenquimáticos (vermelho) e no parênquima modular (azul); E) Distribuição de lipídios na epiderme (vermelho) e tecidos vasculares (azul); F) Detalhe da figura E, mostrando os lipídios nos tecidos vasculares. (Bf: baixa amplificação; Ch: células hipertrofiadas; E: epiderme; Fl: floema; P: parênquima cortical; Pm: parênquima modular; T: tronco; Tl: tubo laticêncio; Xi: xilema).
O sítio de alimentação, ou tecido nutritivo, da gálila, caracteriza-se pela abundância de proteínas, lipídios, água e geralmente ocorre no reto da cavidade larval (Mani, 1964; Friedberg, 1964). Nas gálilhas de *T. rudolphii* observou-se a presença de tecido nutritivo contendo lipídios lipoídios, descritos também para gálilhas de *Rouschella butleri* e *Cisthophora sp.* (Mani, 1964).


O segmento 1 ou pseudocefálico (Fig. 3B) apresenta-se bastante reticulado e rugoso anteriormente e suporta estruturas alimentares, os ganchos bucais. Segundo Heedrick e Goeden (1990a), a presença da região anterior do segmento pseudocéfalo reticulado e rugosa é uma característica de larvas de segundo estádio. Os ganchos bucais (Fig. 3B) utilizados na alimentação das larvas e escavação do túnel de saída do inseto adulto, ocorrem em todos os estádios larvais. As larvas de *Tepeirda* de primeiro e segundo estádios são identificadas, enquanto as de terceiro apresentam um dente acessório rudimentar, pouco visível (Noval e Foose, 1975, 1980; Heedrick e Goeden, 1990a).

Os ganchos frontal e principal, principalmente, são dispositivos nos demais segmentos (Figs. 3A e 4A). São uma prateada adaptação à locomoção e estabilização da larva dentro da gálila. Na porção posterior desse segmento estão os espiráculos anteriores com função respiratória (Fig. 3B). No segmento caudal, insere-se os espiráculos posteriores (Fig. 4B) também com função respiratória. As mudanças mais significativas do sistema respiratório de primeiro e segundo estádio larval, são o aparecimento de espiráculos anteriores e a adição de uma fenda espiracular posterior (Goeden, 1990a; Heedrick e Goeden, 1990a). A cada passagem de um estádio larval para o outro ocorre a retirada do conteúdo do tronco traqueal. O material é absorvido através de uma abertura que se forma posteriormente à cicatriz escleral (Noval e Foose, 1975, 1980; Heedrick e Goeden, 1990a) (Fig. 4B).

Nas gálilhas de *Tepeirda* podem ocorrer uma, duas ou várias gerações por ano (Friedberg, 1964). O ciclo biológico de *T. rudolphii* é bastante curto, com várias gerações por ano (multivoltino) e o período de desenvolvimento larval é bem mais longo que o período adulto. Apesar de ocorrerem durante todo o ano, as gálilhas de *T. rudolphii* são raras. Fernandes et al. (1983) descreveram sua ocorrência de março a abril e de agosto a novembro.

Mortalidade larval e pupal é provavelmente o fator regulador mais importante das populações de tetráédridos gálilhadores. Entre os principais fatores que causam a morte larval e pupal de *T. rudolphii* destacam-se parasitismo, predação e parásitos. Os Braconídeos foram os parasitas mais comuns. Braconídeos e Eurytomidae estão entre as famílias mais importantes de parasitoides de gálilhadores (Friedberg, 1964). O papel dos scarabaeídeos na redução de insetos associados às gálilhas é ainda obscuro. Eles podem ser inquilinos, sucessores ou até competidores pelos tecidos da gálila com o gálilhalhador. Estes questões poderão ser resolvidos com estudos detalhados da comunidade de insetos associados à gálila de *T. rudolphii*.

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**TABELA I**

Frequências de espaços horizontais associados à gálila de *Tomnophyx rudolphii* em *Vernonia polyanthus*.

<table>
<thead>
<tr>
<th>Gênero</th>
<th>N° de gálilhas</th>
<th>Frequência (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Rouschella sp.</em></td>
<td>1</td>
<td>0,25</td>
</tr>
<tr>
<td><em>Phalacophora sp.</em></td>
<td>2</td>
<td>0,45</td>
</tr>
<tr>
<td><em>Paracanthina genuilis</em></td>
<td>3</td>
<td>0,65</td>
</tr>
<tr>
<td><em>Eurytominae</em></td>
<td>4</td>
<td>0,85</td>
</tr>
<tr>
<td><em>Rouschella butleri</em></td>
<td>8</td>
<td>1,65</td>
</tr>
<tr>
<td><em>Stenopa sp.</em></td>
<td>10</td>
<td>2,05</td>
</tr>
</tbody>
</table>

| Total                   | 20             | 4,00           |

---

**TABELA II**

Ocorrência dos gêneros mais comuns de fornalhais associados à gálila de *Tomnophyx rudolphii* em *Vernonia polyanthus*.

<table>
<thead>
<tr>
<th>Gênero</th>
<th>N° de gálilhas</th>
<th>Percentual (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Paracanthina</em></td>
<td>9</td>
<td>40,90</td>
</tr>
<tr>
<td><em>Rouschella</em></td>
<td>3</td>
<td>13,66</td>
</tr>
<tr>
<td><em>Phalacophora</em></td>
<td>3</td>
<td>9,09</td>
</tr>
<tr>
<td><em>Paracanthina</em></td>
<td>2</td>
<td>4,54</td>
</tr>
<tr>
<td><em>Rouschella</em></td>
<td>1</td>
<td>2,25</td>
</tr>
<tr>
<td><em>Eurytominae</em></td>
<td>1</td>
<td>2,25</td>
</tr>
<tr>
<td><em>Stenopa</em></td>
<td>1</td>
<td>2,25</td>
</tr>
<tr>
<td>Total</td>
<td>22</td>
<td>100,00</td>
</tr>
</tbody>
</table>
A presença de formigas estava constatada no estudo de Fernandes e Price (1991) na Serra do Mar, no estado de São Paulo. As formigas desempenham um papel crucial na distribuição de sementes e nutrientes entre plantas e animais. O estudo demonstra que a presença de formigas influencia significativamente o crescimento e a sobrevivência das plantas estudadas.


O estudo de Fernandes e Price (1991) demonstra a importância da presença de formigas na ecologia de diferentes biomas brasileiros. O papel das formigas na dispersão de sementes e na ecologia de diferentes ambientes é crucial para o funcionamento do ecossistema.


O estudo de Fernandes e Price (1991) demonstra a importância da presença de formigas na ecologia de diferentes biomas brasileiros. O papel das formigas na dispersão de sementes e na ecologia de diferentes ambientes é crucial para o funcionamento do ecossistema.
Utilization of Apion sp. (Coleoptera Aplonidae) galls by an ant community in southeastern Brazil

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The ant community associated with Apion sp. (Coleoptera Aplonidae) galls on Despina bipada DC (Ebenaceae) was studied in a cerrado (savanna) area in southeastern Brazil. We asked the following questions: (a) what ant species occupy the galls, (b) are there any relationships among gall occupation, plant height, and gall distance from the ground, and (c) do ants differentially select galls? Seven ant species were found: Camponotus sp. 1 and Camponotus sp. 2, Crematogaster brevispinosa (Mayr. 1870), Zacryptocerus patillus (Klug 1824), Pseudomyrmex gracilis (Fabricius 1804), Solenopsis sp., and Leptothorax sp. Plant height, distance of the gall to the ground, gall volume, number of channels inside the gall, the length of ant's body and the width of ant's head were recorded. Ants occupied the largest galls (t = 2.633, n = 144, P < 0.05). The number of channels in occupied galls was significantly different from that in unoccupied galls (t = 5.565, n = 144, P < 0.05). Differential utilization of galls may be explained by the different biology and competitive interactions of the ant community.

Key words: Ants, Apion sp., community structure, insect galls, resource partitioning.

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INTRODUCTION

The community associated with galls comprises gall makers, their inquilines, predators, parasitoids, fungi, and other succession organisms (MANT 1964, Fernandes et al. 1989). Many arthropods and fungi utilize galls on plants, or even those galls that fall on the ground. Galls are used as food, cover and/or reproductive sites.

Ants are considered the main group of organisms using galls after the emergence of the gall-making species (Wheeler 1910, Mant 1964). The ant genus Leptothorax Mayr
1855 forms small colonies and nests in galls, while other genera can use galls during the early period of colonization (e.g., *Crematogaster* Lund 1831, *Zacryptocerus* Wheeler 1911, and *Comaposus* Mayr 1864) (Wheeler 1910). Some genera are also capable of modifying the interiors of woody galls by excavating wood (see Franks et al. 1989). Nevertheless, gall hardness and the climatic conditions influence the occupation by ants, thus affecting the development of the community (Craig et al. 1992).

We studied a population of galls caused by *Aiptos* sp. (Coleoptera: Aiptaidae) on *Drupmynema buxifolium* DC. (Ebenaceae) in a cerrado vegetation in southeastern Brazil. This work addresses the following questions: 1. What ant species occupy the galls? 2. Are there any relationships among gall occupation by ants, plant height, and gall distance from the ground, and test if ants differentially select galls?

**Material and Methods**

The study was done in a fire-disturbed cerrado vegetation 30 km south of Belo Horizonte, Minas Gerais State, Brazil. We collected 144 *Aiptos* sp. galls collected from 40 *Drupmynema buxifolium* DC. (Ebenaceae) plants. *Aiptos* sp. galls are green, hairy, exposed with a thick wall (Fig. 1), and become woody during gall-fusoid development. The plants studied were 3.95 ± 0.12 cm high, with a mean of 8 gall size.

Gall length and width were measured to the nearest millimeter. Gall volume was obtained by the immersion of the gall in a tube with 30 ml with water, recording the new volume of the water column. The degree of modification in the inner architecture of the galls was measured by the number of chambers in the galls (Franks et al. 1989). Galls were opened and the ants collected, separated, and counted as eggs, larvae, pupae, adults, workers, and queens. We measured the body length and head width of 10 ant workers of each species in order to correlate the ants's body size with gall volume. In this work, "colony" means an assembly of workers and immatures (Fernandes et al. 1989).

**Results**

Seven ant species belonging to six genera were found in 44 of the 144 collected galls: *Zacryptocerus pusillus* (Klug 1824), *Crematogaster brevispinosa* (Mayr 1870), *Pseudomyrmex gracilis* (Fabricius 1804), *Solenopsis sp., Lepidochares sp., Comaposus sp. 1 and Comaposus sp. 2. The number of colonies of each ant species, the mean number of individuals per colony, and the mean volume of the occupied galls are given in Table 1. *Crematogaster brevispinosa* had the highest number of colonies (18), whereas *Solenopsis sp., Comaposus sp. 2 and Lepidochares sp. had only one colony each.

There was no relationship between gall occupation by ants and plant height (P > 0.05), or between ant occupation and the height of the gall in the tree canopy from the ground (P > 0.05).

The volumes of occupied (11.47 ± 0.53 cm^3^), and unoccupied (0.29 ± 0.44 cm^3^) galls were significantly different (t = 2.63, n = 144, P < 0.05, Fig. 2b). The galls occupied by *Comaposus sp. 1, Crematogaster brevispinosa, Pseudomyrmex gracilis,* and *Zacryptocerus pusillus* differed significantly in volume (One-way ANOVA, F = 5.67, P < 0.05). *Comaposus sp. 1* occupied the largest galls (14 cm^3^), whereas *Pseudomyrmex gracilis* occupied the smallest galls (8.0 cm^3^).

**Table 1.** Ant species associated with *Aiptos* sp. galls on *Drupmynema buxifolium*.

<table>
<thead>
<tr>
<th>Ant species</th>
<th>Number of colonies</th>
<th>E</th>
<th>L</th>
<th>WK</th>
<th>T</th>
<th>Volume (cm^3^)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Comaposus sp. 1</em></td>
<td>4</td>
<td>3.7</td>
<td>18.5</td>
<td>12.2</td>
<td>35.7</td>
<td>14.7</td>
</tr>
<tr>
<td><em>Comaposus sp. 2</em></td>
<td>1</td>
<td>1.0</td>
<td>10.0</td>
<td>8.0</td>
<td>15.5</td>
<td>27.0</td>
</tr>
<tr>
<td><em>Crematogaster brevispinosa</em></td>
<td>18</td>
<td>19.0</td>
<td>40.0</td>
<td>58.0</td>
<td>127.0</td>
<td>10.7</td>
</tr>
<tr>
<td><em>Pseudomyrmex gracilis</em></td>
<td>9</td>
<td>24.5</td>
<td>14.8</td>
<td>11.5</td>
<td>51.2</td>
<td>8.2</td>
</tr>
<tr>
<td><em>Solenopsis sp.</em></td>
<td>1</td>
<td>40.0</td>
<td>0.0</td>
<td>8.0</td>
<td>53.0</td>
<td>10.0</td>
</tr>
<tr>
<td><em>Zacryptocerus pusillus</em></td>
<td>10</td>
<td>24.3</td>
<td>9.3</td>
<td>55.5</td>
<td>60.5</td>
<td>12.7</td>
</tr>
<tr>
<td><em>Lepidochares sp.</em></td>
<td>1</td>
<td>14.0</td>
<td>10.0</td>
<td>30.0</td>
<td>35.0</td>
<td>9.0</td>
</tr>
</tbody>
</table>

Average number of individuals per gall: E = egg, L = larva, P = pupa, WK = worker, T = total.
Insect gall use by ants

Many utilize cavities in thin stems, such as *Pseudomyrmex* and *Zacryptocerus* Wheeler (CARROLL 1974). Except for *Solenopsis*, these genera have already been recorded occupying insect galls (WHEELER 1910, FERNANDES et al. 1989, CRAIG et al. 1991).

Plant height and tree height of the gall from the ground were not related with gall occupation by ants in this study. Fire is an important selective factor acting upon cerrado plants and animals. Fire affects mainly species nesting in weak trunks, which do not provide thermal insulation (CARROLL 1974). Stems could offer better protection for ants against fire, enhancing survival, in the upper part of the tree canopy. Consequently, we expected that galls on higher trees would be preferred than galls on short trees.

Furthermore, the distance of galls from the ground could also influence ant occupation. Perhaps, the woody structure of the *Apis* sp. galls provides efficient insulation against fire, even in the lower canopy. For instance, *Collabiasa citriella* (Coleoptera Curculionidae) larvae may survive some fires due to their woody galls formed on *Solanum lycocarpum* (Solanaceae) (G.W. FERNANDES pers. obs). Nevertheless, no study has yet addressed this question.

Ant species partitioned galls of different volumes. *Camponotus* spp. occupied the largest galls. *Camponotus* spp. typically form large colonies with high population densities (LUEDERWALDT 1926). Body size is large (average of 9.5 mm for workers) (KUSNEZOV 1978), and does not show any adaptation for living in narrow cavities. Several studies have considered *Camponotus* as a generalist regarding nesting sites (LUEDERWALDT 1926, KUSNEZOV 1951, MORAI 1980).

Despite having relatively large body size, *Pseudomyrmex gracilis* utilized the smallest galls (8.2 cm²) (KEMP 1960, 1961). *Pseudomyrmex* ants are adapted to live in tubular and narrow cavities due to their capacity to go forth and back with enormous facility and speed. They form small colonies (WHEELER 1910), which would allow the utilization of smaller galls. *Zacryptocerus pusillus* and *Crematogaster brevispinosa* formed dense colonies (Table 1). *Zacryptocerus* is known to live in small stem cavities (MORAI 1980), as well as, in many galls (FERNANDES et al. 1989, CRAIG et al. 1991). This is the first record of a *Solenopsis* colony in a gill. *Solenopsis* is not a characteristically arboreal genus (MORAI 1980), even though it can be found under tree bark (L.M. ARAUJO pers. obs).

The difference between the number of channels in occupied and unoccupied galls may be the result of two different ant strategies: (a)ants select galls based upon the number of channels, or (b) ants modify the internal architecture of galls. Modification of the internal architecture of galls by ants has already been reported (FERNANDES et al. 1989, CRAIG et al. 1991). *Zacryptocerus pusillus*, *Crematogaster brevispinosa*, and many species of *Camponotus* are known to excavate wood (LUEDERWALDT 1926, KEMP 1961). These two alternatives are likely to occur in a complex community like this. Since larger galls are preferred, ants may compete for them and may colonize galls early in the season when the galling larvae are not fully developed.

The dynamics of ant communities on galls have not yet been studied in detail, and this system, as well as that studied by FERNANDES and collaborators (see FERNANDES et al. 1989, CRAIG et al. 1991) provides a beginning.

In summary, this work indicates that ants differentially occupy *Apis* sp. galls. The differential utilization of galls can be related to the biology of the occupying ant.
species, reflecting their colony sizes, body sizes, and capacity to excavate wood. Future studies shall deal with these topics in this dynamic tropical ant community.

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HERBIVORIA POR INSETOS EM CHAMAECRISTA DENTATA (LEGUMINOSAE)

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ABSTRACT: Insect heriboria on Chamaecrista dentata (Leguminosae) were studied in the relationship between glandular trichomes and insect heriboria on Chamaecrista dentata in the State of Minas Gerais (Brazil). Twenty plants were hand-pollinated with the C. dentata population studied. Trichome density varied significantly among the several plant tissues (One way ANOVA, F = 13.77, P < 0.0001). Trichomes (50) per cm²) for flowers and flowers per plant (r = 0.25, P < 0.01). The damage caused by herbivores leaves, flowers, and fruits also varied significantly (One way ANOVA, F = 7.25, P < 0.005). Nevertheless, damage was higher on leaves compared to the other organs. The relationship between damage and insect heriboria damage, suggesting a preference by insects on the function of glandular trichomes on these plant species.

Keywords: Chamaecrista, Glandular trichomes, Insect heriboria, Plant damage.

INTRODUÇÃO

A ação de insetos herbívoros pode provocar danos consideráveis que reduzem a capacidade reprodutiva das plantas atacadas. Assim, as plantas estão sujeitas a freqüentes pressões seletivas para reduzir o impacto produzido por herbívoros e compensar as perdas quando as defesas falham (Marquis, 1984, 1991). O aparecimento de substâncias secundárias nas meta-bioquímicas dos vegetais, bem como características morfológicas (globo, tricomas, esclerófitos), tem sido frequentemente relacionado a pressões exercidas por herbívoros (McNaughton, 1991; Whitham et al., 1991; Fernandes, 1994).


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Efeitos comportamentais e ecotóxicos (Fernandes & Sousa, 1986). Embora existam trabalhos desse natureza, a maturação dos diversos tipos de tricomas glandulares e suas substâncias contidas são investigadas e identificadas (e.g., Riedel & Lev., 1976), pouco tem sido realizado sobre o significado adaptativo deste mecanismo de defesa em plantas tóxicas (Fernandes, 1991).

Observações preliminares indicaram uma grande produção de secreção em tricomas glandulares em diversas raças vegetais e espécies de Chamaecrista dentata (e.g., Irwin & Barnes, 1983). Tendo em vista a falta de estudos sobre a eficácia destes tecidos como herbívoros, dois insetos foram testados. A primeira hipótese proposta é que os tecidos mais velhos para a planta deveriam possuir maior dano de triquinas e maior produção de secreção do que os tecidos menos velhos. A segunda hipótese proposta é que os tecidos mais velhos com maior densidade de triquinas glandulares por unidade de área deveriam apresentar melhores defensas contra insetos herbívoros do que os tecidos com menor densidade destes tecidos.

MATERIAL E MÉTODOS

Local de estudo

O estudo foi realizado na Serra do Capo que se localiza na região do Extremo Sul do Brasil. A vegetação compreende matas de galeria, estepes e campos rupestres associados com diferentes tipos de solo (Meneghini & Guarnieri, 1986). O local de coleta encontra-se a uma altitude de 1360 metros, no km 125 da rodovia MG 010.

Espécie estudada

Chamaecrista dentata apresenta porte arbóreo (1 a 6 metros), ocorre em áreas de matas de galeria e produz flores e frutos durante todo o ano (G.W. Fernandes, observ. pers.). Tricomas glandulares estão presentes em todos os órgãos da planta. Na base de cada tricoma filamentosos, há uma grande glândula secretora, que é visível a olho nu devido ao seu tamanho. Geralmente o únca tricoma apresenta-se contínuo às paredes da glândula devido à abundante secreção produzida. A população de C. dentata amostrada compreende algumas centenas de indivíduos que se agrupam de forma homogênea ou discreta. Os estudos foram realizados entre julho e dezembro de 1992.

Medidas de densidade de tricomas glandulares

Para quantificar o número de tricomas glandulares nos diversos órgãos da planta, foram coletadas aleatoriamente amostras de caules, folhas, flores e frutos em 50 indivíduos da população. As amostras foram acondicionadas em sacos de plástico e levadas para o laboratório, onde o número de tricomas por cm² em cada órgão foi contado sob estereomicroscópio. Cinco contagens em cada órgão foram feitas por placa e a média destas utilizada nos testes estatísticos.
Medidas de densidade das tricomas glândulas.

O número de tricomas variou significativamente entre os diversos tecidos da planta (one way ANOVA, F = 13,77, P < 0,0001). O caule de C. dentata apresentou um número significativamente maior de tricomas/cm² (x = 49,9 ± 2,7) do que folhas (x = 25,8 ± 2,7), flores (x = 26,2 ± 1,1) e frutos (x = 24,1 ± 1,5) (teste de Tukey; P < 0,001; todos). Entretanto, não houve diferenças estatisticamente significativas entre folhas, flores e frutos (teste de Tukey; P > 0,05; todos).

Houve grande variação na espessura dos caules utilizados para medir os valores de densidade de tricomas, bem como o número de tricomas/cm². A possível influência da largura do caule na densidade de tricomas glândulas foi testada através de regressão simples. Entretanto, apenas 8% da variação no número de tricomas no caule foi explicada pela variação na largura do mesmo (r² = 0,08; p < 0,005; y = 57,94 - 21,78x).

Herbívoros.

O número de galhas em caules variou significativamente na população estudada. O número de galhas em árvores variou de 8 a 46 enquanto a média de galhas por árvore foi de 25,5 ± 13,2 (n = 20). O número de galhas não variou em função da idade das árvores (regressão linear simples; r² = 0,01; n = 20; p > 0,05).

Danos causados por insetos herbívoros em folhas, flores e frutos variaram significativamente (One way ANOVA; F = 7,239, P < 0,005). Os órgãos com maiores porcentagens de danos foram as folhas (x = 23,3 ± 0,2; n = 40) e as flores (x = 15,0 ± 0,4; n = 40). Os frutos tiveram uma porcentagem de dano de 16,0 ± 0,1 (n = 40). Flores foram significativamente menos atacadas do que folhas e frutos (teste de Tukey; p < 0,0001 e p < 0,05, respectivamente). Danos em flores compreenderam a perda de tecidos por magostadores, ninhais e galhas em pecíolos. Os danos em folhas foram visíveis somente nas sépalas, pétalas e estames e foram causados por insetos magostadores, enquanto os danos causados nos frutos foram devido a predação de sementes principalmente por uma espécie de borróide.
atividade dos tricomas glandulares. A maturação da planta pode produzir extensiva variação dentro do indivíduo, devido a variações sazonais e espaciais na qualidade nutricional e nos níveis de defesa dos tecidos (Wittman et al., 1991). Deste modo a densidade de tricomas glandulares em uma planta pode ser alterada à medida que o amadurece, podendo a atividade secretora aumentar ou simplesmente acalmar (Roberts & Levy, 1976). Tomando-se a espessura dos caules como medida indicativa de suas idades, pode-se notar que, ao contrário, a correlação com a densidade de tricomas foi negativamente significativa. Isto demonstra que, no caule, a densidade de tricomas tende a diminuir. Emba o meio de quantidades de secreções produzidas por órgãos que não tenham sido folhas, teores mais elevados aparecem produzir uma quantidade maior de secreções do que os folhosos. O consumo de folhosos por herbívoros causa maior impacto sobre a aptidão das plantas do que o consumo de tecidos maduros por máscar, pois a presença de nutrientes em solos contendo água, nitrogênio e proteínas solúveis estes podem ser fotoassinteticamente ativos (Diniz, 1984; Goulart, 1991).

Herbivoria diferencial

Embora a densidade de tricomas glandulares em folhas e folhos tenha sido a mesma e a maioritária dos insetos encontrados seja a ambas as plantas, a porcentagem de rato em folhas foi maior do que em folhos. Comparado com os de outros órgãos de C. dentata, o dente em frutos foi igual, o que não se verifica em folhos. Em média, cada fruto produz 4,9 sementes, com cerca de 20% das sementes sendo aboradadas e 10% sendo destruídas por insetos herbívoros. Entretanto, o tempo de vida destes ovos é diferenciado, os ovos de insetos herbívoros variam entre os estudos mais detalhados que possam estabelecer uma relação entre tempo disponível para a colonização e defesa da planta.

O mecanismo de defesa de C. dentata não se dá apenas por "gumose", uma vez que foram encontrados poucos insetos adultos às secreções dos tricomas glandulares. Entretanto, o pequeno número de insetos presentes às secreções poderia ser o resultado de predação, vento ou chuva. Não houve correlação entre as densidades de tecidos e o dente em folhos, pois os dentes em folhos de C. dentata. Todavia, estes resultados não descartam a posibilidade dos tricomas glandulares e suas secreções estarem agindo como um mecanismo de defesa ou mesmo atratividade contra insetos herbívoros. As secreções podem interferir no comportamento e fisiologia de insetos herbívoros através da toxidade e/ou repulsão. Por outro lado, insetos galhardes e minhados possuem geralmente dieta restritas, e por isso os tecidos da planta hospedarão pelo menos se dos pelos e secreções para localização dos plantas hospedadas. não espaço (órgãos) livres de ninhos naturais (conquistas, predadores e parasitóides). Assim os pelos e secreções produzidos em C. dentata poderiam ter papel anti-herbívoro como ativo. No entanto, estudos detalhados de preferência alimentar dos insetos associados à C. dentata, bem como estudos quantitativos e qualitativos das secreções nos diversos órgãos da planta são necessários para o entendimento completo sobre o papel dos tricomas glandulares na defesa contra insetos herbívoros.

ARTRÓPODOS DE UM GRADIENTE ALTITUDINAL NA SERRA DO CIPO, MINAS GERAIS, BRASIL.

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ABSTRACT. Arthropods of an altitudinal gradient in the Serra do Cipo, Minas Gerais, Brazil. The distribution of arthropods along an altitudinal gradient in the Serra do Cipo, MG, Brazil was studied. Two hypotheses were tested: (a) the altitudinal gradient hypothesis, and (b) favorability hypothesis. Pairs of habitats were established from 800 m to 1400 m at each 100 m elevation. Habitats were separated into xeric (away from water sources) and mesic (along streams and rivers). Pairs of xeric and mesic habitats were replicated three times per elevation. Arthropods were collected by sweeping the vegetation in the rainy and dry seasons. Arthropods were separated to morphospecies and identified to the family level. Contrary to expected, arthropod richness did not increase with decreasing elevation. Nevertheless, mesic habitats were generally richer in arthropod species than xeric habitats. Distribution patterns were more clear when smaller taxon level (e.g., family) were studied, indicating that the grouping of species into a large taxa can mask individual responses to environment.

KEYWORDS: Altitudinal gradient, Diversity, Insect assemblages, Patterns, Richness.

INTRODUÇÃO


Ao longo de gradientes altitudinais ocorrem habitats xéricos e mesóicos, ideais para o teste de hipóteses que tentam explicar padrões de distribuição relacionados a temperatura e umidade. De modo geral, as bases de montanhas são mais quentes e úmidas que os topos. Em regiões tropicais a temperatura do ar diminui em média 0,6 °C a cada 100 m, enquanto a precipitação aumenta de baixas altitudes para o topo (Holdridge, 1967; Sarnat, 1986). Assim sendo, acreditamos que as bases de montanhas desempenhem um papel crucial na diversidade e riqueza de artrópodes ao longo do gradiente altitudinal, devendo ser estudados adequadamente (Fernandes & Price, 1988).

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Taxons menos resistentes a variações de temperatura e umidade seriam mais diversos em habitats mísicos do que aqueles mais resistentes, os quais seriam mais diversos em habitats xéricos (e.g., Fernandes & Price, 1992). Estudos desta natureza nos trópicos foram realizados na Serra do Cipó para insetos galhadores (Fernandes & Price, 1988; 1991). Entretanto, não foram ainda realizados estudos que descrevam a distribuição de todos os artrópodos. Embora padrões possam ser encontrados para alguns taxons específicos, uma visão do todo e também necessária para a elaboração de hipóteses gerais de trabalho.

Neste trabalho descrevemos os padrões de distribuição de artrópodos e, separadamente, das cinco famílias de insetos herbívoros de vida livre mais abundantes ao longo de um gradiente altitudinal na Serra do Cipó, MG. Foram testadas duas hipóteses: a) hipótese do gradiente altitudinal: que prediz que a riqueza de espécies diminui com o aumento da altitude (e.g., Lawton et al., 1987; Fernandes & Price, 1988); e b) a hipótese da favorabilidade: que prediz que a riqueza de espécies é maior em habitats mísicos do que em habitats xéricos devido a condições mais favoráveis para insetos de vida livre encontrados nos habitats mísicos (veja Fernandes & Price, 1991, 1992).

MATERIAL E MÉTODOS

Área de estudo

A área de estudo localiza-se na Serra do Cipó, MG, na porção sul da Cadeia do Espinhão, entre 19° 15' e 19° 30' S e 43° 53' W. Na Serra do Cipó a cobertura vegetal é muito diversificada, ocorrendo um predominio de campos rupestres (Gigliotti et al., 1987). O solo é arenoso, roxo, de baixa capacidade de retenção de água e de natureza oligotrofica (Gigliotti et al., 1987).

Sítios amostrais

As coletas foram realizadas num gradiente entre 800 e 1500 metros de altitude, em intervalos de 100 metros, totalizando oito estações amostrais. Os sítios de coleta foram estabelecidos ao longo da rodovia MG-010, entre Lagoa Santa e a Serra do Alto Palácio (veja Ribeiro, 1992).

Para cada altitude foram estabelecidos três sítios amostrais, distanciados um dos outros por pelo menos 1 km para evitar possíveis pseudoreplicações. Cada sítio consistia em um habitat xérico (longe de cursos de água) e um habitat mísico (ao longo de cursos de água) (Fernandes & Price, 1988), exceto os sítios de 1500 m e um sítio de 1400 m onde não existiam habitats mísicos. Os habitats xéricos de 800 a 1000 metros eram cobertos por vegetação de cerrado e de 1100 a 1500 m predominavam campos rupestres e campos antiluminais. Ao longo deste gradiente fisionômico, os habitat mísicos eram representados por matas ciliárias que acompanhavam os rios.

Coleta de artrópodos

As coletas de artrópodos foram realizadas com uma rede de varredura de 38 cm de diâmetro durante a estação chuvosa (fevereiro) e seca (julho) de 1991. Em cada habitat foram realizadas cinco amostras de 30 batidas cada, ao longo de uma linha imaginária, totalizando 150 batidas por habitat e 900 por elevação (habitats xéricos + habitats mísicos) em cada estação. Ao longo do gradiente altitudinal, em cada estação, foram realizadas 6600 batidas, 3600 batidas em habitats xéricos e 3000 em mísicos. Para a realização de análises estatísticas foi considerado o valor médio das cinco amostras por habitat.

Para maximizar a amostragem sobre a folhagem nos habitats mísicos e diminuir a perda de eficiência devido à rede de varredura em vegetação fechada, as batidas foram feitas nas bordas das matas ciliárias, sobre a folhagem. As coletas foram realizadas entre 9:00 e 16:00h e nunca sob vento forte ou chuva. Não foi nosso objetivo estimar a diversidade de artrópodos, e sim geral dados comparativos para análise de padrões. Segundo Whittaker (1952), a coleta com rede de varredura fornece dados absolutos questionáveis, mas dados relativos de alto valor comparativo. Assim, esta metodologia atendeu nosso objetivo de descobrir padrões gerais da distribuição de artrópodos na região (veja também Janzen, 1973).

Os artrópodos coletados foram separados ao nível de morfoespecie. A divisão de insetos em morfoespecies têm-se mostrado extremamente eficiente na realização de estudos prévios com comunidades de artrópodos e suprindo de forma temporária a deficiência de taxonomistas de vários grupos de insetos (McCoty, 1990). Devido a dificuldades em separar ninhos de Heteroptera e Orthoptera em morfoespecies, estes não foram computados. De qualquer maneira, ninhos de Hemiptera e Orthoptera não foram frequentes nas nossas coletas (menos de 5%). Insetos herbívoros foram identificados ao nível de família, sendo aquelas mais abundantes neste estudo analisadas separadamente: Aracnídeos (Orthoptera), Cicadellidae (Hemiptera), Chrysomelidae (Coleoptera) e Curculionidae (Coleoptera). Os insetos foram depositados na coleção da Universidade Federal de Minas Gerais.

Análises estatísticas

Os dados apresentaram distribuição, permitindo o uso de modelos paramétricos de regressão linear simples para testar a hipótese do gradiente altitudinal. Para testar a hipótese da favorabilidade foi utilizado "Wilcoxon sign rank test" (Zar, 1984).

RESULTADOS

Hipoéstese do gradiente altitudinal

A riqueza total de espécies de artrópodos não variou em função da altitude na estação chuvosa nos habitats xéricos (F122 = 3.093; P > 0.05) e mísicos (F122 = 1.999; P > 0.05, Tabela I). Nesta mesma estação, a riqueza de espécies de insetos herbívoros também não variou com a altitude em habitats xéricos (Aracnídeos: F122 = 2.162, P > 0.05; Chrysomelidae: F122 = 0.196, P > 0.05 e Curculionidae: F122 = 2.791, P > 0.05). Em habitats mísicos também não foi observada nenhuma relação entre a riqueza de espécies de herbívoros e altitude (Aracnídeos: F122 = 0.332, P > 0.05; Cicadellidae: F122 = 0.337, P > 0.05; Chrysomelidae: F122 = 0.018, P > 0.05 e Curculionidae: F122 = 0.939, P > 0.05, Tabela I).

Na estação seca o mesmo padrão foi observado, ou seja, a riqueza total de artrópodos não variou em função da altitude nos habitats xéricos (F122 = 0.066; P >
0,05). Ao contrário do esperado, nos habitats mísicos, houve um aumento significativo do número total de espécies de artrópodes com o aumento da altitude (F_{1,24} = 5,256; P < 0,05; Tabela II). Nos habitats xéricos, a riqueza de espécies das famílias Acridiidae (F_{1,6} = 0,052; P > 0,05), Cicadellidae (F_{1,22} = 0,000; P > 0,05) e Curculionidae (F_{1,22} = 2,574; P > 0,05) não variaram com a altitude. O mesmo pode ser visto para as espécies de Acridiidae (F_{1,6} = 0,848; P > 0,05) e Cicadellidae (F_{1,6} = 1,000; P > 0,05) nos habitats mísicos. Por outro lado, a riqueza de espécies de Cicadellidae aumentou com o aumento da altitude nos habitats mísicos (F_{1,14} = 51,757; P < 0,05). O número de espécies de Chrysomelidae aumentou com o aumento da altitude nos habitats xéricos (F_{1,24} = 41,859; P < 0,05) e mísicos (F_{1,14} = 21,451; P < 0,05) nesta estação (Tabela II). O aumento da riqueza total de artrópodes foi influenciado pela relação positiva entre o número de Cicadellidae e Chrysomelidae com a altitude.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Habitat</th>
<th>r²</th>
<th>Equação y = a + bx</th>
<th>Valores P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acridiidae</td>
<td>xérico</td>
<td>0,12</td>
<td>21,223 - 0,048</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>mísico</td>
<td>0,10</td>
<td>3,935 + 0,089</td>
<td>ns</td>
</tr>
<tr>
<td>Cicadellidae</td>
<td>xérico</td>
<td>0,09</td>
<td>1,455 - 0,001</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>mísico</td>
<td>0,01</td>
<td>0,777 + 0,001</td>
<td>ns</td>
</tr>
<tr>
<td>Chrysomelidae</td>
<td>xérico</td>
<td>0,65</td>
<td>0,633 + 0,001</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>mísico</td>
<td>0,00</td>
<td>-0,000 + 0,001</td>
<td>ns</td>
</tr>
</tbody>
</table>

m = não significativo, P > 0,05.

Tabela II: Regressões lineares simples de riqueza de espécies em habitats xéricos e mísicos na estação chuvosa, entre 800 e 1500 metros de altitude, na serra do Cipó, MG. Para habitats xéricos e mísicos, n = 24 e n = 20 habitats, respectivamente.

A riqueza de espécies de artrópodes e de Curculionidae foi significativamente maior nos habitats mísicos em relação aos habitats xéricos na estação seca (Tabela IV). Entretanto, a riqueza de espécies de Cicadellidae e Chrysomelidae não variou entre os habitats xéricos e mísicos nesta estação (Tabela IV). A riqueza de espécies de Acridiidae na estação seca foi maior aos habitats xéricos do que aos mísicos, repetindo o encontrado na estação chuvosa.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Habitat</th>
<th>r²</th>
<th>Equação y = a + bx</th>
<th>Valores P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acridiidae</td>
<td>xérico</td>
<td>0,50</td>
<td>1,067 - 0,001</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>mísico</td>
<td>0,65</td>
<td>0,180 + 0,001</td>
<td>ns</td>
</tr>
</tbody>
</table>

m = não significativo, P > 0,05.

Tabela III: Regressões lineares simples de riqueza de espécies em habitats xéricos e mísicos na estação seca, entre 800 e 1500 metros de altitude, na serra do Cipó, MG. Para habitats xéricos e mísicos, n = 24 e n = 20 habitats, respectivamente.

Hipótese da favorabilidade

A riqueza de espécies de artrópodes foi maior em habitats mísicos do que em habitats xéricos na estação chuvosa (Tabela III). Entretanto, a riqueza de espécies de Chrysomelidae, Curculionidae e Cicadellidae não variou entre os habitats xéricos e mísicos nesta estação. Ao contrário do esperado, a riqueza de Acridiidae foi maior em habitats xéricos do que em habitats mísicos (Tabela III).

Tabela IV: Riqueza de artrópodes em habitats xéricos e mísicos em um gradiente de altitude de 800 a 1400 m na Serra do Cipó, durante a estação chuvosa de 1991 (em todos os casos n = 20 habitats).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Habitat</th>
<th>r²</th>
<th>Equação y = a + bx</th>
<th>Valores P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acridiidae</td>
<td>xérico</td>
<td>0,15</td>
<td>2,472 + 0,001</td>
<td>&lt; 0,05</td>
</tr>
<tr>
<td></td>
<td>mísico</td>
<td>0,78</td>
<td>3,780 + 0,001</td>
<td>&lt; 0,05</td>
</tr>
<tr>
<td>Cicadellidae</td>
<td>xérico</td>
<td>0,00</td>
<td>-0,001 + 0,001</td>
<td>&lt; 0,05</td>
</tr>
<tr>
<td></td>
<td>mísico</td>
<td>0,00</td>
<td>-0,001 + 0,001</td>
<td>&lt; 0,05</td>
</tr>
<tr>
<td>Chrysomelidae</td>
<td>xérico</td>
<td>0,65</td>
<td>0,633 + 0,001</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>mísico</td>
<td>0,00</td>
<td>-0,001 + 0,001</td>
<td>&lt; 0,05</td>
</tr>
</tbody>
</table>

m = não significativo, P > 0,05.

DISCUSSÃO

Não foram encontrados padrões consistentes entre a riqueza total de espécies de artrópodes e das famílias de insetos herbívoros com a altitude. Ao contrário do esperado, na estação seca houve um aumento da riqueza de espécies com o aumento da altitude para Cicadellidae e Chrysomelidae nos habitats xéricos, e de Chrysomelidae nos habitats mísicos. Provavelmente, este fato esteja associado a uma maior severidade climática nas bases das montanhas, como mencionado em Fernandes & Pinto (1988). Claramente, o estresse ao qual referimos trata-se do aumento da temperatura e diminuição da umidade. Por outro lado, os valores das correlações entre riqueza de espécies e altitude foram baixos, indicando que outras variáveis são de relevância e portanto, devem ser estudadas mais detalhadamente.
Ao longo dos gráficos, ajustados, gráficos, alguns fatores podem influenciar o desenvolvimento da espécie, como o tempo, a luz e a temperatura. As condições climáticas, altura da vegetação e a qualidade do solo também podem influenciar o desenvolvimento do inseto. As condições climáticas, em particular, podem afetar o desenvolvimento do inseto, aumentando ou reduzindo a qualidade do solo e a qualidade da vegetação. As condições climáticas podem variar de uma região para outra, o que pode afetar a distribuição e o desenvolvimento do inseto. 

No entanto, dependendo das condições climáticas e de vegetação, alguns fatores podem influenciar o desenvolvimento do inseto. Assim, para melhor compreender o desenvolvimento e a distribuição do inseto, é necessário considerar os fatores climáticos e vegetacionais.


Keysan, J.I.; T.F. Brennan; R.F. Schreiber & W.E. Steiner, 1981. Elevation of "Diabrotica virgifera" (Coleoptera: Chrysomelidae) to the subspecies level with notes on the altitudinal distribution of "Diabrotica" species in the Cuzco Department of Peru. Entomol. News 95: 91-98.


Received on 03.11.1993; accepted on 03.08.1995.
DISTRIBUIÇÃO DIFERENCIAL DE INSETOS GALHADORES ENTRE HABITATS E SEU POSSÍVEL USO COMO BIOINDICADORES

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RESUMO

Neste estudo, descrevemos a distribuição e riqueza de espécies de insetos galhadores em dois habitats distintos de um empreendimento hidrelétrico no sudeste brasileiro, durante as estações seca e chuvosa. Os habitats coletados foram separados por diferenças em umidade e temperatura. Foram amostradas galhas ao longo de transectos durante a hora de caminhada diurna, posteriormente separadas em morfo-espécies. Não houve diferenças estatísticas entre a época média total de espécies de galhas nas estações, chuvosa e seca, para ambos os habitats. O número de espécies de galhas foi significativamente maior nas estações úmidas, com diferença de 11% nas estações seca e chuvosa. Essas diferenças corroboram a hipótese de que insetos galhadores são mais ativos em habitats úmidos e temperados. Dados sobre a composição e diversidade de galhas podem fornecer informações relevantes para o estudo de sistemas ecológicos e de habitats, e assim, serem importantes como espécies bioindicadoras.

PALAVRAS-CHAVE: adaptações, bioindicadores, especificidade, galhas de insetos, impacto ambiental, preferência por habitats

RESUMEN

En este estudio, describimos la distribución y riqueza de especies de insectos que forman galhas en dos hábitats distintos de una planta hidroeléctrica en el sudeste de Brasil. Las galhas fueron medidas durante las épocas luna y seca, tanto en hábitats húmedos como secos. Las galhas fueron colectadas en transectos durante una caminata de una hora, y después separadas en morfo-espécies. No se encontró diferencias estadísticas en el número medio total de galhas entre las épocas seca y lluviosa en los dos hábitats medidas. La riqueza de las galhas fue significativamente mayor en los hábitats secos comparados con los hábitats húmedos en ambas épocas. Estos datos corroboran la hipótesis de que los insectos que forman galhas son especies ricas en hábitats estresados en términos hidrológicos. Los datos sobre la composición y diversidad de insectos que forman galhas pueden ofrecer información importante sobre los estados fisiológico y nutricional de las plantas y su hábitat, y así servir como especies bioindicadoras.

PALABRAS-CLAVE: adaptaciones, bioindicadores, especificidad, galhas de insectos, impacto ambiental, preferencia por hábitats

ABSTRACT

In this study we describe the distribution and richness of gall-forming insects in two distinct habitats of a hydroelectric power plant in southeastern Brazil. Galls were sampled during the dry and rainy seasons in wet and dry habitats. Galls were collected in transects during 1-hr walks, and then separated into morpho-species. There was no statistical difference in the mean total number of galls between the dry and rainy seasons in both habitats sampled. Gall richness was significantly greater in dry habitats compared to moist habitats in both seasons. These data corroborate the hypothesis that gall-forming insects are more species-rich in hydrothermally stressed habitats. Data on the composition and diversity of gall-forming insects may provide important information on the physiological and nutritional status of plants and habitat, and thus serve as bioindicator species.

KEY WORDS: adaptations, bioindicators, specificity, insect galls, environmental impact, habitat preference

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habitats definidos pelo estresse hídrico, térmico e até distúrbios antrópicos (e.g., lavouras, florestas de eucaliptos, áreas de mineração, etc.). Galhas de insetos têm sido amplamente utilizadas também para o monitoramento de áreas poluídas por metais pesados (Fernandes 1987, Heliövaara 1986, Heliövaara et al. 1987).

Este estudo descreve a distribuição e a riqueza de espécies de insetos galhadores em dois habitats distintos, na área de implantação de um novo empreendimento hidreletrico. Este é o primeiro estudo no qual insetos galhadores são utilizados na avaliação de qualidade de habitats na região tropical. De modo geral, insetos terrestres são raramente coletados em projetos de avaliação ambiental, não obstante sua importância central na manutenção e funcionamento de comunidades de plantas e animais (Collins e Thomas 1991, Wilson 1987).

METODOLOGIA

Locais de Estudo

As coletas foram realizadas em diversas localidades do norte de Minas Gerais: Soberbo (Município de Cristália), Fazenda Cabelo (Município de Cristália), Lameçim (Eixu) (Município de Itiruglo e Itamogi), Posse (Município de Minas Novas) e Peixe Crú (Município de Turmalina) (Fig. 1). Para a escolha dos locais de coleta foram utilizadas aerofotografias na escala de 1:30.000 e mapas do Instituto Brasileiro de Geografia na escala 1:100.000. Posteriormente, efetuou-se um reconhecimento da área a partir do qual foram selecionados locais para amostragem.

As principais formações vegetais nativas das localidades amostradas e suas correlações com as principais unidades de solo são as seguintes: a) vegetação campestre e campos limpos quase-típicos em afloramentos rochosos com baixa fertilidade e formação de solos; b) campo cerrado em lotossóis com baixa fertilidade; c) cerrado "stricto sensu" e cerradão em lotossóis com baixa fertilidade; d) floresta estacional (florestas mesófilas deciduas e semidecidual) em cambissóis com baixas torres de nutrientes e em podzólicos com maior fertilidade; e) floresta pluvial ripária (mata ciliar), principalmente em terraços fluviais dos tributários de menor porte do cerrado; f) veredas em solos hídromórficos com relativa fertilidade.

O clima regional, condicionado pela topografia muito acidentada da região, sofre a influência das frentes polares e do sistema de circulação do anticiclone do Atlântico Sul que se opõem em equilíbrio dinâmico. Segundo a classificação de Köppen, a região apresenta um predomínio do clima AW, representado pelo clima tropical úmido de savanas (Antunes 1986, Nimer 1979). Este tipo de clima é caracterizado por inverno seco e verão chuvoso. A temperatura média do mês mais frio é superior a 18°C. A precipitação do mês mais seco é inferior a 60 mm e também inferior a 100 cm, sendo P a precipitação média anual (Antunes 1986). A seguir são descritos os ambientes dos locais amostrados.

Sobrala - Localiza-se próximo à conflúncia do ribeirão Sobral com o rio Jequitinhonha, a 42°46'W e 17°08'S, no município de Cristália. A vegetação consta por campo cerrado sobre afloramentos de rocha e lotossóis alvoa; floresta mesófila decidua e semidecidual sobre solo eutrófico e floresta pluvial ripária nos terraços fluviais.

Fazenda Cabral - Localiza-se a 42°47'W e 16°34'S, no município de Cristália, apresentando pouco afloramento de rocha e predominio de associação lotossolo + cambissolo. A vegetação é constituída por floresta pluvial ripária descontinua às margens do rio Iacambiruçu, ocorrendo floresta estacional nos terraços fluviais e nas encostas em cotas altimétricas mais baixas: campo cerrado e cerrados degradados nas regiões mais altas.

Lamaú (Exo) - Localizado em uma região encalhada no vale do rio Jequitinhonha, a 42°36'W e 16°44'S, nos municípios de Belo e Giau Mogol. Trata-se de uma região sem distúrbios antrópicos com ocorrência de lotossolo eutrófico. Nas altitudes mais elevadas ocorrem cerrado, campo sujo e campo rupestre, com predominio de floresta mesófila decidua e semidecidual ao longo das vertentes e nos terraços fluviais. São poucos os elementos da floresta pluvial ripária nas margens do rio Jequitinhonha, sendo uma localidade seca com solos bastante ricos e que não conduzem a retenção de água. A decíduidade da floresta estacional é quase total durante o período seco do ano, o que não ocorre com tanta intensidade no campo cerrado e campo rupestre.

Passos - Localizada na margem direita do rio Jequitinhonha, a 42°47'W e 17°02'S, no município de Minas Novas. A região amostrada compreende várias áreas de Iavuma em lotossolo distrofico onde ocorre cerrado e uma associação de lotossolo + cambissolo sob floresta estacional.

Petrolândia - Localizado na margem direita do rio Jequitinhonha, a 42°57'W e 17°S, no município de Turnalina. A área está constituída por floresta estacional nos terraços fluviais e em solos compostos por uma associação de lotossolo + cambissolo. O cerrado ocorre sobre lotossolo localizado em manchas atenuadas.

Amostragem

Para a avaliação da riqueza de espécies de galhas nas áreas e habitats estudados, foram realizadas três coletas (ampliadas aleatórias) de uma hora cada (Price 1991). Durante este período, todas as espécies de galhas e plantas hospedeiras encontradas nas vegetações foram coletadas e armazenadas em saco plástico para posterior identificação. Nos usamos a forma das galhas, cor, pilosidade, distribuição, órgão hospedeiro, e família dos insetos galhadores e plantas hospedeiras para separar as morf-especies de galhas. As descrições das galhas e identificação das plantas hospedeiras foram realizadas conforme descrito por Fernandes et al. (1988). Logo após a termino das coletas, plantas e galhas foram pressas e herborizadas. As galhas foram depositadas na Coleção de Galhas do Insetos do Herbário do Departamento de Botânica da Universidade Federal de Minas Gerais. Uma listagem das galhas, plantas hospedeiras e insetos galhadores encontrados está sendo preparada e será posteriormente publicada.

Um ponto controverso nos estudos da distribuição de insetos e a sazonalidade das comunidades de insetos, e em alguns casos os métodos utilizados (McCoy 1990). O uso de insetos galhadores é apropriado devido a simplicidade e persistência das galhas nas plantas hospedeiras, diminuindo assim os problemas de sazonalidade características de insetos herbívoros de vida livre (Lara e Fernandes, in pressa). Devido a alta diversidade de formas e enorme grau de especificidade com suas plantas

Duas coletas foram realizadas durante o período do estudo, sendo a primeira durante a estação chuvosa (abril de 1991) e a segunda durante o período de seca (julho-agosto de 1991). Estas duas coletas foram necessárias diante da possibilidade de variação na composição e riqueza de espécies de insetos herbívoros com as mudanças estacionais. As comparações da riqueza de espécies entre estações e habitats foram realizadas através do teste t de Student e de Wilcoxon (Zar 1984).

RESULTADOS

Não houve diferenças estatisticamente significativas entre a riqueza média total de espécies de galhas nas estações chuvosa e seca e dos habitats úmido e seco. O número médio de espécies galhadoras em habitats úmidos foi de 7,8±1,2 na estação chuvosa e de 8,5±1,6 na estação seca (t=0,355, n=27, P<0,9, Fig. 2). Em habitats secos, o número médio de espécies galhadoras foi de 20,9±2,3 na estação chuvosa e 24,4±3,5 na estação seca (t=0,882, n=27, P=0,8, Fig. 2).

O número de espécies de galhas diferiu significativamente entre habitats secos e úmidos na estação chuvosa e seca. Na estação chuvosa o número médio de espécies de galhas foi estatisticamente superior em habitats secos do que em habitats úmidos em todas as localidades amostradas (Wilcoxon=3,411, n=15, P<0,001, Fig. 3). O mesmo padrão de riqueza de espécies de insetos galhadores foi observada na estação seca (Wilcoxon=3,063, n=12, P<0,001, Fig. 4).

DICUSSÃO

Uma coleta durante uma estação climática teria sido suficiente para a avaliação do número de espécies de galhas por habitat dado e não diferença estatística entre este parâmetro no presente estudo. Esta observação reforça a importância do uso de galhas como bioindicadores pois são sóveis e permanecem aderidas às plantas hospedeiras após a emergência dos adultos, podendo ser realizados sensores com facilidade. Entretanto, o simples número de galhas presente no habitat durante uma estação pode não retratar a composição total de espécies. Espécies encontradas na estação chuvosa podem não ser as mesmas encontradas na estação seca e vice-versa. Devido à natureza preliminar deste estudo, posições sólidas sobre este fato precisam ser apoiadas em mais exemplos empíricos. Portanto, as duas coletas serão analisadas ainda em separado neste estudo.
Diferenças na riqueza de galhas de insetos tropicais entre habitats secos e úmidos foram descritas por Fernandes e Price (1988). O padrão de uma maior riqueza de galhas em habitats estressados nutricional e higrotermicamente foi encontrado tanto para a região tropical como para a temperada. Estudos mais detalhados realizados na Serra do Cipó, MG (Fernandes et al. 1994, Lura e Fernandes 1994) juntamente com o presente estudo reforçam a hipótese de que insetos galhadores são comuns em habitats áridos (Fernandes e Price 1988).

A maior riqueza de galhas em habitats secos pode estar relacionada a diversos mecanismos ecológicos e processos evolutivos. Estudos recentes (Fernandes e Price 1992) indicam que insetos galhadores sofrem maiores pressões seletivas exercidas por inimigos naturais e resistência de plantas em habitats úmidos comparados a habitats secos. A maior susceptibilidade de plantas que ocupam habitats secos pode ser devida à escassez de água e nutrientes relevantes nos processos de defesa contra herbivoria (Fernandes 1992). Mudanças na disponibilidade de nutrientes e/ou água alteram os balanços limnológicos e fisiológicos de plantas (Fitter e Hay 1987). Respostas de hiperosensibilidade, um mecanismo eficiente na defesa contra microrganismos e insetos galhadores, diminui consideravelmente com o aumento do estresse nutricional e hídrico das plantas (Fernandes 1990). Além disso, a preferência das fêmeas dos insetos galhadores por plantas hospedeiras em habitats secos durante o período de oviposição reforçam o padrão de distribuição diferencial das galhas (Fernandes 1992). Estudos sobre a mortalidade e sobrevivência de espécies de galhadores em habitats tropicais distintos são necessários para o conhecimento dos mecanismos que moldam os padrões de distribuição diferencial entre habitats. Neste sentido, fazem-se necessários estudos de campo nos quais as taxas de sobrevivência e mortalidade de espécies-chave são avaliadas antes de um empreendimento, para que modificações futuras sejam adequadamente avaliadas.

A listagem simples de espécies por habitats sem informações ecológicas que visem a preservação e manejo não fornece as bases necessárias para uma avaliação precisa dos mecanismos ecológicos e processos evolutivos que moldam os padrões de biodiversidade. Uma visão funcional da distribuição de espécies ao longo de gradientes biogeográficos e de distúrbios antrópicos é vital para o entendimento de padrões ecológicos.

A correlação entre estresse do habitat e número de insetos galhadores fornece um importante entro de estudo para o entendimento das relações parasita-hospedeiro, resistência de plantas, biodiversidade e monitoramento ambiental. Por serem sérios, as galhas podem ser facilmente visualizadas, coletadas e estudadas através de tabelas de vida (Fernandes e Price 1992, Price et al. 1990). A preparação de curvas de mortalidade e sobrevivência para insetos galhadores em habitats distintos é importante para a elaboração de medidas que auxiliem no entendimento das características do habitat que influenciam as dinâmicas populacionais e controle populacional de insetos galhadores. Por estarem intimamente associadas às suas plantas hospedeiras, o estudo das galhas fornece dados de enorme relevância para o conhecimento do status fisiológico e nutricional das plantas e do habitat (Fernandes 1992).

Insetos galhadores são potenciais indicadores da diversidade e qualidade do habitat. Os melhores indicadores biológicos são aqueles que facilitam o programa de conservação e monitoramento (Collins e Thomas 1991). Insetos galhadores apresentam valores úteis ou superiores aos grupos mais importantes de insetos utilizados como biomarcadores (térmitas, formigas e lepidópteros das subfamílias Heliconiinae e Ithomiinae) (veja Brown 1991). Os insetos galhadores são taxonomicamente e ecológicamente diversificados, apresentam alta fidelidade ecológica, são sedentarios na sua fase larval, são de fácil identificação através de suas galhas (morfoespécies), são abundantes e facilmente detectáveis no campo, podem ser colhidos em abundância, são importantes no funcionamento de ecossistemas, apresentam respostas previsíveis a variações
AGRADECIMENTOS

REFERENCIAS CITADAS
91 81-87.


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TOMÉCIÊNCIA

OS TUMORES VEGETAIS E SEU IMPACTO NAS PLANTAS

Assim como os animais, as plantas também podem desenvolver tumores. Pesquisa realizada por IVONEIDE M. SILVA, GIOVANNA J. ANDRADE e G. WILSON FERNANDES, do Laboratório de Biologia Evolutiva de Herbívoros da Universidade Federal de Minas Gerais, verificou os impactos de tumores induzidos por uma mosca sobre as plantas assa-PEIXE, comum em todo o território brasileiro.

Os tumores vegetais, ou galhas, caracterizam-se pelo aumento do número (hipertrofia) ou do volume (hiperplasia) de células, tecidos ou órgãos e são induzidos por vários tipos de organismos: fungos, vírus, bactérias e, em sua grande maioria, insetos (ver CIBERCI 10, no 19). As galhas podem desenvolver-se em todas as partes das plantas, da extremidade da raiz até as gomas apicais do caule, incluindo órgãos vegetativos e reprodutivos.

Na região tropical, entre as famílias de plantas hospedeiras mais atacadas destacam-se as compostas (alêncrin, prevena, girassol), leguminosas (mimosas, feijão, cadávia) e mirtáceas (babosca, eucalipto, goiaba).

A relação galha-planta é normalmente parasitária. Quase todas as plantas de plantas estão sujeitas ao fenômeno, sobretudo as plantas com flores, que apresentam grande abundância e diversidade de espécies galhadoras.

As galhas causadas por insetos interferem de várias maneiras em suas plantas hospedeiras, danificando órgãos ou tecidos da planta. Como o crescimento e a manutenção da galha requerem recursos energéticos adicionais, elas atuam como desvios de recursos, desviando para si nutrientes destinados aos tecidos normais da planta.

Em determinadas ocasiões, as galhas podem funcionar como uma pista, causando um retrocesso intenso. Essa modificação na arquitetura normal da planta pode levar a uma taxa de crescimento acelerada, com um aumento da biomassa total e da produção de flores e frutos, num processo chamado de supercompensação.

Alguns autores consideram que esse crescimento seja um recurso desenvolvido pela planta para beneficiar-se da herbivoria. Para outros, entretanto, ainda não há evidências suficientes de que a herbivoria seja benéfica. Esses autores acreditam que a otimização da produtividade, ocasionalmente encontrada após a herbivoria, é apenas uma estratégia da planta para minimizar qualquer tipo de dano, como, por exemplo, os provocados por fogo, verdo, gado ou pobreza, e não apenas os danos causados por herbívoros.

A pressão dos herbívoros sobre suas plantas hospedeiras pode ser estimada através de estudos específicos das alterações causadas. Quando a reprodução sexual é afetada pela herbivoria, por exemplo, os impactos negativos podem ser detectados em características reprodutivas como a produção, o peso e o tamanho de flores, sementes ou frutos e a taxa de germinação das sementes.

Em estudo recente, verificaram os impactos causados por uma galha característica em assa-PEIXE (Vernonia polyanthea), induzida por um inseto da família Tephrillidae (Tephrillidae F. Muller) (Figura 1).

O assa-PEIXE, planta invasora largamente encontrada no Brasil, é uma das pragas mais freqüentes e temidas, porque tende a dominar as pastagens, inutilizando-as. Em contraste, além de sua importância medicinal, para o tratamento de doenças respiratórias e urinárias, é bastante conhecida como excelente melhice.

O período de maior abundância anual da galha assa-PEIXE ocorre entre os meses de setembro a dezembro, e o ciclo de larva e adulto do inseto galhador dura de 65-60 dias. A fêmea põe os ovos nos tecidos indiferenciados do ápice dos ramos e, após a eclosão, as larvas...
desenvolvem-se às custas do conteúdo das células desses tecidos.

Com o crescimento das larvas, ocorre uma expansão dos tecidos do caule ao seu redor, originando uma galha globulete, mostrada na figura 1. Ao final do desenvolvimento, as larvas escavam um orifício para a saída do inseto adulto e, em seguida, empupam. Nossa fase a galha pós de crescer. Logo após o período pupal (15-20 dias) dá-se a eclo- são dos adultos, que reiniciam o ciclo (figura 2).

Para verificar o impacto da galha na arquitetura de *V. Polyacanthus*, comparou-se o número de ramificações laterais presentes nos ramos galhados com o número produzido por ramos não-galhados em 130 plantas. Além disso, para analisar o efeito da galha na viabilidade das sementes, foram pesadas e colocadas para germinar 50 sementes de 45 plantas.

A arquitetura da planta hospedeira foi consideravelmente afetada pela formação e manutenção da galha.

Verificou-se um aumento do número de ramificações laterais produzidas pelos ramos frutificando, dando origem a um maior número de inflorescências.

Quanto às sementes, a consequência da ação da galha foi uma redução no peso e na porcentagem de germinação (figura 3), o que diminuiu a viabilidade das sementes, principalmente daquelas localizadas após a galha. Essa perda no potencial reprodutivo poderia ser atribuída a um redirecionamento para a galha de recursos necessários à reproducção da planta, tendo-se observado em plantas da região temperada.

Diversos autores têm estudado os impactos causados pelas galhas em suas plantas. Por exemplo, Sarchi e colaboradores, em 1988, demonstraram que galhas causadas por vetas em salgueiro reduzem significativamente a produção de sementes. Em um estudo mais recente, Fernandes e colaboradores também observaram uma redução na produção de sementes e frutos e um declínio na taxa de crescimento da plân- tula *Linaria lutea* (Nyctaginaceae) depois da acção.

As alterações causadas por galhas são fatores reveladores no crescimento e na história de vida da planta hospedeira. Uma evidência desse potencial é o uso de galhas no controle do crescimento populacional de ervas daninhas terrestres e aquáticas. Os insetos galhado- res são parasitas e, em geral, diminuem a performance de suas plantas hos- pedeiras.

---

<table>
<thead>
<tr>
<th>Ramo Galhado</th>
<th>Ramo Não-Galhado</th>
</tr>
</thead>
<tbody>
<tr>
<td>N° de ramificações</td>
<td>7.31 +/- 0.45</td>
</tr>
<tr>
<td>Peso das sementes</td>
<td>13.98 +/- 1.0</td>
</tr>
<tr>
<td>Taxa de germinação</td>
<td>26.4%</td>
</tr>
</tbody>
</table>

Figura 3. Comparação das médias obtidas para número de ramificações, peso de sementes e taxa de germinação de ramos galhados e não-galhados de *V. Polyacanthus*. 
As relações conflitantes entre plantas e insetos

SEXO, drogas e herbívoria

SEXO
A diversidade e a complexidade alcançada pelos seres vivos provavelmente não seria possível sem a reprodução sexual. Mas sexo e reprodução não devem ser confundidos nem tomados como sinônimos. A reprodução ocorre mesmo sem o sexo — uma bactéria, por exemplo, divide-se originando duas células-filhas idênticas à célula-mãe.

Na reprodução sexual, caracterizada pela troca de material genético, duas células — denominadas gametas — fundem-se para formar o novo organismo. Em seres eucariontes (cujas células têm núcleo diferenciado), a variação genética decorre da meiose, processo em que uma célula diploide, que tem o dobro de cromossomos de um gameta, divide-se em duas células haploides, cada uma com metade dos cromossomos da célula-mãe. Em geral, células resultantes da meiose são gametas (para a grande maioria dos animais ou esporos em vegetais).

Os cromossomos, na meiose, distribuem-se ao acaso entre as células-filhas. Um homem, por exemplo, tem 46 cromossomos (número haploide = 23), o que o torna capaz de produzir 2^23 tipos de espermatozoides, ou 8.388.608 combinações diferentes de cromossomos. O total de combinações pode até aumentar, com variações internas em cromossomos causadas por recombinações genéticas durante a meiose — ao se emparelharem, os cromossomos podem ligar-se em alguns pontos e trocar pedaços. A reprodução sexual é energeticamente mais onerosa do que a assenital, mas aumenta a variabilidade das células-filhas, essencial aos processos evolutivos, e reduz genes desvantajosos (dêtertios).

Plantas com flores (denominadas fértergas) reproduzem-se sexualmente, por gametas (fase gametofítica), e também assexuadamente, por esporos (fase esporofítica). Por causa dessa característica peculiar, a aplicação de termos com conotações sexuais a estruturas assexuais tem gerado grande confusão (ver 'Sexualidade das plantas', em Ciência Hoje nº 106, 1995).

Alguns biólogos questionam o uso de termos sexuais para expressar a condição esporofítica, como hermafrodita (para plantas que têm flores com pistilos e estames e produzem esporos masculinos e femininos) e também feminino e masculino respectivamente para plantas que têm, em indivíduos separados, flores com pistilos ou flores com estames, produzindo apenas gêneros (no primeiro caso) e andrósporos (no segundo).

Entretanto, inúmeros ecólogos e evolucionistas que trabalham com vegetais utilizam as expressões planta feminina e planta masculina. No artigo 'Sex determinação in flowering plants', de 1993, por exemplo, Stephen L. Dellaporta e Alejandro Calderón-Urra, da Universidade de Yale (Connecticut, EUA), apresentam as diferentes formas de expressão do sexo para flores individuais (figura 1), plantas individuais (figura 2) e populações de plantas (figura 3). Estes termos, mais próximos dos usados na literatura científica sobre interações entre insetos e plantas, são os empregados neste trabalho, embora os autores concordem com a necessidade da unificação da nomenclatura botânica sobre o assunto.

Plantas dioicas (do grego di, que significa dois), e ovais, que significa casa, caracterizam-se por apresentarem flores com pistilos (femininas) e com estames (masculinas) em indivíduos separados. O dioíctico, mais comum no grupo das zingiberáceas, ocorre mais em ecossistemas tropicais do que em temperados. Vários fatores têm influenciado a evolução do dioíctico, entre eles a dispersão de sementes, a polinização e a pressão exercida por herbívoros e pelo ambiente.

Em ambientes pobres em nutrientes, onde as plantas podem escoiá-los a moléculas energéticas e seus respectos?

Na reprodução, no crescimento ou na produção de compostos químicos para se defenderem? Na produção de insetos ou de outros inimigos naturais?

Estudos em áreas temperadas sugerem que plantas femininas, por serem mais longevas e frutíferas, têm melhor potencial para resistir a desastres e para competitividade em ecossistemas de sucesso rápido.

Sten et al. (1988) sugerem que plantas masculinas (estaminadas) e bem atacadas por insectos, enquanto plantas femininas (estéreis) que também atacam, produzem compostos mais comuns e são mais atacadas por insetos. Entretanto, pesquisas sobre determinado gênero vegetal, na Serra do Cipó, em Minas Gerais, revelam que este padrão de ataque não é inteiramente válido para áreas neotropicas.
Dias dois tipos defensas químicas

Quando os recursos são limitados, as plantas 'escolhem' onde investir energia e nutrientes: no crescimento ou em defesas químicas. Como a deficiência de nutrientes limita o crescimento (mais do que a fotossíntese), grande parte dos carboidratos produzidos com essa finalidade não é utilizada.

O excesso de carboidratos (formados por fotossíntese), hidrogênio e oxigênio favorece a síntese e 'escoamento' de compostos químicos, como polifenóis (figura 4) com base de carbono e contendo os dois elementos - substâncias de elevado peso molecular e, portanto, de ação química eficaz para a planta. Classificados como defensas químicas, compostos nitrogenados estão presentes em grandes concentrações e atuam como toxinas. Com seu efeito não é direcionado, a grau de defesa da planta está vinculado à concentração do composto em seu tecido.

O excesso de recursos, particularmente de nitrogênio, não empregado no crescimento também é transferido para a produção de compostos nitrogenados. Substâncias com bases de nitrogênio são, portanto, baixo peso molecular e, portanto, de ação química eficaz. Como seus efeitos parecem ser apenas genitoradis.


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### Tabela 1

<table>
<thead>
<tr>
<th>Espécie de Insetos</th>
<th>Altitude (m)</th>
<th>900</th>
<th>1.000</th>
<th>1.100</th>
<th>1.300</th>
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<tbody>
<tr>
<td>Curculionidae</td>
<td>(sp 1)</td>
<td>(F)</td>
<td>(F)</td>
<td>(F)</td>
<td>(M)</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>(sp 2)</td>
<td>(F)</td>
<td>(F)</td>
<td>(F)</td>
<td>(M)</td>
</tr>
<tr>
<td>Cecidomyiidae</td>
<td>(sp 3)</td>
<td>(F)</td>
<td>(F)</td>
<td>(F)</td>
<td>(F)</td>
</tr>
<tr>
<td>Curculionidae</td>
<td>(sp 4)</td>
<td>(M)</td>
<td>(F)</td>
<td>(F)</td>
<td>(F)</td>
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<tr>
<td>Cecidomyiidae</td>
<td>(sp 5)</td>
<td>(F)</td>
<td>(F)</td>
<td>(F)</td>
<td>(F)</td>
</tr>
<tr>
<td>Cecidomyiidae</td>
<td>(sp 6)</td>
<td>(F)</td>
<td>(F)</td>
<td>(M)</td>
<td>(F)</td>
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<tr>
<td>Total (todas)</td>
<td></td>
<td>(F)</td>
<td>(F)</td>
<td>(M)</td>
<td>(F)</td>
</tr>
</tbody>
</table>

Figura 8. Comparação entre taxa de ataques de insetos galladores em plantas masculinas (linha-d'água) e femininas (linhas-pontilhadas) de Bacterianon. Os sinais indicam se a diferença entre os sexos foi estatisticamente significativa (*), ou não significativa (**), e as letras indicam o sexo mais atraente (F ou M).
Galling insects on neotropical species of *Baccharis* (Asteraceae)


*Ecologia Evolutiva de Herbívoros Tropicais* [DBG, CP 486, ICB/Universidade Federal de Minas Gerais, 30161-970 Belo Horizonte, MG, Brazil]

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We report on the insect galls on neotropical species of *Baccharis* (Asteraceae) and describe new kinds of galls on *Baccharis* spp. of the cerrado and rupestrian fields of Brazil. Gall collections were made in several localities in Minas Gerais (Belo Horizonte, Caratinga; Lagoa Santa, Moeda, Ouro Preto, and Serra do Cipó). *Baccharis* may support the richest galling fauna of the neotropics (121 galling species on only 40 species of *Baccharis*). Nevertheless, gallers were not evenly distributed across host plant species. Four species of *Baccharis* alone supported 46% of the galling fauna. The most diverse fauna occurred on *B. dracunculifolia* (17 galls), *B. concinna* (12 galls), *B. siliquifolia* (13 galls) and *Baccharis* sp. 1 (11 galls). The most numerous galling taxa were, in decreasing order, Cecidomyiidae (Diptera), Lepidoptera (several Gelechiidae, Psylliidae (Hemiptera), and Tephritidae (Diptera). The most diverse gall communities were on *Baccharis* species that inhabit harsh environments, such as *B. concinna* in the rupestrian fields of Minas Gerais, *B. siliquifolia* in the dry chaco vegetation of Argentina, and *B. dracunculifolia* and *Baccharis* sp. 1 of the cerrado of Lagoa Santa in Minas Gerais.

**Key Words:** *Baccharis*, insect community, insect galls, neotropics, species richness

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**Introduction**

Gall-forming insects are very common in all biogeographical regions of the world, except the poles (see Mani 1964, Gagné 1989, Fernandes et al. 1994). They achieve the highest diversity in warm temperate ecosystems; i.e., between 25° and 40° north or south (Price et al. 1996). In the Neotropical region, they are most species-rich in
sp. 3 to B. mexicanus sp. 9 were sampled from Lagos Santa to Serra do Cipó (between 19°10' and 19°40'S, and 43°30' and 43°55'W). Gall collection methods are reported in Fernandes et al. (1998). Complementary bibliographical surveys utilized several checklists and lists of galls on neotropical species of *Baccharis* as sources of additional information. These are listed in the reference column of Table 1 and additional field site description can be found in these references.

Insect gall formation in *Baccharis* is influenced by host organ, volume, number of internal larval chambers, and epidermal cover (Mani 1964), and we utilized these variables to characterize them. Because of the many problems with the taxonomy of tropical insects, we identify most gallers only to family level. Whenever possible, we give the genus and species names. Insects are commonly being reared from galls and these will be identified to the species level in the near future. Some Baccharis were listed as sp. 1, sp. 2, etc. to sp. 9 due to taxonomical problems. The identification of *Baccharis* at the species level is generally complex due to the large number of species in the genus, approximately 500 (Boyle 1989). Ninety percent of these species occur in South America (Nixon 1990), and more than 120 species are known to occur in southeastern Brazil alone (Barbosa 1976). In addition, hybridization is common in the genus (e.g., Pain et al. 1992) making identification complicated. Nevertheless, all plants are being identified by specialists and will be reported in the near future as studies develop.

**RESULTS AND DISCUSSION**

*Baccharis* may have the richest galling fauna of the neotropics. One hundred and twenty-one species of galling insects were found on 40 species of *Baccharis* (Table 1). Gallers were not evenly distributed across host plant species. Four species of *Baccharis* (10% of the species studied) supported 46% of the galling insects (36 galling species) (Table 1). The host plants with the most diversity were *B. dracunculoides* (17 gall species), *B. concinna* (15 gall species), *B. salicifolia* (13 gall species) and *B. mexicanus* (11 gall species). We also found a galling induced by an unidentified species of fungus on *B. concinna*, while other authors reported unidentified insect galls on *B. nitida* and *B. poepigiana* (these galls were not used in the analysis). The diversity of galls on *Baccharis* sp. is certainly much higher than there are approximately 500 Baccharis species in the neotropics (Barbosa 1976, Hurlwitz 1990) and practically no comprehensive attempt has been made to survey their galling insects. The data we present beg the question of whether, despite having rich galling communities, gall abundance is equal across the species and the habitats occupied by them. Future studies will focus on comparisons of richness and abundance between *B. concinna* and *B. dracunculoides* in Brazil.

The most numerous galling taxa belonged to the ecidiopteryidae (*Diptera Cecidomyiidae*, Lepadotera (several Goechididae), Ptyllidae (Hoplotalpa), and Tephrithidae (Diptera) (Fig. 5). The common occurrence of ecidiopteryid galls on *Baccharis* has already been reported (Fernandes et al. 1994, Gaeta 1995).

This is the first time that broad patterns in gall distribution are examined within a single host plant taxon (genus) in the tropics (but see Docters van Leeuwen & Docters van Leeuwen 1956, Fernandes 1992b). Our findings add to and corroborate the latest findings on the ecology of galling insects (see Fernandes &

the rupiastrian fields and in the cerrado (savanna) vegetation of southeastern Brazil (Fernandes & Price 1988, 1993). The mechanisms that influence this global distribution of gall formation are still under investigation, but it appears that plant species and their related emergent properties have influenced the evolution of galling insects (see Fernandes & Price 1993, 1994, 1995). Other studies have addressed other hypotheses on the evolution of the galling habit (e.g., Connell 1983, Warner & Price 1990, Hartley & Lawton 1992, Blanchard 1993, see review by Price et al. 1987).

Studies on insect galls are now very common in ecology. Galls are often conspicuous and easy to find all year round, which limits methodological problems of seasonality and number rates characteristic of other insect herbivores (see Lara & Fernandes 1990b). The majority of galling insects are host-plant and plant-organ specific, and gall morphology is specific to each inducing species (Price et al. 1987) making identification a useful tool for the estimation of the patterns of abundance and richness (Fernandes & Price 1985, 1988, Fernandes et al. 1994). In addition, galls may be seen as extended phenotypes of their inducers (Dodd & Price 1989). Various ecological hypotheses have been generated from studies of gall communities on many temperate plants (e.g., Sexton spp. (Price & Robinson 1993), Quercus (Kearns 1987, Cornell 1983), Arctostaphylos (Hawkins 1984), Carya tomentosa (Fernandes 1992a), and Salsibury (Gaeta 1989). Tropical insect galling communities are, however, poorly known and mostly undescribed. We do not know of any community of tropical insect galls that has been studied in as much detail as the ones mentioned above.

Neotropical studies on galling insects have been primarily descriptive (e.g., Fernandes et al. 1985, 1988, 1994 and references therein), or centered on the natural history of single species (e.g., Fernandes et al. 1987, Fernandes et al. 1991). We believe that a better understanding of gall distribution, gall ecology, and insect plant relationships would be achieved if diverse tropical communities were studied in detail over the long-term to enable appropriate comparisons with corresponding temperate systems. For this reason we have chosen to study the highly diverse galling community on the neotropical species of *Baccharis* (see summary). In this study we present a list, partially extracted from the literature, of the insect galls on neotropical species of *Baccharis* and report for the first time new types of insect galls found on several species of *Baccharis* of the cerrado and rupiastrian fields of Brazil.

**MATERIALS AND METHODS**

This paper is a combination of data extracted from the literature and data obtained by us during a 4 year study. Insect galls on *B. concinna* Hurlwitz, *B. dracunculoides* D.C., and on *Baccharis* sp. 2 to sp. 9 were collected from 1990 to 1993 by our research group while performing several studies on these plants. On *B. concinna* and *B. dracunculoides* galls were counted on 100 plants twice a year from 1991 to 1993. The other species were surveyed once a year from 1990 to 1993. Surveys were performed in several localities, but primarily in the cerrado and rupiastrian fields of the State of Minas Gerais (Belo Horizonte, Lagoin Santa, Mocia, Ouro Preto, and Serra do Cipó), and in the Atlantic rain forest (Catinga) in southeastern Brazil. *Baccharis* sp. 2 was sampled in Belo Horizonte, while *Baccharis*
<table>
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<tr>
<th>Host plant</th>
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* Male flowers only, **both male and female flower, ' = Cecidomyiidae, ' = Psyllidae, ' = Tephritidae, ' = Gelseciidae*
Fig. 4. — Galling insects on Baccharis spp. (Baccharis sp. 3 to Baccharis sp. 8, and B. platypoda) from Serra do Cipó, Minas Gerais (see Table 1).

Fig. 5. — Proportion of galling insect taxa on neotropical species of Baccharis (Asteraceae).

Price 1988, 1991; Fernandes et al. 1994) and add to them. A few important observations are of central interest: first, the most diverse gall communities were on Baccharis species that inhabit harsh environments, such as B. concinna in the rupestrian, high altitudinal fields of Minas Gerais, Brazil, B. salicifolia in the dry and low-nutrient chaco vegetation of Argentina (see Hueck 1972), and B. dracunculifolia and Baccharis sp. 1 of the dry and low nutrient cerrado of Lagoa Santa in Minas Gerais. Although many galling species on B. dracunculifolia were found in Argentina and Chile, all of them were also found in the dry cerrado vegetation of Minas Gerais. In these localities, habitat harshness may be produced primarily by nutrient stress as rainfall is generally high (see Hariadasan 1982). This pattern fits the harsh environment hypothesis on gall diversity as proposed by Fernandes & Price (1988, 1991) and Price et al. (1996). Second, host plant area (distribution over space) may not affect gall diversity as approximately equal numbers of galls may be found on widely distributed as well as restricted host species. This is in agreement with the findings of Fernandes & Price (1988) for temperate species. Nevertheless, more detailed studies should be performed to confirm this finding.

Descriptive knowledge of the diverse community of galling insects on Baccharis spp. is important and is the first step for the development of detailed studies. Baccharis spp. are distributed in tropical and temperate regions of the New World, and thus are appropriate for broad comparisons on the evolutionary ecology of galling insects. The evolutionary questions we are interested in were only briefly mentioned here. Future studies will focus on the diversity patterns and mechanisms that influence gall diversity on species of Baccharis of the cerrado and rupestrian fields of Brazil.
ACKNOWLEDGMENTS

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REFERENCES


Distinguishing intrapopulational categories of plants by their insect faunas: galls on rabbitbrush

Abstract

Within a population of rabbitbrush, <i>Crotalaria nematica</i>, the subspecies <i>C. n. contorta</i> and <i>C. n. hioicola</i>, and a third unidentified group were better segregated by their insect galls, than by differences in plant morphology. This level of segregation was further increased when morphological measurements and counts of insect galls were analyzed simultaneously. We interpret this result to mean that plant morphology and insect distributions reflect two different, perhaps overlapping, portions of the host's genome. By using both sets of characters concurrently, rather than either set independently, we increased the portion of the plant's genome being sampled and increased the probability of detecting differences among host genotypes. Hence, knowledge of the distributions of insect galls may be useful for augmenting the level of separation, obtained by morphological measurements, among intrapopulational categories of plant genotypes. This application may be of greatest benefit when hybridization blurs morphological distinctions among plant taxa, when morphological traits are highly variable within genotypes, or when ephemeral morphological traits (e.g., leaves, flowers) are not available for measurements.

Key words: Plant systematics - Discriminant function analyses - Taxonomy - Arizona

Introduction

Reliance solely on morphological traits limits the ability of researchers to segregate plant taxa in the field. This occurs frequently when hybridization blurs the morphological distinctions between plant species (Alston and Turner 1962, DePamphilis and Wyatt 1989; Kier et al. 1991), when traits are highly variable within plant genotypes (e.g., leafy spurge, <i>Euphorbia</i> spp., Harvey et al. 1988), or when distinguishing characters are ephemeral. Floral characters used to distinguish plant species may be present for only a brief period, and a lack of leaf and floral characters may make field identifications of plants during winter months virtually impossible.

The galls of phytophagous arthropods also are "traits" associated with plants and may be useful for separating plant taxa. Gall-formers are typically "host, organ and tissue specific" (Shorthouse 1982) and have an intimate relationship with their host plant that enables them to induce a proliferation of plant cells (the gall) in a pattern characteristic of the galling species. Because of this relationship, gall-formers are sensitive to small differences in host genotype and may discriminate among plants within populations of the host plant species (e.g., Askew 1962; Fritz and Price 1988; Schowalter and Haverty 1989; Akimoto 1990).

Recently, the distributions of galling insects and mites have been shown to separate partially or almost completely hybrid from parental categories of plants in overlap/hybrid zones of oak (<i>Quercus</i>, Aguilar and Bueckl 1992), willow (<i>Salix</i>, Fritz et al. 1994), and cottonwood (<i>Populus</i>, Floate and Whitham 1995). Hence, the distributions of gall-forming insects may serve to distinguish intrapopulational categories of plant genotypes, regardless of whether these categories correspond to subspecies or are categories without formal taxonomic status (e.g., categories of hybrid plants).
To test the hypothesis that galls can be used to segregate categories of plants within a plant population, we study the distribution of galls in a genetically diverse population of rubber rabbitbrush, *Chrysothamnus nauseosus* (Pall.) Britton. Insect distributions have been previously suggested as a method for clarifying the systematics of *Eucryphia* (Pryor 197b), and have seen limited application in separating rabbitbrush subgenera (Leitner 1985). A greater level of discrimination was achieved by Floate and Whitham (1995), who reported a 98% level of concordance for categories of Fremont cottonwood, *F. thyrsoides*, and complex backcross hybrids (*Populus fremontii × Populus angustifolia*), separated by either their leaf morphologies or by their associated insects and miles. The current study expands upon the findings of McArthur et al. (1979) and tests the generality of those of Floate and Whitham (1995) by examining a different family of plants, i.e., *rabbitbrush* (*Asteraceae*) vs cottonwood (*Salicaceae*).

We also test the novel hypothesis that plant categories may be best distinguished by joint examination of both their morphological traits and their associated insects, rather than by independent examination of these two character sets. Differences in plant morphology reflect differences within a subset of a plant's genome and may affect insect distribution (see examples in Floate and DeClerck-Floate 1993). However, insects also may respond to differences in anatomical, phenological and chemical traits among others, which correspond to additional subsets of the plant's genome. Thus, insect distributions reflect differences in subsets of the plant's genome that may or may not overlap with the subset affecting only plant morphology. By considering both sets of characters simultaneously, we postulate that differences in a greater portion of the plant's genome will be detected, allowing better segregation of host categories.

**Materials and methods**

**Study system**

Rubber rabbitbrush (*C. nauseosum*) is a common and morphologically diverse shrub that grows throughout the southwestern United States and northern Mexico. It is characterized by erect, slender, flexible branches covered with a dense mat of gray-green or white trichomes. Leaves are very narrow and yellow flowers are formed in dense clusters at the ends of stems in late summer. Currently, 32 subspecies of *C. nauseosum* are recognized (Andersson 1986), but intergradation of morphological traits, occasional hybridization, and intraspecific population differences can greatly complicate their identifications (Anderson 1996, 1997; Hanks et al. 1995; Hedges et al. 1987; McArthur et al. 1987).


**Table 1: Descriptions of galls on rabbitbrush (Chrysothamnus nauseosum) surveyed in present study**

<table>
<thead>
<tr>
<th>Gall species</th>
<th>Gall no.</th>
<th>Organ galled</th>
<th>Illustration in Fig. 1</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Diplocaulus</em></td>
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<tr>
<td><em>Rhaphidophora</em></td>
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<tr>
<td><em>Leptopoeta</em></td>
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<td><em>Acitrus</em></td>
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<tr>
<td><em>Acontia</em></td>
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<tr>
<td><em>Fusiophora</em></td>
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</tr>
<tr>
<td><em>Asteraceae</em></td>
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<tr>
<td><em>Sporophila</em></td>
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<tr>
<td><em>Leptopoeta</em></td>
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</tbody>
</table>
### Table 3: Univariate statistics on plant morphological traits. Values are means ± SE. The different letters following the mean indicate significant differences (P < 0.05) for within-row values (Tukey-HSD post-hoc test). Critical P-values have been adjusted using sequential Bonferroni using pairwise to the dependence of some traits.

<table>
<thead>
<tr>
<th>Morphological trait</th>
<th>C. mezzalupi sp. compositum (n = 25)</th>
<th>C. mezzalupi sp. holodonum (n = 25)</th>
<th>C. mezzalupi Group 3 (n = 25)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height (cm)</td>
<td>71.00 ± 3.44a</td>
<td>74.52 ± 3.43b</td>
<td>63.56 ± 3.11a</td>
</tr>
<tr>
<td>Plant length (cm)</td>
<td>114.40 ± 6.70a</td>
<td>112.28 ± 5.97a</td>
<td>98.85 ± 6.92a</td>
</tr>
<tr>
<td>Plant width (cm)</td>
<td>90.20 ± 6.92a</td>
<td>76.91 ± 5.21a</td>
<td>75.92 ± 6.56a</td>
</tr>
<tr>
<td>Stem length (cm)</td>
<td>12.81 ± 0.67a</td>
<td>16.33 ± 1.09a</td>
<td>10.05 ± 0.70a</td>
</tr>
<tr>
<td>Stem diameter (mm)</td>
<td>0.44 ± 0.04a</td>
<td>0.88 ± 0.06b</td>
<td>1.82 ± 0.07a</td>
</tr>
<tr>
<td>Leaf length (mm)</td>
<td>10.89 ± 0.68a</td>
<td>36.87 ± 3.43b</td>
<td>25.10 ± 2.18a</td>
</tr>
<tr>
<td>Leaf width (mm)</td>
<td>0.21 ± 0.15a</td>
<td>0.71 ± 0.43a</td>
<td>1.03 ± 0.86a</td>
</tr>
<tr>
<td>No. flowers/stem</td>
<td>11.82 ± 1.10a</td>
<td>20.29 ± 2.68a</td>
<td>12.97 ± 3.62a</td>
</tr>
<tr>
<td>No. fruits/stem</td>
<td>11.82 ± 1.10a</td>
<td>1.04 ± 0.73a</td>
<td>7.27 ± 1.17c</td>
</tr>
</tbody>
</table>

### Results

#### Segregation by plant morphology

Univariate analyses of morphological traits are summarized in Table 2. Plant width and length were the only two characters that did not differ significantly across plant categories. Hence, they were excluded from subsequent multivariate analyses.

The three plant categories differed significantly in their overall morphologies (MANOVA, Wilks’ Lambda = 0.012, F-statistic = 10.886, df = 0.001), which separated them in ordination space (Fig. 2a). There was no overlap of C. n. sp. holodonum and C. n. compositum along the discriminant function (DF) axis 1, and group 3 attained partial separation from these sub-species along DF axes 1 and 2. DF 1 explained 91% of the variation among plants, and primarily reflected differences in leaf length, the number of fruits per stem, and leaf width. DF 2 described 6% of the remaining variation among plants, which primarily reflected differences in stem length, leaf length, and the number of flowers per stem. Axes described significant differences among categories (DF 1, χ² statistic = 156.55, df = 0.001; DF 2, χ² statistic = 33.21, df = 0.001). Canonical coefficients, indicating the relative importance of leaf parameters in defining DF 1, 2, are listed in Table 3. Predicted group memberships based on morphological traits differed from our a priori classifications using plant color and architecture for 6 of the 75 study plants. Two plants of sp. C. n. compositum were identified as members of group 3. For group 3, one plant was identified as sp. C. n. holodonum and three other plants were identified as C. n. sp. compositum.

#### Segregation by gall assemblages

The three plant categories had similar numbers of galling species (11–12 species per category), but different species compositions (Table 4). For example,
Segregation of plant categories by their insect faunas

Our results expand upon previous reports of insect faunas associated with specific plant categories. Earlier studies found the distributions of three gall-forming species to be useful in distinguishing subspecies of raspberry bush, particularly during winter months when leaf and floral characters normally used for this purpose were absent (McArthur et al. 1979; McArthur 1986). We increased the rigor of this galling bioassay by considering the relative abundances of all galling insects as useful indicators of our subspecies, rather than the presence or absence of a few select species. For example, if we had restricted our attention to galls occurring on only one host category, we would have overlooked the distribution of this galling species, which provided the greatest separation of the three categories of raspberry brush along DF axis 2 (Fig. 2b, Table 3).

In a larger context, our study illustrates the value of insect galls to distinguish intrapopulational categories of plants, which may provide insights into the genetic structure of plant populations. We obtained a level of separation among two subspecies of C. nanus and C. n. subsp. tessulata, that was previously identified using linear measurements (Fig. 2b) that exceeded the level obtained using morphological measurements (Fig. 2a). Our results are not unique. Fritz et al. (1994) used genetic analyses to identify a group of individuals at a common area on the prairie, Salix eriocephala, or their hybrids. Segregation by stipule and leaf hair measurements produced considerable overlap between hybrids and S. eriocephala, but the distributions of phytoseiid mites that we determined were separated the third groups. Similarly, Flosate and Whitham (1995) achieved a high level of segregation among hybrid and parental cottonwoods (Populus deltoides and P. trichocarpa), but their distributions reflect two different, perhaps overlapping, populations of the host's genome. Because insects are affected by plant traits in addition to morphology (e.g., chemistry, anatomy, and phenology), the analysis of leaf and stipule characters may reflect differences in subsets of the host's genome in addition to the subset affecting plant morphology. By using both character sets concurrently, in effect, we strengthen the available data and, therefore, increased the probability of detecting differences among host genotypes.

Considerations

Because galls, e.g., are among the most specialized of phytophagous insects, we expect that their distributions will be the most valuable in discriminating among plant categories. Generalist species do not have the same intimacy with galling insects as the more specialized species, and are less likely to respond to relatively small differences in host genotype. This prediction is supported by distributions of insects in plant hybrid zones. In a zone of hybridizing ecotypes (C. nanus var. tenuis × Eucalyptus rigidula), generalist insects were more likely to occur on hybrid trees than were specialist insects, and tended to be equally distributed among the parental categories. In contrast, specialists were less likely to occur on hybrid trees, and were concentrated on the hybrid category that most closely resembled their host species (Whitham et al. 1994; also see Morrow et al. 1994). Similarly, gall-formers were of greater value in segregating hybrid and parental categories of cottonwood than were free-feeding species (Flosate and Whitham 1995).

As is true for other methods, the availability of galls (i.e., characters) will limit their use in discriminating among plant categories. Taxonomists do not rely on morphological traits to segregate closely related plant categories, and accurate DNA analyses may require the use of more than 20 genetic loci (see Flosate et al. 1994). It is important to note that galls are a type of gall-forming insects that can be used accurately to separate genetically similar host categories. Hence, the galla bioassay will be more useful for perennial woody species with numerous galling species than for annual species, which typically have a shorter gall fauna. We note that many plant species with abundant and diverse gall faunas hybridize with their congeners (e.g., Bauharia, Eucalyptus, Macquaria, Populus, Quercus, Rosa, Salix). Because hybridization blurs the morphological distinctions between parental species, the use of galls as distinguishing features may be particularly valuable in segregating categories of hybrid and parental plants.

Greater discrimination of plant categories is evident in our results than in galls by examining the distributions of individual galling species, rather than the distributions of guilds or taxa containing several species. Each gall species represents a single character and does not convey information that will typically increase with the number of characters used. Unless all gall species have exactly the same pattern of distribution among host categories, combining galls into larger groups will reduce separation of host categories. For example, the distributions of five ecologically and taxonomically similar species of leaf-falling aphids segregate parental and hybrid types in cottonwood. However, the same information is lost when these species are pooled into a guild of leaf-falling aphids (Flosate and Whitham 1995; also see Morrow et al. 1994).

Molecular versus morphological methods

Why should researchers use either morphological traits or insect distributions for segregating plant categories when more precise methods are available? Genetic analyses examine DNA directly to detect differences among plant genotypes. This not only largely eliminates nonheritable variation as a factor confounding analysis, but it permits a larger number of traits to be used, limited only by the number of nucleotides in the organism's DNA (e.g., 5 x 10^9 for 4 x 10^11, Hillis 1987). In contrast, relatively few morphological traits and insect distributions can be used, and environmental factors are indicators of plant genotype, which is affected by environmental factors.

The extent of variation is broadened by Hillis (1987) and Patterson et al. (1993) in their reviews on the merits of molecular versus morphological methods in systematics. Both reviews conclude that each method has its distinct advantages and disadvantages, and that results in conjunction with another alone. However, the cost of genetic analyses is a major obstacle to the use of molecular studies in systematics, e.g., to establish
maintain molecular laboratories may require tens of thousands to hundreds of thousands of dollars (US Hults 1987). Further, molecular methods typically support the findings of previous morphological studies, such that “molecular sequences have contributed most significantly in areas where morphological data are inconclusive, deficient, nonexistent, or poorly analyzed” (Patterson et al. 1993). We have shown that insect gall can be used to augment the segregation of plant categories achieved by morphological studies. In this regard, the gall biology described here may be best suited to find fields where molecular methods of discriminating among plant categories are unnecessary or impractical. Ultimately, it is the researcher who determines which of the available methods for segregating plant categories are best suited to their particular study. Our objective has been met if the current study increases the reader’s awareness of insect galls as tools to provide insights into the genetic structure of plant populations.

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References


The highest diversity of galling insects: Serra do Cipó, Brazil

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Abstract. During the past decade many studies have been carried out on the distribution of gall- forming insects along gradients of temperature, humidity, elevation, and latitude. Over 300 localities have already been sampled around the world representing numerous vegetation types such as shrubland, desert, chaparral, cerrado, savanna, tropical rainforest, taiga, tundra, and pine forest using sound and field-tested methods. The peak of species richness has been found at low and dry elevations, in areas of sclerophyllous vegetation. Nevertheless, gallers are most species rich and abundant in dry habitats. Among all habitats studied, the Brazilian cerrado has the richest fauna of galling insects. At 900 m altitude in a cerrado area at the base of the Serra do Cipó in south-east Brazil, we found the richest galling insect fauna (forty-six species in a census of forty-five trees, 100 shrubs and 1000 herbs per site). At this elevation, the soil is rocky and sandy, nutrient-poor, and the vegetation is dominated by woody, sclerophyllous plants, with few herbs. The plant most attacked was Baccharis concinna (Asteraceae) which supported fifteen galling species.

Key words. Biogeography, cerrado, diversity, insect galls, richness, savanna, Serra do Cipó.

INTRODUCTION

The question “how many species are there?” is central to evolutionary ecology and conservation biology. This question has engaged for more than 160 years, since it was first raised by Westwood (1833). Estimates of species diversity have been made for many plant and animal taxa, but detailed and long-term studies have been carried out for only a few groups. Perhaps the major problem being faced is the variation in sampling procedures which can impair comparisons across taxa and biogeographical regions. Hence, instead of describing absolute numbers of species, it is necessary to develop sound and replicable sampling techniques so that numbers can be compared with confidence across habitats and microhabitats (Erwin, 1991). Data...
must also be obtained directly from the field in a context in which the same question can be asked repeatedly, and enabling as much global evaluations (Fernandes & Price, 1998; Erwin, 1991). Some guilds of gallformers have been sampled in this way (see Erwin 1963, 1988), although to obtain more accurate estimates of biodiversity on earth, these studies need to be extended to a greater number of insect groups.

During the last 10 years, numerous studies have been conducted to examine the patterns of gall-forming insect diversity in several biomes. Samples have been concentrated in Australia, Brazil, Canada, Costa Rica, England, Fiji, Finland, Israel, Japan, Mexico, Panama, Russia, South Africa, and the United States. More than 300 localities have been sampled representing a variety of vegetation types including shrubland, desert, chaparral, cerrado, rupestrum field, African savanna, tropical rainforest, mangrove, and pine forest (Price et al., 1996). Hence, galling diversity can be compared in numerous latitudes (from 90° to 60°N and 45°S), and elevations from 0 m at sea level to 4000 m.

Because of the peculiar way of living most of the life time immersed in the issues of the galls, it is difficult to evaluate the numbers of adult life forms of gall-forming insects. In addition, many insect gallers live only few days (see Matti, 1964) and it is difficult to classify the species if host plant records are not available. Such a situation has been documented in the family Cecidomyiidae (Diptera), the most common galling taxa (Gagné, 1989, 1994). Thus, counts of gall-forming insects are difficult to obtain by using conventional sampling techniques (light traps, fogging).

Here we report on ground and field tested methods of galling insect diversity surveys two methods were used. In method 1, transects 10 m wide were staked out at each sample site, and subsequently searched for galls above ground until forty-five trees. 101 shrubs and 1000 herbs had been sampled. These numbers were defined through the species-area curves described in Fernandes & Price (1998) to obtain an asymptotic accumulation of galling species. The difference in the numbers of samples of tree, shrub and herbs is an attempt to minimize the influence of the structural complexity of plants on the richness of insect communities (see Strong, Lawton, & Southwood, 1984).

Sampling method 2 consisted of a one-hour census, walking through an area and examining plants carefully, searching for galls. In both methods, galling insects and their host plants were recorded as morphospecies (Price 1991). A detailed description and comparison of these methods can be found in Price et al., (1996). The Brazilian cerrado has found to have the richest fauna of galling insects based upon the survey method 1.

THE RICHEST HABITAT

The cerrado comprises an area of 1.8 million km² and is highly variable in its plant composition and structure (Eiten, 1978). Cerrado is a complex woodland and grassland vegetation province in central Brazil that presents a xeromorphic aspect with Vochysiaceae, Annonaceae, Myrtaceae, Asteraceae, and Leguminosae being the most representative plant families (Giglietti & Pitard, 1988; Oliveira-Filho & Ratter, 1993). This region has a mean annual rainfall of 1500 mm, and the cerrado occurs on infertile and deep soils called latosols (Harr, 1972). Patches of richer soils are covered by mesophytic forests, and rivers and streams are bordered by gallery forest. The cerrado vegetation sampled along the Espinhaço mountains in Minas Gerais State were in the localities Lagoa Santa, Serra do Cipó, Caracá, Cristalina, Grão Mogol, Belo, Minas Novas, and Turmalina, along an altitudinal gradient ranging from 800 m (in Lagoa Santa) to 1700 m (in Serra do Cipó).

We sampled insect galls on all major cerrado habitat types: campo limpo, campos sujo, cerradão (stricto sensu), cerrado, rupestrum field, 'buriti forest', and gallery forest.

In the Espinhaço mountains the vegetation is dominated by cerrado and high altitude rupestrum fields. The sclerophyllous vegetation in lithostels in the mountains are called rupestrum fields (rocky fields). In the Serra do Cipó, the high altitude rupestrum fields occur from 900 m (intermixed with cerrado until 1100 m) to the mountain top at approximately 1700 m altitude. The flora is largely endemic and highly diverse (Giglietti, 1996). The woody plants of rupestrum fields may form groves of open or even closed scrub over undergapping hard bedrock (Eiten, 1978; Goulding & Fern, 1979). To enable a broader view on galling distribution and richness, other Brazilian forest formations were also sampled during the study: Atlantic forest, Amazonian rain forest, estuaries (floury and scrubby vegetation), campina vegetation, along the Rio Negro, and coastal dune vegetation locally called restinga.

At an altitude of 900 m in a cerrado area at the base...
of the Serra do Cipó we found the richest galling insect fauna (forty-six species using method 1). At this elevation, the soil is rocky and sandy, and the vegetation is dominated by woody, sclerophyllous plants, with a few herbs. The richness of galling insects in communities with these characteristics is known to be very high (Price, 1991; Lara & Fernandes, 1996). The plant most attacked, Banisteria caapi (Asteraceae), supported fifteen galling species. To our knowledge, this plant supports the richest insect galling community in the Neotropics (Fernandes et al., 1996b).

Gallers are the most common, and perhaps most important herbivores in this vegetation type. The influence of gallers on the population dynamics of their host plants and habitat dynamics is under investigation, but we feel that gallers could drive many important processes in this type of ecosystem. For instance, the field woodpecker, Colaptes campestris, was frequently seen to feed on the woody galls caused by the weevil Collabriae cithoide (Cololoeoptera, Curculionidae) on Solanum luteovatum (Solanaceae). After the emergence of the galling insect, galls are often occupied by other species such as ants, spiders, termites, and even small frogs (Marc, 1984). The latter of many galls are often used by cerrado birds to construct their nests (e.g. the hummingbird Epistomus plumifrons). Gallers were also noted to be the most common herbivores in a similar habitat, the campina vegetation along Rio Negro, Amazonia (D. H. Janzen, pers. comm.; Fernandes & Price, 1991). Although not described, more than 99% of the cerrado galling species were new to science, and of these a large proportion were endemic to this vegetation type (J. W. Fernandes, unpubl. data).

In addition to the description of the distribution patterns, we found some interesting characteristics of this insect guild. Comparisons of galling richness along altitudinal and latitudinal gradients have shown that the peak of species occurs at low and dry elevations, mainly between 25 to 30° N or S, in areas covered by sclerophyllous vegetation (Price, 1991; Price et al., 1994). Comparisons between dry and humid habitats also showed that gallers were most species-rich and abundant in dry habitats (Fernandes & Price, 1988, 1991; Fernandes & Lara, 1993; Fernandes, Paula & Loyola, 1995; Fernandes et al., 1996a; Lara & Fernandes, 1996b).

Despite its importance, representing 22% of Brazilian vegetation (Hoch, 1972), the cerrado ecosystem has been severely endangered for the expansion of agriculture, eucalyptus plantation, and the production of charcoal. The cerrado ecosystem is of enormous interest to ecologists because of the richness and high endemicity of the plants and animal species (Vanzolini & Hoyer, 1987). Within the cerrado domain, the high altitude savannas fields are unique in their degree of endemism (see Giupellet, 1996).

Despite sampling in the most diverse high altitude savannas fields, and covering the major cerrado formations, the area covered by the census is small compared to the area of the cerrado in Brazil. Nonetheless, the primary goal of this study will have been met if students pursue and broaden our knowledge on the richness of gallers and generate questions which attempt to unravel the ecological mechanisms and biogeographical relationships involving gallers, host plants and habitats.

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tropical and temperate galling species reflect the roles of environmental harshness and plant nutrient status.


Parasitic Relationships between a Gall-forming Insect *Tomoplagia rudolphii* (Diptera: Tephritidae) and its Host Plant (*Vernonia polyanthes*, Asteraceae)

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We studied the impact caused by *Tomoplagia rudolphii* Lutz & Costa Lima (Diptera, Tephritidae) on the architecture, flower production, seed germination and seed viability of its host plant *Vernonia polyanthes* Less (Asteraceae). We measured the gall influence on the number of lateral shoots, on the production of flower heads and on seed viability. Gall formation induced a significant increase in the number of lateral shoots modifying the host plant normal growth pattern. Galled stems produced an average of 7.3 ± 0.45 shoots, whereas un-galled stems produced 3.6 ± 0.69 shoots. Gall formation also caused a significant reduction in seed viability. Seeds of galled stems had a total percent seed germination mean of 25.4%, while seeds of un-galled stems had a mean of 33.8%. However, flower head production and seed germination velocity were not affected by the gall. This study showed that *T. rudolphii* galls influence the architecture and seed viability of its host plant.

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Key words: Insect galls, herbivory, herbivore impact, plant growth, *Tomoplagia rudolphii*, *Vernonia polyanthes*

INTRODUCTION

Consequences of the interactions between herbivores and plants are often contradictory. Herbivore impact upon plants may be harmful (Belsky, 1986, 1987) or positive (e.g. Hendrix, 1979; Whitham et al., 1991). Some species may present an assemblage of compensatory responses, which range from negative to positive, depending on both plant and abiotic variables. The increase in growth rate, total biomass, and seed production occasionally found in damaged plants has been argued to be an evolved response to herbivory (e.g. Paige and Whitham, 1987). However, this plant response would probably be more related to a strategy to diminish the impact to injury than a strategy to improve fitness and/or productivity after herbivory (Belsky et al., 1993).

Insect galls develop in the host plant meristematic tissues, where the gall-forming insect modify the tissue growth processes, transforming the attacked cells into gall structure (Rohrfrisch and Shorhouse, 1982). Most galls affect the plants only locally, but in some instances they may have systemic effects (Mani, 1984; Fernandes, 1987; Larson and Whitham, 1991; Fernandes, Souza and Sacchi, 1993). Gall formation on apical meristems may lead to the activation of dormant meristems, resulting in the development of lateral ramifications affecting secondary flower and fruit production (Mani, 1964; Craig, Price and Imai, 1986). In some cases stem galls may significantly reduce seed production (Denill, 1985; Sacchi et al., 1988; Fernandes et al., 1993).

Preliminary observations of galls induced by *Tomoplagia rudolphii* Lutz and Costa Lima (Diptera: Tephritidae) on *Vernonia polyanthes* Less (Asteraceae) indicated that galls may disrupt normal host plant development. Andrade et al. (1995) suggested that branching in galled stems is due to the break down of apical meristems, probably caused by inhibition of apical hormone transfer. This phenomenon causes an increased number of flowers and fruits, resulting in an increase on the reproductive performance of the host plant. Nevertheless, gall growth and maintenance drain host plant resources (Harnett and Abrahamson, 1979; Fernandes and Ribeiro, 1988; Fernandes et al., 1993). Therefore, gall formation could result in the reduction on flower head production and/or decrease seed viability. In this study we describe in detail the gall influence on plant architecture and flower head production. We also investigate whether viability and germination velocity of the seeds produced are influenced by the gall.

MATERIALS AND METHODS

Study system

*Vernonia polyanthes* is a woody weed species of cultivated and disturbed areas (Lențo-Filho, Aranha and Bacchi, 1972). The tephritid, *T. rudolphii*, oviposits during July-August in shoot apical meristems. Later, eggs hatch and the larvae feed on cells of the medullar parenchyma. As the larvae develop, gall tissue proliferates surrounding the larva, resulting in a globulous gall (Fig. 1). Later during gall development, larvae excavate a hole through which the adult leave the gall. Larvae then pupate and adults emerge 15 to 20 d later to begin a new reproductive cycle (Andrade et al., 1995).
et al., 1995, see also Alvarenga, 1959). The life cycle lasts 45 to 60 d. The galls are rare with low abundance per plant (Fernandes, Neto and Martins, 1988). Greatest gall abundance occurs between Sep. and Dec., being scarce in the other months.

Study area

Galls were collected at the Campus of the Universidade Federal de Minas Gerais, Belo Horizonte (MG) and Lagoa Santa, in southeastern Brazil during two consecutive flowering periods of *V. polyanthes* (1991 and 1992). The campus area has a heterogeneous vegetation with native, introduced, ornamental, and fruitiferous plants, and is at 800 m above sea level. The native vegetation is much modified by human disturbances (Fernandes, Neto and Martins, 1988). Lagoa Santa is located 42 km away from Belo Horizonte at an altitude of 835 m. Samples were taken in pasture areas around Lagoa Santa. The natural floristic composition of Lagoa Santa has also been changed by human activities (see Warming, 1908). These conditions are ideal for the development of *V. polyanthes* (Leitão-Filho et al., 1972).

Impact on plant architecture

We measured gall influence on the external morphology of 129 plants of *V. polyanthes*. The number of lateral shoots were counted on galled stems and on the nearest ungalled stems (see Craig et al., 1986; Fernandes and Ribeiro, 1990) (Fig. 1). As the data were not normally distributed, the Wilcoxon sign-rank tests for the comparisons on the effect of galling on galled and ungalled stems (Zar, 1984) were used. All statistical means are followed by their respective standard errors (± 1 s.e.).

Impact on flower production

We verified the influence of galls on the flower head production of 45 plants. All inflorescences of galled stems and nearest ungalled stems were collected and counted. We used Wilcoxon sign-rank tests to test for differences in
flower production because the data were not normally distributed (Zar, 1984).

**Impact on seed viability and germination time**

The influence of gall formation on seed viability was measured on flower heads produced on galled and on nearest neighbour ungalled stems. Fifty seeds were randomly selected from each stem, weighed and then placed in Petri dishes with filter paper for germination. Seeds were maintained in an incubator at mean temperature of 27 ± 1°C. Seeds that produced primary roots (2 mm long) were considered viable (Metcalf, 1986). Again, we used the Wilcoxon sign-rank tests to test for differences in seed weight (Zar, 1984).

The germination of each seed group was monitored daily for 18 d on 19 plants. This is the time period after which the seeds were no longer viable. For statistical analysis, the data were percentage transformed arcsine and then compared by the Wilcoxon sign-rank tests. Moreover, the maximum germination rate (Gmax) was calculated by the ratio between the highest value of daily germination to total number of germinated seeds. This rate describes the maximum proportion of seeds that germinate on a single day (Sheffy and Parent, 1991). The average germination time (t) was evaluated as (see Laboriau, 1983).

\[ t = \frac{\sum n_i t_i}{\sum n_i} \]

where, \( n_i \) is number of seeds that germinate in \( t_i \) time.

**RESULTS**

Lateral shoot production was significantly increased by gall formation (Wilcoxon = 4.937, \( n = 129 \), \( P < 0.001 \)). Galled stems produced an average of 7.3 ± 0.45 shoots, whereas ungalled stems produced 5.6 ± 0.40 shoots.

The number of flower heads produced by galled stems showed no difference to ungalled stems (Wilcoxon = 0.937, \( n = 45 \), \( P > 0.05 \)). Galled stems produced 295.3 ± 76.1 flower heads, whereas ungalled stems produced 303.5 ± 70.4 flower heads. Therefore, even though galled stems had more lateral shoots, a concomitant increase in flower head production was not observed.

Seeds on galled stems weighed less compared to seeds on ungalled stems (Wilcoxon = 3.370, \( n = 45 \), \( P < 0.001 \)). Seeds on galled stems weighed 14.0 ± 1.0 mg, whereas seeds on ungalled stems weighed 15.5 ± 1.1 mg. The total percent seed germination (G%) on galled stems was also statistically smaller than the G% of seeds on ungalled stems (Wilcoxon = 2.906, \( n = 45 \), \( P < 0.05 \)). Seeds of galled stems had a G% mean of 28.4%, while seeds of ungalled stems had a G% mean of 33.8%.

There was no difference between the average germination time (t) and the maximum germination ratio (Gmax) of seeds on galled and ungalled stems (\( P > 0.05 \)). Viable seeds germinated within approximately 7 d with most of the germination occurring between the second and third days of incubation.

**DISCUSSION**

The galls of *T. rudolphii* caused significant alterations in the architecture and performance of *V. polyanthus*. Galled stems produced more lateral shoots than ungalled stems. Gall-forming insects are known to break apical dominance and are thus responsible for an intensive lateral ramification (Fernandes and Ribeiro, 1990; Whitham et al., 1991; Fernandes et al., 1993). Several studies suggest that after an attack by herbivores, plants can exhibit an under-, non- or over-compensation pattern of growth (Belsky, 1986, 1987; Whitham et al., 1991; Ritenour and Rittenhouse, 1993). The increase in shoot production may be a response to the gall establishment (Crang et al., 1986; Sacchi et al., 1988; Maschinski and Whitham, 1989), or a generalized tolerance strategy against any kind of natural damage (Fernandes and Ribeiro, 1990; Belsky et al., 1983). Almost all cases of over-compensation result in an increase in the number of modular units after apical bud damage by herbivory. In *Jurinea mollis* (Asteraceae), removing the apical bud caused an increase in the number of modules per plant, and consequently an increase in the number of ovules per modules (Whitham et al., 1991). However, the modules produced distally to the galls on galled stems of *V. polyanthus* produced fewer flower heads than on ungalled stems. Such reduction can be due to the limited resource supply available for reproduction and allocation among more shoots.

The negative impact of gall formation on plant performance was evident on the weight and total percentage germination of seeds. This loss in reproductive potential may be caused by a sink effect exerted by the gall (Fernandes, 1987; Sacchi et al., 1988; Larson and Whitham, 1991). However, a better understanding of the plant response to gall formation and the total carbon balance is necessary to establish how plant resources are reallocated.

Gall formation did not influence the G% or the daily Gmax. This fact demonstrates that galls affect the formation and development of seeds, but once viable they achieve normal phenological behaviour.

In summary, this study demonstrates that *T. rudolphii* galls caused changes in *V. polyanthus* architecture and viability, corroborating the hypothesis that galls are plant parasites (Price, Waring and Fernandes, 1986; Price, Rosenau and Tahvanainen, 1987). Nevertheless, it cannot be assumed that host plant responses are specific to the herbivores. Apical bud dominance break can be caused by other physical factors, and plants can react in the same way (see Belsky et al., 1993). Studies on plant responses to gall formation are needed to unravel the mechanisms involved in the impact of herbivores on host plant performance. Modifications on plant development and phenology due to gall establishment are important factors promoting changes in plant population growth (Denill, 1985).

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LITERATURE CITED


Multiple responses of insect herbivores to plant vigor

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The patterns of herbivore attack on plants have been extensively studied and many hypotheses were raised to account for them. In this work we evaluated the response of three different species of insect herbivores, one free-feeding Geometridae species (Lepidoptera) and two gall-forming Cecidomyiidae (Diptera), to plant vigor and level of plant stress during two consecutive years. The abundance of the geometrid was not influenced by shoot length in 1993 and 1994 (p > 0.05; both years), hence supporting the null hypothesis. The abundance of Cecidomyiidae A increased with increasing shoot length class both in 1993 (r² = 0.59; p < 0.05; y = -0.8102 + 0.2779x) and 1994 (r² = 0.80; p < 0.0001; y = -0.3707 + 0.1974x), supporting the plant vigor hypothesis. Cecidomyiidae B attack was concentrated on the most stressed shoots (the smallest shoot length classes), but only the 1993 relationship was significant (r² = 0.66; p < 0.005; y = 0.0249 - 0.0008x). These data support the plant stress hypothesis for 1993 but the null hypothesis for 1994. They also corroborate the idea of the existence of a continuum of responses to plant quality, and that herbivores may have idiosyncratic responses to plant quality even when feeding on the same host.

The patterns of herbivore attack on plants have been extensively studied and many hypotheses were raised to account for them. The host plant vigor hypothesis predicts that insect herbivores which have a close relationship between adult oviposition and offspring feeding sites, and whose larval development is associated with plant growth processes, exhibit an oviposition preference for, and enhanced larval performance on, vigorous plants and/or plant modules (1,2,3,4). Therefore, insect herbivores that meet such conditions will be more abundant on plant individuals and/or modules which are fast growing than on slow growing ones (2,5). Several guilds of insect herbivores are known to preferentially choose the most vigorous plants or plant modules for oviposition (1).

Opposing the plant vigor hypothesis, White (6,7) and Mattson and Haack (8,9) argued that herbivore abundance is higher on hosts under stressful conditions. The mechanisms producing this pattern would be the increased quality of host plant tissue and decreased chemical defenses in stressed host tissue (6). This apparent paradox has led to the hypothesis that herbivorous insects with different feeding habits should respond differentially to host plant quality (10).

While these hypotheses have been
tested in several temperate systems, no comparative study has yet been undertaken in the tropics. In a field study, we evaluated the response of three different species of insect herbivores to plant modules (stem shoots). We addressed the following question: How do the insect herbivores respond to module length (module vigor)? To answer this question, three hypotheses were tested simultaneously in the field: 1) The plant vigor hypothesis, which predicts that attack will be centered on the most vigorous modules (the longest shoots in the shoot population) (2); 2) the plant stress hypothesis, which predicts that attack will be centered on the most stressed shoots (the shortest shoots in the shoot population) (6,7) and 3) the null hypothesis, which predicts that shoot size should not influence herbivore attack.

The study was performed at the Estação Ecológica de Pirapitinga (IBAMA) in Três Marias (MG), southeastern Brazil. The biological station is a man-made island which was built in 1965 in the Três Marias reservoir (18°23'5"S, 45°20'20"W) at an altitude of 560 m above sea level. The island appeared as a result of the filling of the reservoir. The island has 1100 ha and its vegetation is primarily cerrado (savanna) (11).

Bauhinia brevipes Vog. (Leguminosae) is a leguminous shrub, up to 3 meters high. It is abundant in the station, and flowers from June to August. We studied the patterns of an attack by a free-feeding geometrid species and another caused by two species of leaf galls. Several free-feeding insects attack the plant, but during the study attacks were primarily made by an unidentified Geometridae (Lepidoptera) species. Its larvae feed on the plant leaves causing distinct marks. Seven gall feeding species attack B. brevipes [three leaf-gallers (Cecidomyiidae: Diptera), and four stem gallers: one Cecidomyiidae, one Lepidoptera, and two Curculionidae (Coleoptera) species]. The leaf galls studied are caused by two undescribed Cecidomyiidae species. External gall morphology is a good indicator of species (12,13) and we used gall morphology to separate species in this study. Galling species A develops on the adaxial leaf surface, and the galls are spherical, with red hairs covering their external walls, are one-chambered, and have one galling larva per chamber (14). Galling species B also develops on the adaxial leaf surface. The galls are spherical, with short whitish hairs covering their walls, and are one-chambered, with one single larva per chamber. Leaf blades become connected by the gall walls.

To answer how the insect herbivores respond to module vigor, 50 shoots per plant were randomly collected around the canopy of 41 randomly selected B. brevipes plants in November 1993 and 40 other plants in November 1994. All collected shoots were placed in plastic bags, numbered, and then taken to the laboratory where stem length (to the nearest mm), total number of leaves, and number of attacked leaves by the three herbivore species were recorded. In the present study shoot length (cm) was used as an indicator of the degree of plant stress (2). The data were transformed into shoot length classes of 3 cm (n=18) classes, and then analyzed statistically by linear regressions (1,2). The probability of herbivore attack on plant shoots was calculated through the frequency of shoots in each class (2).

The proportion of shoots of B. brevipes per shoot length class showed the described distribution pattern observed by Price et al (1). Short shoots (>13.5 cm) were the most abundant in the shoot population while long shoots were rare in both years (Fig. 1). The number of leaves increased with increasing shoot length in both years (1993: r² = 0.92; F₁₁ₒ = 115.916; y = 3.028 + 0.395x; p < 0.0001; 1994: r² = 0.95; F₁₁₂ = 254.537; y = 3.187 + 0.345x; p < 0.001). Nevertheless, longer shoots did not present more leaves per unit length, as the number of leaves per cm decreases with shoot length (1993: r² = 0.65; F₁₈ = 18.266; y = 1.009 - 0.018x; p < 0.002; 1994: r² = 0.60; F₁₉ = 17.888; y = 1.025 - 0.018x; p < 0.001). Thus, longer stems had longer internodes; therefore longer shoots did not provide additional resources for the herbivores. Instead, they provided less resources per unit length (Table 1). These data contrast with that presented in the literature (1,2), consequently calling for more studies.

Herbivores showed divergent responses to shoot length classes. The abundance of the geometrid larvae was not influenced by shoot length class in both 1993 and 1994 (see Fig. 1, Table 1). None of the regressions was statistically significant (p > 0.05), therefore these data support the null hypothesis.

On the other hand, galling species A showed a strong preference for the most rare shoot length classes, i.e., the longest ones (see Fig. 1). The abundance of galling species A increased.

![Figure 1. Proportion of available shoots per shoot length class and proportion of shoots attacked by a geometrid species, galling species A, and galling species B in 1993 and 1994.](image)
with increasing shoot length class in both 1993 (\(r^2 = 0.59; F_{1,5} = 14.153; p < 0.005\); \(y = -0.8102 + 0.2779x\)) and 1994 (\(r^2 = 0.80; F_{1,5} = 47.873; p < 0.0001\); \(y = -0.3707 + 0.1974x\)). Although representing the smallest proportion of the available shoot population, attack by the galling species A was centered on the largest shoots. Attack reached 100% of the longest shoots in both years, hence supporting the plant vigor hypothesis.

The results obtained from galling species B were not clear, however. Galling species B abundance was negatively influenced by shoot length class in 1993 (\(r^2 = 0.66; F_{1,5} = 19.561; y = 0.0249 - 0.0008x; p < 0.005\)) (see Fig. 1) but in 1994 the relationship was not statistically significant (\(p > 0.05\)). Because of the scale used in Figure 1, the relationship between attack rate and shoot length class is not apparent for 1993. Hence, the data on the distribution of galling species B supported the plant stress hypothesis in the year 1993 but the null hypothesis in 1994.

Two of the three hypotheses (plant vigor and the null model) tested were supported in this two-year long field study, whereas the stress hypothesis was only supported in 1993. Stress and vigor may be considered opposite extremes on a continuum of strategies of attack by herbivores (2). Some herbivores may prefer and perform better on vigorous modules, some may prefer and perform better on stressed modules, while some may not be influenced by vigor and stress (1,4,5). We may have seen an interesting case which illustrates the continuum of responses of herbivores to plant quality. Future studies should investigate the influence of plant shoot length on the performance of the herbivores. Only when the hypothetical link between female preference and larval performance and larval performance is studied in detail will we be able to provide a mechanistic explanation for these findings (16). The diversity of herbivores and complex interactions with their tropical plants and natural enemies could also influence...
observed preference patterns. Furthermore, the statistical analysis of this type of data must be critically evaluated. We feel that the statistical procedure, i.e., grouping shoot length into arbitrarily chosen size classes may provoke unbalanced data repetition. It may force the relationship where the longest shoots are always attacked just because of chance alone. Hence, selection may not be acting in the system for it to occur (17).

References and notes

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MODULE SELECTION BY A SCARABAEIDAE BEETLE ON 
**ERYTHROXYLUM SUBEROSUM** IN SERRA DO CIPÓ, 
MINAS GERAIS, BRAZIL

**SELECCIÓN DE BROTES DE ERYTHROXYLUM SUBEROSUM** POR UN 
COLEÓPTERO SCARABAEIDAE EN LA SIERRA DE CIPÓ, 
MINAS GERAIS, BRASIL

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Key words: herbivory, insect-plant interactions, plant stress, plant vigor, Scarabaeidae, Serra do Cipó.

Palabras clave: herbivoria, interacciones insecto-planta, estrés en plantas, vigor en plantas, Scarabaeidae, Sierra de Cipó.

Understanding the pattern of herbivore attack on plants has been a concern of many farmers and ecologists. Many patterns have been extensively investigated and several hypotheses have been suggested. White (1969, 1970) proposed that under stressful conditions, plants would be more vulnerable to herbivore attack. The mechanism accounting for this pattern would be the decrease in protein synthesis coupled with an increase in amino acid content in plant tissue. Concurrently, stressed plants have less ability to produce chemical defenses (Rhoades 1979). Since the eighties, studies have focused on the mechanisms of plant stress and outbreaks of insect herbivore populations on stressed hosts. Hence, plant quality started to be better investigated as an important component in plant-herbivore interactions (Price 1984, Mattson and Hanck 1987).

On the other hand, the hypothesis of plant vigor suggests that herbivore attack primarily occurs on younger, relatively fast growing individuals (Price 1991). Price defines vigor as a plant or module, that grows rapidly and ultimately reaches a larger size, relative to the mean growth rate. Preferential attack on vigorous modules may be related to greater success obtained by the offspring that feed on a better quality resource. Thus, there should be a strong relationship between herbivore preference and offspring performance (see Craig et al. 1986, Thompson 1988).

Stress and vigor hypothesis may be considered as opposite extremes of a continuous strategy of herbivore attack (Price 1991). These hypotheses have been widely tested on several temperate systems, but relatively few studies have been attempted in the tropics (e.g., Prada et al. 1995).

In this study we tested the following hypotheses: a) the plant vigor hypothesis that predicts that the largest shoots (modules) are preferentially attacked by herbivores, and b) the plant stress hypothesis that predicts that stressed plants suffer more attacks by herbivores.

*Erythroxylum suberosum* (Erythroxylaceae) is a perennial shrub, characteristic of cerrado
MODULE SELECTION BY A SCARABAEID BEETLE ON *ERYTHROXYLUM SUBEROSUM*

![Graph showing distribution of shoot size and attack prevalence](image)

**Figure 1.** Size distribution of all shoots (○) of *E. suberorum* and attacked shoots (■) by scarabaeid beetle in Serra do Cipó, Brazil.

Vegetation, with a height between 1 and 3 meters (Rizzini 1979). Casual observations indicated that a species of adult Scarabaeidae (Coleoptera) is a very common herbivore that chews on the leaf borders of this plant species.

This work was done in Serra do Cipó (19° 15'S; 43° 30'W), Minas Gerais, Brazil, in the Espinhaço mountains at 1,300 m above sea level in October 1993. The soil is sandy with low capacity for water retention (Giulietti et al. 1987). In the dry season (June to September) soil water is restricted to riparian vegetation, and fire is very frequent. The plant population studied had been burned in August 1993. As all shoots had been burned, the shoot population studied was of similar age.

Fifteen individuals of the *E. suberorum* population were randomly selected near a stream and arranged along a gradient that simulated water availability in the soil. On each individual we randomly collected 30 shoots around the crown. Two assumptions were made: shoots were randomly dispersed and herbivory was similar on all crowns. Trunk circumference and height of each plant were also measured to evaluate differences among individual plants. All shoots were collected and taken to the laboratory where we measured their length. We measured herbivory as presence or absence, and recorded the proportion of attacked shoots. To test hypothesis (a), data were grouped into 15 size classes (see Price 1991). To test hypothesis (b), data was averaged by plant. Data were analyzed by simple regression analysis (Zar 1984, Price 1991).

Adult beetles concentrated their attack on certain branches, and fed in groups. Rates of scarabaeid attack increased with increasing shoot length, although smaller shoots were more abundant (Figure 1). Attack on the longest shoots approached 100%. The regression model between attack rate on shoot size class explained 87% of the variation in beetle attack ($r^2 = 0.87$, $n = 15$, $p < 0.001$, $y = 33.9 + 0.34x$). Although representing the smallest proportion of the available shoot population, attack was primarily on the longest shoots. These data corroborate the vigor hypothesis (Price 1991). Similar results were found by Craig et al. (1986) on the attack by the gall-forming sawfly, *Eura lasiolepis*, on *Salix lasiolepis*. Price et al. (1990) revised 43 examples of insects that feed on the most vigorous plants (or shoots), but only one species was an adult form.
As predicted by the stress hypothesis, plants that were more distant from the water source were more heavily attacked than plants close to the water \((r^2 = 0.52, n = 15, p < 0.005, y = 20.63 + 0.101x\), Figure 2). However, the attack on the most water stressed plants may be a function of plant shoot size. If plants that were farther from the water had the longest shoots, then the vigor hypothesis would be corroborated. However, we found no relationship between mean shoot size and distance from the water \((p > 0.05)\).

One of the complications of the vigor hypothesis is that many herbivores tend to attack larger modules on plants (Price 1991). For instance adult females of Dorcetrix albivittata on Pinus edulis select the longest shoots on plants growing in stressed habitats (Whitham and Mopper 1985, Mopper and Whitham 1986). Many gall-formers also select larger modules in xeric sites (Fernandes 1992). Hence, insect herbivores may use two distinct levels of host selection: scarabaeid individuals select plants that are more susceptible to attack and then select more vigorous modules inside the plant (Fernandes 1992). Future studies shall expand the data presented to observe female beetle selection of plant modules and individuals, and herbivore performance on plant modules and stressed hosts.

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Leaf galls on an aquatic macrophyte, *Nymphoides indica* (Nymphaeaceae), in Rio Doce Valley, Brazil

Galhas em folhas de uma macrófita aquática, *Nymphoides indica* (Nymphaeaceae), no Vale do Rio Doce, Brasil

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RESUMO
Pela primeira vez, é registrada a ocorrência de uma galha de insetos em *Nymphoides indica* Ktze. (Nymphaeaceae) e um caso raro no qual galhas de insetos são encontradas em plantas aquáticas. A macrófita é amplamente distribuída nos inúmeros lagos do Vale do Rio Doce, Minas Gerais, Brasil. A galha esferóide é provavelmente causada por um Cecidomyiidae (Diptera) ainda não identificado. São fornecidos dados sobre a morfologia e abundância da galha na sua planta hospedeira.

Unitermos: Galhas de insetos; Herbívoria; *Nymphoides indica*; Vale do Rio Doce.

ABSTRACT
For the first time, we report on an insect gall on *Nymphoides indica* Ktze. (Nymphaeaceae) and a rare case where a gall is described from an aquatic plant. The macrophyte is widely distributed in the several lakes of the Rio Doce Valley, Minas Gerais, Brazil. The spheroid gall is probably induced by an undescribed species of Cecidomyiidae (Diptera). We provide data on gall morphology and abundance on its host plant.

Keywords: Herbivory; Insect galls; *Nymphoides indica*; Rio Doce Valley.
I Introduction

Galls are found on most of the plant families throughout the world (Mani 1964, Fernandes 1992ab). Nevertheless, galls on aquatic plants have seldom been reported in the literature (see Docters van Leeuwen-Reijnvaan & Docters van Leeuwen 1926, Houard 1933, Felt 1940, Mani 1964, Gagné 1989). This is the first report of an insect gall on Nymphoides indica Ktze. (Nymphaeaceae) and a rare case where a gall is described from an aquatic plant. The macrophyte is widely distributed in the several lakes of the Rio Doce Valley, Minas Gerais, Brazil (Ikegami & Gentil 1985).

The galls are spheroid, light green, glabrous, occur on both leaf surfaces and are coalescent in some instances (Fig. 1). Gall tissue is whitish, soft and juicy, probably due to its high water content in the gall and leaf tissue. No distinguishable larval chamber was found within the gall. Only one insect larva was found in 34 dissected galls. The larva was whitish, one millimeter long and belonged to the family Cecidomyiidae (Diptera). Despite of the wide occurrence of galls caused by the cecidomyiids in Brazil and especially in the Rio Doce Valley, studies should be performed to confirm the identity and role of the larva in this system. Cecidomyiids can be gallers, gall incinerines, as well as organisms that occupy the gall after the emergence of the galling herbivore (see Mani 1964).

Galls were not abundant. Twenty one out of 153 examined leaves of Nymphoides indica at Lagoa Carroca were galled. There was an average of 41.8 galls per galled leaf (SD = 49.1; n = 21). Gall diameter averaged 2.47 mm (SD = 0.09 mm, n = 50). Galled leaves were frequently abscised. Nevertheless, many abscised leaves were also mined by an unidentified microlepidopteran larva.

The paucity of galls on some plant groups is not well understood and remains largely unknown (see Kamy 1926, Fernandes 1992a,b). The question on why there are so few species of insect galls on aquatic plant is of vital importance to understand the evolution and adaptive nature of galls. Our present knowl-

edge on the patterns of insect gall richness indicates that galls evolved primarily in water-stressed habitats (Fernandes 1992a). An important factor hampering gall colonization on plants in humid habitats is the high mortality rates exerted by pathogens (Fernandes 1992a). The occurrence of an insect gall on an aquatic plant makes this system very interesting to study in an attempt to unravel the rarity of galls in some habitat and plant groups.

Acknowledgments

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Figure 1: Leaf galls on Nymphoides indica. (not in scale).
Leaf galls on an aquatic macrophyte, Nymphoides indica (Nymphaceae), in Rio Doce valley, Brazil

References


INSECT GALLS FROM SAVANNA AND ROCKY FIELDS OF THE JEQUITINHONHA VALLEY, MINAS GERAIS, BRAZIL

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ABSTRACT: The distribution of galls formed by insects on several host plants in xeric and mesic habitats was studied in several localities of the Jequitinhonha Valley (Espirito Santo Mountains), northeast of Minas Gerais State. 236 morphologically distinct insect galls were obtained. Galls were found on several organs of 53 plant species of 27 families. Most insect galls (82.6%) were caused by the Cecidomyiidae (Diptera). Leaves were the most frequently galled plant organs (51.7%). Gall external morphology was highly variable, but the most common shape was elliptical, of single occurrence and glabrous.

KEYWORDS: Galls, herbivory, insect galls, Jequitinhonha, host plants, gall richness.

Introduction

Galls or plant tumors are cells, tissues or plant organs induced by the increase of cellular volume (hypertrophy) and/or cellular number (hyperplasia) provoked by parasites or pathogens which normally develop in these structures. This abnormal
of atypical growth normally coincides with the loss of function caused by changes in normal pattern of cellular growth and differentiation. 14 Induced by a vast spectrum of organisms, galls are usually formed by insects, which have been recognized as the most common agents of gall induction. Within this group, the dicotyledons can be emphasized due to the overwhelming number, abundance and richness of gall types produced by them. 15,16 The insects adapted to induce galls find in the host tissues abundant and better feeding sites which are formed by several layers of highly nutritious cells. As the gall surrounds the insect in a sheltered chamber it also protects the larvae against natural enemies and environmental stresses. 17 Galls can be induced on all organs of the host plant, from the root apex to the apical stems, on vegetative and reproductive parts. Furthermore, they are sessile, diverse and abundant, therefore becoming a very important tool for ecological studies. 3

With the development of many studies in different biogeographical regions, a global pattern on the distribution of gall species is emerging. 3,11,18 Latitudinal, altitude, temperature and humidity strongly influence insect gall richness. In habitats distant from water sources gall diversity is significantly higher than in habitats along water sources. 6 Differential rates of parasitism, predation and plant resistance between xeric and mesic habitats have been seen as the most important ecological mechanisms which influence the differential diversity of gall forming insects between habitats. 6 Therefore, galls can be considered as adaptations of some insects to stresses provoked by natural enemies, plant resistance and climate (primarily high temperature and low humidity). 2,4,5,10,11,14,17

Despite the high diversity of galls in the tropical regions, the majority of the studies have been mainly descriptive. 2 Moreover, few studies have been developed in some biomes, especially in tropical savannas and rupestral fields, where their diversity is the highest of the world. 12,13 This is the first survey of gall forming insects in rupestral fields and savannas of Brazil. Studies in other Brazilian vegetation were done by Tavares 9,20,21 in the beginning of this century in Atlantic forest, and by Fernandes et al. 8 in secondary mesophytic forest. Other studies are primarily represented by single contributions. 9 In this initial phase of studies developed in the Espinhaço Mountains, we have described insect galls, identified the host plants, and recorded the most common galls and plant organs attacked.

Material and methods

Studies were performed in several localities in the mountains of the Espinhaço Range, northeastern Minas Gerais, Brazil. The localities studied were: Saberbo in Cristalina County (Cr); Fazenda Cabral in Grão Mogol County (G姆); Laranão in Berilo County (Bо); Posses in Minas Novas County (МиN) and Peixe Cru in Turnalina County (Ту). Descriptions of the environment in sampled localities are given below:

Saberbo — Located near the confluence of Saberbo and Jequitinhonha rivers, at 42°40'.W and 17°08’S. The vegetation is primarily composed of rupestral fields on rocky sites and alluvial soils. Deciduous and semi-deciduous mesophytic forests occur above alluvial soils while riparian pluvial forest grows on pluvial sites.

Fazenda Cabral — Located at 42°47'.W and 16°34’S, on patches of rocky sites and predominant association of itosol and cambisol. The vegetation is formed by broken pluvial riparian forest on the Jequitinhonha river. Seasonal forest grows on pluvial sites and on mountains in the lowest altitudinal belts while rupestral fields and disturbed savannas occur at higher altitudes.

Lamarão — Located in a canyon in the Jequitinhonha river valley, at 43°36'.W and 16°44’S. This is a pristine region on eutrophic lakes. On the higher altitudes savannas (late sensu) and rupestral fields are predominant, while along the slopes and on fluvial sites deciduous and semi-deciduous mesophytic forests are more common. There are few pluvial riparian forests along the Jequitinhonha river, as little is a dry region with shallow soils unable to retain water. Leaf fall in the deciduous seasonal forest occurs in the dry period of the year, a phenomenon that does not occur with so much intensity on savannas and rupestral fields.

Posses — Located on the right bank of the Jequitinhonha river, at 42°49’.W and 17°02’S. Sampled areas consisted of cultivated lands on dystrophic itosol, where savannas occur, and a mixture of itosol and cambisol occurs under seasonal forest.

Peixe Cru — Located on the right bank of the Jequitinhonha river, at 42°57’.W and 17°S. The vegetation is composed of seasonal forest spread on fluvial sites. Soils are composed by an association of itosol and cambisol. Savannas occur above a itosol located on the highest altitudes.

Xeric and mesic habitats were sampled on all localities on wet and dry seasons. Xeric habitats were those distant from water sources in the savanna and rupestral fields. 1 On the other hand, mesic habitats were those near rivers, streams, and arroyos in areas of gallery and mesophytic forests. The region of the studied savanna has a dry season of four or five months with an average rainfall of about 1,450 mm. 6

Results of an analysis on the differential distribution of galls sampled between xeric and mesic habitats can be found in Fernandes et al. 8

To evaluate gall species richness on the studied areas and habitats, three samples (random walks) of one hour each were made on all habitats. 8,15 During the studied period, all gall species and host plants found were collected and placed in plastic bags. Later, plants were pressed and stored in the Insect Gall Collection of the Department of Botany Herbarium, Universidade Federal de Minas Gerais (BHCQ). Subsequently, plants were categorized in morphospecies and then identified at the species level. Galls were characterized according to the methodology described in Fernandes et al. 8 and then illustrated with hand drawings (Table 1).
Table 1 – Host plants, galling insect families, gall description, and studied localities in the State of Minas Gerais, Brazil (Bettio, G.M.: Grão Mogol, Crl: Cristália, Crl: Curral Velho, Min: Minas Novas, Tur: Turmalina).

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Although it was not possible to identify the galling insect species, descriptions and illustrations of all the galls collected are here presented. Gall morphology is a good predictor of species and has been intensively used in cases such as the present one. As new research develops, these galling species will be identified at the species level. Some plant species could not be identified at the species level of species at the sampled individual's stage, but future studies will hopefully fill this gap.

Two samples were realized during the study period, the first during the wet season (April, 1991) and the second during the wet season (July/August, 1991). Sampling in the rainy and dry seasons was necessary due to possible variations in insect herbivore richness in response to seasonal variations.

**Results and discussion**

We have found 236 morphologically distinct types of insect galls on several organs of 134 host plant species belonging to 27 families (Table 1). Leguminosae, Malpighiaceae, Asteraceae, and Myrtaceae were the most attacked families of host plants. Eighteen Leguminosae species supported 34 galling species, 16 Malpighiaceae species supported 32 galling species, 19 Asteraceae species supported 32 galling species, while 18 Myrtaceae species supported 26 galling species (Table 2).

The most frequently galled organs were leaves (53.7%), followed by stems (45.0%), and flowers (1.3%). According to the external morphology of the galls, the most frequent shapes were elliptical, discoidal, spherical, and globular (Figure 1). Most of the galls (60%) occurred singly while 33.8% were found only in groups or in clusters. 35.9% of the galls were covered by trichomes (hairy) while 64.1% did not present trichomes on their external walls (glabrous).

The most frequent galling insects were Cecidomyiidae (Diptera) (22.5%) followed by Coccinellidae (3.5%), Psyllidae (0.9%), and Tephritidae (0.5%) (Table 3). Hymenopterans caused 16.0% of the galls while lepidopterans caused 25.5% of the galls sampled. Only 1.5% of the galls could not be identified.

The Cecidomyiidae (Diptera) were responsible for the induction of galls in most of the plant species studied and galled all observed organs, but especially on leaves (51.7%). The diversity of morphological features of galls caused by insects of this family was enormous, including elliptical, discoidal, spherical, globular, conical, spiny, cylindrical, fower-like, hairy, and glabrous galls. These results corroborate with the general patterns found in Brazil and elsewhere in the world.

Among the galls caused by hymenopterans, stems were the most attacked organs. Gall morphology varied between globular and elliptical shapes, most of them occurred singly and were glabrous. On the other hand, leaf galls caused by hymenopterans were rare and always glabrous.

### Table 2 - Distribution of insect galls by plant families in the Jequitinhonha Valley, MG

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<thead>
<tr>
<th>Family</th>
<th>Number</th>
<th>Galls (%)</th>
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<tr>
<td>Leguminosae</td>
<td>34</td>
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<tr>
<td>Malpighiaceae</td>
<td>32</td>
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<tr>
<td>Asteraceae</td>
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<td>13.6</td>
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<td>Myrtaceae</td>
<td>28</td>
<td>11.0</td>
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<td>Vochysiaceae</td>
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<tr>
<td>Bignoniaceae</td>
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<td>0.9</td>
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<td>Rutaceae</td>
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<td>Total</td>
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### Table 3 - Number of galls induced by the major taxa of gall-forming insects, and their relative frequency in the Jequitinhonha Valley, MG

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<tr>
<th>Taxa</th>
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<tr>
<td>Cecidomyiidae</td>
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<td>Hymenoptera</td>
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<td>Tephritidae</td>
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<td>0.9</td>
</tr>
<tr>
<td>Psyllidae</td>
<td>2</td>
<td>0.9</td>
</tr>
<tr>
<td>Not identified</td>
<td>3</td>
<td>1.3</td>
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</table>
Cytosphora, the only insect species that caused galls, provoking only one spherical and hairy-leaf gall. The globular-shaped stem galls were glabrous, while ellipsoid galls could be covered with trichomes or yet be glabrous. Other coleoptera galls were found on stems, occurred singly, and were glabrous.

Psyllidae (Homoptera) caused leaf galls generally covered by green trichomes, whereas Tephritidae caused single stem galls of elliptical shape on Brachyotum bidentatum (Figure 15), and on Vanuferousa erythrocephala (both Asclepiadoideae).

Due to the acidity and poor nutritional states of the soils, the Espinhaco mountains may render the richest galling insect fauna of the world. Further survey studies are fundamental for the understanding of ecological patterns and mechanisms that influence species distribution along biogeographical gradients.

FIGURE 1 - Frequency (bars) and respective percentages (lines) of external insect gall morphology of Jequitinhonha Valley, MG (Brazil).

Figures 152-181 - Galls on several host plants of the Jequitinhonha Valley (see Table 1 for details): 152-153: S. urucum; 154-155: S. urucum; 156-159: unidentified species (sp. 2) of Malvaceae; 157-158: Lycium sp.; 159-160: Monarda oblonga; 161: unidentified species (sp. 1) of Myrtaceae; 162: Eugenia adenophora; 163: E. hystrix; 164: Myrcia multiflora; 165-167: M. rubra; 168: M. sarsa; 169: M. cana; 170: Myrtaceae sp.; 171: Psychotria scabra; 172: unidentified species (sp. 1) of Myrtaceae; 173-174: M. sarsa; 175: M. cana; 176: unidentified species (sp. 2) of Myrtaceae; 177-180: unidentified species (sp. 3) of Myrtaceae.

Figures 182-211 - Galls on several host plants of the Jequitinhonha Valley (see Table 1 for details): 182-183: unidentified species (sp. 4) of Malvaceae; 184: unidentified species (sp. 5) of Malvaceae; 185: unidentified species (sp. 6) of Malvaceae; 186: unidentified species (sp. 7) of Myrtaceae; 187: unidentified species (sp. 8) of Myrtaceae; 188-189: Cissus scabra; 190-191: C. cana; 192-193: C. rubra; 194: unidentified species (sp. 9) of Malvaceae; 195-196: unidentified species (sp. 2) of Rubiaceae; 197-198: unidentified species (sp. 3) of Rubiaceae; 199: unidentified species (sp. 4) of Rubiaceae; 200-201: unidentified species (sp. 5) of Rubiaceae; 202-204: unidentified species (sp. 6) of Rubiaceae; 205: unidentified species (sp. 7) of Rubiaceae; 206: unidentified species (sp. 8) of Rubiaceae; 207-209: Staphylea coronaria; 210: S. carica; 211: Psychotria sp.
Acknowledgments

We would like to thank R. Mata-Machado and two anonymous reviewers for their helpful comments on early drafts of this manuscript.

References

ÍNDICE DE ASSUNTOS

Formiga; trato digestivo; morfologia; p.9
Leguminosas; papilionoides; floresta parvial; p.9
Germinação; crescimento; solo; p.61
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Hypersensitivity as a Phenotypic Basis of Plant Induced Resistance Against a Galling Insect (Diptera: Cecidomyiidae)

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ABSTRACT The pattern of attack of a leaf galling Contarinia sp. (Diptera: Cecidomyiidae) on its host plant Bauhinia brevicaulis Vogel (Leguminosae) was studied in southeastern Brazil for 2 yr to test the plant vigor hypothesis, which predicts that attack will be centered on the most vigorous (longest) shoots. Most attacks by the leaf galling herbivore occurred on the longest shoots, although these represented the smallest proportion of the available shoot population. Virtually all (98%) of the longest shoots were attacked in 1993 and 1994. Variation in shoot length explained 70% of the variation in the number of galls per shoot in 1993 and 72% in 1994, supporting the plant vigor hypothesis. Nevertheless, no relationship was found between female preference for longer, more vigorous shoots and larval performance. Progeny of females that attacked the longest shoot did not experience higher success than progeny raised on shorter shoots. The hypersensitive reaction of the hosts to galling was observed only as a brown circular spot around the oviposition site. This reaction to galling initiation was the major mortality factor, killing 90.3% of the galls in 1993 and 85.5% in 1994, hence leaving few galls to natural enemies such as parasites, predators, and pathogens. Overall, only 4.7% of the galls produced adults in 1993 and 8.7% in 1994.

KEY WORDS Contarinia, Cecidomyiidae, hypersensitive reactions, insect herbivory, insect galls, plant vigor

Studies of host plant resistance to insects have centered on a wide range of features, which include secondary chemistry, nutrition, phenology, age, induced defenses, and mechanical traits (e.g., Edwards and Watten 1983, Baldwin 1989, Woodman and Fernandes 1991, Fritz and Sims 1992, Herm and Mattson 1982, Fernandes 1991). Nevertheless, an important type of induced defense, plant hypersensitivity, has seldom been studied as a source of host plant resistance to insect herbivores.

Hypersensitivity is a defensive response that encompasses morphological and histological changes terminating in the death of the attacked tissue, and thus in the localization, containment, inactivation, and eventual death of the herbivore. This induced reaction of the host is the primary event in resistance to fungal parasites (MacLean et al. 1974). It leads to a disruption of nutrient supplies to the invading organism and in the production of toxic metabolites, resulting in the cessation of the microorganism's growth (Bayley and Mansfield 1982). The supply of water and oxygen is also reduced, decreasing the probabilities of establishment and success by the invading organism (Wong and Berryman 1977). The necrotic response is the result of a disturbance in the balance between oxidative and reductive processes, which results in an excessive oxidation of polyphenolic compounds and a breakdown of cellular and subcellular structures (Király 1980).

Although the occurrence of this induced defense against microorganisms is well documented, there are relatively few examples of hypersensitive reactions of plants against insect herbivores, with the exception of back beetles (e.g., Berryman 1978, Dafna and Berryman 1983, Berryman and Ferrell 1988). The elicitation of a hypersensitive reaction has been observed among those insects with a tight association with their host plants, such as galling insects, bark beetles, and wood borers (reviewed by Fernandes 1990). Although some authors argue that this induced defense is irrelevant in the insect-plant interaction (e.g., Painter 1991), some studies have addressed its impact on herbivore populations (e.g., Anderson et al. 1991) and have established its frequency and distribution in nature. The hypersensitive reaction has been shown to vary among plant genotypes (Skukle et al. 1992, Bentur and Kaloze 1996) but how this resistance mechanism varies according to plant growth (vigor), phenology, and physiology has never been demonstrated (but see Anderson et al. 1991). In an attempt to describe and document the frequency of this mechanism against herbivory and to relate it to the most relevant hypotheses on insect-plant relationships, I studied the pattern of attack of a leaf galling Contarinia sp. on Bauhinia brevicaulis Vogel.
taria sp. (Diptera: Cecidomyiidae) on its host plant, Bauhinia brasiiens Vogel (Leguminosae).

A recent hypothesis on insect-plant relationships, the host plant vigor hypothesis, argues that many insect herbivores select the fastest growing host individuals or host modules (leaves and stems) (Price et al. 1990, Price 1991, Pressler and Price 1995). The mechanistic explanation for female preference is an increased larval performance on the most vigorous individuals or modules, or both. Several guilds of insect herbivores that are tightly linked to their hosts prefer the most vigorous plants or plant tissues (Price et al. 1990). Most gallers oviposit at the site of gall initiation, and gall formation is directly influenced by the development of actively growing plant modules. Many studies have documented the influence of the growth patterns of plants on the success of gall-forming insects (Mani 1964, Whitman 1980, Ahman 1984, Craig et al. 1989, Glynn and Larson 1994). However, the population dynamics of insect herbivores are not influenced solely by the host, but also by natural enemies such as parasites, predators, and pathogens (e.g., Clancy and Price 1986, 1990, Fernandes and Price 1993).

The 3 questions I addressed were as follows: (1) How does the galling herbivore respond to module vigor (here measured as stem length)? To answer this question in the field I tested the plant vigor hypothesis which predicts that attack will be concentrated on the most vigorously growing shoots (the longest shoots in the shoot population) (see Price 1991), against the null hypothesis, which predicts that herbivore attack will not vary in relation to shoot length. (2) Is the preferential response of adult females of the leaf galling cecidomyiid for longer shoots related to larval survivorship? (3) Is there a strong linkage between oviposition preference and larval survival? I also provide a preliminary description of the external morphology and an anatomical observation of the hypersensitive host-induced defense against the galling insect, and I document its impact and consistency during a 2-yr study.

Materials and Methods

The study was performed in the Estação Ecológica de Pirapitinga in Três Marias, Minas Gerais, southeastern Brazil. The biological station is on an island that was formed in 1965 upon completion of the Três Marias Reservoir (18° 25′ S, 45° 20′ W) at an altitude of 560 m above sea level. The island is 1,000 ha in area and its natural vegetation is primarily cerrado (savanna), which is typical of the entire area flooded (Azevedo et al. 1987). Samples of shoots and galls were taken in November of both 1993 and 1994 at the end of the galling period.

Bauhinia brasiiens is a leguminous shrub up to 3 m high and is abundant on the island. Plants flower from May to August. Seven insect species induce galls on B. brasiiens; 3 are leaf-gallers (Cecidomyiidae: Dipiura), and 4 are stem galler (1 Cecidomyiidae, 1 Lepidoptera, and 2 Curculionidae: Colleteras) (unpublished data). The leaf galls studied are caused by an undescribed species of Contarinia sp. (Diptera: Cecidomyiidae). The genus Contarinia includes species with elongate, tapered ovipositors to allow oviposition in narrow places (bud scales, closely fitted parts of developing buds, crevices) near the feeding sites (Cagné 1994). Upon hatching, larvae search for an adequate feeding site and immediately start boring into the plant tissue to initiate the gall (Shorthouse and Hofbirsch 1998). Mature larvae of Contarinia sp. leave the gall to pupate in the ground beneath the host tree. Voucher specimens of insects and Contarinia sp. galls have been placed in the Herbarium at the Instituto de Ciências Biológicas, Belo Horizonte, Brazil. Galls (Fig. 1) are located on the adaxial leaf surface, are spherical in shape, with long red hairs covering their external walls. They have a single chamber, with 1 larva per chamber. They may occur singly or in conelike groups.

To answer the 1st question "How does the galling herbivore respond to module vigor?" 50 shoots were collected haphazardly around the canopy of 41 haphazardly selected B. brasiiens plants in 1993 and 40 different plants in 1994. All collected shoots were placed in plastic bags, numbered, and then taken to the laboratory where stem length (to the nearest mm), total number of leaves, and number of galled leaves were recorded and then transformed into shoot length classes of 3 cm (n = 18 classes). The data were then analyzed statistically by linear regression, using shoot length as the independent variable and the logarithm of the number of galled shoots and the logarithm of galled leaves as the response variables to reduce data heteroscedasticity (Zar 1984).

Fig. 1. Illustration of the cecidomyiid leaf gall and hypersensitive reaction (small black spots on lower and top leaves) against galling.
To determine if oviposition preference of Conotraria sp. was related to survival of their larvae, galls were opened for observation of their contents, and factors associated with mortality recorded (see Fernandes and Price 1992). Galls killed by the hypersensitivity of the plant could not be opened, however, because the necrotic reaction fuses the gall walls. The hypersensitive tissue was prepared for scanning electron microscopy according to the methods described by Murphy and Romsas (1984). The mortality factors included hymenopteran parasitoids, lepidopteran larvae that eat the gall walls and larvae or indirectly kill them through desiccation, fungi pathogenic on the galling larvae, and hypersensitive reaction of the host. Galls in which I was unable to identify the mortality factor were assigned to a mortality category named “other.” Percent mortality and survivorship are followed by their respective standard errors.

I also examined the data to determine if there was a link between female oviposition preference and larval performance. The data on the percent mortality and survival of the galling insects were regressed against shoot length class to test this hypothesis (see Price 1991).

Results

Herbivore Response to Module Vigor and Mechanisms. The majority of shoots and leaves in each shoot-length class were concentrated in the shorter categories (Fig. 2). The distribution of shoot length had a long tail of shoots falling in the long shoot-length categories. Although these long shoots were rare, representing the smallest proportion of the available shoots, they were the most heavily attacked by the galler, with 100% of the shoots greater than 34.5 cm long and longer being galled in 1993, and 100% of those longer than 43.5 cm being galled in 1994.

Variation in shoot-length class explained 32% of the variation in the number of galls per leaf in 1993 ($r^2 = 0.32; df = 1, 10; F = 4.64; logy = -1.717 (SE = 0.290) + 0.029 (SE = 0.013) x; F < 0.05$) and 56% in 1994 ($r^2 = 0.56; df = 1, 12; F = 15.69; logy = -1.892 (SE = 0.204) + 0.0678 (SE = 0.008) x; F < 0.001$) (Fig. 3A). Variation in shoot length class explained...
Fig. 2. Linear regressions of the (A) number of galls per leaf and (B) number of galls per shoot in 1993 and 1994. Closed circles and solid line, 1993; open circles and dashed lines, 1994. Refer to text for statistical data.

70% of the variation in the number of galls per shoot in 1993 ($r^2 = 0.70; df = 1, 10; F = 23.76; \text{log}_y = -0.297 (SE = 0.320) + 0.072 (SE = 0.015); x; P < 0.001$) and 78% in 1994 ($r^2 = 0.78; df = 1, 12; F = 41.75; \text{log}_y = 150.348 (SE = 0.249) + 0.061 (SE = 0.010) x; P < 0.0001$) (Fig. 3B). These results support the plant vigor hypothesis.

Major Mechanism of Plant Resistance to Galling. Hypersensitive reaction by the host plant was the most important mortality factor in the galling population. This plant resistance mechanism, whereby plants inhibit gall formation, killed 90.3 $\pm$ 1.3% (mean $\pm$ SE) of the gall formers in 1993 and 93.2 $\pm$ 0.9% in 1994 (Fig. 4). Parasitism by microhymenopteran wasps killed 1.9% of the galls in 1993 and 1994. Fungal pathogens killed 1% of the galling larvae in 1993 but were not found in 1994. Unknown factors (other) killed 1.9% in 1993 but again were not found in 1994. Overall, only 4.7 $\sim$ 0.1% of the galls produced adults of Contarinia sp in 1993 and 6.7 $\sim$ 0.1% in 1994.

The most important factor contributing to gall mortality, the hypersensitive reaction of the host, was easily observed as a brown circular spot around the oviposition site (Fig. 5). In $\sim$ 88% of the hypersensitive reactions the gall development never began, whereas in the other 12% the larva inside the gall was killed while it was probably in its 1st instar. The round circular area was observed on both leaf surfaces, but was darker on the adaxial leaf surface where the gall develops. Microscopical observation indicated that all mesophyll structures...
were necrotic, lacked transport tissues, and the corky dead tissue was filled with polyphenolic compounds (unpublished data), as reported in hypersensitive reactions against fungal pathogens (Agrios 1988).

Lack of Preference and Performance in the System. The hypothetical link between female preference and larval performance was not supported by these data. In both years, no relationship was found between the length of the shoot and the percentage of galls that survived or were killed by the plant (hypersensitive reactions) or by natural enemies (parasites, predators, pathogens) (linear regressions of percent survivorship/mortality factors against shoot length exist; \( r^2 > 0.05 \) for all regressions [1993: \( n = 1,618 \) galls; 1994: \( n = 1,045 \) galls, Fig. 6]). Thus, selection of the most vigorous shoots by the females did not increase survival of their young.

Discussion

Price (1991) proposed that insect herbivores that display a tight linkage between the site of adult oviposition and the feeding sites of their offspring primarily attack individual young plants or modules within plants that are growing faster, because this will increase the chance of their offspring surviving (see also Thompson 1988, Craig et al. 1989, Price et al. 1990). The leaf galling Contarinia sp. satisfied only 1 of the 2 predictions of this hypothesis. The mechanism whereby female preference should be explained (increased larval success on the most vigorous modules) was not supported by this study. Similar findings have been reported in several other systems (Tischendorf 1988, Fernandes 1992, Bruyn 1995, Pesslner and Price 1995). However, longer shoots might support more galls just because they are bigger or have more resources (Madeira et al. 1997; M. L. Fast and G.W.P., unpublished data). Cornishsen et al. (1997) observed that the number of leaves in B. buxifolia increased with increasing shoot length in 1993 \( (r^2 = 0.93, P < 0.0001) \) and 1994 \( (r^2 = 0.95, P < 0.001) \), but that longer shoots did not present more leaves per unit length because the number of leaves per centimeter decreased with shoot length \( (1993: r^2 = 0.63, P < 0.002; 1994: r^2 = 0.60, P < 0.003) \). Hence, longer shoots had longer internodes; therefore they did not provide additional resources for the herbivores. Craig et al. (1989) and Pesslner and Price (1995) showed that the performance of insect herbivore and host vigor and insect performance was strongly influenced by the abscission rates of leaves on longer shoots. Leaves abscised more frequently on shorter shoots than on longer shoots; therefore, herbivores preferred and survived better on longer shoots. Although this study did not address abscission-based
It is possible that plant interactions with the other galling herbivores could also affect the pattern of response to Contarinia sp. However, despite the high richness of the galling community on B. brevipes (n = 7 morphologically distinct species), the other galling species were rare in both years and are not likely to have contributed significantly to the development of the hypersensitive response. An alternative explanation is that the selection for the most vigorous plant modules was adaptive 30 yr ago when the area was a dry cerrado before the formation of the reservoir. The increased water volume in the area has undoubtedly dramatically changed the climate close to the lake; and Fernandes (1990) suggested that plant hypersensitive reactions to galling would be more efficient and thus common in more humid habitats (see Puritch and Mullick 1975, Christiansen et al. 1987). However, no direct climatic data are available to support this hypothesis. Studies should be carried out on the efficiency of this resistance mechanism under different field and experimental climatic conditions.

Questions currently debated in ecology relate to the selective pressure of natural enemies on the pattern of attack by herbivores and what are the relative strengths of the bottom-up (plant-driven) versus the top-down (natural enemy-driven) effects in 3-trophic-level interactions (Clancy and Price 1956, Hunter and Price 1992, Fressler et al. 1996). In this study, effects driven by the host plant (the hypersensitive reaction) strongly influenced the herbivore population in the absence of other factors. Natural enemies of the galling fly were weak mortality factors during the study period. Nevertheless, trophic relationships vary both within and among systems and are strongly affected by abiotic heterogeneity (Whittaker and Fenzy 1971, Hunter and Price 1992, Fressler and Boecklen 1994). Moreover, hypersensitive reactions may be influenced by temperature and humidity gradients, as well as plant quality. This system may offer an interesting opportunity to observe the strength of this induced response to an insect herbivore and possibly help reveal the dynamic interplay between bottom-up and top-down effects under various environmental conditions.

Hypersensitivity was the most important mechanism whereby B. brevipes terminated attack by the major galling Cecidomyiidae fly. Mattson et al. (1988) suggested that the intimate interactions between herbivores and hosts may select for more specific and more complex defenses because of the greater and more varied opportunities that the host plant has to regulate the lives of its intimate associates. This induced host reaction should then be effective against galling insects because their larvae cannot leave their galls once formed (Fernandes 1990).

Few studies have documented the occurrence and effectiveness of hypersensitive reactions against galling insects, however (see Anderson et al. 1989). Hypersensitivity may lack documentation for reasons other than the scarcity of its occurrence in...
nature. Studies on plant resistance to herbivory may have missed some of the host reactions, including hypersensitivity, because necrotic spots frequently seen on attacked leaves and stems may have been erroneously treated as spots caused by pathogens, although they too may be involved in the interaction. Biochemical and genetic studies should be initiated on this resistance mechanism to insect attack as well as detailed studies on the process of gall formation, because microorganisms, which are commonly linked to hypersensitive reactions, may be involved with galling (Cornell 1983, Fernandez 1980).

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Influence of the Parasite *Pilostyles ingae* (Rafflesiaceae) on some Physiological Parameters of the Host Plant, *Mimosa naguirei* (Mimosaceae)*

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Abstract: The holoparasite-host interaction of *Pilostyles ingae* (Kasr. Hook. f. (Rafflesiaceae) and *Mimosa naguirei* Barneby (Mimosaceae) was studied in the open campo rupestre vegetation of Serra do Cipó (State of Minas Gerais, Brazil). Infected *M. naguirei* plants found at this site were densely covered by flowers of the parasite on their stems indicating heavy development of cellular threads of the parasite in the bark of the hosts. Cellular threads of the parasite are likely to be richer in lipids and hence depleted in 13C. This may explain the significantly more negative carbon isotope ratios (δ13C values) of the bark of infected host plants observed as compared to other tissues of infected and non-infected host plants. Photosynthetic parameters such as potential quantum yield of photosystem II (Fv/Fm), apparent photosynthetic electron transport rates (ETR) and effective quantum yield of photosystem II (ΔF/Φm) in light dependence curves, as well as δ13C values of leaves as a relative measure of average intercellular CO₂ partial pressure during photosynthesis over the lifetime of the leaves, which is also related to average stomatal conductance via water use efficiency, were remarkably similar. This suggests a well balanced relation between the Mimosa host and the Pilostyles parasite, in contrast to other hemiparasitic angiosperm parasite-host interactions where the parasite (e.g. Strigo) is known to have strong detrimental effects on host photosynthesis.

Key words: Brazil, carbon isotope ratio, chlorophyll fluorescence, holoparasite, Rafflesiaceae.

Abbreviations:

ETR apparent photosynthetic electron transport rate
Fv/Fm potential quantum yield of PS II
ΔF/Φm effective quantum yield of PS II
PFD photosynthetic photon flux density
PS photosystem

Introduction

Like all species of the family Rafflesiaceae the members of the genus *Pilostyles* are holoparasites. Their vegetative organs are reduced to ramifying cellular threads penetrating the tissues of the host plants (Kammerer, 1962; Dell et al., 1982; Küfner et al., 1985). In the case of *Pilostyles* species, which parasitize the aerial parts of their host plants, flowers develop on adventitious shoots on the "mycelium" at the external surface of their hosts (Fig. 1). The diameter of the flowers is about 1 mm. *Pilostyles* species are unusual dioecious plants feeding on Leguminosae. They are unisexual, i.e. very host specific with each species having only one given host (Ule, 1915). They show an unusual geographic distribution: S USA to tropical S America, tropical Africa, Iran; W Australia (Willis, 1972).

In the campo rupestre at Serra do Cipó, Minas Gerais, Brazil, a large number of individuals of *Mimosa naguirei* Barneby (Mimosaceae) are parasitized by *Pilostyles ingae* (Kasr). Hook. f. The parasite influences the architecture of the host plant: parasitized plants have an increased number of branches, which are shorter than branches on non-parasitized individuals. The number of fruits produced by *M. naguirei* is not influenced by the parasite, but the fruits are smaller and have lighter seeds. There are no significant differences in seed germination between parasitized and healthy plants (Küfner and Fernandes, 1994). In general, in spite of the great number of *P. ingae* flowers, also indicating an intensive and extensive intrametrical development of the parasite, the morphologically apparent detrimental effects on the host appear to be rather limited.

In the present study we wanted to find out if and to what extent the heavy development of the parasite possibly impedes host photosynthesis, and therefore checked some ecophysiological aspects of this host/parasite interaction. Carbon isotope ratios (δ13C values) were determined as an indication of chemical compartmentation and average intercellular CO₂ concentration during photosynthesis over the whole life period of leaves as influenced by stomatal conductance and water supply, in leaves of healthy and infected host plants. Measurements of potential quantum yield of photosystem II were performed, and light dependence curves of apparent photosynthetic electron transport rates and effective quantum yield of PS II were obtained to characterize the photosynthetic apparatus.

* Dedicated to Prof. Dr. Rainer Ziegler on the occasion of his 65th birthday.
Materials and Methods

Study site and plant material

The field studies (chlorophyll fluorescence measurements) were carried out at Serra do Chipó in the central part of the state of Minas Gerais, Brazil (19°12' S, 43°28' W) in October 1995. A detailed description of the site is given by Gomes and Fernandes (1994).

Potential quantum yield of photosystem II ($F_0/F_m$) was obtained after 30 min dark adaptation of individual pinnules of the Mimosa leaves using a pulse-amplitude modulated photosynthesis yield analyzer (Mini-PAM, H. Walz, Effeltrich, Germany). Due to overcast cloudy weather on the day of the measurements, ambient photosynthetic photon flux density (PPFD) was only 380 μmol m$^{-2}$ s$^{-1}$ ($\lambda = 400$ – 700 nm). Therefore, photosynthetic capacity of leaves of non-infected and infected Mimosa plants was checked using the light curve programme of the instrument. Actinic light on the leaves was increased up to ca. 2000 μmol m$^{-2}$ s$^{-1}$ during 4 min in 8 steps following each other within 30 s. At each level of actinic light supplied by the instrument a pulse of saturating irradiance (ca. 6000 μmol m$^{-2}$ s$^{-1}$) was applied to obtain chlorophyll fluorescence parameters. The effective quantum yield of PS II is given as $\Delta F/F_m = (F_m - F)/F_m$ where $F$ is chlorophyll fluorescence of the light-adapted sample and $F_m$ is the maximum light-adapted fluorescence during a saturating light pulse. Apparent photosynthetic electron transport rates (ETR) are given as $0.5 \times \Delta F/F_m \times$ PPFD (Schreiber and Bilger, 1991), where the factor 0.5 accounts for excitation of both PS II and PS I. No correction was made for reflection since this was not known numerically for the leaves of M. nogueiri but must have been similar for all leaves measured. Due to the rapid increase in actinic light intensity over only 4 min, photosynthesis of the leaves was not in steady state at any time during these measurements. Hence, steady state values of ETR were not obtained. On the other hand, the method allows rapid comparisons under closely comparable conditions in the field. In fact, it was our aim mainly to compare the compartment of leaves of non-infected and infected plants. Since, except for the infection, all conditions were strictly comparable as non-infected and infected plants grew in close proximity at the same site, such a comparative assessment is warranted.

The carbon isotope ratios ($\delta^{13}C$ values relative to Pee Dee belemnite standard) were determined according to Osmond et al. (1975) using a Heraeus CHN rapid elemental analyser coupled on-line to a trapping box gas isotope mass spectrometer system (Finnigan MAT Delta Sx).

Table 1. $\delta^{13}C$ values (%) of tissues of non-infected and infected hosts (M. nogueiri) and female flower buds of the parasite (P. infortis). Values are $\bar{x} \pm SD$ (n). For the comparisons Latin letters (first letters) only refer to comparisons within vertical columns, i.e. to comparisons of the various tissues of non-infected and infected plants, while Greek letters (second letters) only refer to comparisons in horizontal lines, i.e. between non-infected and infected plants for a given tissue. Values followed by different letters are statistically significantly different at the $p = 0.05$ level and for $\beta^*$ at the $p < 0.001$ level (Mather’s F test).

<table>
<thead>
<tr>
<th>Tissue</th>
<th>non infected</th>
<th>infected</th>
</tr>
</thead>
<tbody>
<tr>
<td>leaf</td>
<td>-28.99 ± 0.65 (11) a, α</td>
<td>-29.61 ± 0.23 (11) a, β</td>
</tr>
<tr>
<td>bark</td>
<td>-28.33 ± 0.39 (4) b, α</td>
<td>-30.33 ± 0.39 (3) b, β'</td>
</tr>
<tr>
<td>wood</td>
<td>-28.33 ± 0.45 (4) b, α</td>
<td>-28.58 ± 0.83 (3) b, α</td>
</tr>
<tr>
<td>female flower buds</td>
<td></td>
<td></td>
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Fig. 1. Female flower buds of the holoparasite Plistyles infortis on stems of the host Mimosa nogueiri (Serra do Chipó, Minas Gerais, Brazil).
Results and Discussion

Among C3 plants carbon isotope ratios ($\delta^{13}C$ values) of the biomass are partly determined by chemical composition, in particular when different types of tissues are compared, and partly by stomatal control, e.g. when leaves are compared as photosynthetic organs. It is well-known, for example, that glycine dehydrogenase discriminates against the heavy ($^{13}C$ rich) pyruvate, and hence, is responsible for reduction of $^{13}C$ levels in fatty acids (Deniro and Epstein, 1977). Thus, the slightly more negative $\delta^{13}C$ values (less $^{13}C$) of leaves of non-infected *M. naguiri* plants as compared to the bark and the wood (statistically significant at the 0.05 level, Table 1) may be due to the leaves containing more lipids due to the presence of chloroplasts. In the infected *M. naguiri* plants there are no statistically significant differences between the $\delta^{13}C$ values of leaves and wood. Conversely, the bark of infected plants has more negative $\delta^{13}C$ values (i.e. a smaller proportion of $^{13}C$) than leaves and wood of infected plants (significant at the 0.05 level) and more negative $\delta^{13}C$ values than the bark (significant at the 0.001 level) and other parts of healthy *M. naguiri*. It is very probable that the clear difference between $\delta^{13}C$ values of the bark of infected and non-infected plants mirrors the strong development of the parasite, which is documented by the dense coverage of the stems of infected plants by flowers of the *P. bugene* parasite (Fig. 1) which must be supported by a vigorous growth of hyphae-like threads of the parasite. These threads are known to be restricted to the infected bark and to be rich in cytoplasm, membranes and lipids (Kummerow, 1962). The $\delta^{13}C$ value of the female flower buds was -28.36±0.28 (2). It did not differ from leaf and wood of the infected host plants and was less negative than the bark of these plants. The flower buds have woody scales and stalks and must have much less lipid than the "hyphae" in the bark of the host.

The light-dependence curves of apparent photosynthetic electron transport rates (ETR) and of effective PS II quantum yield (Δ $F_{v}/F_{m}$) obtained for leaves of healthy and parasitized plants of *M. naguiri*, to our surprise, were practically identical (Fig. 2). The speed at which PPFD was increased with the light curve programme of the MINI-PAud was too fast to reach steady state (see Materials and Methods). Thus, these measurements do not rule out that steady photosynthesis might indeed be different between the leaves of infected and non-infected plants. However, they do show that the speed at which the light reactions of photosynthesis are induced during PPFD increase are similar in the two cases. At the ambient PPFD of about 300 μmol m$^{-2}$ s$^{-1}$ given, neither the parasitized nor the healthy plants of *M. naguiri* were subject to photo-inhibition, since potential quantum yield ($F_{v}/F_{m}$) in both cases was close to 0.8 (inset numbers in Fig. 2; see Björkman and Demmig, 1987). The $\delta^{13}C$ values of leaves of healthy and parasitized plants of *M. naguiri* also do not differ (Table 1). In C3 plants carbon isotope ratios indicate average stomatal conductance and intercellular CO$_2$ concentration during photosynthesis over the whole lifetime of the leaves sampled, which is also related to average stomatal conductance via water use efficiency (Farquhar et al., 1989).

![Light dependence curves](image_url)

The conformity in key parameters of photosynthetic electron transport and stomatal control in parasitized and healthy host plants may be an indication of a well balanced relation between host and parasite, perhaps the result of a relatively old phylogenetical interaction. From a teleological point of view, considering a possible advantage in evolution, this is an optimal situation: the heterotrophic parasite does not impair the food-producing process of the host on which it depends.

It would be interesting to compare the influence of other parasitic angiosperms on the photosynthesis of their host...
plants. Even in hemiparasitic angiosperms there are in fact reports on partial reduction of photosynthetic capacity of host plants, e.g. in sorghum-Striga hermonthica (Graves et al., 1989; Gurney et al., 1995; Ramlan and Graves, 1996), Pemienium typhoides-Striga hermonthica (Graves et al., 1990), and cowpea-Striga gesnerioides (Graves et al., 1992) associations. Evidence for photoinhibition of photosystem II with S. hermonthica, however, is only obtained by chlorophyll fluorescence analysis of parasitized green leaves and not of parasitized cowpea relative to the uninfected hosts (Hibberd et al., 1996).

With the inoparasite, Cucurbita reflexa, it was observed that it may have enhancing effects by creating a sink stimulation which is regulated by supply and assimilation of nitrogone (Jeschke and Hilperti, 1997; Jeschke et al., 1997). The present observations did not suggest any detrimental effects of the P. inoparasite photosynthesis on pollination of M. negutiflora in the field-grown host-parasite consortium.

Acknowledgements
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References


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Photosynthesis of mistletoes in relation to their hosts at various sites in tropical Brazil

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Abstract Chlorophyll a fluorescence parameters showing the instantaneous performance and carbon-isotope ratios reflecting long-term performance of leaves were determined for a large number of mistletoe/host-pairs in the cerrado belt of Brazil. Study sites were a very exposed upland field, a semi-exposed savanna and a highly shaded gallery forest. The major question asked was if photosynthetic capacity of mistletoe leaves differed from that of the leaves of their respective hosts. It was shown that for the very exposed upland field site, photosynthetic capacity appeared to be similar in mistletoes and host leaves. The superior behaviour of host leaves in the upland field was due to particularly expressed sun-plant characteristics of the host. However, mistletoes always had higher average stomatal conductances, lower leaf temperatures at similar or even higher irradiance and higher intercellular CO₂ partial pressures than hosts. Photosynthetic performance of mistletoe leaves was independent of whether a given mistletoe species parasitized aluminium-accumulating or non-accumulating host species in the cerrado with their aluminium-rich soils.

Key words Aluminium · Carbon isotope ratios · Cerrado · Chlorophyll fluorescence · Mistletoes

Introduction

Mistletoes mainly belong to two families of the order Santalales, namely the Loranthaceae (approx. 900 species in 65 genera) and the Viscaceae (approx. 400 species, 11 genera). They occur ubiquitously (Sallé et al. 1993) in the temperate zone and in arid regions, but the large majority of mistletoe taxa is found in the tropics.

Mistletoes are generally considered to be hemiparasites feeding on the transpiration stream of their host tree for water and mineral nutrients. However, it is known that mistletoes may also acquire carbon compounds from their hosts (Ehleringer et al. 1985, Pate et al. 1991a, b; Rey et al. 1991; Marshall and Ehleringer 1990), and a holoparasitic mistletoe taxon has even been discovered, i.e. Tristerix aphyllus, which grows on the tissue of cactus stems (Kraus et al. 1995). Mistletoes can draw part of the host’s transpiration stream towards their own leaves by having a more negative leaf-water potential and a larger leaf conductance for water vapour and hence a higher transpiration rate than the host leaves (Schulze et al. 1984). This implies that there must also be complex responses of the mistletoe/host-associations to environmental factors, such as irradiance, temperature and water supply. However, comparative ecophysiological studies at different sites and under varying environmental stress conditions are still scant.
Here we present for the first time comparative measurements of chlorophyll fluorescence parameters and carbon-isotope analyses of many pairs of different mistletoe species (all of them Loranthaceae) and different hosts. Studies were performed at different sites in the cerrado belt of Brazil, where mistletoes are particularly abundant. The cerrado of the central plains of Brazil comprise a complex of various types of vegetation including seasonal savannas, dry forests and gallery forests with different degrees of sun exposure, so that comparative studies of mistletoes and their hosts can be performed under different light climates. Thus, study sites included a very exposed open site in a riparian field, a semi-exposed savanna site and a highly shaded gallery forest site. Chlorophyll fluorescence measurements provide information on the instantaneous photosynthetic performance while carbon-isotope ratios of C3 plants reflect the average stomatal conductance, intercellular CO2 partial pressure and water use efficiency during photosynthesis over the lifetime of the leaves sampled (Farquhar et al. 1989a, b).

The major question asked was if photosynthetic capacity of mistletoe leaves differed from that of the leaves of their respective hosts. Clearly, under all circumstances mistletoes must have a higher transpiration than their hosts. However, given a certain supply of carbon compounds by the host to the mistletoes, the latter might acquire a lower photosynthetic capacity in comparison to the host. On the other hand this may also depend on the productivity of the host, as determined by the light climate and sun/shade adaptations. Cerrado soils have high levels of aluminium. Given mistletoe species may occur on hosts which are Al-accumulators or non-accumulators. Since they must receive different loads of the toxic metal via the transpiration stream of these hosts the present data also provide information on the possible effects of Al on the parasites.

Chlorophyll fluorescence measurements

The chlorophyll a fluorescence measurements were performed with a pulse-amplitude modulated photosynthesis yield analyzer (Mini PAM) of H. Walz (Effeltrich, Germany) with the leaf clip holder described by Hilger et al. (1995) which allows measurements at a distance of 1 cm and angle 60° to the fibre optics. Measurements of light intensity \( \lambda = 400-700 \text{ nm} \) close to the leaf surface were taken by a micro quantum sensor calibrated against a LI-COR quantum sensor (Nebraska, USA). For measurements of fluorescence parameters in the light adapted state under continuous light to keep the natural leaf exposure on the plant and not to shade the leaves by the fibre optics and the leaf clip. Each measurement took less than 5 s allowing minimum disturbance of the leaf. Readings of potential quantum yield of photosystem II (Fm' -Fp) where Fm' is maximum quantum yield of photosynthesis in light adapted state and Fp is maximum variable fluorescence, Fv/Fm' was taken on leaf predarkened for 30 min. A reduction of Fv/Fm' below values of approximately 0.8 indicates photoinhibition which was not reversible after 30 min of darkening. Mostly for each mistletoe/host pair 5-10 readings on different mistletoe and host leaves were taken and averaged. The effective quantum yield of PSI (Fv'/Fm') was calculated as \( Fv'/Fm' = Fm' - Fp/Fm' \), where Fm' is fluorescence of the light-adapted sample and Fp/Fm' is the maximum light-adapted fluorescence when a saturating light pulse of 600 ms duration is superimposed on the prevailing emission under light levels (Schreiber and Bilger 1993). Apparent rates of electron transport through photosystem II (ETR) were obtained as 0.5 x \( Fv'/Fm' \) x PPFD (PPFD is photosynthetic photon flux density, \( \lambda = 400-700 \text{ nm} \)), where the factor 0.5 accounts for the excitation of both PS I and PS II. No correction was made for reflection as this was not known numerically. The quenching coefficients for photochemical, npq non-photochemical quenching fluorescence could not be calculated since the instrument does not allow determination of the minimum fluorescence of the light-adapted sample; Fm'. Instead relative excess light was observed as \( (Fv'/Fm')_{NPQ} = (Fv'/Fm')_{WPSI} \) (Bilger et al. 1995). Light dependencies of ETR and \( (Fv'/Fm')_{NPQ} \) were determined using a light curve programme of the instrument, where ambient light intensity was increased during 4 min in eight steps followed each other with 30 s. Due to this short time, most likely photosynthesis is the least significant component of the light saturation fast correct absolute values of ETR were not obtained. However, compare the measurements of the performance of leaves of mistletoe and the respective hosts under natural environmental conditions within a six time interval are possible in this way.

All measurements were performed between 12 and 19 October 1995 (beginning of the rainy season) and 0900-1600 hours solar tilt

Materials and methods

Sites and plants

Chlorophyll fluorescence measurements were performed and leaf material for carbon isotope analysis was collected at the following sites in the cerrado belt of Brazil:

1. Two different localities (sites) with similar vegetation of the riparian fields in the Serra do Cipó (State of Minas Gerais) at 1100-1200 m above sea level. 19°23'S, 43°28'W.

2. In a cerrado vegetation at the base of the Serra do Cipó (Rio Cipó) at 800 m above sea level.

3. In the cerrado vegetation around Brasilia (DF), namely, (a) near the Centro Olímpico (15°46'S, 47°52'W), (b) in the University of Brasilia Experimental Station (15°45'S, 47°52'W), and (c) in the Parque Nacional de Brasília (15°44'S, 47°56'W).

4. In a gallery forest at the ecological reserve of the Instituto Brasileiro de Geografia e Estatística (IBGE), Brasilia (DF) (15°56'S, 47°54'W).

Names of the mistletoes and host taxa studied are given in full with authorities where they first appear in the Tables, i.e. most of them in Table 1 and a few in Table 2. More details on the vegetation and the plants are found in Ratter (1986 b, 1986 c), Ferreira et al. (1983) and Ratter et al. (1984). Some of the hosts growing on the aluminium-rich cerrado soils were Al-accumulators while others were non-accumulators.

Carbon isotope analysis

The carbon isotope ratios (δ13C) values are relative deviations to the Pee Dee belemnite standard in parts per ten thousand (‰) determined according to Cook et al. (1975) using a Heraus CHN rapid elemental analyzer coupled on-line to a trapping-box-gas-isotope-mass spectrometer system (Fison MAT Delta S) of the error determinations is 2.0‰ external precision.

Carbon isotope ratios (δ13C) values in the leaves of C3 plants indicate the relations between intercellular CO2 partial pressure and CO2 assimilation rates as determined by the average degree of stomatal opening (stomatal conductance during photosynthesis over the 1 time of the leaf sampled, with more negative values referring to higher conductance). Often, the carbon isotope discrimination (δ) is calculated, which is directly proportional to average conductance over 6 as follows:

\[ \Delta = \frac{\delta^13C_{\text{leaf}} - \delta^13C_{\text{atm}}}{1000 + \delta^13C_{\text{atm}}} \times 10^3 \text{‰} \]

where \( \delta^13C_{\text{leaf}} \) is the value measured for the plant material and \( \delta^13C_{\text{atm}} \) the value for the CO2 of the ambient atmosphere. The latter may be somewhat different for different species. Frequently it is not measured and is set as -8‰ (Farquhar et al. 1989a). In the present study \( \delta^13C_{\text{atm}} \) was
Table 1. Comparison of chlorophyll fluorescence measurements of mistletoe/host pairs at different sites in Brazil. In the sites and species column the first species name indicates that of the mistletoe parasite the second one that of the host. Absolute values are given for the average PPFD at the level of the parasite leaves during measurements. Errors are standard deviations. The other values are comparisons, where Δ (differences) indicates mistletoe minus host values and r (ratios) mistletoe: host values.

<table>
<thead>
<tr>
<th>Sites and Species (Parasite - Host)</th>
<th>PPFD at mistletoe (μmol m-2 s-1)</th>
<th>Δ ETR</th>
<th>Δ PPFD</th>
<th>r</th>
<th>r</th>
<th>r relative excessive PPFD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rupesarian field (Serra do Cipó, Minas Gerais)</td>
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<td>Site 1: <em>Struthanthus margaritae</em> (Drege) J.H. Pisek</td>
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<tr>
<td><em>Trembleya laniflora</em> (Don.) Cognorth.</td>
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<tr>
<td>466±385</td>
<td>-155</td>
<td>-990</td>
<td>0.50</td>
<td>1.03</td>
<td>0.79</td>
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<tr>
<td>Site 2: <em>S. marginatus</em> - <em>T. laniflora</em></td>
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<tr>
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<td>-612</td>
<td>0.86</td>
<td>0.87</td>
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<tr>
<td>Site 1: <em>Pittosporum robustum</em> Mart. - <em>T. laniflora</em></td>
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<tr>
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<td>-139</td>
<td>-3</td>
<td>0.86</td>
<td>0.34</td>
<td>1.38</td>
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<tr>
<td>Site 2: <em>P. robustus</em> - <em>T. laniflora</em></td>
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<tr>
<td>1139±258</td>
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<td>-156</td>
<td>0.82</td>
<td>0.21</td>
<td>1.58</td>
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<td>Cerrado (Brasilia)</td>
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<td>Site 1: Centro Olímpico</td>
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<tr>
<td>346±454</td>
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<td>-168</td>
<td>1.35</td>
<td>1.59</td>
<td>0.79</td>
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<tr>
<td>Site 2: Experimental Station</td>
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<tr>
<td><em>P. robustus</em> - <em>Diplonyxis viridis</em> (Vog.) Malme</td>
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<tr>
<td>250±70</td>
<td>23</td>
<td>112</td>
<td>1.00</td>
<td>1.09</td>
<td>0.64</td>
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<td>Site 3: Parque Nacional</td>
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<tr>
<td><em>P. robustus</em> - <em>Rhynchospora flabellata</em> (Spr.) Kurth.</td>
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<td>203±198</td>
<td>3</td>
<td>94</td>
<td>1.03</td>
<td>0.82</td>
<td>2.02</td>
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<td><em>P. robustus</em> - Quello parviflora Mart.</td>
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<td>64±8</td>
<td>11</td>
<td>32</td>
<td>1.11</td>
<td>1.01</td>
<td>3.03</td>
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<tr>
<td>Gallery Forest (Brasilia, IBGE)</td>
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<td>Site 1: Gallery Forest</td>
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<tr>
<td><em>P. robustus</em> - <em>Clarkea viridissima</em> Camb.</td>
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<tr>
<td>91±71</td>
<td>11</td>
<td>53</td>
<td>0.93</td>
<td>0.92</td>
<td>1.05</td>
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<td><em>P. robustus</em> - <em>Corymbia gallonii</em> Gardner</td>
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<tr>
<td>112±11</td>
<td>14</td>
<td>49</td>
<td>0.88</td>
<td>0.80</td>
<td>0.86</td>
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<td><em>Phoradendrum crassifolium</em> (Pohl) Eichl. - <em>I. cf. ephusa</em></td>
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<tr>
<td>0.10</td>
<td>-9</td>
<td>-24</td>
<td>0.98</td>
<td>0.97</td>
<td>1.15</td>
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<tr>
<td><em>P. crassifolium</em> - <em>Microcarpa spinosa</em> Naud.</td>
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<tr>
<td>30±8</td>
<td>-12</td>
<td>-64</td>
<td>1.01</td>
<td>1.26</td>
<td>0.19</td>
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<tr>
<td><em>P. crassifolium</em> - <em>Toona guianensis</em> Aubl.</td>
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<tr>
<td>18±12</td>
<td>3</td>
<td>8</td>
<td>0.96</td>
<td>0.93</td>
<td>1.48</td>
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<td>Site 2: Ecorena Gallery Forest-Cerrado</td>
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<tr>
<td><em>Phoradendron crassifolium</em> Urb. - <em>T. ruifolius</em></td>
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<tr>
<td>252±71</td>
<td>18</td>
<td>75</td>
<td>0.88</td>
<td>0.94</td>
<td>0.76</td>
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</table>

measured, and therefore we preferred to tabulate the δ13C values which were the direct results of analyses of carbon-isotope ratios of the leaf material sampled. However, we used Eq. 1 and an assumed value of -8.00 % for δ13C to calculate intercellular CO2 partial pressure, pco2 as follows

\[ p\text{co}_2 = \frac{p\text{co}_2 \cdot \Delta - a}{b} \]

where \( p\text{co}_2 \) is CO2 partial pressure of the ambient atmosphere, taken here as 340 Pa/MPa, a given/discrimination due to CO2 diffusion in air (4.4 %a) and b the net fractionation caused by carboxylation in C3 photosynthesis (27.6 %a) (Farquhar et al. 1989a, b; Broadmeadow et al. 1992).

Errors given are always standard deviations.

Results and discussion

Chlorophyll-fluorescence measurements of mistletoe/host pairs at ambient irradiation

In the rupesarian field (Serra do Cipó, Minas Gerais), with the rather open exposed vegetation F'/Fm (potential quantum yield of PS II after 30 min dark adaptation) was always lower in the mistletoes than in the host leaves on a sunny day (Table 1). The range of F'/Fm in the hosts was from 0.677 ± 0.113 to 0.814 ± 0.010 and in the mistletoes 0.542 ± 0.042 to 0.702 ± 0.023. This shows that both mistletoes and host were often under photo-inhibition not reversible during the applied darkening period of 30 min (F'/Fm < 0.8) but the mistletoes more strongly than the host. On an overcast day immediately following the sunny day with only 380 μmol m-2 s-1 ambient irradiance the relationship was inverse, the mistletoes showed F'/Fm values of 0.732 ± 0.035 (Pittosporum robustus) and 0.839 ± 0.011 (Struthanthus marginatus) while the host (Trembleya laniflora, Melastomataceae) had 0.615 ± 0.053 showing that the mistletoes had largely recovered from photo-inhibition under the lower irradiance in contrast to the host.

When irradiance received by leaves of parasite and host was of comparable intensity the mistletoe (P. robustus) on average had much lower ΔF/Fm' (effective quantum yield) (-0.09) and ETR (apparent relative electron transport rate) (-50 μmol m-2 s-1) and higher relative excessive PPFD (-0.87) than the host, where the respective values were ΔF/Fm ~ 0.30, ETR ~ 210 μmol m-2 s-1, and relative excessive PPFD ~ 0.60. For the more shaded mistletoe S. marginatus, of course, values of ΔF/Fm' and relative excessive PPFD were more favourable in comparison to the host than in the more exposed P. robustus due to the light dependency of these variables. However, average ETR was rather low in the mistletoes (~ 40 μmol m-2 s-1). Overall, the comparison
of the mistletoes _S. marginatus_ and _P. robustus_ with their host _T. laniflora_ (Table 1) shows that mistletoe photosynthesis was less effective than host photosynthesis at the rupetran field site.

In the cerrados around Brasilia the more dense vegetation led to lower overall irradiance on both mistletoe and host leaves, and all the chlorophyll fluorescence parameters for the parasite (exclusively _Phoradendron verticillatum_ at the cerrado sites) and its various hosts were much more similar (Table 1). The range of average values measured on leaves of individual plants was as follows for parasites and hosts, respectively: \( \Delta F/F' \_m \) 0.384 ± 0.181 to 0.693 ± 0.044 and 0.250 ± 0.146 to 0.720 ± 0.026, ETR 22 ± 4 to 73 ± 45 and 11 ± 2 to 72 ± 83 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), relative excessive PIPFD 0.171 to 0.499 and 0.040 to 0.644. Photoinhibition also was limited and only occasionally apparent in hosts (e.g., in _Pouteria ramiflora_, Sapotaceae, with an \( F'/F_m \) of 0.576 ± 0.034) with ranges of \( F'/F_m \) values of the mistletoe (_P. verticillatum_) and hosts (excepting _P. ramiflora_) of 0.757 ± 0.075 to 0.838 ± 0.088 and 0.702 ± 0.084 to 0.805 ± 0.007, respectively.

In the gallery forest (IBGE, Brasilia) irradiance was very low during the measurements at midday (1200–1430 hours solar time). The highest PIPFD received by mistletoe leaves measured was 112 ± 11 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) and it was 97 ± 92 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) on host leaves. At the site in the ectomycorrhizal forest/cerrado the irradiance was 252 ± 71 (mistletoe) and 177 ± 132 (host) \( \mu \text{mol m}^{-2} \text{s}^{-1} \). At the shaded gallery forest site chlorophyll fluorescence parameters were rather similar for parasites and hosts (Table 1) with ranges of average values as follows: \( \Delta F/F' \_m \) 0.619 ± 0.156 to 0.790 ± 0.035 and 0.626 ± 0.207 to 0.783 ± 0.012, ETR 0 ± 0 to 37 ± 3 and 4 ± 1 to 23 ± 5 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), relative excessive PIPFD 0.045 to 0.207 and 0.062 to 0.233, respectively. There was no or only in a few cases a peak indication of photoinhibition with \( F'/F_m \) values of 0.734 ± 0.049 to 0.827 ± 0.006 and 0.816 ± 0.10 to 0.838 ± 0.012 for mistletoes and host, respectively. By contrast, in the ectocarp with its higher irradiance \( F'/F_m \) values of 0.652 ± 0.110 for the mistletoe _Phoradendron verticillatum_ and 0.741 ± 0.025 for its host _Tupira guianensis_ (Anacardiaceae) did indicate some photoinhibitory reduction of photosynthetic efficiency. ETRs were higher than in the gallery forest with 66 ± 14 and 48 ± 30 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for mistletoe and host respectively, and the other parameters changed accordingly. However, performance of host and mistletoe was still rather similar (Table 1).

An overall comparison of all mistletoe and host measurements is given in Fig. 1. As expected, effective quantum yield of PSII (\( \Delta F/F' \_m \)) with increasing PIPFD, both ETR and relative excessive PIPFD increased with PIPFD with an indication of the typical light-saturation behaviour at higher PIPFDs. These relations do not show differences between the general behaviour of mistletoes and their host plants, except for the three points of host measurements at the highest PIPFDs in Fig. 1A-C which suggests that in these cases at high PIPFD there was better effective quantum yield, higher ETR and lower relative excessive PIPFD in the hosts. These points are all from the measurements of the _T. laniflora_ host plants in the rupetran field site.

Therefore, it appears, on the basis of the actual performance in the field, that the relative behaviour of parasites and hosts in comparison with each other depends on the site and environment and that the strong disadvantage of mistletoes vs hosts was restricted to the rather open and exposed rupetran field site. On the other hand, it may be argued that this pronounced parasite-host difference in the rupetran field was mostly due to the particular behaviour of the dominating or almost exclusive host _T. laniflora_. This may be evaluated comparing the respective light-dependence curves (Table 2) which give more insight into the potential capacities of the plant species involved.
Table 2. Comparison of cardinal points of light dependence curves of chlorophyll-fluorescence measurements of mistletoe and host plants at different sites in Brazil. In the sites and species column the first species name indicates that of the mistletoe parasite, the second one that of the host. ETR_{max}, maximum apparent relative electron transport rate. ParRS, PPFD at half ETR_{max}; yield_{RS} yield (ΔF/F_{m}) at ParRS; Δ, mistletoe minus host values; r, mistletoe divided by host values. Values are averages of two light-dependence curves except for the bright day on Canapi pasture (Serra do Cipó) where averages were obtained from 3-4 curves. * refers to curves which did not saturate below a PPFD of 200 μmol m^{-2} s^{-1}.

<table>
<thead>
<tr>
<th>Sites and Species (Parasite = Host)</th>
<th>Parasite</th>
<th>Host</th>
<th>ParRS</th>
<th>Yield_{RS}</th>
<th>ETR_{max}</th>
<th>Yield_{max}</th>
<th>ETR_{max}</th>
<th>Δ</th>
<th>ParRS</th>
<th>Yield_{RS}</th>
<th>ETR_{max}</th>
<th>Yield_{max}</th>
<th>ETR_{max}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rupesatern field (Serra do Cipó, Minas Gerais)</td>
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</tr>
<tr>
<td>bright day: S. marginata - T. laniflora</td>
<td>285 ± 0.39</td>
<td>105 ± 0.62</td>
<td>&gt;250</td>
<td>-230</td>
<td>0.62</td>
<td>-150</td>
<td></td>
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</tr>
<tr>
<td>P. robustus - T. laniflora</td>
<td>310 ± 0.41</td>
<td>125 ± 0.63</td>
<td>&gt;250</td>
<td>-275</td>
<td>0.65</td>
<td>-215</td>
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</tr>
<tr>
<td>overcast day: S. marginata - T. laniflora</td>
<td>320 ± 0.40</td>
<td>131 ± 0.62</td>
<td>&gt;250</td>
<td>-140</td>
<td>0.65</td>
<td>-150</td>
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</tr>
<tr>
<td>P. robustus - T. laniflora</td>
<td>200 ± 0.54</td>
<td>105 ± 0.62</td>
<td>&gt;280</td>
<td>-260</td>
<td>0.87</td>
<td>-175</td>
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</tr>
<tr>
<td>Cerrado (near Rio do Cipó, Minas Gerais)</td>
<td>S. marginata (dark green) - Vernonia fruticosa Mart.</td>
<td>220 ± 0.61</td>
<td>135 ± 0.63</td>
<td>&gt;295</td>
<td>-260</td>
<td>0.97</td>
<td>-160</td>
<td></td>
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</tr>
<tr>
<td>S. marginata (yellow green) - V. fruticosa</td>
<td>200 ± 0.39</td>
<td>76 ± 0.63</td>
<td>&gt;295</td>
<td>-270</td>
<td>0.62</td>
<td>-220</td>
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<tr>
<td>Cerrado (Brasilia)</td>
<td>V. fruticosa (non parasitized)</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
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</tr>
<tr>
<td>Site 1: Centro Olímpico</td>
<td>P. ocaña - P. ramiflora</td>
<td>300 ± 0.46</td>
<td>160 ± 0.28</td>
<td>110</td>
<td>1.71</td>
<td>60</td>
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</tr>
<tr>
<td>P. ocaña - S. ferrugineus new leaves</td>
<td>250 ± 0.50</td>
<td>125 ± 0.63</td>
<td>180</td>
<td>-55</td>
<td>0.79</td>
<td>-60</td>
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</tr>
<tr>
<td>P. ocaña - old leaves</td>
<td>250 ± 0.50</td>
<td>125 ± 0.62</td>
<td>240</td>
<td>145</td>
<td>0.94</td>
<td>-70</td>
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</tr>
<tr>
<td>Site 2: Experimental Station</td>
<td>P. ocaña - D. violacea</td>
<td>450 ± 0.48</td>
<td>210 ± 0.59</td>
<td>210</td>
<td>60</td>
<td>0.76</td>
<td>0</td>
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<tr>
<td>P. ocaña - D. coelocobolus</td>
<td>245 ± 0.53</td>
<td>135 ± 0.67</td>
<td>95</td>
<td>65</td>
<td>0.79</td>
<td>40</td>
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</tr>
<tr>
<td>P. ocaña - Q. purpurea</td>
<td>320 ± 0.57</td>
<td>&gt;180 ± 0.60</td>
<td>105</td>
<td>140</td>
<td>0.93</td>
<td>75</td>
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</tr>
<tr>
<td>Site 3: Parque Nacional</td>
<td>P. ocaña - K. tomentosa</td>
<td>265 ± 0.59</td>
<td>155 ± 0.53</td>
<td>185</td>
<td>-75</td>
<td>1.11</td>
<td>-30</td>
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<tr>
<td>P. ocaña - V. rufa</td>
<td>280 ± 0.62</td>
<td>175 ± 0.57</td>
<td>130</td>
<td>70</td>
<td>1.09</td>
<td>55</td>
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</tr>
<tr>
<td>Gallery Forest (Brasilia, IBGE)</td>
<td>P. ocaña - C. ericifolia</td>
<td>195 ± 0.67</td>
<td>110 ± 0.61</td>
<td>230</td>
<td>-195</td>
<td>0.98</td>
<td>-125</td>
<td></td>
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</tr>
<tr>
<td>P. ocaña - C. ericifolia</td>
<td>210 ± 0.66</td>
<td>140 ± 0.65</td>
<td>150</td>
<td>-35</td>
<td>1.00</td>
<td>-15</td>
<td></td>
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</tr>
<tr>
<td>P. ocaña - C. ericifolia</td>
<td>100 ± 0.53</td>
<td>60 ± 0.67</td>
<td>65</td>
<td>-60</td>
<td>0.79</td>
<td>-25</td>
<td></td>
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</tr>
<tr>
<td>P. ocaña - C. ericifolia</td>
<td>200 ± 0.55</td>
<td>100 ± 0.59</td>
<td>130</td>
<td>-20</td>
<td>0.90</td>
<td>-30</td>
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</tbody>
</table>

Light-dependence curves of mistletoes and their hosts.

Light-dependence curves of ETR and effective quantum yield (ΔF/F_{m}) of photosynthesis were obtained for many mistletoe/host pairs as summarized in Table 2. A few selected examples are shown in Fig. 2. The host plant of the mistletoes at the rupesatern field site showed the highest maximum ETR (over 250 up to 375 μmol m^{-2} s^{-1}; Fig. 2A, Table 2) although another species measured in the rupesatern field, namely Minosia nagi, even had an ETR < 400 μmol m^{-2} s^{-1} (Fernandes et al. 1997). Another mistletoe-host the Asteraceae Vernonia fruticosa at an open road-side site in the cerrado at the base of Serra do Cipó, and even Canapi crane in the gallery forest also had high ETR_{max} (over 250 and over 200 μmol m^{-2} s^{-1}, respectively). In the mistletoes an ETR_{max} over 200 μmol m^{-2} s^{-1} was only reached in one case. Overall the range of ETR_{max} was much smaller in the mistletoes (60-210 μmol m^{-2} s^{-1}) than in their hosts (85-375 μmol m^{-2} s^{-1}). Thus, the large difference between parasites and hosts in the rupesatern field seems to be a matter of the specific hosts. With the smaller PPFD and effective quantum yield at half saturation of ETR and the lower ETR_{max} the mistletoes behave like shade plants in comparison to the sun-plant characteristics of the host. In the other less exposed sites this strong difference disappears due to the less pronounced sun-plant characteristics of the hosts.

Carbon isotope ratios and calculated internal CO₂ partial pressures of leaves and leaf-temperature differences in mistletoe/host pairs.

Carbon isotope ratios of all mistletoes and hosts studied showed that all taxa were C₃-plants, including C. ericifolia in the gallery forest at IBGE, i.e. the species of a genus
comprising many CAM and C3/CAM intermediate species (Lütge 1996). For all pairs measured the host values of δ13C were always less negative than the parasite values. Among C3-plants more negative δ13C values indicate larger long-term average stomatal conductance and transpirational loss of water. Larger transpiration should lead to increased transpirational cooling of the leaves, and indeed, this prediction from the long-term average behaviour given by the carbon-isotope analyses of leaf biomass is also borne out by the instantaneous determinations of actual leaf temperatures (Lr) during chlorophyll fluorescence measurements. Leaf temperatures in the present study ranged from 23.5 ± 1.1 to 29.2 ± 0.5 and 25.1 ± 0.1 to 32.5 ± 0.3°C in parasites and hosts, respectively. Lr was consistently lower in the leaves of mistletoes as compared to the leaves of hosts. Only in a few cases was Lr equal in mistletoes and hosts, but this only occurred at low absolute irradiance (compare Table 3 with Table 1 for PPFD) at the level of mistletoe leaves. The lower Lr of mistletoes in some cases can be explained by lower irradiance received by the leaves of mistletoes when these are shaded by the host. However, mistletoe Lr was also lower than host Lr in cases where the mistletoe leaves received similar or higher average irradiance than the host leaves. The lower Lr in the mistletoes then must have been due to higher transpirational cooling. In many cases these temperature differences were large enough to be sensed by touching the leaves with the fingers. The larger stomatal conductance of mistletoes as compared to their hosts also implies that internal CO₂-partial pressure of mistletoe leaves was higher than that of host leaves (Eq. 2; Table 3).

Mistletoes on aluminium accumulating and non-accumulating hosts

The cerrado soils are very rich in aluminium. Some of the host plants are known to be strong Al-accumulators, namely Qualea parviflora, Vochysia rafa and Miconia chantinsois (Haridasan 1982). The other host plants (Tables 1–3) of this study were non-accumulators. However, comparisons show that there were no significant differences in potential quantum yield of dark adapted leaves (Fv/Fm) and leaf temperatures (data not presented) and δ13C-values (Table 3) for a given mistletoe species, e.g. Phthiriusa ovata or Phoradendron crassifolium, on Al-accumulating and non-accumulating hosts. Since the mistletoes receive much more Al on Al-accumulating than on non-accumulating hosts (data not shown), this implies that their photosynthetic apparatus and stomatal regulation are well adapted to increased Al-levels as there is no increased photo-inhibition (no reduced Fv/Fm) or reduced transpirational cooling (no less negative δ13C-values, no increased leaf temperatures) in the mistletoes on the Al-accumulating in relation to the non-accumulating hosts.

General discussion

Is it now well established that in addition to water and mineral ions, mistletoe parasites also receive more or less considerable amounts of photosynthetic products from their hosts, and in extreme cases mistletoes have even become
Table 3. Comparison of carbon isotope ratios (δ¹³C, PDB) calculated internal CO₂ partial pressures (pCO₂) and leaf temperatures (T) of mistletoe/host pairs at different sites in Brazil. In the sites and species column the first species name indicates that of the mistletoe parasite the second one that of the host. δ mistletoe minus host values. Leaf temperatures are those obtained during the measurements of Table 1. Values of δ¹³C marked by asterisks are averages of two samples, otherwise values are for single samples analysed.

<table>
<thead>
<tr>
<th>Sites and Species (Parasite - Host)</th>
<th>δ¹³C (%)</th>
<th>pCO₂ (Pa/MPa)</th>
<th>Δ</th>
<th>T (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rupenstinian field (Serra do Cipó, Minas Gerais)</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Site 1: <em>S. marginatus</em> - <em>T. longiflora</em></td>
<td>-29.25</td>
<td>-2.73</td>
<td>306</td>
<td>263</td>
</tr>
<tr>
<td>Site 2: <em>S. marginatus</em> - <em>T. flammea</em></td>
<td>-31.42</td>
<td>-3.47</td>
<td>298</td>
<td>235</td>
</tr>
<tr>
<td>Site 1: <em>P. robiniae</em> - <em>T. longiflora</em></td>
<td>-30.26</td>
<td>-3.31</td>
<td>300</td>
<td>247</td>
</tr>
<tr>
<td>Site 2: <em>P. robiniae</em> - <em>T. flammea</em></td>
<td>-29.53</td>
<td>-4.64</td>
<td>268</td>
<td>242</td>
</tr>
<tr>
<td>Cerrado (near Rio do Cipó, Minas Gerais)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. marginatus</em> (yellow-green) - <em>V. franciscana</em></td>
<td>-32.09</td>
<td>-2.86</td>
<td>308</td>
<td>263</td>
</tr>
<tr>
<td><em>S. marginatus</em> (dark-green) - <em>V. franciscana</em></td>
<td>-31.83</td>
<td>-5.48</td>
<td>304</td>
<td>217</td>
</tr>
<tr>
<td>Cerrado (Brazilia)</td>
<td></td>
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<tr>
<td>Site 1: Centro Olimpico</td>
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<tr>
<td><em>P. bracteata</em> - <em>P. trichodes</em></td>
<td>-28.65</td>
<td>-2.71</td>
<td>297</td>
<td>254</td>
</tr>
<tr>
<td><em>P. bracteata</em> - <em>S. carenius</em></td>
<td>-29.46</td>
<td>-2.17</td>
<td>301</td>
<td>266</td>
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<tr>
<td>Site 2: Experimental Station</td>
<td></td>
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</tr>
<tr>
<td><em>P. bracteata</em> - <em>D. violacea</em></td>
<td>-29.59</td>
<td>-6.09</td>
<td>311</td>
<td>205</td>
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<td><em>P. bracteata</em> - <em>C. pachysperma</em></td>
<td>-29.76</td>
<td>-2.21</td>
<td>306</td>
<td>211</td>
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<tr>
<td><em>P. bracteata</em> - <em>Q. paraflorana</em></td>
<td>-28.69</td>
<td>-2.78</td>
<td>298</td>
<td>234</td>
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<tr>
<td>Site 3: Parque Nacional</td>
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<tr>
<td><em>P. bracteata</em> - <em>K. coracent</em></td>
<td>-27.63</td>
<td>-5.85</td>
<td>330</td>
<td>238</td>
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<tr>
<td><em>P. bracteata</em> - <em>V. ruba</em></td>
<td>-26.19</td>
<td>-4.86</td>
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<td>220</td>
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<tr>
<td>Gallery Forest (Brazilia, IBGE)</td>
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<tr>
<td>Site 1: Gallery Forest</td>
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<tr>
<td><em>P. bracteata</em> - <em>C. triloba</em></td>
<td>-26.72</td>
<td>-5.18</td>
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<td><em>P. bracteata</em> - <em>I. affinis</em></td>
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<td>-1.64</td>
<td>313</td>
<td>229</td>
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<td><em>P. bracteata</em> - <em>M. lagenaria</em></td>
<td>-28.77</td>
<td>-1.95</td>
<td>304</td>
<td>271</td>
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<tr>
<td><em>P. bracteata</em> - <em>M. africana</em></td>
<td>-30.57</td>
<td>-2.80</td>
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<td>264</td>
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<td>-30.68</td>
<td>-1.20</td>
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<tr>
<td><em>P. bracteata</em> - <em>M. glabrescens</em></td>
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<td>-3.19</td>
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<td><em>P. bracteata</em> - <em>M. choroanthos</em></td>
<td>-28.43</td>
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<td><em>P. bracteata</em> - <em>T. guamae</em></td>
<td>-26.97</td>
<td>-1.00</td>
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<td>227</td>
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</tbody>
</table>

holoparasites and are entirely dependent on their hosts (see Introduction). Thus, one might have expected that mistletoes could afford a lower photosynthetic capacity than the leaves of their hosts. The present chlorophyll fluorescence measurements of mistletoe/host pairs apparently do not bear out such a relationship between parasite and host photosynthesis. In only a few cases did the host show a superior photosynthetic capacity, but this can be explained by a particular adaptation of the host to high irradiance in an open habitat. It is not a general feature of host/mistletoe-relations because largely photosynthetic capacity of host and parasite leaves appeared to be similar. However, the carbon isotope analyses show that mistletoes have a lower average stomatal conductance than the host leaves. This is already well known (Ziegler 1980; Richter et al. 1995) and a prerequisite for the mistletoes to drag the host transpiration stream with dissolved mineral nutrients to their own stems and leaves (Schulze et al. 1984). It has, however, additional consequences. One of them is the fact that mistletoe photosynthesis operates at higher intercellular leaf CO₂ partial pressures (pCO₂) than host photosynthesis. The present carbon isotope data suggest that on average pCO₂ in mistletoes was 52±25 (21) Pa/MPa larger than that of hosts (Table 3). Thus, host leaves have a handicap as compared to parasites. Achievement of similar ETR and effective quantum yields (AF/AFₑ) by mistletoe leaves as compared to hosts leaves may then well be due to compensation of lower intrinsic capacity by higher substrate (CO₂) concentration. When mistletoes have similar rates of photosynthesis at larger stomatal conductance this also implies that they have smaller water-use-efficiencies than hosts.

Another consequence of higher stomatal conductance of mistletoes dragging mineral solutes towards the mistletoe leaves is that also toxic metals dissolved in the transpiration stream should accumulate in the mistletoes. Thus, the mistletoes must receive much more Al from Al-including hosts than from non-includers on the Al rich cerrado soils. Since there were no differences between mistletoes of given species on the two types of hosts, the mistletoes must be quite Al-resistant. Finally, the consistently lower mistletoe leaf temperature as compared to host leaf temperature, of course, is also a consequence of higher stomatal conductance of the mistletoes. It is an intriguing question if this cooling is only an unavoidable side effect of the higher transpiration of the parasites or if it has other advantages for the mistletoes, e.g. reducing stress in a hot environment.
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References


Global patterns in local number of insect galling species

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Abstract. We evaluate a three-part hypothesis explaining why gall-inducing insect species richness is so high in sclerophyllous vegetation. (1) persistence of low nutrient status scleromorphic leaves facilitates the galling habit in warm temperate latitudes; (2) favorable colonization sites for gallers result from reduced hygrothermal stress, high phenolics in the outer cortex of the gall, and reduced carnivore and fungal attack in the gall; and (3) in more mesic sites, mortality is high due to carnivore attack and invasion of galls by fungi. Over 280 samples of local species of galling herbivorous insects from fourteen countries on all continents except Antarctica revealed a strong pattern of highest richness in warm temperate latitudes, or their altitudinal equivalents. The peak of galling species richness on the latitudinal gradient from the equator into the Arctic was between 25° to 38°N or S. Galling species were particularly diverse in sclerophyllous vegetation, which commonly had greater than twelve species per local sample.

In mesic, non-sclerophyllous vegetation types the number of galling species was lower with twelve or fewer species present. Many sites in sclerophyllous vegetation supported between thirteen and forty-six galling species locally, including carpinia islands in Amazonia, cerrado savanna in central Brazil, the Sonoran Desert in Arizona and Mexico, shrubland in Israel, fynbos in South Africa and coastal scleromorphic vegetation in Australia. At the same latitude, or its elevational equivalent, galling species richness was significantly higher in relatively xeric sites when compared to riparian or otherwise mesic habitats, even when scleromorphic vegetation dominated the mesic sites. The results were consistent with the hypothesis and extend to a more general level the patterns and predictions on the biogeography of gall-inducing insects.

Key words. Biodiversity, galling insects, latitudinal gradients, local species richness, scleromorphic vegetation.

INTRODUCTION

The discovery of broad patterns in nature stimulates the generation of factually based theory in biology. Hence, one of the preoccupations among ecologists has been the search for pattern and the mechanisms that shape pattern (e.g. MacArthur, 1972; Tilman, 1989; Brown, 1995). Phytoecologists and biongeographers have been particularly strong in employing broadly comparative studies. Most of the faunal studies in global patterns have been based on comparisons of regional species richness, depending on compilations from many sources and diverse sampling techniques (e.g. Fischer, 1960; Williams, 1964; Wilson, 1992, and review by Stevens, 1989). Problems with direct comparisons arise because of different sampling intensities, sampling methods, unequal areas sampled, and lack of tests on how such methodological differences influence the data base. (Alternatively, only one taxon of plants has been sampled, such as bracken fern by Lawton and colleagues [e.g. Lawton, Lawton & Compston, 1993], providing less general views of pattern.)

For the past 12 years we have employed a broad and more directly comparable approach by sampling in standardized ways the local number of insect herbivore galling species around the world. The small number of people engaged in the sampling and the use of standardized methods, minimize sampling error and unwanted sources of bias. With over 280 samples completed from around the world, we are able to report on patterns of local species richness.

We are unaware of a similarly cosmopolitan data set for any other group of animals or plants. The small size of galling species, their abundance and ubiquity, the persistence of galls on plant parts, and their commonly conspicuous form, make them easy subjects for such a study. However, with issues of biodiversity and conservation becoming central concerns among naturalists, and given the longstanding debate on the cause of latitudinal gradients in species richness (e.g. Dobzhansky, 1950; Rohde, 1992),

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we feel that similar studies on other groups should be encouraged.

In the search for more general patterns and synthesis we extended previously reported results by more than doubling the number of previous samples, increasing the geographical range of samples, and testing the validity of ground-based samples in forest vegetation with tall canopy trees, especially those in tropical forests. We have also tested the comparability of the two sampling methods employed. Comparisons of galling species distribution in Arizona, U.S.A., and Minas Gerais, Brazil, were reported by Fernandes & Price (1988, 1991, 1992). Price (1991) provided additional data covering a latitudinal gradient from Amazonia into the Arctic. The mechanisms driving the pattern were investigated by Fernandes & Price (1991, 1992).

We based our questions on the following steps in the study of local galling species richness: (1) initially superficial observations in Arizona; (2) the subsequent research results reported by Fernandes & Price (1988); (3) a more global view in Price (1991); and (4) hypotheses on mechanisms driving the pattern suggested by Fernandes & Price (1991, 1992). Our studies in Arizona and Minas Gerais showed similar and strong increases in galling species richness with increasing elevation and from more mesic to more xeric environments. Local samples at one elevation indicated the same kind of pattern with consistently more galling species in xeric than adjacent riparian and mesic sites. Correlated with increasing aridity and gall species numbers was a shift in vegetation from mesophytic woody plants to xerophytic, sclerophyllous shrubs and small trees. Further studies showed that galls in mesic sites were exposed to significantly higher mortality from carnivores and fungal attack, suggesting a mechanistic explanation for the patterns. Based on general knowledge of galling insects and sclerophyllous plants we erected the following hypothesis (Fernandes & Price, 1991). Scleromorphic vegetation develops on nutrient-poor soils, and conservation of nutrients results from the evolution of long-lived and therefore tough leaves, with reduced probability of abscission. The high carbon gain from photosynthesis in low-nitrogen-status plants also results in carbon-based chemical defenses, notably phenolics and tannins. Nutrient concentration in the feeding zone for insects in galls is well documented (White, 1983), as are the increased concentrations of chemical defenses in the outer cortex (Fernandes & Price, 1994). Therefore, sclerophyllous plants provide favorable sites for colonization because of reduced abscission, reduced hygro-thermal stress in xeric habitats, nutrient concentration, and increased chemical defense against other herbivores and fungal pathogens. Over evolutionary time galling species will tend to increase in richness in scleromorphic vegetation more rapidly than in mesophytic vegetation. A clear prediction from this hypothesis is that in warm-temperate, Mediterranean types of vegetation, dominated by woody scleromorphic species, galling species richness should reach a peak on latitudinal gradients. We were interested to discover if this prediction were evident over a much more extensive biogeographical range.

The questions we addressed in our research were as follows. (1) Are the patterns found in Arizona and Minas Gerais general on a more global basis? (2) Is the peak in galling species richness with warm temperatures a general pattern? (3) Is high richness in insect galling species associated with sclerophyllous vegetation? (4) At the same latitude, are mesic sites generally depauperate relative to drier sites in galling species richness? (5) Does this broad-based sampling approach provide clues to the mechanisms that shape the pattern? (6) Can galling species richness be predicted for an unsampled region?

METHODS

Sampling was conducted between 1984 and 1994, intensively in Arizona and Minas Gerais, and intermittently elsewhere as opportunities materialized. Basic assumptions have been that each gall morph is unique to a galling species and that gall species are specific to a single plant species. Small errors may have resulted from dimorphism of galls within species of aphids, cynipids, and eriophyds, but few sites contained many species in these taxa. The taxonomy of galling species is in a state of flux, and changes in taxonomy increasingly reflect support for host specificity of gallers and gall morphology as an indicator of a morphospecies of insect (cf. Price & Roininen, 1993; Roininen et al., 1993; Kopeik, 1989). Galls were opened to determine if they had been induced by an insect species.

There is no doubt that after much sampling experience observers could anticipate the kind of galler species richness to be found at a particular latitude and in a certain vegetation type. Thus, potential biases may be of concern. However, the range in richness at one latitude and even within one geographical region was considerable, as will be seen in the results, so there was a persistent challenge to find as many species as possible. Therefore, any subjective bias was probably very small, and certainly diminutive relative to the strength of the patterns revealed.

Sampling Method I—architectural census

At each site a 10-m-wide transect was staked out and all plants were searched for galls above ground until 1000 herba, 100 shrubs, and forty-five trees had been sampled, representing the three major architectural types of plants. Previous tests on the adequacy of this sampling intensity showed that an asymptotic species richness was always reached before the total sample was completed (Fernandes & Price, 1988). The different number of plants sampled in each structural category was necessary to compensate for size differences and the frequency of galling insects on each type. Generally, galling species are far more common and abundant on woody plants than on herbs (Fernandes & Price, 1988, 1991). In both the tropics and in the temperate regions, 99% of all galling species discovered per site were included when the following sizes were used: 461.2 ± 288.9 for herba, 58.5 ± 22.1 for shrubs, and 25.9 ± 12.4 for trees (Fernandes & Price, 1988).

Sampling Method 2—60-min census

An alternative sampling procedure was much less time consuming and more practical when extensive traveling was underway. At each site a 60-min census was taken by examining all plants carefully while moving slowly through an area. Paths and roads were commonly used as census routes because foliage is lower in the canopy at their edges, and they provided access through dense vegetation. A record was kept on morphospecies of plants and gall types and the total number of galling species was recorded. Disturbance of vegetation, including trimming, increases the chances of finding galls because many species attack rapidly growing shoots. Therefore, use of paths and roads no doubt increased the rate of discovery of galling species, although the total species richness in a locale would be little affected because all species were usually discovered well within the 1-h sample time.

Comparison of methods

In Arizona both methods were employed on the same elevational gradient at the same sites, for a total of eleven sites from 584 to 3843 m at intervals of 305 m, plus one sample at 3843 m. Pearson's product-moment correlation analysis was employed to test for the similarity between sampling methods (Sokal & Rohlf, 1969).

Comparison of ground-based and canopy samples

The potential for erroneous estimates derived only from ground-based sampling in tall vegetation was evaluated in two tropical forest locations.

In Panama, in September 1993, method 2, the 60-min census, was used to sample from the ground, and compared with paired samples in the canopy taken from a gondola hanging from a crane. The site was in the Parque Natural Metropolitano in Panama City with the crane erected and operated by the Smithsonian Tropical Research Institute in Arenal. A total of 8 h sampling the canopy from the crane and 8 h sampling the understory from the ground covered most of the area available within the 45 m radius of the crane's boom. Each 30-min sample in the canopy was matched with a 30-min sample below, providing sixteen matched pairs for comparison.

In Amazonia, a similar test was conducted near Porto Velho, Rondonia, in February 1994. Thirty-one ground-based samples were matched with thirty-one samples in the canopy of trees which had been lowered to the ground. We used sampling method 2 again. In the young second-growth forest, each tree could be bent over by several people and sampled.

For both sets of samples, the Wilcoxon matched-pairs signed-ranks test was employed to test the null hypothesis that no significant differences existed between canopy and understory samples (Siegel, 1956). Two-tailed tests were used because we had no prediction on how the canopy and ground samples would compare.

Choice of sampling sites

Two approaches were employed in designating sampling sites. A formal design was used in Arizona and Mexico and Minas Gerais, with one or two samples taken at every 305 m elevational interval above sea level, from 0 m in Mexico to 3843 m in Arizona, and from 650 to 1350 m in Minas Gerais (Fernandes & Price, 1988, 1991). Sampling method 1, the architectural census, was used. Informal, opportunistic sampling using method 2, the 60-min census, was conducted during travels principally for other purposes. Samples were taken whenever time allowed when more or less natural vegetation was available. When opportunities permitted, diverse vegetation types within an area were sampled.

Comparison between sampling personnel

We were interested in detecting any personal bias in sampling, so whenever two samplers took independent samples in the same locality, closely associated sites, these matched samples were compared with Pearson's product-moment correlation analysis (Sokal & Rohlf, 1969).

Conversion of altitude to latitudinal equivalents

As elevation above sea level increases at any one latitude, the climate cools to an equivalent climate at sea level but further from the equator north or south (Merriam, 1894, 1898; Holdridge et al., 1971). The alitudinal effect on temperature can be converted to the latitudinal effect by assuming an increase in 4° latitude for every 305 m increase in elevation. We used this conversion to express all data on a latitudinal gradient as if samples were taken at sea level, even though samples were taken at many altitudes from sea level to a maximum of 3843 m above.

Testing predictions based on pattern

After sampling in most biogeographic realms, we predicted that symbioses vegetation in South Africa should have high galling species number. We were aware of no such samples taken in this vegetation type. Subsequent sampling by MCGW, following methods similar to Sampling Method 1, the architectural census, yielded an independent test of the predictability of the patterns discovered in other biogeographic realms. Symbio is a heathland and shrubland vegetation growing on low-nutrient soils and is somewhat representative of the types found in Mediterranean kinds of ecosystems, such as chaparral, matorral, and Kwongan (Wright, 1993; Richardson et al., 1995). The similarity and differences among these Mediterranean-type ecosystems are considered by Hobbs, Richardson & Davis (1995).

Once sampling in symbio vegetation commenced, our direct comparison was rendered more difficult and tentative by the very high diversity of plant species in symbios, accompanied by the small stature of the mainly shrubby species. Species density in the Cape Floristic Region reaches close to that in tropical rain forest, with 94,400 species per 10 km² in South Africa compared to 103,300 species in.
Panamanian rain forest (Wright, 1993). Asymptotic richness of galling species in fynbos was reached only between 400 and 600 individual plants per sample. This is a much larger number of shrubs sampled than in other regions but less than the total plant individuals sampled when herbs, shrubs, and trees were present at a sample size. Therefore, we suggest that samples in fynbos provide an interesting comparison with other regions, although they proved to be less directly comparable than expected.

RESULTS

Sample site locations

Samples were taken in fourteen countries: Australia, Brazil, Canada, Costa Rica, England, Fiji, Finland, Israel, Japan, Mexico, Panama, Russia (Siberia), South Africa, and the United States (mainly Alaska, Arizona, Florida, and Hawaii). The only continent without representation was Antarctica, and the only biogeographic realm unsampled was the Oriental. A map provides the approximate locations of samples (Fig. 1).

General patterns in galling species richness

The latitudinal gradient

In response to question 1 on the generality of patterns initially discovered in Arizona and Minas Gerais, the answer is generally positive, but with important qualifications. Between adjusted latitudes of 23° and 45° N or S in warm temperate climates galling species richness was very high (Fig. 2). The pattern included climates with cool dry winters and warm wet summers (Minas Gerais) and cool moist winters and hot dry summers with little rain (Arizona). Samples taken in these latitudinal equivalents included Australia (galling species richness from eight to fourteen species, six samples), Brazil (richness from zero to forty-six, forty-three samples), Israel (richness from six to twenty, two samples), Mexico (richness from fourteen to fifteen, two samples) and U.S.A. in Arizona (richness from six to twelve, four samples). Samples from South Africa were consistent with the pattern (richness from three to twenty-four, ten samples). Clearly, there is a large range in species richness in these latitudes, but a common feature is high values in the warm temperate zone relative to general values outside the warm temperate zone. This broad generalization needs qualifying on two counts.

In Arizona at elevations equivalent to 45° to 60° North, diversity is high in dry sites reaching up to eighteen galling species per sample. Many elements of the richly galled Sonoran Desert flora each up to 1000 m above sea level and higher and these are the plants that retain a high galling species diversity at latitudinal equivalents of 45 to 60° N.

A major departure from low richness in tropical latitudes was seen in campina vegetation along the Rio Negro in Amazonia. Campina and caatinga are terms referring to similar vegetation types in Amazonia, according to Pires and Prance (1985). Developing on nutrient-poor leached white sand, the campina vegetation has a xeromorphic aspect with thick sclerophyll and bark. After walking for many kilometres in extensive wet tropical forest with low galling richness one can suddenly enter a small island of campina vegetation and find many galls; nine to twenty-six species in the three patches sampled in this study.

Note that high gall species richness, at twenty or more species per sample, was observed in three biogeographic realms: the Palearctic (Jordan Valley, Israel), the Ethiopian (southern Cape Province, South Africa), and the Neotropical (Campina, Amazonas, Serra do Cipó, Minas Gerais, Brazil). The exceptional case from the tropics in campina vegetation leads us into the subsequent questions raised in the introduction.

Warm temperate climates

Our second question addressed the generality of high galling richness in climates just outside the tropics. Mediterranean climates with hot dry summers and warm wet winters are common at latitudes from 32° to 45° N and S. However, hot wet summers and cool dry winters are also found in these latitudes where typhoons bring summer rains, for example, in Japan. Also, in tropical latitudes such as in Minas Gerais, the summers are very wet and the winters are very dry (Hueck, 1972). This latitude at which samples were taken in Minas Gerais moved these tropical locations at 10° S into the equivalent of the warm temperate belt.

Therefore, the answer to question 2 is that galling species richness in warm temperate latitudes and equivalents is commonly high so long as there are distinct dry and wet seasons each year.

Galling species richness in scleromorphic vegetation

We asked in question 3 if galling species richness is related to sclerophyllous vegetation. In warm temperate climates and their equivalents, typical climatic types have hot dry summers and warm wet winters, or warm wet summers and warm dry winters. Both climatic regimes result in scleromorphic elements in the vegetation. Whether or not phytosociologists accept the term sclerophyllous for a particular type, scleromorphy is a common denominator for many species in truly Mediterranean climates, and in climates with wet summers, as in savannas in Brazil (cerrado, with grasses and herbs intermixed with low, tortuous, scleromorphic trees with thick bark), and the evergreen forest types in southern Japan.

Scleromorphic vegetation is defined as a flora dominated by plants with persistent and tough leaves (Schulze, 1982). In fact, a combination of the terms scleromorphy and xeromorphy covers the range of plant types of which gallers become most abundant. Features of scleromorphic plants include reduced stature, reduction in internode lengths, perenniality (Schulze, 1982, p. 649), and small leaves with thick cuticles (Small, 1973). Scleromorphic plants may have large leaves, but leaves are so hardened that they retain their mature shape while drying. At the upper extreme of this leaf type in the cerrado is Pallisera rigida (Rubiaceae) with some leaves the size of those on a large cabbage

FIG. 1. Map of the World showing the approximate distribution of clusters of local sample sites estimating insect herbivore gallig species richness. The map uses the Mercator projection, as if longitude is represented by a set of parallel lines north and south, grossly overrepresenting land and sea areas in northern and southern latitudes. The tropics, temperate and arctic regions are indicated by dashed lines of latitude. Biogeographic realms are indicated. The International Date Line at 180° longitude is the general case and is not accurate for all specific regions.
FIG. 2. Distribution of samples measuring galling species richness on a latitudinal gradient north or south of the equator. The gradient is divided into tropical, warm temperate, cool temperate and arctic zones, and shows a strong peak in richness in warm temperate regions or their equivalents, based on latitude and altitude. Open circles represent samples on scleromorphic vegetation and closed circles are samples in mesic sites on nonscleromorphic vegetation. Samples taken on scleromorphic vegetation in relatively mesic sites are indicated by an x. Squares indicate samples from fynbos vegetation in South Africa which acted as an independent test of the pattern. Twelve xeric sclerophyll (open squares) and two mesic sites (closed squares) in riparian woodland are given. Note that all samples with a richness greater than twelve species are from scleromorphic vegetation types. This apparent limit on species richness in mesic sites is indicated by the broken line horizontal in the X axis.

and almost the toughness of a cyclist’s plastic safety helmet.

The highest estimates of galling species richness around the world are all associated with scleromorphic and xeromorphic vegetation (Fig. 2). In the warm temperate zone and its equivalents, richness reaches a strong peak based on samples in Australia, United States (Arizona), Israel, Brazil (Minas Gerais, Amazonia) and South Africa. Scleromorphic and xeromorphic vegetation in these areas support commonly local galling species of thirteen and more, above any vegetation types that are not sclero- or xero-morphic (Fig. 2). We address the mechanisms driving this strong pattern when discussing Question 5 on mechanisms.
**Galling species in relatively dry and wet sites**

If galling species are strongly associated with scleromorphy in their host plants, are drier (xeric) sites more favourable than wetter (mesic) sites for gallers? (Question 4). Using data in Fig. 2 we have categorized sites as either xeric with scleromorphic plant species or more mesic sites with scleromorphic and nonscleromorphic plant species. If a mesic site was sampled with scleromorphic vegetation it was usually matched with a drier site at the same elevation and latitude, unless no equivalent was available, as for campo-wet vegetation.

The pattern shows a clear preponderance of galling species in xeric sites (Fig. 3). In all but three of the pairwise comparisons per 5° latitudinal range class, out of the eleven comparisons, xeric sites supported more species than mesic sites, a significantly different species richness in general (Wilcoxon's signed-ranks paired-comparisons test: \( n=11; \ T=9, P<0.025 \) one-tailed test). We anticipated this result based on studies by Fernandes & Price (1988, 1991, 1992) on pairwise tests of xeric and riparian habitats in Arizona and Minas Gerais at the same altitude. In the range of latitudes from 60° to 70° the contrast between mesic and xeric sites diminishes and numbers of galling species per habit type tend to converge. Mechanisms driving the general pattern are considered next.

**The mechanisms driving the patterns**

In question 5 we asked if clues on mechanisms were provided by the sampling adopted for this global view on galling insect species richness. In general, the patterns are consistent with the hypothesis developed by Fernandes & Price (1991). Galling species richness increases on scleromorphic vegetation, more so in xeric than mesic sites in the same locality, and a scleromorphic flora is typically associated with nutrient or water limitations in warm temperate regions or equivalents (Loveless, 1982). Each region is likely to have different critical factors associated with the scleromorphic habit: very poor soils, low available water, high concentrations of elements such as aluminium, or a combination of these factors (cf. Haradans, 1982). Deforestation volcanic deposits (e.g. Kagoshima, Japan), ancient soils on old continents like Australia (Barlow, 1981), white alluvial sands (e.g. Rio Negro, Amazonia), weathered limestones producing white sands (e.g. Pirinololos limestone hills, near Brasilia, Brazil) sandy and rocky deserts (e.g. Sonoran Desert, Arizona, U.S.A.), saline soils (e.g. Israel), high concentration of aluminium in soils (e.g. cerrado vegetation in Minas Gerais, Mato Grosso and Goias states and the Federal District of Brasilia, Brazil), all result in a scleromorphic vegetation (cf. Kruger, Mitchell & Jarvis, 1983). Galling insect species respond positively to many of the plant species growing on these less than hospitable soils.

We have not tested mechanisms driving the pattern of galling species richness in the present study. All we can claim is that this large sample from many areas of the world is consistent with the pattern. Nevertheless, we remain optimistic that the hypothesis will prove to be correct because the correlated traits of scleromorphy, poor soil conditions or water shortage, and high galling species richness, persist as a central result in this study.
A test of predictions

In question 6 we asked if it is possible to predict a pattern of gall species richness in a previously unsampled biogeographic realm. Samples in the Western Cape Region of South Africa included twelve from eucalypt sites with fynbos vegetation and two from mesic woodland without the fynbos components represented. Estimates of species numbers fell within the values from the rest of the world, and are indicated with square symbols in Fig. 2. Outside warm-temperature-latitude equivalents, five samples in fynbos vegetation were consistent with those from Arizona between the latitudes of 45°-57° N or S. The results indicate that crude predictions on galling species richness can be made and supported, although deviations from the general sampling methods because of the unique flora diminish the power of our test.

Gall-inducing taxa in the study

The gall midges (Diptera: Cecidomyiidae), a cosmopolitan family, were largely responsible for the patterns detected. They are known to be associated with a wide range of host plant taxa in both tropical and temperate latitudes (cf. Gagne, 1989, 1994). Other taxa with galling insects were much more restricted in the host-plant range and geographic distributions in our samples. Tenthredinid sawfly and aphid gallers were found only in north-temperate latitudes or their Northern Hemisphere elevational equivalents. Cynipids were sampled on oaks and roses providing relatively high local species numbers in adjusted latitudes between 35° and 60° N. However, a small number of samples was dominated by the Cynipidae. Gall-forming Eriocuccidae were found in Australia alone, representing a small component of the samples. Galling insects in the Lepidoptera, the Tephritidae (Diptera) and the Psyllidae (Hemiptera) were not common enough to influence the pattern significantly.

Comparison of sampling methods

Comparison of methods

Method 1, the architectural census, was employed by G.W.F. on the San Francisco Peaks in Arizona down into the Verde Valley at 984 m and beyond and reported in Fernandes & Price (1991). Method 2, the 60-min census, was used by P.W.P. covering the same eleven sites for direct comparison. The correlation between sampling methods was highly significant ($Y = 1.58 + 0.05X$, $n = 11$, $r = 0.93$, $P < 0.01$). The intercept of 1.58 resulted from a slightly higher number of galling species in Method 2 at higher elevations because of the more extensive area searched. This effect also lowered the slope of the correlation to 0.05. However, the relationship predicted differences in galling species richness of 1.38 species per sample as a maximum, if any galls were found by sample method 1 ($X = 1$, $Y = 2.38$), providing confidence in the direct comparison in sampling methods.

Comparison of ground and canopy samples

In Panama, ground-based sampling yielded significantly higher estimates of galling species richness than matched canopy samples (ground mean = 1.88 galling species per 30 min; range 0 to 3; canopy mean = 1.31 galling species per 30 min; range 0 to 2; Wilcoxon $T = 23.5$, $n = 16$, $P < 0.05$, 2-tailed test). When ground and canopy samples were combined to simulate a total sample taken throughout the under- and over-story vegetation an intermediate richness was estimated with a mean of 1.75 galling species per 30-min sample (range 1 to 3). The total samples were not significantly different from the ground-based samples alone (Wilcoxon $T = 39$, $n = 16$, N.S.).

In general, in the wet season in dry tropical forest, sampling from the ground provided a small overestimate of galling species richness in samples combining under- and over-story vegetation. However, in this vegetation with low richness of galls, the ground samples provided a mean estimate within one species of the combined canopy and ground samples. For a 1-h sample this would translate to an overestimate of two species per sample on average. Given the wide range in galling species richness around the world this is a small and acceptable overestimate.

Sampling the canopies of lowered trees in Amazonia provided results similar to those obtained in Panama. Ground samples identified significantly higher gall species numbers than matched canopy samples (ground mean = 1.32 galling species below a canopy; range 0-6; canopy mean = 0.48 galling species in a canopy; range 0-4. Wilcoxon $T = 58.92$, $n = 26$, $P < 0.01$, 2-tailed test). We then combined samples from ground and tree canopy for a composite sample. This provided a mean of 1.71 galling species per tree canopy plus ground sample (range 0-10). In contrast to the samples in Panama, the total samples were significantly higher than ground samples (Wilcoxon $T = 0$, $n = 9$, $P < 0.01$), although in only nine cases were differences observed, and the mean difference was 0.48 galling species. Hence, the ground samples provided an acceptable estimate of total galling species richness.

Comparison among sampling personnel

Two tests were conducted on the correlation between pairs of samples conducted simultaneously by different sapers in at least nine locations. The paired samples were not in identical sites, but displaced by a few metres, enough to introduce the probability that real differences in galling species number would be expected, in addition to biases introduced by the researchers themselves.

At locations with low galling species richness P.W.P. and G.W.F. sampled nine paired sites, each using method 2, and the correlation between samples was significant ($r = 0.54$, $P < 0.05$, slope = 1.00, intercept = 0.00). All samples were taken before a direct comparison of results was planned. In sampled richness ranging from 0 to 6 galling species per hour, there was a consistent bias in which G.W.F. would find on average one gall more than P.W.P. per sample. Such a generally small difference in results between personnel could not alter the general patterns discussed in the next section.

The second test was conducted in the richest galling species habitats we have discovered to date, using method 1, on Serra do Cipó in Minas Gerais, Brazil, near Belo Horizonte. In 1991, samples were spread among wet and dry sites at elevations from 900 to 1400 m a.s.l., with paired
data collected by GWF and ACFL. All samples yielded richness estimates between eleven and thirty-eight galling species per sample, except one pair at the highest elevation with estimates of four and five galling species. Samples were significantly correlated (n = 13, r = 0.33, P < 0.05, slope = 0.59, intercept 10.66). However, the correlation was not as strong as we expected. The extent to which the differences were due to personnel or to real differences in the field needs more study. However, all samples fell within the range, or exceeded the richness of samples taken at equivalent sites by GWF in 1984 and 1986 on Serra do Cipó (Fernandes & Price, 1988). These results indicated that samples were correlated, and strong patterns could be detected repeatedly, even though different people sampled.

**DISCUSSION**

Opportunity and adversity take different forms in the adaptive radiation of insect groups. Tenthredinid sawflies are poorly represented in the tropics as if the cool temperate climates in which they radiated and the important families of plants that they utilize, such as the Salicaeae, have constrained exploitation outside their primordial latitudes (Smith, 1979). Aphids are also depauperate in the tropics, perhaps because their method of finding hosts by trial and error is inefficient in floristically diverse vegetation (Dixon et al., 1987). The galling insects are represented by several families, although the pattern we describe is driven undoubtedly by the abundance of the gall midges (Diptera: Cecidomyiidae). For the galler, opportunities for adaptive radiation obviously have been very extensive in scleromorphic vegetation and the wet tropics present mostly adverse conditions.

Galling insects such as the gall midges appear to be excellent colonizing species. Even though adults are short lived, galls can be found in isolated patches of vegetation after disturbance. They can be rare in a landscape, but common very locally, as we have found for two tenthredinid gallers (e.g. Rothinemen et al., 1993). They colonize newly sprouting host plants rapidly after fire in the cerrado as we have noted around Brasilia and Belo Horizonte (e.g. Vieira, Andréns & Price, 1996). Therefore, the richness of tropical rainforest flora does not seem to pose a significant barrier to colonization by gall species as hypothesized for aphids. Nor do gall midges have evident broad phylogenetic associations with cool temperate climates and host plants, even though specific genera are associated with northern plant taxa. Indeed there may be very ancient links between gallers and cerrado vegetation, for this savannah system may be very old, some 30 million years perhaps (Cole, 1986). Without doubt localities with dry climates have been centres of adaptive radiation, especially for cecidomyiids, with very rich communities in deserts, shrublands and savannas.

The prolonged debate about the adaptive significance of the galling habit, at least since 1899, was discussed by Price et al. (1986, 1987). We argued that the most cogent thesis implicated hypothalamic stress as the selective factor. Sampling in Arizona and Minas Gerais reinforced this argument (Fernandes & Price, 1988, 1991), and the data presented in this paper add further support. The pattern of galling species richness on the latitudinal gradient is clear enough, but the underlying explanation for the pattern is unresolved.

Strong association of galler species richness with scleromorphic vegetation, lower richness in moist sites relative to dry sites at the same latitude, and reduced richness in the wet tropics and cool temperate climates, focused our concern on the special features of scleromorphic vegetation. We argued that scleromorphic hosts provide commonly persistent leaves of low nutrient status and high phenolic concentrations, but gallers could concentrate nutrients and overcome low nutritional status (Fernandes & Price, 1991; White, 1993). Nutrients would be concentrated in the feeding zone of the insect (White, 1993) while phenolics acting as chemical defenses against other herbivores are concentrated in the outer cortex of the gall. In moist sites activity of endophytic fungi, fungal pathogens, and parasitoids would be detrimental to gallers and reduce species richness (Fernandes & Price, 1992). The net result is higher richness in relatively dry sites and in dry latitudes. 'Dryness' in these cases must be viewed as physiologically relevant stresses on the host plants, rather than the amount of precipitation, for canopy vegetation receives about 2200 mm rainfall per year and cerrado about 1500 mm per year (Hueck, 1972). Such 'physiological drought' was recognized as important in xeromorphic and scleromorphic plants a century ago by Schimper (1898).

An interesting consideration concerns the mechanisms by which gall species richness develops in scleromorphic vegetation. Does such richness derive from multiple independent colonizations, or are a small number of initial colonizations followed by extensive speciation in closely related taxa? Focusing on the cecidomyiids as the richest taxon of gall inducers, we favour the latter scenario. With the caution advised by Gagné (1989), that generic categories are subjective, and in the Cecidomyiidae genera may not be monophyletic, we offer the following tentative argument. Several genera of cecidomyiids are large, indicating extensive host-plant shifting without major change in morphology. *Rhabdophaga* contains about seventy species globally, *Rhopalomyia* over 120 species, and *Asphondyliina* contains 247 described species (Gagné, 1989, 1994). On a local scale we know that one genus may radiate into several different ecological niches on the same host plant, with the best examples from deserts in the SW United States and Kenya, *Crescentia* bush, * Larrea tridentata* (DC.) Coville is host in Arizona to sixteen species in the cecidomyiid genus *Asphondyliina* (Gagné, 1989; Waring, 1986, 1987; Waring & Price, 1990). *Asphondyliina* is also represented by eight species on *Atriplex canescens* (Pursh) Nuttall and *A. polycarpa* (Torrey) Watson in southern California (Hawkins & Goeden, 1984; Hawking, Goeden & Gagné, 1986). In Kenya, the genera *Acacidiplois* (13 spp.) and *Apatoschizomyia* (5 spp.) have radiated across *Acacia* host plant species (Gagné & Murouhuy, 1993). One host plant species, *Acacia tortilis* (Forssk.) Hayne, has a total of eighteen cecidomyiid gall-forming species recorded, with eleven *Acacidiplois* and three *Apatoschizomyia* included. Therefore, it is conceivable that ecological opportunities for host shifting in xeric habitats, once cecidomyiids became adapted to such dry
sites, provided the basis for extensive adaptive radiation from a small number of phylogenetic lineages. Knowing that most gall midges attack and utilize only one plant species (Gagné, 1989) suggests that the details of the interaction between host and parasitic gall maker necessitate extreme specialization, as argued by Price (1980). Nevertheless, Gagné (1989) noted that females may lay eggs on plants related to the host plant, with such 'accidents' providing the basis for host shifting and ultimately speciation, in our opinion.

Latitudinal gradients in species richness of plants and animals are more complex than is usually acknowledged in the literature (cf. Pianka, 1966; Price, 1991). Each taxon is under specific constraints in its adaptive radiation, with associated opportunistic outlets for resource exploitation. We have shown that a strong peak in galling species richness is associated with edaphic and climatic conditions resulting in scleromorphic vegetation. We have not invoked any of the forces commonly considered in discussions of latitudinal gradients in diversity, such as competition, species packing, or niche width, and the importance of natural enemies in gall-forming communities is very different from that invoked in general debates. Indeed, in forthcoming papers we will show for galling species assemblages in the wet tropics and at peak richness in the cerrado, that any kind of community organization is very hard to discover, and may well be absent. Gallers in local, favorable environments appear to be radiating opportunistically, in loose assemblages, seemingly unconstrained in evolutionary time. The data on galling insects do not support any of the conventional views of the tropics regarding community organization which date back to the great naturalists of the nineteenth century, and which were summarized by Dobzhansky (1950). As Vandermeer (1989) noted, much of our current ecological 'theory' relies on arguments unfounded in empirical facts.

ACKNOWLEDGMENTS

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Natural History of a Gall-Inducing Weevil *Callobius* clitellae (Coloeoptera: Curculionidae) and Some Effects on its Host Plant *Solanum lycocarpum* (Solanaceae) in Southeastern Brazil

ANDREA LÚCIA TEIXEIRA DE SOUZA, \* GEINALDO WILSON FERNANDES, JOSÉ EUGÊNIO CORTES FIGUEIRA, and MARCELO OKAMOTO TANAKA

**Abstract**

The phytology, general characteristics, and mortality factors acting upon the weevil *Callobius clitellii* Boheman in a population of *Solanum lycocarpum* St. Hil. (Solanaceae) were investigated in southeastern Brazil, as well as its distribution and impact on the host plant. Mating and oviposition of the weevils were observed in the beginning of the summer, with larval development until the autumn and emergence in spring. Most galls were found toward the base on plants 0.5-1.2 m high; a distribution perhaps the result of physiological differences between plants of different height. Natural enemies also may influence this pattern; logistic regression showed that greater gall size and increased height above the ground increased mortality caused by the woodpecker *Colaptes campestris* (Vieillot). Larger galls also were more frequently attacked by the fungus *Pestalotiopsis sp.*. Gall attack rates were correlated with *S. lycocarpum* stem mortality (43.4% of plants sampled), because galls conduct as nutrient sink or favor the breaking of stems. The possible effect of *C. clitellii* on the population dynamics of *S. lycocarpum* is discussed.

**Key Words** *Callobius clitellii*, Coleoptera, Solanaceae, plant-insect interactions, gall mortality

*CALL-INDUCING INSECTS are extremely diverse and have interesting and complex life histories. Most of their life is spent embedded within tissues of their host plants, with which they have perhaps the most intimate relationship of all organisms (Mant 1964, Matton et al. 1988, Fernandes 1990). The understanding of the natural history of Neotropical gall-forming insects is tremendously poor; most studies have centered on the ecological aspects of gall distribution (Fernandes et al. 1988, Fernandes and Prive 1988, 1991). In addition, there are few studies on the frequency and kind of impacts caused by gall-forming insects on their host plants, especially for shoot galls (Saez et al. 1990).

The weevil *Callobius clitellii* Boheman forms galls on shoots of the fruit tree, *Solanum lycocarpum* St. Hil. (solanaceous: *S. grandiflorum* Raddi, variety *Carvalho 1985*) (Solanaceae), a woody shrub that grows to 1 m height. This plant is a common weed in central and southeastern Brazil, occurring along highways, pasture, grasslands, and disturbed areas (Carvalho 1985). This association also was recorded for *S. grandiflorum* in Minas Gerais State (Bondar 1922, Lima 1958).

Here we describe the phytology, general characteristics, and mortality factors acting upon *C. clitellii* in a population of *S. lycocarpum* in southeastern Brazil. We also provide data on the distribution of galls within and between plants and discuss some aspects of the impact of these galls on the host plant.*

**Materials and Methods**

The study was conducted between May 1991 and July 1992 in a population of *S. lycocarpum* located along highway MG-140 (km 80), near Serra do Cipó, Minas Gerais, 840 m above sea level. The dominant vegetation is cerrado, which is regularly cut as a management practice for cow grazing. Plants of *S. lycocarpum* were cut at 5 cm above the ground every other year, and were last pruned in January 1990. The population studied consisted of clones with several ranets patchily distributed. Ranets were 16-18 m old and varied from single small shoots (<10 cm from the ground) to 1.0 m high. Ranets up to 5 m high also were found and examined in the study area.

We randomly collected 355 galls from 67 individuals of *S. lycocarpum*. To identify possible patterns of gall distribution within and between plants, we measured plant height and gall height on the plant relative to the ground. Because plant height was variable, the distribution of galls on different plant parts was analyzed using the gall height/plant height ratio. The distribution on the plants was then measured by dividing gall locations into basal (0-0.33), median (0.33-0.66), and apical (0.66-1.00) parts of the plant. We also recorded the diameter of the galled stem and whether they were wilted or dead, to evaluate the impact of galls on stem survival, using the gall attack rates (see below).
In the laboratory, we measured the length and diameter of galls and estimated their volume with the formula volume = length \times (diameter/2)^2. To test whether this measure provided a statistically reliable estimate of gall size, we randomly subsampled 67 galls whose volume was determined by immersing each gall in a graduated tube filled with water and recording the volume of water displaced. As the relationship between both measurements was linear (r = 0.85, P < 0.001), the former method was used to estimate gall size throughout this study.

The attack rate per stem was evaluated as the sum of chambers in all galls found per stem; later, all galls were dissected and the chambers were counted and opened. This approach was needed because the number of chambers per gall and number of galls per stem were highly variable. Furthermore, there is only 1 beetle larva per chamber, which would be a better estimate of the attack rate.

During oviposition by females of *C. citrella*, we randomly marked 175 egg batches on 40 plants. Of these, we measured the stem diameter, plant height, and the number of starts left by the females on the epicuticle of the stem oviposited upon. We also recorded the number of stems that were broken exactly where the eggs were deposited.

The mortality factors acting upon *C. citrella* in relation to plant height, gall height in relation to ground, and gall volume were analyzed with logistic regressions (Horter and Lemeshow 1989, Steinberg and Coles 1991). The odds ratio (W) was calculated according to an increase of units of the independent variable analyzed, with the following equation:

\[ \text{logit}(p) = \beta + \beta x \]

and 95% confidence limits set by the relation

\[ CI = e^{\beta} \times 1 + PE, \]

where \( \beta \) is the parameter estimate and \( PE \) is the standard error of the estimate (Horter and Lemeshow 1989). A similar model was used to analyze beetles survival in relation to beetle attack rates and stem diameter. The relationship between these factors and stem diameter categories on the breaking off of stems was analyzed using the \( t \)-test (Sokal and Rohlf 1983). Voucher specimens of *C. citrella* were deposited in the Museo de Historia Natural (Universidad Estatal de Campinas).

Results

Biology of *C. citrella*. Mating and oviposition of *C. citrella* occurs in the beginning of summer (November-December). Ovipositing females use their mouthparts to perforate the epidermis of nonwoody stems (shoots) of *S. demissum* to lay their eggs. Each hole is quickly sealed off after egg deposition, leaving a conspicuous scar on the stem. We collected several newly oviposited stems for dissection in the laboratory, and only 1 egg was deposited in each hole. Therefore, the number of eggs laid corresponded to the number of scars left on the surface of the stem. We observed 3 eggs (29.3 \pm 2.6 eggs per oviposition). Eggs were deposited around the entire circumference of a stem, but in a spiral formation. Thus, the length of the oviposition bout varied both with the number of eggs deposited by a female and stem diameter.

Each larva of *C. citrella* (Fig. 1A) was concealed within a single chamber (Fig. 1B), developing between December and May. Galls continued to grow as larvae fed on the galled tissue until larvae terminated feeding and pupated, which occurred in May. Pupae (Fig. 1B) were found from June to July, and adults were found inside galls between July and September. Emergence of adults from their galls (Fig. 1C) took place from September to October.

The adults of *C. citrella* (Fig. 1D) are pale yellow with a dark spot on the elytra. This color matches the pale yellow of the stem of their host plant. Adults are very abundant in the field from October to December, where they are found commonly feeding on newly growing shoots, leaves, and flowers of *S. demissum*, as well as ovipositing on new shoots.

N. formed galls are green, scaly, and soft (Fig. 1F). Their internal tissues have many fibers and a large amount of water. They are bluish, globsular, or eliptoid and may occur singly or in coherence. As galls age, their tissue becomes drier, woody, and brownish.

Gall stems were variable in size, ranging from 1.26 to 16.35 cm (3.35 \pm 1.99 cm, n = 351) long and from 0.59 to 1.65 cm (1.21 \pm 0.31 cm, n = 351) wide. Their width varied from 0.34 to 1.39 cm (21.74 \pm 24.59 cm, n = 351). The number of chambers also was highly variable, ranging from 1 to 78 chambers per gall.

Gall Distribution Between and Within Plants. Galls were distributed on plants that ranged between 40 and 200 cm high, only 3% being recorded on plants higher than 160 cm and the greatest proportion (42%) on plants 60-120 cm tall (Fig. 2A). Within the host plants, they occurred mostly on the median and basal parts, greater numbers in the latter region (C = 9.7, df = 3, P = 0.02). Because only 15 galls were found on spiral stems, they were excluded from the analysis.

Of all galls collected, 210 (65%) were smaller than 20 cm³, containing from 1 to 6 chambers. Large galls (>40 cm³) might have up to 68 chambers, more of them occurring on the basal stems of the plants than on the median region (C = 15.6, df = 3, P = 0.001, Fig. 2B). All galls located on the apical region were < 40 cm³.

Mortality Factors. An unidentified species of the fungus *Penicillium* was the major mortality factor acting upon *C. citrella* during our study (25.9% of studied galls). The external morphology of the gall was not altered by the presence of the pathogen, whereas its growth inside the gall damaged larval chambers and killed the galling larvae. On 35.2% of the galls attacked by *Penicillium*, we observed 1-3 larvae of an unidentified species of *Ophiomyces* (Colletotrichum). None larvae formed tunnels inside the pathogen-damaged galls. The occurrence of the fungus was most frequent in the largest galls, but was independent of plant and gall height (Table 1). According to the analysis, an increase in 10 cm³ in gall size increased the chance of a gall being attacked by a factor of 1.62. For example, if the chance of a gall being attacked in the field is 10%, an increase of 10 cm³ will raise this chance to 12.2%.
Fig 1. Several phases of the galls caused by C. clavigera on S. ipequantum. (A) Larva. (B) Pupa. (C) Adult excavating the gall walls. (D) View of galls showing internal wall. (E) Gall on the host plant. (F) 5 mm. (G) 10 mm. Galls also attacked by the woodpecker Colaptes campestris (Vieillot) (Piciformes: Picidae). These birds perforated the gall walls to reach the juicy larvae inside the chambers, partially or even entirely destroying galls. C. campestris was frequently observed on branches of the host plant, and attacks were commonly recorded in the field. Un attacked galls were frequently attacked by the largest galls or those located in the upper portion of the host plant (Table 1). Analysis indicated that an increase of 10 cm in gall height increased the chance of being attacked by C. campestris by a factor of 1.36, and a 10 cm increase in gall volume led to a factor of 1.33. Despite the fact that plant height had an important effect on the decision of the woodpecker to attack a given gall, plant height alone was not a risk factor because the lower confidence limit of the odds ratio was less than 1.0 (e.g., Haxmeier and Lemerch 1989). Therefore, the most important factors influencing the pattern of attack by C. campestris were gall size and gall height from the ground.

Galls also attacked by 2 species of parasitic hymenoptera; both leave their cocoons inside the gall after emergence. This study did not focus on the relationship between the parasites and gall distribution patterns within plants because parasitism rates were much lower than other mortality factors (14.4%). A large percentage of galls was killed by undetermined factors, possibly including nematodes, ants, and plant resistance (30.7% of galls attacked).
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Fig. 2. Number of galls in (a) plant height classes and (b) gall size classes in different parts of plant. Dark bars represent galls located in apical portion, hatched bars in median portion, gray bars in basal portion.

Impact on Host Plant. The number and size of galls varied enormously among stems. Many galled stems died, probably as a consequence of gall induction; death began with the wilting and drying of the apical region. Of 70 randomly collected stems on 76 plants, 33 (43.4%) were dead. The probability of stem death was positively associated with gall size and negatively associated with stem diameter (Table 2). Therefore, the number of larvae per stem was an important factor influencing stem survival; an increase in 10 chambers per stem (10 individuals) increased 2.4 times the probability of stem death, whereas an increase of 1 cm in stem diameter decreased the probability of death by 0.042 times. Thus, thinner stems without galls are more likely to survive, as would larger stems, even if galled.

Drifting by females during oviposition frequently resulted in stem hercriage by mechanical factors such as wind, rain, and by pasting animals. Among the stems analyzed, 24.4% were broken exactly at the site of oviposition. Breaking was frequently observed in the thinnest stem classes ($G = 11.51$, df = 4, $P = 0.02$, Fig. 3).

Discussion

The mortality of C. cecidicae from external agents is independent of plant height. Thus, the greater occurrence of galls on smaller plants may be caused by inherent factors of the interaction between the galling insect and S. lycoctonum. First, plants or parts of the plant may be in different phenoctical or developmental stages, which could influence the survival and performance of C. cecidicae larvae and consequently the attack rates observed (e.g., Keaneey and Wiblum 1999). The aging of host plants can lead to differences in the nutritional quality of young and mature tissues because of distinct chemical or mechanical defense levels, which influences the distribution of herbivores across reder stages (Frankie and Morgan 1984, Wiblum et al. 1984, Craig et al. 1989, Akimoto and Yasunishi 1991). Second, the pattern observed could result from female behavior when choosing oviposition sites as an attempt to maximize the survival and performance of her offspring (Thompson 1998, Craig et al. 1998, Price 1995) (but see Butstein and Wool 1992). A 3rd hypothesis is that this distribution may result from the impact of galls on plants, reducing their growth (Fernandes 1986, 1997). Whether these hypotheses explain the pattern observed will be clarified only with further experiments. In addition to the limitation on the distribution among plants of different heights, galls of C. cecidicae occur more frequently on the basal portions of the attacked plants, where galls attain the largest sizes. An

<table>
<thead>
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<th>Odds ratio</th>
<th>95% CI</th>
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<td>0.609</td>
<td>1.015</td>
<td>0.951</td>
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<td>1.000</td>
<td>0.999</td>
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<tr>
<td><strong>Gall height</strong></td>
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<td>0.002</td>
<td>1.04</td>
<td>1.07</td>
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<tr>
<td><strong>Gall size</strong></td>
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<td>0.005</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
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**Calyptris cephaloides**

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<th>Odds ratio</th>
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<tbody>
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<td><strong>Stem diameter</strong></td>
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<td>0.005</td>
<td>1.025</td>
<td>1.020</td>
</tr>
<tr>
<td><strong>Plant height</strong></td>
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<td>0.001</td>
<td>1.025</td>
<td>1.051</td>
</tr>
<tr>
<td><strong>Gall height</strong></td>
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<td>0.003</td>
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<tr>
<td><strong>Gall size</strong></td>
<td>0.018</td>
<td>0.005</td>
<td>1.03</td>
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</table>

C = 15.04, df = 3, $P = 0.005$.
C = 14.12, df = 3, $P = 0.005$.

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A87-08177
important factor determining these distribution patterns was the attack of the woodpecker C. cancrivorus, because the chances of being attacked increase with gall size and height on the plant. Birds of the family Picidae search for insect larvae, mainly beetles in wood, which constitute the preferred food item of many Brazilian species (Sick 1984). Generally, insects or birds hunt by visual search, and individuals of this species should detect the galls most easily visualized at greater distances. Attack of insect galls by the woodpecker Picidae ruber or the Canadian gold-crown, Scolia cancrivora, also are intensive on large galls on tall stems (Confer and Faires 1983). The attack rates recorded for C. cancrivora (19% of all galls) seems to be relatively high and may assume a larger importance for those galls located on the higher portions of the plants, where gall occurrence is lower than on the basal region.

Mortality caused by fungous also was higher on the largest galls. In 38.5% of the attacked galls, we observed larvae of a cecumiroid that probably fed on the mycelia, and adults may be acting as a dispersal agent of this pathogen. Fungal transport by several coleopteran families has been recorded in Scytotrophine (Lavrén et al. 1981), Curculionidae (Nevill and Alexander 1992), Notocoliidae (Cook 1992), and Anobiidae (Hoover et al. 1995). Thus, the behavior of this cecumiroid could influence the distribution of Fusicladium sp. and ultimately gall survival.

Salix geniculata stems died according to a balance between gall infestation rate and stem diameter. The mean size progressively from the apex, modifying or interrupting the development of galls located at greater heights. This suggests the possibility of competition among C. citellae galls. Those in the basal parts of the plants may be draining resources otherwise available for galls in the apical parts (e.g., galls on different leaf parts [Whitham 1980]). These galls not only contributed to stem breaking, they also reduced plant fitness; stem mortality caused by gall attack was 43.8%. The direct effect of herbivory on plants can be very strong, influencing the net production of inflorescences and seeds, modifying plant architecture or sex expression (or both), or inducing shoot mortality (Gaia et al. 1986, Sacchi et al. 1988, Whitham et al. 1991). The presence of galls can influence the physiology of the host plant, acting as metabolic sinks for energy and mineral nutrients and modifying tissues that otherwise could serve for growth and reproduction (Abrahamson and Weis 1987, Price and Louw 1996). Indirect effects include the susceptibility to other herbivore species because of the modification of plant tissue and/or plant resistance caused by a specific herbivore (Whitham et al. 1991, Price and Louw 1996, McGoch and Chown 1997).

The damage of herbivores to the reproductive characters of plants may depend on the phenology of the plant (Harper 1977). Because gall frequency was higher on smaller plants, young dead plants were observed several times. In larger plants, the infection rates were smaller, and there was less damage to the plants. Sacchi et al. (1988) observed that the sawfly Eurytoma laeviventris influenced the production of inflorescences by Salix laeviventris only during the year of infestation, rather than in subsequent years. The artificial cut of S. geniculata keeps a high resource availability to C. citellae, maintaining young branches highly susceptible to attack by the herbivore. Thus, the pruning season of these agricultural and pasture fields should influence the effect of C. citellae on S. geniculata when adjusted to the life cycle of this insect.

Acknowledgments

We are most grateful for critical discussions of this work with P. F. Martín and H. B. Fontes. We thank W. Burke for the identification of the galls, and the Parque Nacional do Serra do Cipó IBAMA for logistical support. We also thank C. Schaeer and an anonymous referee for critically reviewing the manuscript. This study was funded by Conselho Nacional de Desenvolvimento.
A diversidade padronizada

Quantas espécies existem na Terra? A primeira vista, essa questão pode parecer insignificante, mas a maioria dos biólogos acredita que conhecer esse número é essencial para entender como funcionam os ecossistemas e garantir a manutenção da diversidade de seres vivos no planeta. Manter a biodiversidade é uma das principais preocupações da atualidade, principalmente em função dos efeitos negativos da degradação ambiental e do crescimento da cidade.

Desse modo, o número de espécies ameaçadas de extinção. Desde a pré-história, o homem demonstra seu interesse pelos organismos e por seu comportamento. Como revelam as pinturas e desenhos em cavernas. Já naquela época o homem registava desse número de espécies. Ainda se perguntam qual seria o número total de espécies. Hoje, passados mais de 160 anos, não é conhecido sequer o número aproximado dos diferentes seres vivos existentes. Nós sabemos que estamos falando em milhões ou bilhões (ver "Espécies terrestres versus espécies marinhos").

Os insetos podem exemplificar essa dúvida. No início dos anos 70, a estimativa do número de espécies de insetos girava em torno de 10 milhões. Mas no início dos anos 80 o entomólogo Terry L. Erwin, do Museu Nacional de História Natural dos Estados Unidos, mudou esse quadro. Ao estudar artrópodes de copos de árvores em florestas tropicais pluviais na América do Sul (uma das amazônicas), Erwin estimou a existência de 30 milhões de espécies desses organismos só nessas florestas. O trabalho ressuscitou a polêmica do número de espécies da Terra e estimulou a realização de grandes números de trabalhos sobre o tema nos anos 80 e 90.

Até o momento, o número de espécies vivas conhecidas (descritas pela ciência), incluindo microorganismos, animais e plantas, está em torno de 1,4 milhão. É provável que essa quantidade não chegue a 10% do total de espécies vivas na Terra. Lamentavelmente, a ciência não conhecerá todas, pois a interferência humana está extinguindo muitas espécies ainda desconhecidas.

Embora o número total ainda seja um estigma, é evidente que a maior parte é composta pelos artrópodes. Os insetos representam cerca de 70% das espécies animais e metade dos seres conhecidos. Portanto, não entre em pânico se alguém disser que os insetos estão invadindo o mundo. Isso aconteceu há muito tempo, no período geológico Devoniano (figura 2). Os paleontólogos chamam o Devoniano...
Esperamos que você esteja satisfeito com o resultado.
As escalas da diversidade

Os padrões de diversidade são analisados em três escalas espaciais: local, regional e global (figura 4). É difícil obter uma definição geral, dado que os limites entre essas escalas, por vezes, não são claros.

Na escala local, cada padrão de diversidade é caracterizado por um único número de espécies e a sua distribuição em diferentes ambientes. Por exemplo, a diversidade de plantas em um jardim ou em um campo é determinada pelas espécies presentes naquele local.

Na escala regional, a diversidade de espécies é medida a nível de uma paisagem ou de uma comunidade. Por exemplo, a diversidade de espécies de aves em uma floresta ou em uma praia.

Na escala global, a diversidade de espécies é medida em termos de diversidade biológica a nível do globo. Por exemplo, a diversidade de espécies de mamíferos a nível global.

O primeiro padrão

A ecologia procura identificar e descrever padrões de diversidade e a sua distribuição e abundância dos organismos. Por causa disso, os ecologistas têm de estar cientes de que os padrões de diversidade de várias espécies que se apresentam em diferentes escalas geográficas (regional ou global) recebem mais atenção do que o padrão local.

Os padrões de diversidade que se apresentam em diferentes escalas geográficas são determinados por uma variedade de fatores, incluindo a disponibilidade de recursos, o nível de pressão humana e a interação entre as espécies.

O padrão por latitude

Na escala global, o padrão de diversidade mais evidente é a redução do número de espécies com o aumento da latitude — que vai de 0º na linha do Equador a 90º nos polos (Norte ou Sul). Segundo essa regra, as espécies mais desenvolvidas e complexas têm uma distribuição mais localizada e estão menos propensas a se expandir para novas regiões.

Os Exemplos mais conhecidos desse padrão são a diminuição da diversidade de espécies em direção ao norte e ao sul do mundo. Nestas regiões, a temperatura é mais baixa e, como resultado, as espécies estão menos desenvolvidas e complexas.

Embora em geral e número de espécies diminua para o pólo, a diversidade de espécies é diferente, mostrando que outros fatores influenciam a diversidade.
Em uma escala regional, o padrão altitudinal de diversidade é a redução do número de espécies com o aumento da altitude. Em estudos clássicos realizados nas montanhas do Himalaia, no Nepal, o número de espécies de aves, mamíferos e plantas vasculares diminui com a altitude. Da mesma forma, a redução do número de espécies de insetos galhadores com a altitude foi confirmada em diferentes regiões do planeta (figura 6). Na serra do Cipó, o mesmo ocorreu com outros organismos, como formigas. Já a diversidade de insetos herbívoros de vida livre não diminuiu com o aumento da altitude.

**Ação de outros fatores**

Mesmo mantendo iguais a distância do Equador (19° S) e a altitude das coletas (1.000 m), foram observados na serra do Cipó locais com diversidades diferentes. Isso revela que outros fatores, além de latitude e altitude, influem na distribuição das espécies. Entre esses fatores, em geral locais, podem estar diferenças nas espécies de plantas, nos nutrientes do solo, na umidade e nas histórias evolutivas de cada área.

Um padrão local bem conhecido, para insetos herbívoros, é o aumento do número de espécies a medida que cresce a diversidade de plantas hospedeiras. Se cada espécie de planta tem uma estratégia de vida, uma qualidade nutricional e uma história evolutiva, e se insetos herbívoros respondem de modo diverso a essas plantas, mais 'tipos' de plantas sustentarão mais 'tipos' de insetos. Mas na serra do Cipó a diversidade, considerando só os insetos galhadores, não acompanhou o aumento de espécies de plantas hospedeiras.

Outro fator que pode ter influência, independentemente da diversidade das plantas, é a chamada 'arquitetura' vegetal, definida pelo tamanho das plantas, pela maneira como se desenvolvem e pela persistência (ou perda sazonal) de folhas e outras partes. Estudos mostram que a diversidade de insetos herbívoros aumenta com a complexidade estrutural das plantas hospedeiras: árvores são atacadas por mais espécies de insetos herbívoros do que arbustos, e estes servem de alimento a mais insetos do que as ervas. No entanto, os insetos galhadores da serra do Cipó não aumentaram esse padrão, sendo mais diversos em arbustos do que em árvores ou ervas. E esse resultado ainda é parcial, e novos estudos verificando se é um padrão geral para galhadores.

Mas por que processar padrões de diversidade? A resposta é simples: conhecer esses padrões de distribuição permitirá explicar cada vez mais a diversidade. Um padrão, por ser uma 'descrição' de um fenômeno, é o primeiro passo para entendê-lo. Assim que a existência de qualquer padrão é comprovada, como os observados na serra do Cipó, é preciso saber 'como' e 'por que' ele ocorre, que fatores o determinam, qual a contribuição relativa dos diferentes fatores, como eles interagem etc. Obter respostas para essas questões, e para muitas outras, é um dos desígnios que movem os ecólogos.
Free-feeding insect herbivores along environmental gradients in Serra do Cipó: basis for a management plan

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The distribution of free-feeding insect herbivores in Brazilian savanna was studied in the National Park of Serra do Cipó. Insect samples were obtained with sweep nets across cerrado (savanna), rupestrian field and altitudinal grassland vegetation from 800 to 1500 m above sea level. We found a low species richness in xeric and mesic habitats during both wet and dry seasons. Sap-sucking insects were the most abundant guild (53.4%) with Cicadellidae the most abundant family (27.2%). The hypothesis that xeronomic richness of free-feeding insects decreases with increasing altitude was supported in xeric habitats during the wet season only, mainly as a function of mountain summit effect. There was a decrease of 65% in the number of families occurring at 1400 and 1500 m compared with lower elevations. The exclusion of sites of rupestrian vegetation at mid-elevations from the analysis increased significantly the proportion of variation explained by the model. An examination of taxon distribution using canonical variate analysis supported this result. The hypothesis that mesic habitats are richer in species of free-feeding insect herbivores than are xeric habitats was not supported. The data indicate that plant sclerophyly may exert a strong negative influence on insect species richness, and that variation due to particular characteristics of each site strongly affected the studied guilds. The present results should inform conservation strategies for the National Park Management Plan, which is currently being developed.

Keywords: altitudinal gradient; cerrado; free-feeding insect herbivores; high altitude grassland vegetation; sclerophyly.

Introduction

Patterns of insect species distribution in the tropics have not been sufficiently explored, despite many recent studies (e.g. Leahey and Proctor, 1987; Fernandes and Price, 1988, 1991; McCoy, 1990; Olson, 1994; Lopatin, 1996). In montane ecosystems, where climate variation and natural habitat fragmentation are common traits (Olson, 1994; Boggs and Murphy, 1997; Fernandes et al., 1997; Haslett, 1997), it is important to understand the variation in species distribution within and between habitats, its ecological meaning and its relevance to species conservation (Janzen, 1967). Species endemisms and insect assemblages are influenced by landscape patches, and thus easily affected by impacts like anthropogenic fragmentation or change in forest composition (Umpster, 1991; Samways, 1995; Brown, 1997). Distribution of insect species richness along environmental gradients corresponds, to some extent, to the patches in the environmental matrix. Therefore, consideration of specific habitat characteristics in studies of gradients may elucidate ecological processes in natural ecosystems and human expanded habitat edges (review of landscape ecology and insect conservation in Samways, 1995).

Whilst most studies point to a negative correlation between species richness and altitude, mid-elevation peaks of insect richness have been reported for tropical mountains (Janzen, 1973; Young, 1982; McCoy, 1990). Severe physical conditions associated with high altitudes have been used to explain the decreased species number in mountain ecosystems (Mani, 1962; Smith and Young, 1987; Walla, 1987; Boggs and Murphy, 1997). However, the importance of spatial complexity of mountain ecosystems and its effects on invertebrate communities have been recognized recently (Haslett, 1997), and may nullify a gradual decrease in species number along gradients (Ribeiro et al., 1994; Ribeiro and Fernandes, 1998).

Significant changes in insect species richness are greater on mountain tops or on rough slopes due to a conspicuous rise in climatic severity or the harshness of the habitat (Sarmiento, 1986; but see Leahey and Proctor, 1987).
tor, 1987; Fernandes and Price, 1988). However, since most studies on species richness along altitudinal gradients do not include replicate samples at any given altitude (e.g. Janzen, 1973; Janzen et al., 1976; Keyser et al., 1984; Wolda, 1987; McCoy, 1990), they do not account for the relative importance of horizontal habitat variation. Recent reviews of spatial heterogeneity in montane ecosystems are found in Boggs and Murphy (1997) and Hadley (1997).

The Serra do Cipó is a high altitude area within the Espinhaço Mountain Range, in the south-eastern Brazilian Central Plateau. The most pristine and complex mountains were declared a National Park of 33000 ha in 1984. However, a strategy for use and management of this Park has yet to be developed, and ecological data are needed. The region is covered by cerrado (savanna) vegetation which changes in structure gradually with altitude. There is a predominance of xeric habitats, and most plant species are sclerophyllous. The landscape is composed of patches of different plant species, though there are various levels of overlap within any environmental gradient (Eiten, 1972, 1977; Giulietti and Pirani, 1988).

The arboreal cerrado occurs at lower altitudes (800 and 900 m). Between 900 and 1000 m the cerrado is present only as isolated patches on deeper lateritic soils. On quartzite rocks, a rupestrian vegetation dominates, i.e. a combination of sclerophyllous shrubs growing in cracks or gaps between rocks, and fragments of high altitude grassland vegetation. It occurs from 900 m up to the summit (1500-1600 m) and contains several endemic plant species. Most belong to genera which are highly diverse within, or unique to, the Neotropical region, such as Baccharis (Poligonaceae), Vochysia (Vochysiaceae), Xyris (Xyridaceae) and Tribolium (Melastomataceae). High altitude grassland predominates on sand quartzite soils from 1200 m up to the summit, and is more frequent and continuous than the rupestrian vegetation in the study area. In companion studies using the same sampling sites, a negative effect of altitude on gall-forming and mining insects and ants was found in these xeric habitats (Lara and Fernandes, 1996; Fernandes et al., 1997). Nevertheless, it appears that this pattern does not apply to free-feeding herbivorous insects (Ribeiro et al., 1994; Carneiro et al., 1995; Fernandes et al., 1997).

Narrow corridors of moist gallery forest predominate along streams and rivers across the altitudinal range, up to 1400 m (Meguro et al., 1996a, b). Fernandes and Price (1988, 1991, 1992) argued that the species richness of free-feeding insects should be favoured by microclimate and physical conditions associated with gallery forests in comparison with the surrounding sclerophyllous cerrado vegetation. They expected similarities in physical conditions among gallery forests along the altitudinal gradient, due to relatively consistent structure and physical conditions in these mesic habitats.

The aim of this work was to study the variation in species richness of free-feeding insect herbivores along an altitudinal gradient in the Serra do Cipó. Two hypotheses were tested: (i) that insect species richness decreases with increasing altitude (e.g. Pianka, 1966), tested in xeric and mesic habitats independently (see Fernandes and Price, 1988), both in wet and dry seasons; and (ii) that mesic habitats are more favourable, constant and therefore, richer in free-feeding insect herbivores than xeric habitats in both dry and wet seasons (Fernandes and Price, 1988). Implications for the elaboration of a management plan for the National Park are discussed in the conclusion section.

Methods: study sites

The study sites were established in the region of the Serra do Cipó National Park, in Minas Gerais State, Brazil (between 19° 15' and 19° 30' S, and 43° 30' and 43° 55' W). The altitudinal range in the study area varies from 800 to 1500 m. The study region is in the Brazilian Central Plateau which is, on average, 800 m high, with an area of over 1500000 km², almost all covered with cerrado vegetation (Goodland and Ferri, 1979). Three sample sites widely distant from each other (> 1 km) were established for every 100 m of altitude from 800 to 1500 m. Each sample site comprised one xeric habitat sample point and the closest mesic habitat sample point. Cerrado was sampled at 800 and 900 m, rupestrian vegetation between 900 and 1200 m, and high altitude grassland between 1200 and 1500 m. The mesic habitats (gallery forests) were sampled from 800 to 1400 m. Only two sample sites could be established at 1400 m because there were few springs at this altitude surrounded with gallery forests. For a detailed site description see Ribeiro and Fernandes (1998) and Meguro et al. (1996a, b).

Sampling of insect herbivores

Insects were sampled in 1991, in the wet (January-February) and dry (July-August) seasons. In the dry season, we began sampling four months after rain. Samples were taken with a sweep-sample net of 38 cm diameter. The sweeps were done by the same personnel in all sample sites, always between 09:00 and 16:00 h, though never while there was rain or strong
wind. Both seasonal samples were completed in approximately three days. Sites from high, middle and low altitudes were randomly chosen to be sampled within each day. Both herbaceous and arboreal (when present) strata were sampled. In rupesrestrial vegetation, samples were taken mainly in fragments of grassland, on sedentary sandy soil between the rocks. Five sub-samples of 30 sweeps were taken walking along one line of approximately 30 m, at each sample point. Altogether, the 150 sweeps by point, 300 by sample site (two sample points per sample sites: xeric and mesic), provided a total of 6600 sweeps per season.

The cumulative sum of morphospecies from each set of 150 sweeps of a sample point was used to estimate species richness. All adult insect herbivores were considered, with the exception of flower feeders (Cantharidae, Dasytidae and some Braconidae spp. (Chrysomelidae), known flower eating species), because flowers are typically a non-sclerophyllous resource (Ribeiro et al., 1994). However, it is probable that there were not many species among these excluded taxa, since the two sampling seasons were not during the flowering period for most plant species in the region.

Insects were identified to morphospecies and estimates of species richness may be conservative, owing to the possibility of the presence of cryptic species. For instance, cryptic species are known to be frequent in the Chrysomelidae (Young, 1982; Lopatin, 1996), an abundant family in the region (Ribeiro et al., 1994; Carneiro et al., 1995). Conversely, similarity between species, due to common adaptations to vegetation, altitude and high solar radiation exposure might be confused with high colour and size variability of some species of Chrysomelidae, which could lead to incorrect assignation of morphospecies (Basset and Samuelson, 1996; Knoll et al., 1996). Therefore, the present study concentrated on distribution patterns and not on general diversity estimates. Since most families were distributed equally along sites (see discriminant analysis below), different bias in species richness estimates along altitudes or between xeric and mesic habitats was not anticipated.

**Data analysis**

The altitudinal gradient effect on insect species richness was analysed using simple linear regression models. Although altitudinal data per habitat were distributed normally, there was some pattern in the residues of the overall data set. Therefore, in order to compare xeric and mesic habitats, and wet and dry season, Wilcoxon signed-rank test (Zar, 1984; Wilkinson, 1989) was used.

Ecological communities in mountain ecosystems are inadequately characterized by species richness estimates alone (Haslett, 1997). The distribution of insect abundance by taxa was analysed using canonical variate analysis, or discriminant analysis, hereafter, CVA (Digby and Kempton, 1987; Chatfield and Collins, 1996). This analysis was performed only for data from xeric habitats during the wet season, when insect species richness varied with altitude and when the differential effects of habitat types were identified (see results below). Insects were grouped by recognizable higher taxa level, namely superfamily, family and subfamily, or by feeding guild when individuals were not identified, since there were no biological data or reliable taxonomy available for most species. However, it is possible to infer from family level some biological information about the individuals. Further analyses of taxa distribution along altitude for the xeric versus mesic habitats are detailed in Carneiro et al. (1995).

Canonical correspondence analysis (CCA) has been considered the most accurate technique to identify community gradients along multi-dimensional environment data (Ter Braak, 1986; Digby and Kempton, 1987). CVA is the variant to CCA when just one p-dimensional environment variable is used to separate species abundance (Chatfield and Collins, 1996). In this study, the altitude is an axis that defines gradual habitat and, consequently, community changes, fitting the assumptions of the CVA model. Therefore, an altitude-by-taxon group matrix was computed, using the abundance of the 19 most common taxa (listed in Table 2), according to the procedures in Ter Braak (1986), Basset (1992) and Basset and Samuelson (1996). Each altitude was considered as one dimensional variable and sites were replicates of these variables, grouped by insect taxa.

**Results: general patterns**

A total of 4351 specimens of free-feeding insect herbivore, belonging to 36 families, were sampled during two seasons on the altitudinal gradient, in both xeric and mesic habitats. Hemiptera (adopted as Homoptera and Heteroptera united) was the most abundant order (52.4%), while the Cicadellidae was the most abundant family (27.2% of all families). Orthoptera represented 23.8% of sampled insects, followed by Coleoptera (20%), Blattidae (3.4%) and Phasmodea (0.2%).

When separated into feeding guilds, sap-sucking composed 56.2% of identified morphospecies against
43.8% of chewing insects. During the wet season, the proportions of sap-sucking and chewing insects were approximately the same in both xeric (51.8% and 48.2%, respectively) and mesic (53.2% and 46.8%, respectively) habitats. A similar trend was found in the dry season, however the proportion of sap-sucking was slightly higher than that of chewing in xeric (60.6% and 39.4%, respectively) and mesic (60.3% and 38.8%, respectively) habitats.

The overall number of morphospecies was low per site (mean = 6.0; range: 0–20) and per altitude (mean = 31.0; range: 11–42). In xeric habitats in the dry season, the number of species sampled was low across all altitudinal gradients, and was also significantly lower than in the wet season (Wilcoxon signed-rank test z = 2.78, p < 0.01, Fig. 1A). However, in mesic habitats the number of insect species did not change between the dry and wet season (Wilcoxon signed-rank test z = 1.9, p > 0.05, Fig. 1B).

Hypothesis of altitudinal gradient

There was no consistent relationship between species richness and altitude. In the wet season, insect species richness decreased with increasing altitude in xeric habitats ($r^2 = 0.33$, $y = 29.96 - 0.013x$, $F_{1,22} = 11.002$, $p < 0.01$, Fig. 2A), but not in mesic habitats ($r^2 = 0.01$, $p > 0.05$). In the dry season, altitude did not affect insect richness in xeric habitats ($r^2 = 0.03$, $p > 0.05$). However, contrary to expectation, species richness increased with increasing altitude in the mesic habitats.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Functions</th>
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</thead>
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<tr>
<td></td>
<td>Func. 1</td>
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<tr>
<td>Eigenvalues</td>
<td>31.0299</td>
</tr>
<tr>
<td>Variance explained %</td>
<td>81.13</td>
</tr>
</tbody>
</table>

Standardized canonical discriminant function coefficients

| X800 | 1.27215 | -0.01775 | 0.13489 | -0.44002 |
| X900 | 0.31016 | 0.13622  | 0.20110 | 0.64176  |
| X1000| -0.01283| 0.48901  | 0.12913 | 0.65293  |
| X1100| 0.52854 | -0.19769 | -0.22703| 0.43502  |
| X1200| 0.20217 | 0.93693  | -0.58065| -0.33261 |
| X1300| 1.06738 | -0.96502 | -0.23250| -0.32765 |
| X1400| 0.41947 | -0.03181 | 0.93537 | 0.05418  |
| X1500| 0.03688 | 1.12150  | 0.07643 | -0.19564 |

Pooled within-groups correlations between discriminating variables and canonical discriminant functions

| X1400| 0.20292 | 0.01978 | 0.65530 | -0.27143 |
| X1200| 0.19891 | 0.35282 | -0.38326| -0.24143 |
| X800 | 0.21479 | 0.17216 | 0.12543 | 0.03306  |
| X1300| 0.38336 | -0.23922| -0.17775| -0.21240 |
| X900 | 0.10211 | 0.10808 | 0.08591 | 0.48597  |
| X1100| 0.29764 | -0.15627| -0.37710| 0.39997  |
| X1500| 0.14653 | 0.24197 | 0.12982 | -0.21470 |
| X1000| 0.16794 | 0.24640 | -0.05068| 0.53698  |
in the dry season \( (r^2 = 0.39, \quad y = -1.74 + 0.014x, \quad F_{1,34} = 11.756, \quad p < 0.01, \quad \text{Fig. 2B}) \).

To test the effect of altitude further and search for a more ecological explanation for species distribution patterns, a second set of linear regression models without the 1400 and 1500 m sample sites were made. No relationship between species richness of free-feeding insect herbivores and altitude was found when these data were excluded from the analysis. Even the positive relationship found in the xeric habitats in the wet season was not supported \( (r^2 = 0.03, \quad p > 0.05) \). This analysis suggests that the decline in richness with altitude was an artefact of severe reduction in species richness at the highest sites within the altitudinal gradient and not due to a steady decline in species richness with altitude.

A new set of analyses examining the effects of vegetation physiognomy on species richness of free-feeding insects were performed. It was found that the lowest values in species richness observed at intermediate altitudes came from sites of grassland vegetation. This vegetation increased the variability in species number between sites. A new model omitting values from grassland vegetation sites explained 59% of variance in species richness \( (r^2 = 0.59, \quad y = 35.87 - 0.017x, \quad F_{1,33} = 7.921, \quad p < 0.001) \) in comparison with 33.3% in the previous model, but did not change the slope of the model \( (t = 0.732, \quad p > 0.05) \), indicating that there is an expressive variance in the number of species within a certain altitudinal range.

**Change in taxa abundance distribution with altitude**

Discriminant analysis functions were computed for xeric habitats in the wet season. The abundance of the 19 studied taxa varied within each altitude (U-statistics, \( p < 0.05 \)), except at 900 m (U-statistics, \( p < 0.13 \)) where most taxa occurred, but in low densities. The first and second discriminant functions explained 92.78% of data variation (function 1 = 81.13% and function 2 = 11.65%). Table 1 summarizes the eigenvalues and correlation coefficients of this analysis. The first function was highly correlated with altitudes 800 m and 1300 m whilst the second function was correlated with altitudes 1200 m, 1300 m and 1500 m.

Canonical discriminant function by group centroids showed Cicadellidae, Acrididae, and Tettigoniidae as having the highest correlation coefficients with function 1 (Table 2). Basically, this means that these families were distinctive for the number of individuals in 800 m and 1300 m, especially C. in the former altitude. Also Cicadellidae, Acrididae and C. had the highest correlation coefficients with function 2, showing high abundance of these families (and, therefore, total high abundance) for 800, 1200 and 1300 m (Table 2). The CVA diagram of function 1 versus function 2 (Fig. 3) distinguished Cicadellidae, Acrididae and C. from other taxa, highly clustered in the co-ordinates of intermediate sites. Also, Tettigoniidae appeared slightly separated from the other taxa.

The occurrence of families reflected the pattern found for species richness: there was an average of 20.2 taxa per altitude between 800 and 1300 m (range: 18-23), and just 13 taxa at 1400 and 1500 m, which means a loss of 27% of taxa from 1300 to 1400 m and an overall loss of 65% of identified taxa at the highest elevation.

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**Figure 1.** Species richness of free-feeding insects in wet and dry season in Serra do Cipó. The number of species decreased in the dry season in (A) xeric (Wilcoxon signed-rank, \( p < 0.05 \)), but not in (B) mesic habitats (Wilcoxon signed-rank, \( p > 0.05 \)).
Cicadellidae were abundant throughout all altitudes, with highest values at 800 m (77 individuals), and at one specific site at 1500 m (21 individuals). Acradidae were most abundant at 800 and 1300 m (each altitude with 38 individuals), Curculionidae at 1200 m (18 individuals), while Lethrigidae had 24 individuals sampled at 1300 m.

The discriminant analysis showed: (i) a uniform distribution of most insect taxa at low and intermediate altitudes; (ii) a high abundance of few taxa at some specific sites, however not clearly correlated with the altitudinal gradient; and finally (iii) a sharp decrease in the occurrence of taxa at the highest sites. Therefore, the discriminant analysis reinforces the influence of mountain tops and habitat effects on species richness of free-feeding insect herbivores.

![Graph A](image1)

![Graph B](image2)

**Figure 2.** Species richness of free-feeding insects in Serra do Cipo (A) in xeric habitats, in wet season, along the altitudinal gradient (blanket points delimited are riparian vegetation sites). Model estimated for all sites: \( y = 29.96 - 0.013x \). (B) In mesic habitats, in dry season, along the altitudinal gradient. Model estimated from every site: \( y = -1.74 + 0.014x \).
Hypothesis of favourable conditions in mesic habitats

Although comparisons of wet versus dry season suggest that mesic habitats are more constant in species richness than xeric habitats (Fig. 1), no statistical difference was found between the number of insect species in both seasons when comparing mesic with xeric habitats (Wilcoxon signed-rank test: wet season $z = 0.13$, $p > 0.05$; dry season $z = 0.87$, $p > 0.05$). Therefore, these data did not support the hypothesis that mesic habitats are more favourable to free-feeding insect herbivores, even if they had been constant in species richness between seasons.

Discussion

The prevalence of harsh environmental conditions, such as poor soils and a nutritionally poor plant community, may have influenced the low free-feeding insect species richness across the whole studied area, contrasting with other tropical mountains (Janzen, 1973; Krysan et al., 1984; Wolda, 1987; Fernandes and Price, 1988; McCoy, 1990). The Serra do Cipó is located in the Espinhaço mountain range, which has an old and eroded relief, formed by the rise of Pre-Cambrian and Cretaceous soils in the Tertiary period (Freitas, 1951). Still in the Tertiary, the hot and sunny climate and the already poor soils influenced the spread of a sclerophyllous plant community (Rizzini, 1979). Most studies on insect diversity in tropical mountains were made on higher and more recent areas, covered by richer soils (e.g. Janzen, 1973; Simpson, 1975; Wolda, 1987). The present basic assumption is that sclerophyll would have been favorable to the specialization of free-feeding herbivores, but not so favorable to their speciation, owing to nutritional and chemical restrictions and phylogenetic constraints on this guild (Coley et al., 1985; Salatino, 1993; Ribeiro et al., 1994; Turner, 1994).

The pattern of distribution of free-feeding insect herbivores along altitudinal gradients was supported, albeit weakly, by our data. Species declined with altitude only in the wet season in xeric habitats, but this was primarily influenced by the harsh conditions on mountain tops (see Young, 1982; Lawton et al., 1987; Boggs and Murphy, 1997). Stochastic decreases in temperature may result in a sudden reduction in insect abundance on the mountain tops during the early wet season (Galvão and Nimer, 1965), while intermediate and low altitudes are buffered by a more stable and warmed air mass, protected by a constant high solar radiation and physical wind barrier. Moreover, the primary cause of decline of insect species on mountain tops seems to be influenced by increasingly harsh conditions (Kingsolver and Watt, 1983, 1984; Lawton et al., 1987; Boggs and Murphy, 1997), rather than reduction in plant species number or smaller overlap between plant patches on the top (Eiten, 1972; Giulietti and Pireni, 1988; Ribeiro et al., 1994). The combination of these characteristics can severely reduce species diversification (Kole et al., 1996), and benefit a few resource specialist species, as described for species of Brachypoecia in Serra do Cipó (Ribeiro et al., 1994).

The effect of habitat diversification at low and intermediate altitudes reduced the explanatory capability of the regression model for xeric habitats in the wet season. This result indicates that the complexity of habitats across any geographical range, along with different levels of habitat fragmentation, may be an important

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**Table 2. Canonical discriminant functions by group centroids for functions 1, 2, 3 and 4 of the CVA analysis**

<table>
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<th>Func. 4</th>
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<td>-0.53083</td>
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</table>

Group centroids codes: a, Acrididae; b, Heteroptera; c, Curculionidae; d, Tetragonidae; e, Membraeolidae; f, Cicadellidae; g, Scolistellidae; h, Megastigmidae; i, Blattodea; j, Pentatomidae; k, Roripinae; l, Fulgoridae; m, Dactylopiidae; n, Pseudococcidae; o, Cercopidae; p, Cryptoccephalidae; q, Tingidae; r, Delphacidae; s, Cicadidae.
determinant of species richness (Ribeiro and Fernandes, 1998). For instance, some highly diverse sites at 1200 m and 1300 m could be interpreted as intermediate peaks, but this was not a consistent pattern among all intermediate sites and, in addition, the few peaks were defined primarily by Cricadellidae.

The maintenance of higher richness and abundance of sap-sucking, especially Cricadellidae, than of other insect groups along altitudes was one important component of the variability at intermediate sites. Cricadellidae species did not decrease between seasons in xeric habitats (Carneiro et al., 1995), and the present results indicated that sap-sucking insects can perform better than chewing insects in both xeric and mesic habitats in the dry season. These data are in accordance with the hypothesis that sclerophyllous has negative effects on free-feeding insects, while sap-sucking may avoid some of the sclerophyllous traits by feeding directly from the plant’s vascular system.

The maintenance of similar numbers of insect species in mesic habitats between both seasons contrasts with the decline of species number in xeric habitats and, in a first analysis, corroborates Fernandes and Price’s (1988, 1992) hypothesis. However, there was high variability among the mesic sites. Although Fernandes and Price’s hypothesis considered mesic habitat homogeneous compared with xeric habitats, the coefficients of variation of species number among sites for mesic (0.27) and xeric (0.25) habitats were both low and extremely similar in the wet season. Therefore, the pattern of higher free-feeding insect species richness in mesic than in xeric habitats, obtained by Fernandes and Price (1988, 1992), may have been influenced by some locally rich mesic sites, though the really favourable conditions for these insects in gallery forests are not understood completely and do not exist in all mesic habitats. All gallery forests are narrow (between 2 and 20 m) and are restricted to immediate borders of streams and washes (Machado et al., 1996a,b). The surrounding soils (xeric habitats) are poor, and any autochthoneous nutrients would be leached by the tropical storms. Therefore, these habitats may be composed, similarly to xeric habitats, of nutrient-poor and chemically deterrent plant species.

Conclusions: insect species richness and habitat conservation

Preservation of pristine, unique habitats and endemic species, scientific research, conservation associated
with education and sustainability of surrounding agricultural communities, and public leisure are priority objectives of the National Park of Serra do Cipó (G.W. Fernandes, unpublished technical report). Reliable ecological data are required in order to define where a certain activity may occur, or which management technique should be applied. Knowledge of insect assemblages has been used to evaluate habitats in a biogeographic and landscape ecology perspective (Dempster, 1991; Samways, 1995; Stork and Samways, 1995; McGeoch and Chown, 1998). In the case of the National Park of Serra do Cipó, further surveys and a more precise definition of species composition of assemblages (and their ecological functionality) are required for accurate habitat labelling and evaluation of conservation status (Dufrêne and Legendre, 1997). However, the present results suggest aspects of insect assemblages and their habitats which should be explored further, and provide valuable baseline information for the setting of conservation priorities.

Our study emphasizes that the development of conservation strategies in this region must consider the landscape as a mosaic of habitat types, rather than just a set of altitudinal zones. The pattern of species richness described here underlines two contrasting components of the landscape that may require special attention: the extremely low species richness of xeric sites in the mountain tops and in the rupestrian vegetation, and the unexpectedly low species richness in mesic habitats.

Beyond a simplified analysis based on comparison of diversity among sites, there is evidence that the paucity of species on the mountain tops and in the rupestrian vegetation may result from special characteristics of these sites, such as natural fragmentation, small sizes and environmental harshness (Janzén, 1967; Leakey and Proctor, 1987; Olson, 1994; Boggs and Murphy, 1997). These particular habitats may support a distinctive fauna, perhaps more vulnerable as a consequence of its spatial constraints (Young, 1992). For instance, a companion study on Brachypimes distribution showed that this genus is extremely abundant on top sites, and its occurrence is associated with several flowering montane plants (Ribiero et al., 1994). The likely fragility of this habitat is compounded by pressure of human disturbance. Opening of roads at the top of mountains to facilitate tourist access is common practice. Holistic management of these sites will require public access (approval of road building – or denial in favour of footpaths - and road/footpath design on approved routes) to be balanced against potential threats to local habitats.

The data indicate that gallery forests in Serra do Cipó may represent a less buffered system than previously thought, as they may have an intense interaction with the surrounding xeric habitats. These may have resulted in similar richness of free-feeding insects and taxa composition to those of the adjacent xeric habitats. Conversely, mesic habitats along streams and rivers may represent important sites for speciation and maintenance of diversity in the savannas (Smith et al., 1997). Despite general similarities, the richest sampled sites were in mesic habitats connected with patches of forest. To what extent this high species richness could be associated with the patches’ natural condition or human disturbance needs to be further explored. Due to past agricultural activities, patches of high altitude forest and cerrado have been impacted by logging and fire. Consequently, these patches, as well as several areas of gallery forest, might require rehabilitation projects and careful protection against fire, since they might support a less fire resistant fauna than xeric habitats (Louvada et al., 1996; Naves, 1996). As for rupestrian vegetation and mountain tops, natural fragmentation of mesic habitats and their small sizes may exacerbate their vulnerability.

The same adverse conditions that influenced the high diversification of gall-forming insects (see Fernandes and Price, 1991) may have restricted the diversification of free-feeding insects in the Serra do Cipó. The need for specialization, plus the complexity of the landscape, may have created in the Serra do Cipó an ecosystem diverse in terms of insect survival strategies, despite the apparent low number of observed species. The point of concern is the vulnerability of the specialist, endemic and rare species, and the resistance or resilience of this community as a whole.

Provided that basic ecological information is available, targeted experimental work can optimize efforts to establish criteria for land management plans or conservation priorities. Insect herbivore assemblages in Serra do Cipó have been well studied, and ecological and evolutionary hypotheses to explain patterns of species distribution in areas of cerrado have been developed and tested over the last 10 years (Fernandes and Price, 1988; Giuffetti and Pirani, 1988; Lara and Fernandes, 1996; Moguro et al., 1996a; Ribiero and Fernandes, 1998). Knowledge of local insect and plant communities has identified habitat mosaics as one of the key components of this ecosystem, and provides the foundation for further research devoted to identifying specific management requirements.
Acknowledgements

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References


Abundance of Neopelma baccharidis (Homoptera: Psyllidae) Galls on the Dioecious Shrub Baccharis dracunculifolia (Asteraceae)

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ABSTRACT. We assessed whether temporal variation in gall abundance of Neopelma baccharidis on Baccharis dracunculifolia in the Acai belt is determined by climatic conditions, availability of adults for gall colonization, or gall concentration in plant tissue. We divided the reproductive phases (April-October) into three periods (spring, summer, and autumn) and sampled 200 plants per period. Gall density was measured on a weekly basis during the growing season. Our results showed that the abundance of galls was significantly lower in the autumn than in the spring and summer periods. The highest gall density was observed in the summer period, with a peak in the middle of the summer. The number of galls per plant was negatively correlated with the number of adults per plant, indicating that the abundance of galls is determined by the availability of adults for gall colonization. The results of this study suggest that the abundance of Neopelma baccharidis is influenced by climatic conditions and the availability of adults for gall colonization.

KEY WORDS. insect galls, insect herbivory, plant phenology, plant sex, natural enemies

A MULTITUDE of factors, including plant age (Karban 1987), inducible defenses (Haukojo 1983), and production of secondary compounds (Jones 1975) influence the quality of plants to herbivores. The defense provided by these factors may change both seasonally and phenologically (Fenner 1976, Dirzo 1984, Allard 1985, Wolda 1988, Fernandes 1990). Plant phenology affects the concentration of secondary defensive compounds such as tannins and alkaloids, which are important in diminishing herbivore pressure on plants (see Zotova and Shifman 1982, Rockwood 1974, Macnair and Fox 1990, Predhomme 1983, Pablo et al. 1985 and reproductive stages (Jing and Coley 1990).

Plant gender also may affect the biology and population dynamics of some herbivores. The influence of plant sex on herbivores is suggested to be caused by the differential distribution of male and female plants along morphological gradients (Freeman et al. 1976), differential patterns of biomass allocation (Agron 1985, Boekhien and Hoffmann 1993), or differential production of plant defenses such as tannins. Thus, studies on associations between insects and dioecious plants should consider sexual effects and their consequences in time and space.

The importance of parasitoids, predators, and inquilines associated with gall inducers is enormous, and the study of these communities has contributed to knowledge of ecological mechanisms and evolutionary processes involved in gall formation, distribution, and differentiation (Ashe 1975, Price et al. 1987, Schonroth et al. 1996). Nevertheless, parasitism on gall-inducing insects is mediated by many factors: habitat (Fernandes and Pense 1992), plant genetics (Craig et al. 1990), gall location on the plant, gall anatomical structure (Gilg et al. 1990, Weis 1991), and possibly sex of host plant and seasonality.

Baccharis dracunculifolia (Dioecious Asteraceae) is a widespread dioecious perennial shrub, 2–3 m in height, that occurs in southeastern and southern Brazil, Argentina, Uruguay, Paraguay, and Bolivia (Barrero 1976). Neopelma baccharidis Burchard (Homoptera: Psyllidae) is the most common gall inducer found on B. dracunculifolia (Araujo et al. 1998). The galls induced by this psyllid are elliptical, green, glabrous, and 1 cm in diameter, and probably have several overlapping generations per year (Lara and Fernandes 1994). B. dracunculifolia galls grow throughout the year, continuously producing leaf and pod gall products. B. dracunculifolia females. This constant growth may facilitate the multivoltinism of the gall inducer (Lara and Fernandes 1994). However, variation in population density of N. baccharidis, the number of generations produced, and the differential attack of each generation on the host sexes are unknown.

Fig. 1. Monthly total rainfall (filled circles) and monthly average temperature (open squares) in the study site during the period of observation.

Females of N. baccharidis oviposit on the main vein of leaves of the host plant. Initially, the leaf tissues swell, bending over itself until interaction of borders and thereby forming an elliptical capsule (Lara and Fernandes 1994). Nymphs develop inside the inner chamber of this capsule. Gall walls are succulent throughout the development of the psyllid. Even after the death and emergence of the adults, the gall remains attached to the plant, undergoing gradual desiccation, until it becomes dry and woody. This is common to find galls from many generations on a single plant.

The galls of N. baccharidis contain from 1 to several nymphs inside the gall chamber. The developmental time of the nymph is variable, and the length of the adult stage is unknown. Three preimaginal stages are known: unimaginal gnathors, pupal gnathors, and winged gnathors (Roper and Colvett 1993). The parasitoid Neopelma baccharidis leaf and seed galls in the gall wall after emergence, facilitating the identification of the mortality caused by parasitoids.

In this study we observed the relationship between plant gender, gall concentration in leaves, sexual ratio, and mortality factors and their effects on the abundance of galls in the population. The following questions concerning these interactions were tested: (1) Do seasonal and seasonal variation in gall abundance of N. baccharidis? (2) What is the relationship between gall abundance and gall density in leaves? (3) Are there sex-mediated differences in gall abundance and mortality rates of N. baccharidis? (4) What is the relationship between seasonal variation in gall abundance and gall mortality rates? (5) Do differences in gall abundance and maturity affect the number of females produced in the population?

Material and Methods

Study Area. The study was performed in the Campus of the Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (19° 30' S, 44° 00' W), at 856 m above sea level. The average temperature of the study site varied from 18 to 28°C and the average annual precipitation was 1,200 mm. Figure 1 shows the monthly average temperature and monthly total precipitation during the study period. The vegetation is extremely heterogeneous and diverse, composed of natural, introduced, ornamental and fruit-bearing species. The adjacent native vegetation is composed of forest and cerrado (savannas) species (Ferrari 1977). The study plants were all located in a 2 ha area at an early successional stage, with a predominance of B. dracunculifolia, 2 other species of Baccharis, grasses, herbs, and shrubs (Leguminosae) species (Araujo et al. 1995).

Temporal Variation in Gall Abundance. The seasonal variation in gall abundance was evaluated by monthly collection of all galls of N. baccharidis from 30 randomly selected B. dracunculifolia (10 males and 15 females) from May 1993 to September 1996 (recovery study). Sexes of the host plants were distinguished by observations of morphology of the flowers. Plants were categorized into 1 of 2 phylogenetic groups: reproductive (when the plants were flowering) and nonreproductive (when the plants did not bear any flowers). The term "mature" could not be used in this study because B. dracunculifolia grows continuously throughout the year.

We also recorded the monthly variation in adult abundance of N. baccharidis. Adults were recorded by visual observation for periods of 30 min on 20 male and 20 female plants randomly selected from the same population, from September 1993 to August 1996. The time of observation was determined through a lifetime accumulation curve (C.A. Miranda and G.F.W., unpublished data).

Because the host plant flowers several times a year, gall abundance during the reproductive and nonreproductive phases was analyzed separately. Differences between phases were tested using Mann-Whitney U test, as our data did not follow a normal distribution (Zar 1984). We also grouped the abundance of adults during the reproductive and nonreproductive phases separately. Differences between phases were tested using a 2-tailed t-test (Zar 1984). Furthermore, we observed whether there was a relationship between monthly gall abundance, monthly average temperature, and monthly total precipitation by multiple linear regression.

We determined the number of generations of galls during 2 mo by marking all newly formed galls each month on 3 trees and females of B. dracunculifolia randomly selected from the host plant population (cohort study). All galls were marked and counted from February to October 1996. Galls produced each month were marked with different colors of water-resistant paint and considered as belonging to different cohorts (the total number of galls produced in a given month).

Field Concentration. The concentration of leaf tannins in the plants collected monthly during the removal study was measured using the radial diffusion method. The data were analyzed to verify the effectiveness of these compounds to defend the plant against attack by the galling psyllid. Tannins in plant extracts were determined by reaction with borsic acid and quinone solution.
Results

Temporal Variation in Gall Abundance. The abundance of galls varied throughout the study period (Fig. 2). Gall abundance per plant was higher in the reproductive phases (10.53 ± 0.67 [mean ± SE]; n = 30) than in the nonreproductive phases (8.08 ± 0.67; n = 30). Of the abundance of adults in the field was also highly variable during the study, but did not follow the same pattern observed in gall abundance (Fig. 2). Abundance of adults in the reproductive phases (6.30 ± 1.58; n = 40) did not differ statistically from the nonreproductive phases (5.33 ± 1.16; n = 40; t = 0.55, P > 0.05). The abundance of galls per plant in the field was not influenced by total precipitation and average monthly temperature (y = 5.40 + 0.385 * precipitation + 0.118 * temperature; r² = 0.01, F = 1.32, df = 2, P = 0.26).

The developmental time of N. bachtiaris galls on B. dracunculus was highly variable, lasting from 1 to 6 mo. Five cohorts were observed during the 9 mo of study. Overlapping generations were observed during the 3 later cohorts. The 1st cohort was composed by the open galls found at the beginning of the study, whereas the 2nd cohort was composed by immature galls that already existed on the plants at the beginning of the study; hence, we could not determine when these 2 cohorts were produced. All other cohorts were produced in the reproductive phases of the host plant (Fig. 3). Seven percent of the galls of the 3 later cohorts produced adults in May, 26.3% in June, 7.0% in July, 23% in August, and 22.2% in October; no adults emerged in September.

Tannin Concentration. There was a higher concentration of tannins in leaf tissues in the reproductive phase (0.117 ± 0.017 mg/g, n = 30) than in the nonreproductive phase (0.12 ± 0.004 mg/g, n = 30; U = 131.5, P > 0.05). However, no relationship was found between gall abundance and tannin concentration both in the reproductive phase (p = 3.70 ± 0.12; r² = 0.01; F = 0.42, df = 1.29, P = 0.52) and nonreproductive phase (p = 0.22 ± 0.06; r² = 0.00; F = 0.46, df = 1.28; P = 0.76). The concentration of tannins did not differ between male and female plants of B. dracunculus in the 2 phenological phases. The mean concentration of tannins was 0.117 ± 0.027 mg/g in males (n = 15) and 0.117 ± 0.020 mg/g in females (n = 15, U = 93.0, P = 0.42). During the nonreproductive phase, mean concentration of tannins was 0.043 ± 0.003 mg/g in male (n = 15) and 0.040 ± 0.003 mg/g in females (n = 15, U = 100.0, P = 0.60).

Interspecific Differences. The sex of B. dracunculus may influence the abundance of N. bachtiaris galls. Male plants supported 5.83 ± 0.74 galls per plant per month (n = 253), whereas female plants supported 5.01 ± 0.57 galls per plant per month (n = 255, U = 31783.5, P = 0.66). The mean number of galls per plant per month (pooled by sex) was 5.43 ± 0.47 (n = 518). Plant sex also did not influence the mortality factors and survivorship of N. bachtiaris (Fig. 4). Although there was a tendency for more galls being lost by parasites on female plants, the difference was not statistically significant (U = 142.5, P = 0.48). Attacking by external chewing herbivores on the gall walls that indirectly caused mortality of the galls nymphs showed no trend (U = 170.5, P = 0.68). Therefore, survival rates were not statistically different between male and female plants (U = 163.5, P = 0.30).

Gall Abundance and Mortality Rates. The most important mortality factors on N. bachtiaris galls were parasitoids, pathogens, and plant resistance (other factors). Overall, parasitoids accounted for 3.03 ± 3.57% of gall mortality whereas other factors accounted for another 27.04 ± 4.81%. The average mortality caused by external feeding was only 2.82 ± 0.01%. Hence, the overall survivorship rate was 47.76 ± 4.06%. The mortality caused by these factors varied extremely throughout the study period and no trend was apparent. Parasitoids emerged from galls on all months except in April and September when no galls detached. Parasitism rates varied from 16.2 to 80% during the study period. Mortality caused by other factors was observed in February, March, June, August, and September, and varied from 7.4 to 41.5. External feeding was highly variable and often unrecorded among the months studied (Fig. 5). Although gall abundance varied enormously throughout the study period (from zero in April and September to 109 [February, Fig. 5]), it did not influence the mortality caused by parasitoids, external feeders, and other factors. Neither of these factors was found between rates of mortality and gall abundance per plant (Table 1).

Discussion

The abundance of N. bachtiaris galls on B. dracunculus was highly variable throughout the study period. There were 2 peaks of abundance during the 17 mo of observation, and these fluctuations in density coincided with the phenological variations of B. dracunculus. Twelve times more galls were found in the reproductive phases than in the nonreproductive phases.

Table 1. Linear regression statistics between gall abundance and rates of parasitism, external feeding, stress, and survivorship.

<table>
<thead>
<tr>
<th>Factors</th>
<th>y = b + ax</th>
<th>SE</th>
<th>r²</th>
<th>P</th>
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<tr>
<td>Parasites</td>
<td>-22.6 ± 0.05</td>
<td>3.96</td>
<td>0.37</td>
<td>0.05</td>
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<tr>
<td>External feeding</td>
<td>0.66 ± 0.65</td>
<td>1.11</td>
<td>0.95</td>
<td>0.02</td>
</tr>
<tr>
<td>Stress</td>
<td>0.50 ± 0.12</td>
<td>3.39</td>
<td>0.49</td>
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<tr>
<td>Survivorship</td>
<td>0.07 ± 0.01</td>
<td>6.62</td>
<td>0.03</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Note: None of the factors were influenced by the observed variation in gall abundance (P > 0.05) (y = mortality factor and x = gall abundance).
phases. In contrast, the abundance of adults of N. bactracoides showed several peaks during the study, with no coincidence with the reproductive phases of the gall host. Furthermore, there was a marked difference in adult abundance in the field between the reproductive and nonreproductive phases.

The timing of the activity and the shape of the oviposition peak strongly influence on life history characteristics of the species concerned (Woda 1984). These characteristics may include the rate of development of immatures, adult longevity, synchronization of mating, and components of reproduction and volatiles. The complete development of galls of N. bactracoides may last from 1 to 6 mo, overlapping with later generations, and no synchronization in adult emergence. Although a high population density of moth cohorts occurred in the reproductive phases of the host plant, galls with nymphs persisted even in nonreproductive phases, maintaining the abundance of N. bactracoides during these periods. The nutritional reserves available in the reproductive and nonreproductive phases was similar, suggesting that the success of colonization by N. bactracoides is influenced by other factors, because the adult population in the field did not show a seasonal pattern in abundance.

Climatic factors are known to influence the abundance of insects, especially in tropical areas where seasonal variations in temperature are common (Woda 1984). In tropical areas, the dry season seems to be more important than the wet season in influencing the population density of insects (Woda 1984). The abundance of adults of N. bactracoides was not related to the rainfall, temperature, and precipitation, as their activity remained high in both dry and wet seasons. Gall abundance also was not correlated with seasonal variations. Other factors, such as the suitability of the host plant, may play an important role in the seasonality of herbivores, and their abundance is known to vary greatly with host quality (e.g., nutrient content and concentration of secondary compounds) (Feeny 1970, Moran 1981, Hunter and McNeil 1997). The success of N. bactracoides to induce galls on its host plant is highly seasonal and controlled by the plant trait that varies between the reproductive and nonreproductive phases.

The allocation of resources in plants may show seasonal variations according to climatic changes (Feeny 1970, Macauley and Fox 1980, Royal et al. 1983). Ting and Coley (1990) proposed the occurrence of a trade-off between defense and reproduction in Acer negundo Willdenow, induced by higher larval rates on this plant during flowering. Nevertheless, in our study, the concentration found in leaves of B. dracaena was not as expected if a trade-off existed. The allocation of resources in the reproductive phase was higher than in the nonreproductive phase, indicating no trade-off with reproductive investment.

Furthermore, N. bactracoides did not show increased success (higher oviposition rate) on plants with low concentration of tannins. A possible explanation is that these compounds may not have the same harmful effects on gall inducers as on free-feeding herbivores. Gall-inducing insects are able to modify the normal cellular differentiation process of the plant, promoting the development of a suitable feeding site (Rohfritsch and Sharthorne 1982). Phenolic compounds encountered in the early stages of gall development may rapidly disappear from the feeding tissue during gall development (Rohfritsch and Sharthorne 1982). The concentration of tannins may not affect gall inducers due to the natural ability of the compounds to overcome this defense strategy of the host. However, the relationship between the concentration of these compounds and the effects on gall-inducing insects was not observed. Tannin concentration in B. dracaena was also unlikely to be responsible for the abundance pattern observed, possibly as a consequence of its lack of effects on gall-inducing insects. Thus, it is possible that the colonization success of N. bactracoides on B. dracaena is driven by intrinsic characteristics of the plant that vary between phenological phases and that are still undetermined, such as other kinds of secondary compounds, availability and dynamics of meristematic tissues, and physiological or mechanical defenses. Future studies should report on the effects that these mechanisms may have on the abundance of N. bactracoides on B. dracaena.

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Effect of Cone Size on Adult and Larval Foraging Behavior of Strobilomyia neantricina and Strobilomyia appalachensis (Diptera: Anthomyiidae)

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ABSTRACT: A 2-y field study was carried out to determine if adult female cone maggot, Strobilomyia neantricina Michelsen, and Strobilomyia appalachensis Michelsen, oviposit preferentially on larger rather than shorter cones of white spruce (Picea glauca (Moench) Voss), and black spruce (P. mariana (Mill.) Britton, Sterns & Poggenburg), respectively. The study also examined if resources increased with cone size and were limiting in small cones, and whether maggot feeding maintained in sections of the cone where seeds are heaviest. Females of both species laid more eggs on longer cones than shorter cones. Number of seeds per cone and number of seeds eaten per cone were positively related to cone length. However, the proportion of seeds eaten per cone was positively related to the number of seeds per cone in only 1 of 2 yr for white spruce and in neither year for black spruce, providing only very weak support for the prediction that resources were limiting in small cones. We evaluated the influence of cone length and seed position within cones on seed weight for white spruce only. Seed weight was positively related to cone length and was heaviest in the central sections of the cone. Larvae consumed the fewest seeds in the basal sections of the cone but nearly equal proportions in the central and apical sections. Our results demonstrate that the foraging behavior of adult females and larval cone maggots results in larvae consuming more and bigger seeds during development.

Key words: Strobilomyia neantricina, Strobilomyia appalachensis, Picea glauca, Picea mariana, preference, oviposition.

For female phytotrophous insects whose offspring are restricted to 1 host for development, there is strong selection pressure to select the host best suited for larval development (Janzen 1978, Craig et al. 1989, but see Larson and Ekbom 1995). Quiring and McNeil (1987) showed that when foraging on oviposition sites, females of an agromyzid leaf miner, Agromyza frontalis Rondani, ranked leaves according to the incidence or type of exploitation by conspecifics. This ranking corresponded to the level of fitness associated with laying 1 egg on each host. Similarly, selection of large hosts by ovipositing females has been associated with increased larval performance for seed and fruit feeders (Mitchell 1975, Jones 1994), that of Craig et al. 1989, Robertson (1991) and leaf (Glynn and Larson 1994) gallers, and leafminers (Faith 1991) (but see Burnstein and Wool 1995 and Aikin and Yamaguchi 1994).

Strobilomyia appalachensis Michelsen and Strobilomyia neantricina Michelsen are cone maggots found in developing cones of black spruce, Picea mariana (Miller) Britton, Sterns & Poggenburg, and white spruce, Picea glauca (Moench) Voss, respectively (Turgeon and Sweeney 1993). S. appalachensis also is found in cones of Picea rubens Sargant (Michelsen 1985, Turgeon and Sweeney 1993) and S. neantricina in cones of P. engelmannii (Bongard) Carriere and Picea engelmannii Parry ex Engelmann (Michelsen 1985). Females of both species lay eggs singly beneath cone scales when scales have closed and cones have started to turn down after pollination (Tripp and Hedlin 1985, Sweeney and Turgeon 1994). Both species have 3 instars, the 1st of which completes development in the egg. The 2nd instar emerges from the egg and commences feeding on developing ovules. Larval feeding continues for 1 mo after which time 3rd instars exit cones during rainfall and fall to the ground. Larvae burrow into the soil to pupate and remain there until the following spring, when adults emerge, or may remain in extended diapause for several years (Tripp and Hedlin 1985, Sweeney and Turgeon 1994). Both cone maggot species are considered major pests of spruce seed in Canada (Tripp and Hedlin 1985, Sweeney and Turgeon 1994). Because cone maggot larvae are restricted to 1 cone for development, natural selection should favor females that select cones with sufficient resources for larval development. Selecting cones with limited resources could result in decreased fitness of the offspring females as a result of either the death, reduced developmental rate, or size (if related to fecundity) of its offspring. Faden and Powell (1988) found that the total number of seeds per cone was positively corre-
LEAF TANNIN CONCENTRATION, TOUGHNESS, AND SCLEROPHYLLY IN SOME TYPICAL WOODY SPECIES OF THE SAVANNAS OF SOUTHEASTERN BRAZIL

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RESUMO

Estudamos as relações entre a concentração de taninos, esclerofilia e dureza de folhas em 14 espécies de plantas lenhosas de vegetação de cerrado no sudeste do Brasil. Taninos foram encontrados em apenas quatro das 14 espécies (Hyomenaea sp. x = 262.5 mg/g, Bauhinia sp. x = 340.8 mg/g, Stryphnodendron adstringens x = 368.3 mg/g; Kielmeyera coriacea x = 479.7 mg/g). Uma relação positiva entre a concentração de taninos em folhas e a dureza de folhas foi encontrada apenas em Kielmeyera coriacea ($r^2 = 0.73$, $F_{1,3} = 13.397$; $y = 157.657 + 0.277$, $p < 0.05$). Esclerofilia e dureza de folhas foram significativamente diferentes ($p < 0.001$) entre as espécies de plantas.

Unitermos: Cerrado, Dureza de folha, Esclerofilia, Taninos.
ABSTRACT
We studied the relationship between tannin concentration, sclerophyll, and toughness in the leaves of 14 species of woody plants of the cerrado vegetation in southeastern Brazil. Tannins in leaves were only found in four out of the 14 species (Hymenaea sp. x = 262.5 mg/g, Bauhinia sp. x = 340.8 mg/g; Stryphnodendron adstringens x = 368.3 mg/g; Kielmeyera coriacea x = 479.7 mg/g). A positive relationship between leaf tannin concentration and leaf toughness was found only in Kielmeyera coriacea ($r^2 = 0.73$; $F_{1,3} = 13.397$, $y = 157.657 + 0.277$, $p < 0.05$). Leaf sclerophyll and toughness differed significantly ($p < 0.001$) among plant species.

Keywords: Cerrado, Leaf toughness, Sclerophyll, Tannins
I. INTRODUCTION

Information about the distribution of tannins in plant taxa is fundamental to the study of plant-animal relationships. Tannins are polyphenolic compounds, mostly found as soluble components in the sap of living cells (Levin, 1971). They are reported to be present in approximately 35% of plant species (see Mole, 1993) and 80% of woody perennial dicotyledonous plants have been reported to have them (Rhoades, 1979).

Tannins are thought to protect plants against herbivores, fungi and bacteria (Janzen, 1974; Swain, 1977). For this reason, tannins are a major factor in ecological studies in plant-natural enemy interactions (e.g., Feeny, 1976; Rhoades, 1979; Mole & Waterman, 1987a; Bornays et al., 1989). The knowledge of tannin distribution in the plant kingdom is also of interest for evaluating the patterns and mechanisms of herbivore distribution on their host plants (Feeny, 1976; Rhoades & Cates, 1976; Harborne, 1993). They are also very important in the phylogenetic classification of plants (e.g., Mole, 1993).

The production, translocation and storage of tannins are costly for plants and their synthesis competes with the Krebs cycle and induce protein precipitation (Swain, 1977; Crawley, 1983). Hence, their synthesis reduces the productivity of tannin-producing plants (Coley, 1986; Skogsmyr & Fagerstrom, 1992). Quantitative chemical defenses (e.g., tannins) should be favored in nutrient-poor environments and therefore any biomass loss to herbivores can have strong impact on plant fitness (see Janzen, 1974; Coley, 1983; Coley et al., 1985). Tannins are thus expected to be produced in high concentrations by plants that occur in habitats where there is lower availability of energy/protein for plant maintenance or reproduction (see Janzen, 1974; Coley et al., 1985; Coley, 1986). Such a situation is thought to prevail in several types of vegetation such as in the “cerrado” (savanna) of central Brazil. Woody plants of the cerrado have photosynthesis rates in the
range of 6 to 14 μmol m⁻² s⁻¹ (Prado, 1994). We expect that these high rates would produce large quantities of carbon-based molecules such as sugars, but no studies of carbon balance have been conducted on cerrado plants to our knowledge. However, we hypothesize that rates in this range, associated with low fertility levels and high irradiancy typical of cerrado, would result in an excess of carbon that could be allocated in many ways such as fibers and tannins (Eiten, 1978).

Both the apparent energy (Feney, 1976) and C/N balance hypothesis (Bryant et al., 1983) predict that tannin concentration should be higher in sclerophyllous plants that inhabit nutrient-poor soils (see also Janzen, 1974). Hypotheses accounting for the significance of sclerophyll argue that it is an adaptation for water conservation, nutrient conservation or damage prevention (e.g., Loveless, 1961, 1962; Grubb, 1977; see review by Turner 1994). In most studies, toughness and sclerophyll have been considered the same thing and usually toughness has been used as a measure of sclerophyll (e.g., Coley, 1983). Toughness has been defined as the force required to push a blunt rod through a leaf lamina (Coley 1983). Foliar toughness is mainly related to leaf anatomy and morphology while sclerophyll is mainly related to the amount of fibers in the plant, independently of their organization in living tissues (Witkowski & Lamont, 1991). Nevertheless, recent studies consider that leaf resistance is not a measure of sclerophyll (Turner, 1994; Turner et al., 1993, Lucas et al., 1995). The plants of cerrado may offer an interesting system to the study of the relationship between tannin distribution and sclerophyll, given the special characteristics of its flora and abiotic conditions.

The distribution and concentration of condensed and hydrolyzable tannins of 14 species of dicotyledoneous cerrado plants in southeastern Brazil are reported. This study,
which is the first in this topic and vegetation type, adds to those developed by Bate-Smith and Metcalfe (1957), Bate-Smith (1968) and Mole (1993) concerning the distribution of tannins in the plant kingdom. Furthermore, three questions regarding tannin concentration, sclerophyllly and toughness in these 14 species were addressed: a) Do cerrado plants differ in tannin concentration? b) What is the relationship between tannin concentration and leaf toughness among these plant species? c) Is there any relationship between leaf toughness and sclerophyllly in cerrado woody plants?

II. METHODS

Study Site and Species

This study was done between January 1994 and June 1995 in Pampulha, Belo Horizonte, Minas Gerais, at an elevation of 805 meters above sea level (10° 30' S and 44° W) in cerrado vegetation. The climate is montane, tropical, with an average annual temperature of 21° C, and average annual rainfall of 1500 mm, with the rainy season from December to March. We studied the most abundant woody species found in cerrado without taking into account their phylogenetic relationships or growth forms. The fourteen species were: Aegiphila lhostskyana Cham. (Verbenaceae), Bauhinia sp. (Leguminosae), Dalbergia violacea (Vog.) Malme (Leguminosae), Didymopanax macrocarpum Seem. (Araliaceae), Hymenaea sp. (Leguminosae), Hyptis cana Pohl. (Labiatae), Kielmeyera coriacea Mart. (Clusiaceae), Lantana camara L. (Verbenaceae), Neea theifera Oersted (Nyctaginaceae), Pterocaulon lanatum (Asteraceae), Solanum lycoctearpum St. Hil. (Solanaceae), Styphnodendron adstringens Mart. (Leguminosae), Tabebuia ochracea (Cham.) Standley (Bignoniaceae) and Xylopia aromatica Mart. (Annonaceae).
Tannin concentration, leaf toughness and sclerophyll

We measured leaf tannin concentration (mg/g), leaf toughness (g m/s) and sclerophyll (g/cm²) in all plant species. To measure tannin concentration, 9 individuals were sampled per plant species. Three branches from each individual were randomly collected around the canopy of the plants, totalling 27 samples per plant species. Branches were placed in plastic bags, stored in an insulated box with ice and then taken to the laboratory for immediate analysis (see Mole & Waterman, 1987bc). Tannin concentrations (mg/g) were obtained through the radial diffusion method (see Hagerman, 1987). The average tannin concentration was calculated for each species followed by the standard errors.

To measure foliar toughness, 5 fully expanded leaves were randomly collected around the canopy of each plant individual (n= 9 plants) totalling 45 samples per plant species. Measurements of toughness were obtained with a penetrometer, which measures the force (N m/s) necessary for a 2mm-diameter cylinder to break the leaf lamina. Leaf veins were avoided as they could interfere with the measurement.

Leaf sclerophyll measurements were obtained through a random collection of 10 leaves per 9 plant individuals, totaling 90 leaves per species. The individuals from this sample were not the same as those from the previous samples. Sclerophyll was measured as the product of leaf-specific area multiplied by the leaf dry weight (Turner, 1994). Leaf-specific area was calculated as dry weight (g)/leaf area (cm²) (Turner, 1994). The dry weight was obtained by submitting the leaves to a drying cycle of 72 h at 70°C. Dried leaves were weighed on an analytical scale (Metler PM 2500). Leaf area was measured with a leaf area meter (Licor 3000 A).

Data were checked for normality and linear regression was used to test the
correlation between leaf tannin concentration and leaf toughness for the tannin-containing species. Analysis of variance were used to test differences in leaf sclerophyll and toughness among species (Zar, 1996).

III. RESULTS AND DISCUSSION

Tannins were only found in four of the 14 species studied (Hymenaea sp. x = 262.5 ± 9.4 mg/g; Bauhinia sp. x = 340.8 ± 27.2 mg/g; Stryphnodendron adstringens x = 368.3 ± 35 mg/g; Kielmeyera coriacea x = 479.7 ± 29.5 mg/g; Fig. 1). These results do not corroborate the current views that plant species that inhabit water and nutrient-deficient environments should produce and accumulate tannin in higher amounts than plants living in more favorable environments (e.g., Goodland & Ferri, 1979, Coley, 1983). They may also suggest that, despite living sympatrically, these cerrado plant species are utilizing different defense strategies and are probably allocating the carbon produced by photosynthesis to different chemical pathways. Similar results were also observed by Perevolotsky (1994) studying tannins in Mediterranean woodland species. Nevertheless, tannins may not be the major group of substances used as carbon storage. Plants may allocate the excess of photosyntate into waxes or starch or even export them to the ground to be used in root development (Gottlieb, 1990, Salatino, 1993). While not studied, these are common strategies utilized by plants in this complex tropical ecosystem.

Contrary to our expectation, we did not find a clear relationship between leaf tannin concentration and leaf toughness. Although the relationship was positive, it was highly variable within the tannin-containing species (Fig. 1). 73% of the variation in tannin concentration was correlated with leaf toughness in Kielmeyera coriacea (r² = 0.73; F₁,₅ =
13.397; \( y = 157.657 + 0.277x; \) p < 0.05) but not in *Stryphnodendron adstringens* \( (r^2 = 0.25; \)
\( F_{1,7} = 2.413; \) \( y = 727.3 + 1.235x; \) p > 0.05), *Hymenaea* sp. \( (r^2 = 0.08; \) \( F_{1,7} = 0.5906; \) \( y = 197.968 + 0.2215x; \) p > 0.05) and *Bauninia* sp. \( (r^2 = 0.01; \) \( F_{1,6} = 0.045; \) \( y = 432.16 + 0.0746x; \) p > 0.05).

The values found for *K. coriacea* showed a positive relationship between tannin concentration and toughness in this species (Coley, 1983). However, this relationship was not found in the other plant species which presented tannins, invalidating a generalization of this hypothesis at this moment. This is indeed very important as new evidence indicates that the biochemistry of many secondary metabolites does not necessarily corroborate the previous models of plant chemical defenses (e.g., Gershenson et al., 1993).

The weakness of the relationship between tannin concentration and toughness is very interesting. Tannins and toughness are considered strategies to accumulate carbon (Coley et al., 1985). Nevertheless, the way these strategies are utilized may be related to the evolutionary history of each plant species, as well as to variations in the need of investment into these resources (Makkar & Becker, 1994). Sagers & Coley (1995) evaluated the benefits and costs of defense in a neotropical shrub, *Psychotria horizontalis*, and found that total tannin and toughness were not correlated, therefore they could be treated as independent traits.

Leaf sclerophyll and toughness differed significantly among the plant species (ANOVA, \( F = 342.543, p < 0.001 \)). We did not find a clear relationship between the average leaf toughness and sclerophyll (Fig. 2). Plants of the *cerrado* vegetation are under the influence of high light intensity and water stress which reflect on leaf traits (Upadhyaya & Furness, 1994). Witkowski & Lamont (1991), studying six plant species submitted to a varying soil nutrient, moisture and light regimes in California and Australia, found that
toughness and leaf-specific mass can vary independently in the same species. Our results corroborate their hypothesis because we measured sclerophyly by the relationships of leaf dry weight/leaf area, i.e., we considered only the amount of fibers in the leaf. On the other hand, we considered toughness as a measure of the leaf resistance force when the leaf lamina was broken. In this case, anatomical features such as abundance of air spaces, sclereids and fiber orientation could also influence leaf resistance (Witkowski & Lamont, 1991).

If these traits are uncorrelated as the present study suggests, different plant species might be employing different defenses or a combination of defense strategies. Of the 14 plant species studied, 4 contained tannins, 6 other species were very sclerophyllus (more than 0.01 g/cm²), excluding plants with tannins, 1 species Solanum lycopersicum is known to have alkaloids (Harborne 1993) and the genus Dalbergia is known to have associations with nitrogen fixing bacteria which could promote defenses by nitrogen-based compounds (Kirkbride 1984). Hymenoclea sanguinolenta and Tabebua ochracea had tough leaves (0.01 and 0.017 g/cm² respectively) which could be assumed to be utilized as defense mechanisms against herbivores. Therefore, different plant species could be utilizing different defense strategies based on their physiology and evolutionary histories.

This study described an interesting, yet poorly studied, aspect of plants that is of enormous importance to insect herbivores and community organization. Although preliminary, the results indicate interesting aspects on the physiological ecology of cerrado plants that must be further studied. The cerrado is tremendously rich in plant species (Ratter & Dargie, 1992), hence an extension of this study is necessary before any generalization is attempted. A phenological approach is also needed to observe seasonal variations in tannin concentration in different parts of these plants (e.g., Salatino et al.,
IV. ACKNOWLEDGMENTS

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FIGURE LEGENDS

Fig. 1 - Average leaf toughness (full dots) and leaf tannin concentration (bars) in fourteen plant species of the cerrado vegetation, Belo Horizonte, MG. Plants were ordered by average leaf toughness. Letters representing species stand for the initials of each scientific name (Al = Aegiphila lhostskyana, Ba = Bauhinia sp., Dv = Dalbergia violacea, Dm = Didymopanax macrocarpum, Hy = Hymenaea sp., Hc = Hyptis cana, Kc = Kielmeyera coriacea, Lc = Lantana camara, Nt = Neea theifera, Pl = Pterocaulon lanatum, Sl = Solanum lycocarpum, Sa = Stryphnodendron adstringens, To = Tabebuia ochracea, Xa = Xylopia aromatica).

Fig. 2 - Average leaf toughness (full dots) and sclerophyll (bars) in fourteen plant species of the cerrado vegetation, Belo Horizonte, MG. Plants were ordered by average sclerophyll. Letters representing species stand for the initials of each scientific name (Al = Aegiphila lhostskyana, Ba = Bauhinia sp., Dv = Dalbergia violacea, Dm = Didymopanax macrocarpum, Hy = Hymenaea sp., Hc = Hyptis cana, Kc = Kielmeyera coriacea, Lc = Lantana camara, Nt = Neea theifera, Pl = Pterocaulon lanatum, Sl = Solanum lycocarpum, Sa = Stryphnodendron adstringens, To = Tabebuia ochracea, Xa = Xylopia aromatica).
Fig. 1

The graph shows the relationship between average toughness and tannin concentration across different species. The x-axis represents the species code (Lc, Sl, Pp, Al, Dv, Sa, Hy, Xa, Nt, Dm, Hc, Ba, Kc, To), and the y-axis shows average toughness (g.m/s). The tannin concentration (mg/g) is also indicated on the right y-axis.
Vigour of a dioecious shrub and attack by a galling herbivore

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Short title: Vigour and attack by a galling herbivore
Abstract

1- The pattern of attack by the leaf-galling insect *Neopelma baccharidis* (Hemoptera: Psyllidae) was studied in three populations of the dioecious shrub *Baccharis dracunculifolia* (Asteraceae) in southeastern Brazil. The plant vigour hypothesis, which predicts higher rates of attack and increased herbivore performance on the longest plant shoots was tested. This work also provides important elements for the study of differential herbivory in dioecious plants.

2- In full 9200 shoots were randomly collected from 46 male and 47 female plants belonging to the three populations. Shoot length, number of leaves per shoot, rate of galling, and survival of psyllids did not differ between male and female plants. Another population in Campus of Federal University of Minas Gerais was only used to determine the pattern of shoot growth.

3- The hypothesis of sex-mediated herbivory was not corroborated in this study.

4- The frequency of galling increased with increasing shoot length, as predicted by the plant vigour hypothesis. Nevertheless, the number of oviposition sites (leaf buds) increased with shoot length.

5- The performance of the galling herbivore was not related to shoot length in the plant populations studied.

6- In conclusion, *Neopelma baccharidis* did not select shoots based on length only.

**Key words;** *Baccharis dracunculifolia*, herbivory, host selection, insect galls, *Neopelma baccharidis*, plant vigour.
Introduction

In the last two decades there has been an exponential increase in the number of studies of herbivore-plant interactions. A large number of the hypotheses generated include plant quality as an important factor that influences the interactions (e.g. White, 1969, Feeny, 1975, 1976; Bryant et al., 1983; Coley, 1983, Coley et al., 1985, Price et al., 1990; Herm & Mattson, 1992). The plant stress hypothesis (White, 1969, 1974, 1984; Larsson, 1989; Waring & Cobb, 1992) proposes that plants, when submitted to any of a range of environmental stresses, become more susceptible to attack by herbivores (White, 1993; Cobb et al., 1997). Some studies suggest that the pattern of higher rates of attack on stressed plants would emerge through the combined influence of two factors, higher nutritional quality and lower levels of chemical defences (e.g. Rhoades, 1979; Mattson & Haack, 1987a,b).

Since the 1980s, hypotheses have begun to incorporate differential investment in growth or in chemical defences by the plants in an attempt to explain the higher rate of attack on some plants (e.g. Bryant et al., 1983; Coley et al., 1985; Herm & Mattson, 1992). Herbivores that attacked young and vigorous plants more frequently than older and mature plants were until then considered exceptions to the rule (Price et al., 1990; Price, 1991). However, based on many studies of galls produced by sawflies (Hymenoptera: Tenthredinidae) on Salix spp. (Salicaceae), Price et al. (1987a,b, 1990) and Price (1989) formulated the plant vigour hypothesis. This argues that plant modules that grow vigorously are more favourable to certain kinds of herbivores. The archetypes of these herbivores are the gall-forming insects (Price, 1991). The term vigour was defined as applying to any plant in a plant population or any module in a population of modules that grows faster than the mean growth of the plant or the population of modules, reaching a
final size greater than the mean population size. The term stress is used in this context when for any reason the performance of a plant or module is reduced compared to that observed under optimal conditions (Price, 1991). The plant vigour hypothesis should not be understood as a strict alternative to the plant stress hypothesis, however. Price (1991) suggested that these hypotheses should be considered as the two ends of a continuum of possible strategies where some kinds of herbivores will tend to attack more vigorous modules while others will tend to attack more stressed modules. Therefore, the plant vigour hypothesis intends to produce predictions as to what kinds, taxa, or guilds of herbivores would use vigorous or stressed modules (Price et al., 1987b; Caouette & Price, 1989; Preszler & Price, 1995; Price et al., 1995b; Price & Ohgushi, 1995).

The goal of this work was to test the plant vigour hypothesis using a gall-forming insect, Neopelma haccharidis (Homoptera: Psyllidae), on the dioecious shrub Baccharis dracunculifolia (Asteraceae) in south-eastern Brazil. As the host plant has male and female flowers on distinct individuals, the possibility of sex-mediation in herbivore attack should precede the test of the plant vigour hypothesis. Differences in ecological specializations between male and female individuals of dioecious plants can influence their carbon-nutrient balance (Bryant et al., 1983; Herms & Mattson, 1992). This difference tends to produce greater rates of growth in male plants than in female plants (Freeman et al., 1976, 1980; Jing & Coley, 1990; Mutikainen & Delph, 1996). If female plants differ from male plants in growth, nutrition, and defence, it should be expected that sexes might also exhibit differences in susceptibility to herbivore attack (e.g. Wilson, 1979; Danell et al., 1985; Agreen, 1987; Elmqvist et al., 1988; Boecklen et al., 1990, Jing & Coley, 1990; Mutikainen & Delph, 1996). In fact, many studies have reported that male plants are generally more attacked by herbivores than female plants (e.g. Krischik & Denno,
1990a,b). Hence, this work also provides important elements for the study of differential herbivory in dioecious plants. On this topic the following hypotheses were tested: (a) The *sex-mediated growth hypothesis*, which predicts that male plants have longer shoots with more leaves than female plants, (b) *sex-mediated herbivory hypothesis*, which predicts that male plants are more frequently attacked by herbivores than female plants.

In testing the plant vigour hypothesis, special emphasis was given to the comparison of results obtained by the protocol directly required by the present definition of vigour (Price *et al*., 1987a,b, 1990; Craig *et al*., 1989; Price, 1989, 1991) with an alternative proposed in order to answer the following questions: (a) does the definition of vigour fulfill the requirements for conducting the test?; (b) does *N. baccharidis* attack longer shoots more frequently?; (c) is there any relationship between concentration of resources in a shoot and attack by the gall-former?

**Methods**

*The system* Neopelma baccharidis - *Baccharis dracunculifolia*

*Baccharis dracunculifolia* is a perennial dioecious shrub, characteristically an invader of disturbed sites, with a height between 1 and 4 meters and a flowering period from February to July (Barroso, 1976; Boldt, 1989), with growth throughout the year. This plant probably supports one of the richest faunas of galling species in the tropics (Fernandes *et al*., 1996), and 17 species of gall-forming insects have been described from *B. dracunculifolia*. Neopelma baccharidis (Psyllidae) is the most abundant of these (Lara & Fernandes, 1994; Araújo *et al*., 1995; Sperber & Collevatti, 1996). This galling psyllid is restricted to the Neotropics and all of its known hosts belong to the genus *Baccharis* (Buckhardt, 1987). Females lay eggs on the central veins of unfolded young leaves. Upon
hatching, the newly-emerged first-instar nymphs start feeding on the host tissue, causing hypertrophy and/or hyperplasia in the attacked tissue. The two sides of the leaf lamina bend over to form an elliptical or legume-like gall. Thus, each gall occupies the whole surface of a leaf. In most of the galls, only one nymph is found per chamber (see Lara & Fernandes, 1994), and in this study this was also the case. The galled tissue remains succulent during the development of the nymph, but gradually dries and assumes a woody aspect after the adult has emerged (Lara & Fernandes, 1994). The empty gall remains attached to the galled shoot for months. Adults and galls of *N. baccharidis* are present on the host plant throughout the year (Espírito-Santo & Fernandes 1998).

**Study site**

The study was conducted in four populations of *B. dracunculifolia* in the Espinhaço Mountains, Minas Gerais, Brazil: (a) Morro do Pilar (MP), located on the eastern slope of the Serra do Cipó (19°41'S, 43°59'W) in an abandoned cattle ranch along highway MG-232; (b) Serra do Cipó (SC), located along the highway MG-010, on the western slope of Serra do Cipó (19°40'S, 43°55'W); (c) Confins (CON), located along the highway MG 010 in the International Airport of Confins (19°10'S, 43°30'W); and (d) Pampulha (PAM), located on the Campus of the Federal University of Minas Gerais in the urban region of Belo Horizonte MG (19°30'S, 44°W). The predominant vegetation in the sampled areas is savanna (cerrado), except at Morro do Pilar, which is characterized as an ecotone between the Atlantic forest and the cerrado vegetation (Ferri, 1974). The studied areas have a marked dry period of 3 to 4 months during the winter and a rainy season of 7 to 8 months.
during the summer. Annual average precipitation is 1400 mm, with the annual average temperature varying from 18 to 20°C (Nimer, 1977, Fernandes, 1994).

Sampling

Sampling was carried out between March and May 1994. For the tests of the hypotheses 100 terminal shoots were collected randomly per individual from at least 20 plants in populations of the Morro do Pilar, Serra do Cipó, and Confins. Only adult plants that were flowering on the date of sampling and with a height of about 2m were collected. Hence, 18 males and 21 females plants were sampled in Morro do Pilar (n = 3900 shoots), 15 males and 19 females in Serra do Cipó (n = 3400 shoots), and 13 males and 7 females in Confins (n = 2000 shoots). Sampled shoots were taken to the laboratory where the length of each was measured and the number of leaves counted. All *N. baccharidis* galls found had their length measured and were opened to determine the fate of the nymph within. Mortality factors were grouped in the following categories: parasitism, plant resistance, predation, fungus, and other (nymphs dead from unknown causes - see Fernandes & Price, 1992). Plant resistance was identified by a clear hypersensitive reaction (observed as a necrotic spot) in initial stages of gall development.

Plant sex and herbivory

To test the hypotheses of differential growth between sexes and sex-mediated herbivory, in each population, the data were grouped by taking each plant as a sample unit. The mean values of length of shoots, number of leaves, number and survival rates of galls
per shoot on male and female plants were then compared with the Student's t-test as the data were distributed normally (Zar, 1984)

**Shoot growth**

The Pampulha population was only used to determine the pattern of shoot growth. In this population, twenty terminal non-galled shoots were marked randomly on ten distinct individuals of *B. dracunculifolia*, totalling 200 shoots. Sex of host plant was not considered in this analysis. The length of each shoot was measured at the beginning of the study, and 30 and 60 days later. As some shoots died during the experiment, the number of shoots in each interval decreased. In this way, only 115 shoots were present in the end of the experiment. The presence of galls that appeared in each period was recorded. For the determination of shoot growth, and analysis of the definition of vigour, the relationship between the initial and final shoot lengths of the marked shoots in the Pampulha population allowed the construction of growth curves. The relative growth rate was obtained by the ratio of the length added to the shoot during the experiment versus the initial length.

Measurements were taken from April to June 1994. At this time adults of *N. haccharidis* are very abundant in the field. Furthermore, the gall-former is multivoltine (Espírito-Santo & Fernandes, 1998). Each individual shoot was considered as a sample unit (see Price, 1991) and analyzed by linear and nonlinear regressions (Zar, 1984).

**Preference - performance**

To test for the existence of any relationship between preference and performance of the galling insect, male and female shoots were grouped into one set of data in each population, where each shoot was considered as a sample unit. The lengths of galled and
non-galled shoots were grouped in size classes of 1 cm. Since for each gall formed a leaf meristem is needed, the number of leaves in each size class was taken as a measure of the available unit of resource, one leaf being the smallest parcel of resource liable to be used as an oviposition site by any single \textit{N. buccaridis} female. The estimated number of galled shoots expected was determined by two distinct methods:

(a) Let R be the probability of any particular shoot being galled, where:

\[
R = \frac{\text{Sum total of galled shoots in the sample}}{\text{Sum total of shoots in the sample}}
\]

If a class \(i\) is made of \(M\) shoots, then \(MR\) shoots will be galled. Thus, the ratio between galled shoots and non-galled shoots in a sample is taken as a measure of probability of attack.

(b) Let \(R_i\) be the probability of any \(i\) size class shoot being galled:

\[
R_i = 1 - (1-p)^{Ni}
\]

where \(p\) stands for the proportion of galled leaves in the sample, taken as a measure of probability of any particular leaf being galled and \(N\) is the mean number of leaves of a shoot size class \(i\). If class \(i\) has \(M\) shoots, then \(MR_i\) shoots will be galled.

The reason for these two estimates is to compare the results obtained by the \textit{method a} taken directly from the definition of “vigour” (see Price, 1991; Price et al., 1995a), with that obtained by \textit{method b}, which allows associating a special probability of attack rate to shoots of different size classes.

The expected and observed distributions were compared by chi-square test (Sigel, 1973, Zar, 1984).
Results

Sex, differential growth and mediation of herbivory

Mean shoot length and mean number of leaves per shoot did not differ significantly between male and female plants in any of the three populations (all, \( p > 0.05 \), Table 1), indicating that male plants do not have shoots consistently longer than female plants. As *B. dracunculifolia* grows continuously throughout the year (M L. Faria unpb. data), a static measure of shoot length may provide a good indication of plant growth. Therefore, the hypothesis of differential growth between sexes must be rejected in this study.

The mean number of galls per shoot and rate of survival of *N. baccharidis* nymphs did not differ significantly between male and female plants in any of the three populations (all, \( p > 0.05 \), Table 2). Therefore, the hypothesis of sex-mediated herbivory must also be rejected in this study. Since no differences were found between male and female plants, all samples were pooled within each population in the following analysis.

Shoot growth

Longer shoots grew less than shorter shoots during the experiment. There was a tendency for the stabilization of the absolute growth of longer shoots (\( y = 8.792x^{0.548} \), \( r^2 = 0.55 \), \( p < 0.05 \), Fig. 1a). Hence, the mean rate of relative growth varied negatively with shoot length when shoots were grouped in size classes (\( y = 4.006x^{-0.727} \), \( r^2 = 0.80 \), \( p < 0.05 \)). Therefore, by the definition of *vigour*, the most vigorous shoots in the shoot population at the moment of sampling were the smallest shoots.

The absolute growth in the second time interval (31st to 60th day) was positively correlated with that in the first time interval (1st to 30th day). A total of 64% of the variation in growth in the second time interval was explained only by the growth in the first
time interval \( y = 1.359 + 0.599x \), \( r^2 = 0.64 \), \( F = 201.341 \), \( n = 115 \), \( p < 0.001 \), Fig. 1b). A large part of the unexplained variation (36%) was due to the initial shoot length. For the initial size class of 15mm, for instance, 85% of the growth variation in the second time interval was explained by the growth in the first time interval \( y = -2.711 + 0.726x \), \( r^2 = 0.85 \), \( F = 102.917 \), \( n = 20 \), \( p < 0.001 \). In the same way, shoot length at the end of the 60th day of growth was significantly correlated with the absolute growth in the first time interval, when considering shoots with similar initial sizes \( y = 10.188 + 1.785x \), \( r^2 = 0.96 \), \( F = 384.859 \), \( n = 20 \), \( p < 0.001 \), Fig. 1c). These results are consistent with the definition of vigour, i.e. shoots that grow at greater rates at a given instant \( t \) will produce larger shoots at the end of the growth season.

Preference and performance

The mean growth rate of galled shoots \( X_{galled\ shoots} = 12.710 \pm 2.074 \), \( n = 10 \) in first time interval of the experiment did not differ statistically from the mean growth rate of non-galled shoots \( X_{non-galled\ shoots} = 12.580 \pm 1.067 \), \( n = 137 \) in the Pampulha population \( t = 0.032 \), \( n = 147 \), \( p = \text{NS} \). The attack was occurring while the measurements were being taken, suggesting that \( N.\ bucerharidis \) did not select shoots by growth rate.

In the Morro do Pilar, Serra do Cipó, and Confins populations, smaller shoots were always very abundant while long shoots were rare. The proportion of galled shoots in each size class did not correlate with shoot size in any of the populations. However, in all three populations, a consistent tendency was observed: the proportion of attacked shoots increased positively with shoot length. This tendency was very clear in the shoot classes of smaller size, where the number of shoots in each class was relatively large. In the larger
shoot classes, the small number of shoots in each class produced a great deal of variation in the proportion of attacked shoots (Fig. 2). In fact, the number of galled shoots in each size class in the three populations was significantly different from the expected value when method a was used (Morro do Pilar: $\chi^2 = 60.55$, d.f. = 16, $p < 0.001$; Serra do Cipó: $\chi^2 = 95.33$, d.f. = 19, $p < 0.001$; Confins: $\chi^2 = 30.09$, d.f. = 14, $p < 0.001$). Particularly in the smaller shoot classes the number of galls observed was always smaller than that expected. From the class of 4.5 cm upward there was an inversion of the tendency and the number of galls observed was always greater than expected (Fig. 3). The results suggest that longer shoots were attacked more frequently than smaller shoots. Interpreted in this way, the results support the plant vigour hypothesis.

However, there was a positive relationship between shoot length and resource abundance in B. dracunculifolia. The number of leaves per shoot correlated positively with shoot length in the three populations. Shoot length explained 67% (Serra do Cipó), 73% (Morro do Pilar), and 75% (Confins) of the observed variation in the number of leaves per shoot (Morro do Pilar: $y = 0.61 + 4.9x$, $r^2 = 0.73$, $F = 10600.892$, $p < 0.001$; Serra do Cipó: $y = 7.20 + 3.56x$, $r^2 = 0.67$, $F = 6923.170$, $p < 0.001$; Confins: $y = 5.33 + 3.76x$, $r^2 = 0.75$, $F = 5913.949$, $p < 0.001$). Thus, longer shoots had more leaves or resources (meristems) available to be used by the gall-formers.

The frequency distribution of leaves in each size class in the three populations showed a similar pattern to that observed for the frequency distribution of shoots. However, in the smaller size classes, the number of leaves was smaller than would be expected merely on the basis of the frequency of the shoots in these classes, whereas in the larger size classes the number of leaves was greater than would be expected on the basis of
shoot frequency (Fig. 2). Therefore, if the number of leaves in each shoot is taken as a measure of resource concentration, smaller size classes have relatively fewer resources per shoot than larger size classes.

The number of galled shoots per size class correlated significantly with the total number of leaves in each size class (Table 3). On the other hand, the number of galled shoots did not differ from the expected when the expected probability of a shoot being attacked was calculated using the mean number of leaves per shoot (method b). Only in the Serra do Cipó population did the observed distribution differ statistically from the expected distribution. Again, no pattern similar to that obtained by the method a was observed (Morro do Pilar: $\chi^2 = 15.69$, d.f. = 15, $p > 0.05$; Serra do Cipó: $\chi^2 = 31.72$, d.f. = 17, $p < 0.05$, Confins: $\chi^2 = 15.35$, d.f. = 13, $p > 0.05$, Fig. 4). Therefore, larger shoots were attacked more frequently by *N. baccharidis* than smaller shoots because they had more resources, i.e. leaf meristems. Thus, the probability of a given shoot having galled leaves may simply be a direct function of the number of leaves it possesses, regardless of its growth rate or total length.

The rates of survival of *N. baccharidis* and size of gall did not correlate with the length of shoot in any of the studied populations (Morro do Pilar: $y_{\text{surv.}} = 0.42 + 0.02x$, $r^2 = 0.01$, $F = 2.334$, $p = \text{NS}$; $y_{\text{size}} = 8.46 + 0.08x$, $r^2 = 0.00$, $F = 1.043$, $p = \text{NS}$; Serra do Cipó: $y_{\text{surv.}} = 0.44 + 0.012x$, $r^2 = 0.00$, $F = 0.697$, $p = \text{NS}$; $y_{\text{size}} = 6.06 + 0.19x$, $r^2 = 0.01$, $F = 1.711$, $p = \text{NS}$, Confins: $y_{\text{surv.}} = 0.249 + 0.003x$, $r^2 = 0.00$, $F = 0.019$, $p = \text{NS}$; $y_{\text{size}} = 5.56 + 0.19x$, $r^2 = 0.04$, $F = 2.734$, $p = \text{NS}$). Hence, no preference or increase in performance of *N. baccharidis* was detected on larger size classes of shoots in this study.
Discussion

Herbivory and plant sex

Contrary to what has been predicted by the hypothesis of differential growth between sexes (see Krischick & Denno, 1990a,b), the mean size (length) and mean number of leaves per shoots on B. dracunculifolia were not statistically larger in male plants than in female plants. These data confirm the observations made previously in a B. dracunculifolia population in Belo Horizonte, Brazil (Lara & Fernandes, 1994, Araújo et al., 1995). The temperate species B. hastifolia only shows measurable growth differences during the adult stage (Kraft & Denno, 1982; Palmer, 1987; Krischik & Denno, 1990b), while the plants studied were all adults that had flowered several times before.

The hypothesis of sex-mediated herbivory (e.g. Boecklen et al., 1990, Herms & Mattson, 1992) was also not confirmed by the results. Male plants did not support larger numbers of N. baccharidis galls than female plants. In the same way, the survival rate of the gall-former did not differ between male and female plants. These results corroborate the data obtained by Carneiro & Fernandes (1996) in B. concinna populations in Serra do Cipó. The hypothesis of sex-mediated herbivory is based on the assumption that differential rates of growth between male and female plants influence the levels of plant defence (Bryant et al., 1983). Since no differences in growth between male and female plants were found, it is probable that the amount of energy expended in growth does not differ between sexes in this species to the point of producing differences in shoot size and in the level of plant defences (see also Delph et al., 1993). If plants do not differ in these attributes, neither should rates at which they are attacked. The physiology and resource allocation pattern in this species have yet to be studied in detail.
On the definition of vigour

The plant vigour hypothesis (Craig et al., 1986, 1989, Price et al., 1987a,b, 1990; Fritz & Price, 1988; Price, 1991) is based on the assumption that differential growth rates of plant modules explain differences in behaviour of host/module selection by females and offspring performance. The definition of vigour has two distinct terms that are related directly to the protocol employed in testing the hypothesis. The first term refers to the growth rates of shoots in relation to the means obtained in the population of shoots. The second term deals with the final size that vigorous shoots will reach. The inclusion of the second term in the definition is of course necessary, as it makes it possible to organize the protocol to test the hypothesis by using only shoot length as an independent variable in the analysis. Despite the advantages of this approach, which allows the test using a single sample of shoots, there are some difficulties with its use in some tropical systems. If the herbivore selects more vigorous shoots, i.e. those that grow at a faster rate than the mean rate of the shoot population and, at the time of sampling smaller shoots were growing faster, then it would be expected that females of *N. baccharidis* prefer smaller shoots. Hence, results are likely to be influenced by the timing of sampling. Moreover, on the basis of the definition of vigour, vigorous shoots will be larger at the end of the growing season. This problem might be avoided by sampling at the end of the growing season and using the final size of the shoot as an estimate of the rate of growth at any given moment. However, it is only possible to distinguish vigour if all shoots that are present at the sampling moment are also present at the moment of attack by the gall-former. In tropical systems, however, the growth seasons are less clearly defined than in temperate environments (Krebs, 1978). Therefore, the timing of sampling must always coincide with the moment of attack. The system studied represents such a case, where the host
Baccharis dracunculifolia grows throughout the year even when flowering and, the galling herbivore, Neopelma baccharidis, is multivoltine and has several overlapping generations (Espírito-Santo & Fernandes 1998).

**Lack of preference and performance**

The frequency distribution of shoot sizes in B. dracunculifolia was very similar in the three populations, and in general they agree with those observed for other plant species (see Bruyn, 1995, Price et al., 1995a), including other tropical species (e.g. Price et al. 1995b; Cornelissen et al., 1997). Small shoots were always very abundant, whereas large shoots were rare. Attack frequencies in the three populations tended to increase with the increase in the length of shoots, despite the great variation in attack rates in the longest size classes, where the number of shoots was small. In fact, the use of the method a (in which the estimate of attack probability does not include the number of leaves per shoot) leads to the observation that larger shoots tend to be more attacked than would be expected if attacks were random. However, by this method it is only possible to affirm that longer shoots are attacked more frequently than smaller shoots. The chi-square test is not sensitive to differences in the number of sites available for attack on shoots. In contrast, it is assumed that if shoots are attacked at random, the probability of attack is equal across shoot length. However, a larger shoot does have a greater probability of being attacked than a smaller shoot. When a leaf is considered as the smallest unit of resource liable to be used by a gall-former as an oviposition site, and the number of leaves on a shoot as a measure of the amount of resource available, the amount of resources in the classes of small shoots is overestimated if it is taken simply as a function of the abundance of shoots in that class. On the other hand, in larger size classes, the amount of resource is underestimated. Hence, when the chi-square test is made by the method b, which incorporates the amount of
resources in a shoot in estimating the random probability of attack, no pattern is observed in any populations. In conclusion longer shoots of *B. dracunculifolia* were attacked more frequently by *N. baccharidis* without being selected preferentially.

If the analysis has to be reduced to a unit that does not vary with shoot length, then the arrangement of the results using shoot length may be ineffective. When the frequency distribution of shoots and leaves in the population of Morro do Pilar is taken as an example, it is observed that as the density of attack increases, rare and long shoots tend to be galled more frequently. Nevertheless, no shoot selection factor was acting in this case. This effect may be amplified when data in discrete classes of shoot size are grouped. The abundance of shoots in each class tended to decrease with increasing shoot size. Thus, the error associated with the estimates of proportion of attack per size class tended to increase as the abundance of shoots in each size class decreased. Consequently, under high densities of attack, in the size classes of lower shoot abundance the observed proportion of attack tended to the upper limit (100% of shoots attacked). Therefore, the length of shoots is in this context a confounding variable, as it was correlated positively with both the availability of sites for colonization and the age of shoots. These two new variables produced greater attack frequencies in longer shoots perhaps without the occurrence of an active selection by the female. Hence, the term *vigour* may need to be redefined. Otherwise, the results will always tend to support the plant vigour hypothesis (but see Price, 1989; Glynn & Larsson, 1994, Prada *et al.*, 1995; Fernandes, 1998). The protocol required by the definition should necessarily evaluate the attack simultaneously with shoot growth. Therefore, spurious effects of resource concentration and shoot age would no longer exist.
Acknowledgments

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References


Table 1. Shoot length (cm) and number of leaves per shoot (mean ± SE) in male and female plants in three populations of *Baccharis dracunculifolia*.

<table>
<thead>
<tr>
<th>Population</th>
<th>Shoot length (cm)</th>
<th>Number of leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>Morro do Pilar</td>
<td>3.9 ± 0.25</td>
<td>3.6 ± 0.16</td>
</tr>
<tr>
<td>Serra do Cipó</td>
<td>4.3 ± 0.30</td>
<td>4.0 ± 0.28</td>
</tr>
<tr>
<td>Confins</td>
<td>3.1 ± 0.23</td>
<td>3.7 ± 0.24</td>
</tr>
</tbody>
</table>
Table 2. Number of galls per shoot (mean ± SE) and survival rate (%) of *N. baccharidis* in male and female individuals in three populations of *B. dracunculifolia*.

<table>
<thead>
<tr>
<th>Population</th>
<th>Number of galls</th>
<th>Survival rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td>Morro do Pilar</td>
<td>0.33 ± 0.22</td>
<td>0.08 ± 0.01</td>
</tr>
<tr>
<td>Serra do Cipó</td>
<td>0.04 ± 0.01</td>
<td>0.04 ± 0.01</td>
</tr>
<tr>
<td>Confinas</td>
<td>0.04 ± 0.01</td>
<td>0.03 ± 0.01</td>
</tr>
</tbody>
</table>
Table 3. Relationship between number of galled shoots and sum total of leaves in each size class in three populations of *B. dracunculifolia*.

<table>
<thead>
<tr>
<th>Population</th>
<th>$y = a + bx$</th>
<th>$r^2$</th>
<th>F-Ratio</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Morro do Pilar</td>
<td>$y = -0.72 + 0.003x$</td>
<td>0.95</td>
<td>255.427</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Serra do Cipó</td>
<td>$y = 0.37 + 0.001x$</td>
<td>0.87</td>
<td>114.526</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Conins</td>
<td>$y = 0.09 + 0.001x$</td>
<td>0.60</td>
<td>19.721</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
Legends

Fig. 1. Pattern of growth of *B. dracunculifolia* in Pampulha population. (a) Relationship between the final shoot length and the initial shoot length. (b) Relationship between absolute growth in second time interval (31th to 60th day) and the absolute growth in first time interval (1st to 30th day), and (c) Relationship between shoot length at the end of the 60th day of growth and absolute growth in the first time interval for the initial size class of 15 mm.

Fig. 2. Frequency distributions expressed as the percentage of total shoots in each shoot length class, percentage of total number of leaves in each shoot length class, and percentage of shoots galled in each shoot length class, in three populations of *B. dracunculifolia*, Morro do Pilar (MP), Serra do Cipó (SC) and Confins (CON).

Fig. 3. Observed and expected (*method a*) distributions of total number of galled shoots in three populations of *B. dracunculifolia*; Morro do Pilar (MP), Serra do Cipó (SC) and Confins (CON).

Fig. 4. Observed and expected (*method b*) distributions of total number of galled shoots in three populations of *B. dracunculifolia*; Morro do Pilar (MP), Serra do Cipó (SC) and Confins (CON).
Figure 2 in Faria & Fernandes
Figure 4 in Faria & Fernandes

MP

Observed

Expected

Number of galled shoots

0.5  2.5  4.5  6.5  8.5  10.5  12.5  14.5  16.5

SC

Observed

Expected

CON

Observed

Expected

Shoot size class (cm)

0.5  2.5  4.5  6.5  8.5  10.5  12.5  14.5
Ant effects on three-trophic level interactions: plant, galls, and parasitoids

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Abstract. 1. Ants have evolved mutualistic relationships with a diverse array of plant and animal species. Usually, the predatory/aggressive behaviour by ants near food sources can limit herbivore damage.

2. Galls of *Disholcaspis edura* on *Quercus turbinella* produce a secretion that is harvested by three species of ants (*Formica neorufibarbis*, *Liometopium apiculatum*, and *Monomorium cyanenum*) in the chaparral vegetation of Arizona, USA. The present study evidence a mutualistic relationship between these species of ants and the gall-forming wasp *Disholcaspis edura*.

3. An ant exclusion experiment showed that, when ants tended galls, the rate of parasitism by *Platygaster* sp. on *Disholcaspis edura* was nearly halved in comparison to treatment in which ants were excluded.

4. In presence of ants, the galls with the largest diameter suffered lower mortality rate due the parasitoids than when ants were excluded. Thus, ant presence reduced the selective pressure imposed by *Platygaster* sp. on the galls with larger diameter.

Key words. Ant-gall interactions, gall diameter, insect galls, phenotypic selection, parasitism.

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Running head: Ant effects on three-trophic level interactions
Introduction

Studies of plant-herbivore interactions have focused primarily on the direct effects that producers and consumers have upon reciprocal growth, survivorship, and reproduction. However, species at higher trophic levels may exert selective pressures that influence the interaction between species at lower trophic levels (Weis & Abrahamsen, 1985; Coley & Barone, 1996; Roininen et al., 1996). Moreover, spatial and temporal variation in host plant resources can affect herbivore performance greatly. Thus, as insect herbivores feeding on plants are themselves a food source to predators and parasitoids, the effects of variation in plant quality may extend to the third trophic level (Price et al., 1980; Clancy & Price, 1986; Price, 1992; Woods et al., 1996).

Ant-plant interactions have been investigated intensively in the last three decades. Many experimental field studies have demonstrated that predatory/aggressive behaviour by ants near food sources can limit herbivore damage (see Del-Claro et al., 1996; Freitas & Oliveira, 1996; Oliveira, 1997). In systems with extrafloral nectaries, and even more in extrafloral nectary analog situations, ants have been shown to protect certain herbivores from their enemies (Washburn, 1984; Abe, 1992; Seibert, 1993). However, the benefits conferred by ants vary both geographically and temporally, and depend largely on the protective abilities of the ant visitors and the corresponding capacity of specialized herbivores or parasitoids to circumvent the ants' deterring traits (Koptur, 1992, Oliveira, 1997).

A complicating factor that inhibits studies on these trophic systems is the heterogeneity inherent in natural environments (Roininen et al., 1996). Studies of the
influence of the third trophic level are mostly done in simple systems, primarily between single plant species and monophagous insects (Weis & Abrahamson, 1985). Gall-forming insects have high specificity with their host plant, and frequently support a varied fauna of natural enemies, including inquilines, parasitoids, and predators (Weis, 1982; Price et al., 1987). Moreover, the sessile habit of their larvae make the potential number of interactions limited and bounded in space and time (Fernandes et al., 1994), hence making these communities suitable for studies of interactions among trophic levels (Weis, 1982).

The family Cynipidae (Hymenoptera) is dominated by several hundred highly specialized species of herbivores that induce galls on plants of the genera Quercus (Fagaceae) and Rosa (Rosaceae). Each cynipid species attacks one or several closely related plant species, and adult females oviposit on specific sites (Felt, 1940; Cornell, 1986). Quercus does not produce floral or extrafloral nectaries, but some cynipid species induce galls on Quercus whose tissues are able to secrete a sweet honeydew that is highly attractive to ants and other insects (see Washburn, 1984; Abe, 1992). Secretion begins in the early stages of gall development and continues throughout the period of larval development and pupation (Bequaert, 1924; Washburn, 1984).

Galls of Disholcaspis edura Weld (Hymenoptera: Cynipidae) on Quercus turbinella Green are distributed widely in the chaparral vegetation of Arizona, U.S.A. These galls produce a secretion that is harvested by several species of insects. Three species of ants (Formica neorufiharbis Emery, Liometopium apiculatum Mayr, and Monomorium cyaneum Wheeler) were observed to forage continually and guard the
exudate from robbery by other insect species. The present study evidence a mutualistic relationship between ants and the gall-forming wasp *D. edura*. Two questions related to parasitism on *D. edura* were addressed: (1) Can ants that feed on gall secretion affect the efficiency of parasitism by *Platygaster* sp? (2) Can ant presence change the mortality of *D. edura* by *Platygaster* sp. as a function of gall size?

Materials and methods

This study was conducted in the chaparral vegetation, between 1200 and 1500 meters altitude above sea level (adjacent to Highways 1 - 17 and 89A South), near Sedona, Arizona, U.S.A., from April to June 1989. An exclusion experiment was performed to evaluate whether ants attracted to secretions of galls affect the success of parasitism by *Platygaster* sp. on *Disholcaspis edura*. This experiment involved 34 paired branches on 17 trees of *Quercus turbinella*. Plants were separated by at least 10 m. Branches of each experimental and control pair were matched by size and phenology. Branches in each pair were assigned randomly as treatment or control by the toss of a coin. Ants had free access to control branches, while treated branches had their bases pasted with a sticky resin (Tanglefoot®, Tanglefoot Company, Michigan 49504, U.S.A.) to prevent access by ants. Everything that could be used by ants to climb on to the treatment branches, such as neighbouring stems and leaves, was removed. During the field work, plants were checked weekly to ensure that ants were indeed being excluded from treated branches. A total of 306 galls that developed on ant-excluded and control branches were collected before emergence of adults. These galls were maintained in the laboratory,
where gall size and parasitism rate were measured. The parasitism of larvae was
determined by gall dissection at the end of gall developmental time. The parasitoid
exuviae inside the galls and/or the adult parasitoid hole left after its emergence from the
gall were used as direct evidence of parasitism (see Espírito Santo & Fernandes, 1998).

Differences in parasitism between galls on ant-excluded and control branches
were examined using a paired t-test. The effects of gall diameter on parasitism were
analyzed by linear regression. For this purpose, galls were pooled into 1-mm size
categories and the percentage of attack in each category calculated. Arcsin
transformations were used to normalize the variance of data (Zar, 1984). The selection
differential on gall size exerted by the parasitoid *Platygastr* sp., in the presence and
absence of ants, was measured through difference between the average gall diameter for
cynipids escaping *Platygastr* sp. attack and the average diameter for all galls (see

**Results**

The interaction between ants and galls diminished the success of the attack by
*Platygastr* sp. on the gallmaker *Disholcaspis edura* \( t = 2.41, n = 17, p < 0.05 \). The
rate of parasitism on *D. edura* was 58% greater in the ants excluded treatment.

*Disholcaspis edura* galls sampled had a mean diameter of 6.99 mm, and 56.86% of galls
belonged in the intermediate diameter classes (between 5 and 7.99 mm diameter) (Table
1). There were no statistically significant differences in mean gall diameter between the
two treatments \( t = 0.26, n = 17, p > 0.05 \), suggesting that any effects of gall size on
gall selection or survival in *Platygaster* sp. can not be responsible for the observed differences in rates of parasitism between ant excluded and ant presence treatments.

In the ant excluded treatment, the rate of parasitism correlated positively with the diameter of the galls (arcsin $\sqrt{y} = 17.24 + 3.90x$, $r^2 = 0.69$, $F = 13.45$, $p < 0.01$). Therefore, in the absence of ants, the parasitism was higher on galls with the largest diameter. In contrast, in the presence of ants (control branches), the rate of parasitism and the diameter of galls did not show a significant relationship (arcsin $\sqrt{y} = 26.98 + 0.72x$, $r^2 = 0.04$, $F = 0.27$, $p > 0.05$), suggesting that when ants are present, the parasitism is unrelated to gall size. However, the difference between the slopes of these models was only marginally significant ($F = 3.29$, $N = 16$, $0.05 < p < 0.10$) (Fig. 1). Probably, the expressive variation in the parasitism rate in function of gall size, principally in the treatment in which ants were present, may have affected this result.

*Ants diminished the selective pressure imposed by* *Platygaster* *sp.* *on the larger diameter galls* (Fig. 2). In the ant exclusion treatment, the mean diameter of unattacked galls was 6.45 mm, while the overall mean diameter of all galls was 7.02 mm. Therefore, the selection differential was -0.57 mm, or an 8.12% decrease in gall diameter after selection. In the presence of ants, the selection differential was -0.04 mm (6.92 - 6.96), a decrease of only 0.57% in gall diameter of the survivors.
Discussion

The ability to induce galls is a highly successful life-history strategy for phytophagous insects (Price et al., 1987; Hawkins, 1988). However, the reproductive success of galling insects is affected by natural enemies, plant resistance, plant architecture, intra- and inter-specific competition (see Taper et al., 1986; Fernandes & Price, 1991; 1992; Fay et al., 1996; Larson & Whitham, 1997). Moreover, many species of ants have developed a mutualistic relationship with plants and animals, and their presence has become necessary to maintain the system. In this kind of association, ant workers can protect tended species from predators, parasites, and herbivores, and in return the ants receive shelter for nesting and/or a rich food source (e.g., Washburn, 1984; Koptur, 1992; Abe, 1992; Del-Claro et al., 1996; Freitas & Oliveira, 1996). In this study, the ant exclusion experiment clearly showed that ants increase the survival of the gallmaker Disholcaspis edura on Q. turbinella. Despite the positive effect of ant mutualism with the gallmaker, many galls in the control treatments were parasitized (Table 1). In this case, the parasitoids may have oviposited before ant colonization or alternatively, the parasitoid may also be able to circumvent the ants deterring traits.

Many models that focus on host-parasitoid interactions have assumed that the size of the host is a measure of the adequacy for parasitoid development (Harvey et al., 1994). In general, parasitism is high on galls of smaller diameter (see Freezer & Zwölfer, 1996). However, some parasitoids may also attack larger galls preferentially (see Weis et al., 1992). Some traits of parasitoids such as ovipositor size and developmental strategies (idiobionts or koinobionts) can alter this pattern (Weis, 1982;
Harvey et al., 1994). Ant exclusion modified the parasitism success of the parasitoid *Platygaster* sp. on galls of *D. edura* (Fig. 1). Considering that galls of larger diameters produce greater amounts of secretion, and that the amount and quality of the resource are factors that can affect the rate of recruitment of working ants (see Carroll & Janzen, 1973; Abe, 1992), ants are likely to tend large galls more frequently than small galls. This probably contributes to the increase in protection of larger galls against parasitoids, explaining the difference in the gallmaker mortality inflicted by *Platygaster* sp.

Cynipid galls structures are characteristics of the gallmakers rather than of the host-plant. Thus, as gall structures, although constructed of the plant tissues, represent the extended phenotypes of gall wasps genes (Stone & Cook 1998), the selection may act upon the insect to alter this extended phenotype (Weis et al., 1988). Thus, considering that gall size is a heritable trait under field conditions (see Stone & Cook, 1998), the results of ants excluded experiment suggest that the attack by parasitoids imposes a strong directional pressure on larger galls produced by *D. edura* on *Q. turbinella*. However, the established mutualism between ants and galls can decrease the pressure of parasitism on larger galls (Fig. 2), resulting in a selection that would be approximately stabilized and thus favouring an intermediate gall size.

In fact, there is a general consensus that the strongest selection pressure acting on gallmaking insects is probably associated with avoidance of mortality inflicted by natural enemies. For example, parasitoids (Weis & Abrahamson 1985; Price & Clancy, 1986) and vertebrate predators (Weis et al., 1992; Weis & Kapelinski, 1994) can be a significant force in the evolution of gall size. Moreover, symbioses between ants and gall
wasps producing a sweet substance by manipulation of the host plant tissues can too 
modify gall parasitism. This association type is poorly recorded and only three cases are 
known (Washburn, 1984; Abe, 1988; 1992). Therefore, this study is a first experimental 
evidence that association between ants and galls can modify the results of the selective 
pressure imposed by parasitoids on gall size.

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Table 1. Success of parasitism by *Platygaster* sp. in galls of *Disholcaspis edura* on *Quercus turbinella* tended by ants (control) and galls from which ants were excluded.

<table>
<thead>
<tr>
<th>Gall diameter class (mm)</th>
<th>Number of galls</th>
<th>Mean gall diameter (mm)</th>
<th>Parasitism (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ants excluded</td>
<td>Control excluded</td>
<td>Ants excluded</td>
</tr>
<tr>
<td>3 - 3.99</td>
<td>6</td>
<td>4</td>
<td>3.72</td>
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</tr>
<tr>
<td>10 - 10.99</td>
<td>12</td>
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</tr>
<tr>
<td>Total</td>
<td>168</td>
<td>138</td>
<td>7.02</td>
</tr>
</tbody>
</table>
FIGURE LEGENDS

Fig. 1. Relationship between the percentage of parasitism and mean gall diameter based on 86 attacks of *Platigaster* sp. on 168 galls in ant-excluded and 41 attacks on 138 galls in control branches. Percentage of parasitism was arcsin square root transformed.

Fig. 2. Diagrammatic representation of the mean diameter of surviving galls plotted against the mean diameter of all galls, to illustrate the response to selection in the presence and absence of ants.
HERBIVORY, TANNINS AND SCLEROPHYLLY IN Chamaecrista linearifolia ALONG AN ALTITUDINAL GRADIENT

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ABSTRACT:

The concentration of tannins in leaves, fruits, and flowers, leaf sclerophyll, leaf size and herbivore damage in *Chamaecrista linearifolia* (Fabaceae) were measured on three populations along an altitudinal gradient (600m, 850m, and 1100m), in a cerrado vegetation in Minas Gerais, southeastern Brazil. Proportion of leaf area lost to insects was used as an index of herbivore damage, and its relationship with the other variables was analysed. Greater tannin contents were found in leaves, followed by fruits, and flowers, respectively. With increasing altitude leaves tended to be more smaller, more sclerophyllous and less predated, but there was no consistent altitudinal change in tannin concentration in any organ. Damage due to herbivores was related only to the altitudinal gradient, but had no relationship with any of the other measured characteristics. The constancy in tannin concentration across altitudes besides large variations in leaf damage weaks the idea that tannin production is strongly related to herbivore pressure.

Key words: Altitudinal gradient, Cerrado, Insect herbivory, Sclerophyll, Tannins.
RESUMO

As concentrações de taninos em folhas, frutos e flores, esclerofilía e tamanho foliar e pressão de herbivoria foram medidos em Chamaecrista linearifolia (Fabaceae) em três populações ao longo de um gradiente altitudinal (600m, 850m, and 1100m), em uma região de cerrado em Minas Gerais, Brasil. O dano causado por herbívoros foi estimado pela proporção de área foliar perdida, e foi avaliada sua relação com a esclerofilía, área foliar, concentração de taninos nas folhas e altitude. Foram encontradas maiores concentrações de taninos em folhas, seguidas por frutos e flores. Com o aumento da altitude houve redução na área foliar e na pressão de herbivoria e aumento na esclerofilía. Não houve variação altitudinal na concentração de taninos em nenhum órgão. Herbivoria não apresentou correlação com nenhuma das características medidas nas plantas, apenas com o gradiente altitudinal, sugerindo que a abundância de herbívoros em cada local pode estar influenciando os padrões de herbivoria. A constância altitudinal na concentração de taninos junto a uma grande variação em todas as outras variáveis enfraquece a idéia de que a produção de taninos está fortemente vinculada à defesa contra herbívoros.

Palavras-chave: Cerrado, Esclerofilía, Gradiente altitudinal, Herbivoria, Taninos.
INTRODUCTION

Chemical compounds of toxic or digestibility reducing potential have an important role in plant defense against herbivores and pathogens (e.g., 19, 32, 34, 41). Nevertheless, the synthesis, maintenance and sequestration of these compounds may be costly to the plant (7, 10, 31). Most theoretical models on the interactions between herbivores and plant defense consider that plants should be under intense selection to produce an optimal defense level (5, 9, 27, 31, 32). In this cost/benefit relationship, the production of large amounts of defense of high molecular weight, such as tannins, would be advantageous to defend long-lived organs, as observed when comparing tannin concentration in leaves of different plant species (9). The rationale is that these compounds have a high initial cost of production but, in the long term, would be cheaper than low molecular weight substances, due to low turnover rates and maintenance costs (but see 14). We propose that the same pattern may occur between organs of the same plant with different longevities.

Along mountain slopes, variation in abiotic conditions may affect resource availability and, as a consequence, the carbon/nutrient balance of plants. With increasing elevation there is an increase in radiation intensity; also the soils are generally more exposed and shallower and have reduced nutrient availability and lower moisture-retaining capacity (35). If the reduction in water and/or nutrient availability is not accompanied by an inhibition of photosynthesis, plants at higher altitudes should produce an excess of carbon (25). If the production of secondary compounds is strongly related to resource availability (see 6, 25, 39), the concentration of C-based compounds, such as tannins, should increase at higher altitudes. Nevertheless, herbivore pressure may be higher at lower altitudes, as shown by many surveys of insect herbivore abundance along altitudinal gradients both in tropical and temperate zone
(see 12, 21, 23, 42, but see 26, 33). Therefore, tannin production may reflect a balance between herbivore pressure and resource availability.

Tannins are carbon-based compounds of high molecular weight and are believed to reduce the digestibility of plant tissues by precipitating the proteins and enzymes of ingested tissues in the gut of herbivores (27, 31, 38, 41). Tannins also injure the gut of some insects (3, 19). They are viewed as strong anti-herbivory defenses of widespread effectiveness (19, 31, 32, 38) and seem to have a dosage-dependent mode of action (18, 19, but see 20).

Sclerophyll is a leaf trait also closely related to the nutrient status of the plant (28, 40), and plants with high C/N ratios are expected to be highly sclerophyllous (40). However, the role of each evolutionary force that may lead a species to bear sclerophyllous leaves is controversial. Sclerophyll may be an adaptation to water conservation, nutrient conservation and/or prevention of damage (40). In all cases, plant populations at higher elevations are expected to be more sclerophyllous. If sclerophyll is advantageous against herbivory, a negative correlation between sclerophyll and damage due to herbivory would be expected, independent of altitude. As tannin concentration and sclerophyll are similarly influenced by C/N ratio, we would also expect a positive correlation between them.

In this study we estimated tannin concentration in leaves, fruits and flowers, leaf sclerophyll, and herbivore pressure in three populations of Chamaecrista linearifolia var. latifolia Barneby (Fabaceae) along an altitudinal gradient in southeastern Brazil. The following questions were addressed: 1) Is there any difference in tannin concentration between leaves, flowers and fruits? 2) Does tannin concentration and leaf sclerophyll increase with increasing altitude? 3) Does leaf damage by herbivores increase with decreasing elevation? 4) Are leaf tannin concentration and sclerophyll positively correlated? 5) How they are related to leaf damage by herbivores?
MATERIALS AND METHODS

*Chamaecrista linearifolia* var. *latifolia* is a perennial herbaceous legume, typical of cerrado and high elevation vegetations. It has a simple architecture, with many thin branches emerging from the ground. The branches rarely bifurcate and each supports around 10 to 20 leaves. Leaves have two leaflets, are resinous and have high tannin concentrations (37).

**STUDY AREA** - The three populations chosen for this survey are at 600, 850 and 1100m above sea level, along on the western slope of a mountain elevated from the Furnas Dam, in Minas Gerais state, southeastern Brazil (20°40′W, 46°19′S). It is an ancient terrain with quartzite preponderance and nutrient-poor sandy soils (22). The drier months are May to August (1), and this study was conducted in July 1995.

The 1100m population was at the mountaintop, in an open shrubby vegetation called “campo rupestre” (22). It is subject to direct sunlight during all day. The soils are exposed and erosion is intense, increasing the soils’ natural poverty. The population at 850m was on deeper soils, with taller and denser vegetation coverage. Some shade occurs due to sparse trees of the savanna (cerrado). The 600m population was near the dam’s barrage, where the soils were deeper and covered by herbaceous vegetation. More and taller trees are present, increasing shade over this population.

**TANNIN QUANTIFICATION** - 15 individuals of *C. linearifolia* were chosen at random from each population for tannin analysis. All leaves from three branches chosen at random and all fruits and flowers of each individual plant were collected, placed separately in an ice box and quickly taken to laboratory for tannin bioassay. The radial diffusion method (17) was used to
quantify the condensed and hydrolysable tannins. The fresh material was macerated and an extract from 0.3 g of each sample was obtained in 1 ml of aqueous 50% methanol. Extracts were placed in round orifices made on a type I agarose gel cover containing bovine serum albumin (BSA) in petri dishes. Three replicates from each organ were made for each individual. The precipitation of BSA by the extracted tannins produces an opaque halo on the gel, the diameter of which is proportional to the tannin concentration of the extract. From each halo we took two perpendicular diameter measures, and used the mean value. Results were compared to a standard curve obtained for tannic acid and BSA, hence providing an estimation of tannin concentration (mg tannic acid g⁻¹ fresh material) (see 17 for details).

The astringency (protein-precipitation property) depends on the concentration and also on the composition of tannins, because there is great variation in the reactivity of each compound type (20). Therefore, estimating tannin concentration of an extract using a standard curve constructed for a standard polyphenol may lead to errors (8). In this work, we estimated astringency variations within a single plant species, and assumed that the qualitative composition of its tannins, and consequently their reactivity, should not vary consistently between populations or individual plants. Hence, astringency should be proportional to tannin concentration and provide a good relative quantification.

The variation in tannin concentration according to altitude and plant organ was analysed with a two-way ANOVA (43).

SCLEROPHYLLY AND LEAF AREA - Specific leaf weight (SLW = dry weight / area) was used to estimate leaf sclerophyllly (see 40). Ten mature leaves per plant were collected from the same individuals used for tannin quantification (15 plants per altitude). Leaves were dried at 60°C for 48 hours and then weighed on an analytical balance. We used a LICOR 3000 leaf area
meter to measure leaf area. SLW and leaf area values showed normal distribution and homogeneous variances, allowing the utilization of ANOVAs (43). Simple linear regressions were performed between sclerophylly and tannin concentration within plants of each population to test for positive correlations between these traits.

HERBIVORY - Leaf damage by leaf chewers, used as a herbivory index, was estimated as the proportion of lost leaf area. Leaf chewing was probably caused by several insect taxa. Lepidopteran larvae. Orthopteran nymphs and adult beetles were commonly found feeding on C. linearifolia leaves. On each population a transect line was extended and the first ten plants found within a 1m width on both sides of the line were used to estimate herbivory. On each individual we measured the total leaf area and the proportion of leaf area removed by herbivores on 10 old leaves from 5 branches chosen at random. Only leaves with signs of both leaflets were considered, to avoid an overestimation of herbivory, which would occur if abscissed leaflets were considered as eaten. This caution might have lead to underestimation (see 8).

Total and damaged leaf area were estimated using a grid of 0.25 cm² (0.5 x 0.5 cm) drawn on a glass dish. The number of squares touched by the leaf lamina, or by its visual reconstitution, were counted, providing the number of squares containing intact and consumed leaf lamina for each leaf. Mean total leaf area and mean proportion of consumed leaf area by herbivory were calculated for each individual plant. Values were expressed in number of touched squares. Differences in damaged leaf area between populations were tested with a Kruskal-Wallis test as variances were not homogeneous (43). A stepwise multiple regression was employed to verify the effects of sclerophylly, leaf area, leaf tannin concentration and altitude on herbivory.
RESULTS

TANNIN CONCENTRATION - Leaves had significantly higher tannin concentrations than fruits, while flowers had the smallest tannin concentrations. This pattern was consistent in all populations. Nevertheless, tannin concentration within organs did not vary among populations (two-way ANOVA; Organs: F_{2,126} = 28994.96, p < 0.0001; Altitude: F_{2,126} = 152.79, p = ns; Interaction: F_{4,126} = 1.25, p = ns; Fig. 1).

SCLEROPHYLLY AND LEAF AREA - Leaves tended to be smaller and more sclerophyllous at higher altitudes (one-way ANOVAs; Leaf area: F_{2,40} = 14.40, p < 0.0001; Sclerophyll: F_{2,40} = 19.38, p < 0.0001; Fig. 2a,b). There was no significant relationship between leaf sclerophyll and leaf tannin content at any population (600m: r^2 = 0.041, p = n.s.; 850m: r^2 = 0.134, p = n.s.; 1100m: r^2 = 0.012, p = n.s.). The relationship between leaf area and sclerophyll was weak considering all plants together (y = 0.02 - 0.41x; r^2 = 0.17; p < 0.01; n = 43) and not significant when each population was considered separately.

HERBIVORY - The proportion of leaf area consumed by leaf-chewing herbivores increased with decreasing altitude. Nevertheless, herbivory was not correlated with leaf sclerophyll, tannin concentration nor leaf area, and these variables were excluded from the stepwise multiple regression model (herbivory x altitude: y = 22.07 - 0.67x; r^2 = 0.45; p < 0.0001; n = 38; Fig.2c).
DISCUSSION

*Chamaecrista linearifolia* showed increased levels of specific leaf weight and a reduction in mean leaf area with increasing altitude. Smaller leaf area and higher specific leaf weight are two features frequently associated with sclerophyll (29). Furthermore, plant scleromorphism tends to be accentuated at higher altitudes, due to increased radiation intensity and water and nutrients limitation (15, 35). Nevertheless, there was no strong correlation between leaf area and sclerophyll considering plants as units.

In contrast, tannin content within organs (leaves, fruits, and flowers) did not differ statistically between the three populations along the altitudinal gradient. Tannins showed a conservative pattern of higher concentration in leaves, followed by fruits and flowers, respectively.

Herbivory showed no correlation with either tannin concentration, sclerophyll or leaf area, but was clearly more intense at lower altitudes. This pattern may be related to a decrease in herbivore abundance with increasing altitude.

The constancy in tannin concentration across altitudes considering leaves, fruits and also flowers, and the absence of correlation between tannin content and herbivore damage suggest that tannin production is not directly related to herbivore pressure, at least in this species. The idea of a direct relationship between herbivory and concentration of defensive compounds such as tannins is based on the assumption that their production compromise other plant’s functions (7, 13, but see 36). Nevertheless, in plants on poor soils and under high light intensity, its photosynthetic activity may exceed its capacity to acquire nutrients, leading to high abundance of synthesized carbon (25). This is perhaps the reason for a luxuriant accumulation of suber by many cerrado tree species (16, 24). Other studies conducted in sclerophyllous vegetation describe an unexpected constancy in tannin concentration, both in plants of a single species occurring at different habitats at same elevations or at different
altitudes in the cerrado (33) or in Mediterranean plants submitted to severe browsing and thinning treatments (30). In such cases, the negative relationship between herbivory and investment in quantitative defenses may be masked by the carbon excess (39). Furthermore, carbon excess is related to many other features that may negatively affect herbivore performance, as increased leaf toughness and reduced nutritional quality of tissues (33, 40).

The fact that some insect species are either not affected or even benefited by tannins (see 2, 3, 4) may have contributed to this absence of relationships.

It may be interesting to rescue Feeny’s (11) ideas on plant apparenty to interpret the pattern of decreasing tannin concentration from leaves to fruits and then flowers, somehow paralell to a decreasing gradient in longevity. As leaves are usually more “apparent” in time, they should deserve higher investments in “quantitative” defenses, which might deter a wide array of herbivores (11). Moreover, Coley et al. (7) proposed that plants with longer-lived leaves would be benefited if defended by C-based compounds of high molecular weight, with an initial elevated cost of production but low turnover rates. Chamaecrista linearifolia leaves are more persistent than the fruits, while flowers are the most ephemeral of the three organs. This positive relationship between longevity and tannin content suggests the possibility of an extension of Coley et al.’s (7) hypothesis to different organs within a plant. It must be remembered, nevertheless, that a direct relationship between herbivory and tannin production within organs was not found.

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LEGENDS OF FIGURES

Figure 1: Tannin concentration in leaves, fruits and flowers for the three populations of *Chamaecrista linearifolia* (mean ± s.e.). Different letters denote statistically significant differences. ■ = leaves; ■■ = fruits; □ = flowers.

Figure 2: Leaf area, sclerophylly and herbivory (Mean ± s.e. and confidence intervals) on 3 populations of *Chamaecrista linearifolia* along an altitudinal gradient. 2a) Leaf area (number of 0.25cm² squares touched by leaf lamina); 2b) leaf sclerophylly (specific leaf weight [SLW = dry weight / area]); and 2c) herbivory (percent of leaf area [in squares, like 2a] lost due to insect chewing herbivory).
FIGURE 1
**FIGURE 2**

Each graph represents a different aspect of leaf measurements at varying altitudes:

- **Graph A**: Leaf area (No. of squares of 0.25 cm²).
- **Graph B**: Leaf sclerophyll (mg/cm²).
- **Graph C**: Leaf damage (% of consumed leaf area).

Legend:
- A
- B
- C

Altitude levels: 600m, 850m, 1100m.
REPRODUCTIVE PHENOLOGY OF SYMPATRIC SPECIES OF CHAMAECRISTA
(LEGUMINOSAE) IN SERRA DO CIPÓ, BRAZIL

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Running title: Reproductive phenology of sympatric Chamaecrista

Key words: Chamaecrista, Flowering, Fruiting, Reproductive phenology, Rupestrian
field, Seasonality, Seed abortion, Seed predation, Sympatric congeners, Tropical savanna

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ABSTRACT. Reproductive phenology of 13 sympatric plant species of *Chamaecrista*
were surveyed at Serra do Cipó, SE Brazil. Mean abundance of flowers and fruits per
plant and mean of aborted, predated, and surviving seeds per fruit were measured. Four
types of phenological behaviour were distinguished according to the period each species
reproduced, which were related to plant architecture and area of distribution, biotic
factors, and local climatic seasonality. Herbs were more affected by variation in rainfall
than shrubs and trees. Three species did not show any clearly seasonal behaviour. Among
the remaining 10, the widespread species flowered and fructified in the rainy season and
dispersed seeds at the end of the rainy season. All but one of the narrowly distributed
species flowered and set fruits in the dry season or in the transition to the rainy season,
and dispersed seeds at the end of the dry season or beginning of the rainy season. It is
suggested that seed predation may be an important selective force affecting the
reproductive phenology of larger species, while the smaller seemed too constrained by
abiotic factors to be directed by biotic ones. No evidence for any important role of
competition for pollinators was detected.
INTRODUCTION

The distribution in time of the main life history facts, such as growth, leaf flux and fall, flowering, fruiting and seed dispersal has great effects on individual fitness and population or species survival (e.g., Augspurger 1981, English-Loeb & Karban 1992, Eriksson 1995, Grimm 1995, Haddock & Chaplin 1982, Lee & Bazzaz 1982, Mosquin 1971, Opler et al. 1976, Rathcke & Lacey 1985, Schlimmske et al. 1978, Weelwright 1985, Zimmerman 1980a, b). Phenological studies generally look for cyclic patterns due to environmental seasonality. In temperate regions, these cycles are linked to large annual variations in temperature and photoperiod, and are readily detectable.

Nevertheless, there are many examples of seasonal variation in the tropics. Although these are more subtle than in temperate regions, they provide large enough variations to induce cyclic patterns on plants from these sites (Lieberman 1982, Machado et al. 1997, Medway 1972, Frankie et al. 1974, Monasterio & Sarmiento 1976, Rathcke & Lacey 1985, Seghieri et al. 1995). A great distinctiveness from temperate regions is that the main cue to phenological patterns in the tropics is precipitation (Opler et al. 1976), while temperature and photoperiodism may have a secondary role.

included shrubs (Koptur et al. 1988, Opler et al. 1976, 1980), and a few comprised herbs (Croat 1975, Lieberman 1982, Machado et al. 1997, Monasterio & Sarmiento 1976, Seghieri et al. 1995). Hence, the frequency of phenological studies including herbs is far from being representative of their importance in community diversity and structure.


Moreover, some studies claim the possibility of phenological patterns being selectively neutral (Ollerton & Lack 1992).

A small number of phenological studies compared phylogenetically related species, sometimes at family level (Gentry 1974, Proença & Gibbs 1994). Nevertheless, the study of sympatric congeneric species may result in very interesting data, and provide insights both in the ecology and evolution of phenological traits. Studies such as these usually deal with very few species (Haddad & Chaplin 1982, Pickering 1995, Siemens et al. 1992), probably due to the usually small number of congeneric species co-occurring in a relatively small area.

Here we present data on the phenology of 13 sympatric species of the genus Chamaecrista (Leguminosae), all occurring within an area of 28 Km² at Serra do Cipó, SE Brazil. The reproductive phases (flower, fruit, and seed production) of all species were studied during 1996. Among these species there are eight herbs, two small shrubs,
two shrubs and one tree. For the comprehension of the phenological patterns found, we considered the area of distribution of each species, plant habit, biotic and abiotic pressures.

**STUDY AREA**

The study was conducted in an area of rupestrian of approximately 28 Km². This area is located in Serra do Cipó, Minas Gerais State, SE Brazil (Figure 1), a region of high diversity and endemism of higher plants (Giulietti et al. 1987). Serra do Cipó is in the southern portion of Espinhaço range, a quartzitic mountain chain 1100 Km long in north-south direction, with two disjunct parts - Chapada Diamantina in the north and Serra do Espinhaço in the south. This elevation is included in the savanna-like vegetation ("cerrado") domain of Central Brazil (Ab'Saber 1977). Hereafter this southern portion will be referred as "Serra do Espinhaço" and the northern portion as "Chapada Diamantina".

**STUDIED SPECIES**

*Herbs*

*Chamaecrista desvauxii* (Collad.) Killip var. *latistipula* - Widespread from Central Brazil to Paraguay and NE Argentina (R. Barneby, pers. comm.), usually forming small clones with thin ramets, often less than five ramets per clone, 30 to 50 cm tall.

*Chamaecrista micronota* (spreng.) Irwin & Barneby - Occurs along the Serra do Espinhaço and Chapada Diamantina with a more eastern, possibly disjunct population, at Espírito Santo State (Irwin & Barneby 1982). It has lignified branches, usually forming low and dense bushes (ca. 20 cm tall). It is the commonest species at the study area.
Chamaecrista ochracea (Vog.) var. purpurascens (Benth.) Irwin & Barneby - Endemic to Serra do Cipó and vicinity (R. Barneby, pers. comm.). Small branches about 20 cm long produce apical inflorescences with numerous orange flowers, which usually develop into large number of fruits relatively to the small size of their branches.

Chamaecrista desvauxii (Collad.) Killip var. malacophylla Irwin & Barneby - Restricted to Serra do Espinhaço (Irwin & Barneby 1982), grows clonally and close to the ground, sometimes forming dense patches, difficulting the recognition of individuals.

Chamaecrista venulosa (Benth.) Irwin & Barneby - Occurs in the Serra do Espinhaço and Chapada Diamantina (Irwin & Barneby 1982). It is a crawling herb with very thin and branched stems, usually growing close to watercourses and shaded habitats.

Chamaecrista choiriophylla (Vogel) Irwin & Barneby var. latifolia (Benth.) Irwin & Barneby - Restricted to Serra do Espinhaço (Irwin & Barneby 1982), is the rarest species at the study area. Form clones of variable size, has thicker branches than those of the majority of the other herbs. these emerge from the ground without ramifying and support the largest flowers and fruits of the 13 species.

Chamaecrista desvauxii (Collad.) Killip var. molissima (Benth.) Irwin & Barneby - Widespread species, distributed almost all over South and Central Americas (Irwin & Barneby 1982), but is not abundant in the study area, where only two patches were found. Morphologically similar to C.d. latistipula, but slightly larger and more ramified.

Chamaecrista rotundifolia (Pers.) Greene - Cosmopolite invasive species, easily found in pastures, degraded areas and road margins (Irwin & Barneby 1982, Kissman & Groth 1992). Has small rosettes close to the ground, has the smallest flowers, fruits and seeds among the 13 studied species.
Small shrubs

*Chamaecrista ramosa* (Vog.) var. *parvifolia* (Irwin) Irwin & Barneby - Widespread from North to South Brazil (Irwin & Barneby 1982). Highly branched, common and patchily distributed in the lower altitudes in the study area.

*Chamaecrista cathartica* (Mart.) var. *Paucijuga* Irwin & Barneby - Widespread species from North to South Brazil (J.A. Madeira, unpubl. data), but is one of the rarest species in the study area. Only one patch was found. Plants about 70 cm tall, highly branched.

All organs contain glandular trichomes that produce a viscous and smelly secretion.

Shrubby species

*Chamaecrista cipoana* (Irwin & Barneby) I. & B. - Endemic to the crest of Serra do Cipó (R. Barneby, pers. comm.). In the study area it was found in two dense patches. Plants are approximately 150 cm tall, highly ramified and have glandular trichomes in all organs that produce a secretion similar to that of *C. cathartica*.

*Chamaecrista semaphora* (Irwin & Barneby) I. & B.: Endemic to a portion of Serra do Espinhaço, between Serra do Cipó and Serro, 70 Km north off the study site (R. Barneby, pers. comm.). The species was found in three patches in the study area. Larger plants are about 2m tall, very ramified and also have glandular trichomes in all organs which produce a viscous and smelly secretion.

Arboreal species

*Chamaecrista dentata* (Vog.) Irwin & Barneby - Endemic to Serra do Espinhaço (R. Barneby, pers. comm.). Plants reach about 5m tall, are patchily distributed and also have glandular trichomes in all their organs that produce a viscous and smelly secretion.

*Chamaecrista desvauxii latistipula, C. desvauxii malacophylla* and *C. desvauxii molissima* are considered as varieties from the same species (R. Barneby, pers. comm.).
Nevertheless, there are conspicuous differences in their phenology, seed packing, seed size, fruit pubescence, microhabitat and plant architecture (I.A. Madeira, unpubl. data), that justify to treat them as “ecologically distinct species”.

METHODS

Flowering and fruiting phenology

In December 1995 and January 1996, 20 individuals from each species were randomly chosen and labelled for phenological surveys. Around the 20th day of each month, every fruit, flower and flowerbuds from each individual were counted. No gathering was performed on these plants.

* C. cathartica, C. cipoana and C. semaphora * were added latter to the study, the first in February, and the last two in May 1996, because they were discovered when the survey was under progress. Hence, the year of the survey for these species was delayed in relation to the others. The same happened with * C. dentata * due to methodological problems with flower and fruit counts, what caused us to prolonge the observations on this species until January 1997. * C. cathartica * was probably found later due to its local rarity. * C. cipoana * and * C. semaphora * were found only during flowering, and we are sure that these species did not flower between January and May, given the conspicuousness of their flowers.

Some plants were missed due to burning, trail clearing and other accidents, or due to natural motality. These plants were replaced every time the number of plants of any species became lower than 15. The rarity of * C. choriophylla * and * cathartica * did not allow such a replacement, and exceptionaly for these species, a sample of around 10 individuals was accepted.
Seed production

To evaluate seed production, fruits were gathered from different plants, during two or three month surveys. All ripe fruits were collected at every time a fruiting plant was found. We searched as many plants as possible and sampled up to 25 plants. The collection of all fruits per individual was not possible in C. dentata, as many fruits were not accessible due to plant height. Sample size per species per month was variable, since it depended on the proportion of available fruits.

Climatic data

Monthly total precipitation and mean maximum and minimum temperatures of the last ten years were obtained from the nearest meteorological station, distant approximately 30 Km from the study site. To evaluate if it was a typical year, we calculated the averages for each month and for each year, and compared to the data of the year of study. Data from August 1996 are lacking due to technical problems in the meteorological station.
RESULTS

Climatic data

The climate in 1996 was quite similar to the average climatic data in the last ten years. Higher and lower temperatures were practically identical, evidencing the predictability and small variability of these parameters. Temperature had narrow annual and monthly variation. Precipitation showed much more strong seasonality and larger range of variation (Figure 2). There was a rainy season from November to March and a dry season from May to September. Mean annual precipitation for ten years was 1373.56 mm, and total annual precipitation for 1996 was quite similar - 1354.1 mm, with the lack of data from August, which ten year mean is 9.7mm.

Phenological syndromes

The 13 species were grouped into four phenological syndromes in according to the moment they showed flowering and fruiting peak related to dry and rainy seasons. Only the shape of curve was considered for grouping, and not the magnitude of the species’ phenological display, which was relatively proportional to species size (Figures 3 to 6).

Flowering and fruiting during the rainy season - Four out of the eight herbaceous species (C. desvauxii latistipula, C. ochracea, C. desvauxii molissima and C. rotundifolia), and one of the small shrubs (C. ramosa), presented flowering and fruiting peaks in the rainy season. C. desvauxii latistipula presented a low abundance of flowers and fruits per individual (Figure 3a), and a sparse distribution in all the study area. C. ramosa sowed high synchronization in flowering and fruiting between individuals, and large abundance
of flowers and fruits, in relation to the size of its plants (Figure 3e). As it occurs in dense patches, its flowering was concentrated in time and space. C. ochracea, in spite of its small size, presented inflorescences with a relatively large number of flowers, which developed into a large number of fruits per branch, relatively to the species size (Figure 3e). Probably because of this relationship, its fruit development time is slower, perhaps favoring seed predation (Janzen 1969). Supporting this hypothesis, it had the highest seed predation rate among the 13 species (Figure 3f). C. desvauxii molissima also had high synchronization between plants, but with less abundance of flowers and fruits (Figure 3g) and less dense patches. C. rotundifolia occurs specially along road margins in all the study area, and did not form dense patches. It had a more extended flowering and fruiting period, with low variation in abortion rates along the period of seed production (Figure 3i,j). With the exception of C. rotundifolia, the seed abortion rates of these species were lower at peak of fruiting and grew up as the dry season approached (Figure 3b,d,f,h,j).

Herbs flowering in the dry season - Chamaecrista mucronata and C. desvauxii malacophylla showed flowering peaks from the middle to the end of the dry season, and fruiting peak at the transition from dry to rainy season (Figure 4a,c). Nevertheless, they also produced few flowers at other moments, apparently responding to occasional rains. These flowers, however, did not develop into fruits, or resulted in fruits with 100% of seed abortion (Figure 4b,d). The seed abortion rates of C. mucronata were always high, and those of C. desvauxii malacophylla grew up slightly from the beginning to the end of the fruiting station (Figure 4b,d). C. choriophylla had an earlier flowering peak, at the beginning of the dry season and the fruiting peak was at the end of the dry season. The
results for this species were prejudiced by a burning in July, that eliminated the larger accompanied individuals and affected the average number of flowers and fruits per individual (Figure 4e), hence forcing us to maintain a smaller sample \((n = 10)\) in the rest of the year, due to its rarity.

Shrubs with flowering and fruiting at the dry season - The shrub species, *C. cipoana* and *C. semaphora*, had very similar phenological behaviours, with flowering peak at the beginning and fruiting peak at the end of the dry season (Figura 5a,c). Their fruits presented few seeds, and showed small seed abortion rates in the first month, which grewed on the following two months of fruiting. Seed predation rates were relatively high on *C. cipoana* and low on *C. semaphora* (Figure 5b,d).

Species without seasonal pattern - The three remaining species, *C. venulosa* (herb), *C. cathartica* (small shrub) and *C. dentata* (tree), did not present clear peaks of flowering and fruiting, hence being grouped more by the lack of patterns than by the similarity of their phenological behaviour (Figure 6). *C. venulosa* was the only herbaceous species without seasonal phenological behaviour (Figure 6 a,b). *C. dentata* produced flowers and fruits along the hole year, only reducing their abundance at the dry season (Figure 6c). Its seed abortion and predation rates were highly variable (Figure 6d). *C. cathartica* had flowers along all the year, but only a few developed into fruits, and a few fruits reached ripening. The few riped fruits had low seed abortion rates and no seed predation (Figure 6e,f).
DISCUSSION

The climatological pattern found in Sorra do Cipó was typical of the cerrado region, which has rainy summers and dry winters (Freitas & Silveira 1977). This seasonal variation acts as a strong selective force shaping the phenological behaviour of species or populations exposed to these climatic conditions (Monasterio & Sarmiento 1976, Opler et al. 1976).

Herbaceous species were more affected by rainfall conditions, corroborating the views of Seghieri et al. (1995). Herbaceous species that flowered in the rainy season were those of smaller size, while larger species had flowering peaks in the dry season, probably enabled by a greater capacity of capture and accumulation of resources.

Flowering in the dry season may provide their seeds with a greater chance of survival, because they are dispersed near the beginning of the rainy season, with a long favorable period for germination and establishment. Only C. venulosa appeared not to be strongly affected by variations in rainfall, probably due to its occurrence nearby watercourses and shaded habitats (Irwin & Barneby 1982 and J.A. Madeira, pers. obs.).

The small shrubby species showed distinct behaviours. C. cathartica did not present clear flowering and fruiting peaks, while C. ramosa had pronounced flowering and fruiting peaks at the rainy season. Both are widespread species, but C. ramosa is quite abundant at the studied site, while C. cathartica is locally rare. So, we were not able to find distinguishable patterns for the small shrubby species.

The abundant flowering and fruiting of C. cipoana and C. semaphora during the dry season suggest a good storage capacity, as proposed by Seghieri et al. (1995). Flowering at the beginning of dry season should allow these species to experience less competition for pollinators (Gentry 1974, Mosquin 1971, Pickering 1995, Rathcke e
Lacey 1983, Thomson 1980, Weelwright 1985, Zimmerman 1980a) and to suffer smaller seed predation rates (Haddock & Chaplin 1982, Janzen 1969, Rathcke & Lacey 1985). Nevertheless, these species should not compete for pollinators with herbaceous species, as these species produce much fewer flowers. If pollinators are limitant, they should compete with each other. However, their flowering time diverged minimally (Figure 5). Thus, our data did not show any evidence that competition for pollinators would be an important selective pressure upon the flowering behaviour of these two species. Seed production during the dry season did not freed these species from bruchid attack (the same *Semnus* species predated both). However, it is possible that these bruchids, usually highly specialists, would have difficulty to reach high population densities during the dry season, within the short observed fruiting period. If it is true, these species should be under lighter predation pressures than would be expected if they fructify at the rainy season. On the other hand, it should be argued that this bruchid species has a competitor-free resource at its disposal. Furthermore, *C. eipoana* suffered heavy flowerbud predation by a lepidopteran larvae, in spite of the flowering at the dry season, showing that scaping in time may reduce predator diversity, but not necessarily reduce predator abundance (Augspurger 1981).

*C. dentata*, the only arboreal species, seemed still less affected by rainfall seasonality. All the individuals produced flowers along the hole year, although less abundantly in the dry season. As only the new branches produce flowers, this species may maintain growing branches throughout the year. This may be provided by a greater capacity of water and nutrient captation at deeper soils and a greater resource storage capacity (Seghieri et al. 1995). The variations in seed predation rates (Figure 5d) may be explained by the regulation exerted by microhymenopteran parasitoids that attack the
Sennius (Coleoptera: Bruchidae) species that predate its seeds (J.A. Madeira, unpubl. data).

Among the herbaceous species we found three classes of distribution areas. Those widespread (C. desvauxii latistipula, C. desvauxii mollissima and C. rotundifolia), those restricted to Serra do Espinhaço and Chapada Diamantina (C. mucronata and C. venulosa), and those restricted to Serra do Cipó and vicinity or only to Serra do Espinhaço (C. ochracea, C. desvauxii malacophylla and C. choriophylla). We can observe that all the widespread herbs flowered and fructified in the rainy season. Among the species with intermediate distribution, C. mucronata flowered at the dry season and C. venulosa flowered independently from rainfall variation. Among the restricted species, only C. ochracea had its flowering peak at the rainy season, but its behaviour was not as strongly seasonal as that of the three widespread species. C. desvauxii malacophylla and C. choriophylla produced their flowers in the dry season. There was a clear tendency for widespread species to produce their reproductive organs at the rainy season and for the restricted species, perhaps more finely adapted, to flower in the dry season.

When we include the larger species in this analysis, the trend is maintained. The two small shrubby species (C. ramosa and C. cathartica) are widespread. The first showed flowering and fruiting in the rainy season and the second had a non seasonal behaviour. The shrubby species C. cipoana and C. semaphora are restrict endemics and flowered and fructified the dry season. C. dentata, restricted to Serra do Espinhaço, had a non seasonal behaviour. So, in the case of the genus Chamaecrista on rupestrian fields, the behaviour of flower production in the dry season appear to be related to restricted distributed species. We could also speculate a trend for the restricted distributed species.
being the larger and the widespread being the smaller sized species. The only exception is
C. ochracea, a restricted distributed and small sized species.

The variety of phenological behaviours within a single genus contradicts the
hypothesis of Ollerton & Lack (1992), that the flowering phenological behaviours would
be selectively neutral due to be imposed by phylogenetic constraints. Even though we
focus only similar sized species, as they are better comparable, our data presented large
phenological variations between the eight herbaceous species, showing that there is
sufficient plasticity among a single genus to allow natural selection to act generating a
diversity of behaviours.

A better knowledge of the phylogenetic relations between the species studied
here would be very important to a better comprehension of our results. Studies on this
direction are now being undertaken.

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*Biotropica* 6:64-68.


FIGURE LEGENDS

Figure 1: Study area (inside dotted line) and its location in relation to Serra do Espinhaço and Chapada Diamantina, Brazil.

Figure 2: Monthly total rainfall and mean maximal and minimal temperatures - data for the year of the study (1996) and mean values for the last 10 years (January 1987 - April 1997), with the range of the monthly total precipitation on the ten year period. □ = total month rainfall in 1996; □ = average total month rainfall in 10 years; —•— = month minimal temperautre in 1996; —○— = average month minimal temperature in 10 years; —▲— = month maximal temperature in 1996; —△— = average month maximal temperature in 10 years

Figure 3: Phenological data of the Chamaecrista species that flowered and fructified at the rainy season. Graphics on left: Mean ± standard error of fruits and flowers (opened flowers and flowerbuds) per individual per month and percentual of individuals with fruits or with flowers; □ = fruits; □ = flowers; —•— = % of plants with fruits; —○— = % of plants with flowers. Graphics on right: Mean seed production per fruit. Labels indicate the sample number (number of individuals where the fruits were collected), Y = year average; □ = unfertilized ovules or aborted seeds; ■ = predated seeds, □ = surviving seeds. a-b = C. desvauxii latistipula, c-d = C. ramosa, e-f = C. ochacea, g-h = C. desvauxii molissima, i-j = C. rotundifolia.
Figure 4: Phenological data of the *Chamaecrista* herb species that flowered at the dry season. Graphics on left: Mean ± standard error of fruits and flowers (oppened flowers and flowerbuds) per individual per month and percentual of individuals with fruits or with flowers; □ = fruits, ◻ = flowers; —○— = % of plants with fruits; ——●—— = % of plants with flowers. Graphics on right: Mean seed production per fruit. Labels indicate the sample number (number of individuals where the fruits were collected); Y = year average; □ = unfertilized ovules or aborted seeds; ■ = predated seeds; ◻ = surviving seeds. a-b = *C. mucronata*; c-d = *C. desvauxii malacophylla*; e-f = *C. choriophylia*.

Figure 5: Phenological data of the shrubby *Chamaecrista* species that flowered and fructified at the dry season. Graphics on left: Mean ± standard error of fruits and flowers (oppened flowers and flowerbuds) per individual per month and percentual of individuals with fruits or with flowers; □ = fruits, ◻ = flowers; —○— = % of plants with fruits; ——●—— = % of plants with flowers. Graphics on right: Mean seed production per fruit. Labels indicate the sample number (number of individuals where the fruits were collected), Y = year average; □ = unfertilized ovules or aborted seeds; ■ = predated seeds, ◻ = surviving seeds. a-b = *C. cipoana*; c-d = *C. semaphora*. 

Figure 6: Phenological data of the *Chamaecrista* species that did not present seasonal behaviour. Graphics on left: Mean ± standard error of fruits and flowers (opened flowers and flowerbuds) per individual per month and percentual of individuals with fruits or with flowers; □ = fruits; □ = flowers; —○— = % of plants with fruits; —●— = % of plants with flowers. Graphics on right: Mean seed production per fruit. Labels indicate the sample number (number of individuals where the fruits were collected), Y = year average; □ = unfertilized ovules or aborted seeds; ■ = predated seeds; □ = surviving seeds. a-b = *C. venulosa*, c-d = *C. dentata*, e-f = *C. cathartica*. 
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Effects of light on leaf structure in *Miconia ibaguensis* and

*Miconia stenostachya*

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Abstract:

We explored the relationships between leaf sclerophylly, area, volume, mass, density, thickness, and anatomy on two shrubs species, *Miconia ibaguensis* and *M. stenostachya* (Melastomataceae) in southeastern Brazil. Leaf traits were assessed in an open and sunny, fully exposed, savanna environment and in an adjacent shaded riparian forest. Leaf area, mass, density, thickness, and percentage of carbon varied significantly between sunny and shaded habitats (t tests, p< 0.05, all). Variations in leaf sclerophylly were influenced by leaf mass, density, and thickness in the two plant species (Pearson correlation, p< 0.001). Sun-exposed leaves were denser and thicker due an increase in the length of the cells of the palisade parenchyma (*M. ibaguensis*: sun= 93 ± 3µm; shade= 61 ± 2µm; *M. stenostachya*: sun= 150 ± 5µm, shade= 92 ± 4µm). *Miconia ibaguensis* and *M. stenostachya* presented an increase of 13% and 17% in stomatal density in the sunny habitat. *Miconia ibaguensis* also showed an increase of 57% in trichome density under light conditions. These two species showed high plasticity in leaf structure and physiology in relation to light intensity, that favours survival in both sunny and shaded environments.

**Key Words:** Adaptation, Anatomy, Light intensity, Sclerophylly, Stomatal density, Trichome density
Abstract:

We explored the relationships between leaf sclerophyly, area, volume, mass, density, thickness, and anatomy on two shrub species, *Miconia ibaguensis* and *M. stenostachya* (Melastomataceae) in southeastern Brazil. Leaf traits were assessed in an open and sunny, fully exposed, savanna environment and in an adjacent shaded riparian forest. Leaf area, mass, density, thickness, and percentage of carbon varied significantly between sunny and shaded habitats (t tests, p < 0.05, all). Variations in leaf sclerophyly were influenced by leaf mass, density, and thickness in the two plant species (Pearson correlation, p < 0.001). Sun-exposed leaves were denser and thicker due an increase in the length of the cells of the palisade parenchyma (*M. ibaguensis*: sun = 93 ± 3μm; shade = 61 ± 2μm; *M. stenostachya*: sun = 150 ± 5μm; shade = 92 ± 4μm). *Miconia ibaguensis* and *M. stenostachya* presented an increase of 13% and 17% in stomatal density in the sunny habitat. *Miconia ibaguensis* also showed an increase of 57% in trichome density under light conditions. These two species showed high plasticity in leaf structure and physiology.
INTRODUCTION

Leaves of many plant species are known for their large plasticity in growth. They vary in morphology, anatomy, as well as in physiology (Witkowski and Lamont, 1991; Sims and Pearcy, 1992). Leaf plasticity may be adaptive as it can provide additional mechanisms to adapt to different environments (Grime et al., 1986). Plasticity plays an important role in the survival ability of a species in contrasting environments. Despite the plasticity, they may still maintain similar physiology through an increased competitive ability (e.g., Upadhyaya and Furnes, 1994).

Light intensity affects mesophyll development. Under high irradiance, plants are known to produce thicker leaves which have thinner aerial spaces. These leaves have also more mass and a deep mesophyll (Thompson et al., 1992). Conversely, shade leaves present thinner leaf blades and higher chlorophyll concentration. In sunny and arid habitats water availability limits plant growth. Leaf thickening through the addition of more cell layers increase net carbon gain without increasing the cost for transpiration (Turner, 1994a). Leaf sclerophyll reflects a general increase in the proportion of cellular wall/cytoplasm tissue (Turner et al., 1993).

Sclerophyll may have several advantages under a wide range of environmental conditions, which may explain the ecological and taxonomic parallels among some types of vegetation (Turner, 1994a). Sclerophyllous leaves are generally associated to arid habitats with high irradiance such as the so called Mediterranean type-ecosystems and savannas (e.g., Crawford, 1989). Sclerophyllous leaves are generally small and thick (e.g., Juniper and Southwood, 1986). Leaf thickening involves the increase of all leaf tissues, including the leaf cuticle, epidermal walls, content of fibers, and trichomes (Turner, 1994b). Trichomes may reduce water loss through light reflectance at the leaf surface and thus reduce leaf temperature through an increase in the thickness of the boundary layer (Hsiao, 1973; Johnson, 1975; Harrington and Clark, 1989).
The cerrado vegetation of Brazil is known for its generalized high levels of irradiance (Eiten, 1972; Oliveira-Filho and Ratter, 1995). Nevertheless, the cerrado is composed of a mosaic of neighboring habitats where light penetration is reduced due to the size and architectural complexity of the vegetation. A common feature of the cerrado is the presence of riparian forests along river washes and creeks. In these generally narrow riparian forests, light intensity is lower on the shrub and herb strata because of canopy interception. Trees often reach a height of 10 meters. These features enable the study of leaf plasticity under different light intensities in habitats separated by a few meters.

In this study we investigated the effects of light irradiance on leaf sclerophyllity of two species widely distributed: *Miconia ibaguensis* (Bonpl.) Triana and *Miconia stenostachya* DC. (Melastomataceae) in southeastern Brazil. Several leaf attributes which could be influenced by light were studied concomitantly on these species: area, mass, specific leaf mass, volume, density, thickness, carbon, and anatomy.

**Materials and Methods**

The study was performed in the Serra do Cipó National Park - MG in the southern end of the Espinhaço Mountains (19° 20′S, 43° 44′W) at 800m altitude. *Miconia ibaguensis* and *M. stenostachya* are small shrubs frequently found in open and sunny cerrado as well as in the shaded understorey of riparian forests.

Habitats were selected by their distinctiveness in edaphics and environmental characteristics (Table 1). All environmental data presented were obtained in situ between 7 AM and 5 PM with 30 minutes of intervals. Relative humidity (%), temperature (°C), and vapour pressure deficit (Kpa) of the air were measured by isopiestic thermocouple psychrometry (Boyer and Knipling, 1965). Light irradiance was measured with quantum sensors (LI-189) at ten point in each habitat. The two habitats presented large differences
in light intensity, and hence were categorized as: a) sunny habitat (integrated PPFD of 70 mol m\(^{-2}\) day\(^{-1}\)), and b) shaded habitat (integrated PPFD of 6.8 mol m\(^{-2}\) day\(^{-1}\)).

Soil data were measured at 10 cm and 20 cm depth. Soil water content (SWC) was estimated by the percentage of soil moisture from six samples of 20 cm\(^3\) at 10 and 20 cm depth from the two habitats. Soon after, we calculated the difference in moisture between fresh and dry soil. The weight of dry soil was obtained by uniform drying at 70-80°C for 72 hs. The amount of the organic matter in the soil (SOM) was determined after the incineration of three samples of 20 cm\(^3\) at 500°C for two hours. The percentage of SOM was calculated as the difference between the weights (% C x 1.72). The pH was determined by the method described in Raij and Quaggio (1983).

Five random leaf samples of the first nodes of ten plants were taken per species at each site. Leaves were oven dried at 30°C for a week to obtain leaf mass (mg) and leaf area (mm\(^2\)). Then, leaves were rehydrated and fixed in alcohol 70% to determine leaf density (μg/mm\(^3\)). Leaf area was obtained by drawing the leaf in sheets of paper, followed by cutting its contour and then weighing it (Rizzini, 1976). An sclerophyly index (leaf specific mass - LSM) was calculated based on leaf mass and area (Witkowski and Lamont, 1991). Leaf density was calculated by dividing LSM by leaf thickness (Witkowski and Lamont, 1991). Leaf thickness (μm) was measured midway between the margin and the midrib at the widest part of leaf. Major leaf veins were avoided. Leaf volume (m\(^3\)) was calculated as the product leaf area by mean leaf thickness (Garnier and Launert, 1994). The percentage of carbon was determined by uniform incinerating a known weight of sample at 500°C. We used Pearson linear correlations to statistically analyse the relationship between LSM and the various leaf attributes of the plant species. We used the Student t test to observe differences between leaf traits under sun and shade conditions (Zar, 1984).

Some leaves were fixed in alcohol 70% and then transferred to Jeffrey Solution (Johansen, 1940) for epidermis dissociation, stomatal counting, and measurements of
trichome density. Ten fields of view of known area (1 mm$^2$) were examined per leaf and the mean counting converted to stomata and trichome density. Mesophyll comparisons were done by leaf transverse sections in paraffin. Cross sections 10 μm thick were cut with a microtome, and slides with mounted tissue were stained with blue astra and fucsina (see Johansen, 1940). Leaf anatomical features and thickness were then quantified under a one micrometer eyepiece microscope. Cell counting was done using the number of cells over ten lines (1 mm) for palisade parenchyma and number of cells per mm$^2$ for spongy parenchyma on ten different sections from each species in both sun and shade sites. We used the Student test to statistically compare these leaf traits under the two distinct light regimes (Zar, 1984).
RESULTS

Overall, both plant species showed consistent differences in leaf area, volume, LSM, thickness, and percentage of carbon between sun and shade habitats (Table 2). The areas of leaves of plants in the shade of both *M. ibaguensis* and *M. stenostachya* were 70% and 12% greater than leaves of plants in the sun, respectively. However, leaves of plants of *M. ibaguensis* in the shade had 20% more volume than the leaves of plants in the sun. In *M. stenostachya*, leaves of plants in the sun had 91% more volume than leaves of plants in the shade. The dry mass of leaves of *M. stenostachya* in the sun was 92% greater than of leaves of plants in the shade. Plants in the sun presented leaves with higher LSM and density compared to leaves of plants in the shade (Table 2). The same pattern was presented by carbon which was 77% greater in *M. ibaguensis* and 114% greater in *M. stenostachya* in plants in the sun than in the shade. Likewise, leaves of plants in the sun of both species had thicker than leaves of plants in the shade (Table 2).

LSM was highly correlated with leaf dry mass and leaf density in both habitats (Table 3). However, LSM did not correlate with leaf area, while correlated significantly with volume in leaves of shade plants of both species (Table 3). Likewise, LSM correlated significantly with leaf thickness only in shade habitats in both species (*M. ibaguensis*, \( r = 0.66 \); *M. stenostachya*, \( r = 0.54 \)).

The differences in LSM were influenced by changes in the thickness of the cuticle, epidermis, palisade, and spongy parenchyma. All measured anatomical parameters differed between sun and shade habitats in the two plant species. Structural development of the mesophyll of leaves in plants in the sun was greater compared to plants in the shade. Light-induced changes in the development of the mesophyll were probably caused by increasing tissue thickness, cell number per area, and cell size (Table 4).

Leaves of *M. ibaguensis* in the sun were thicker than in the shade habitat (Fig. 1). Although the upper epidermis did not differ in thickness, the thickness of leaf cuticle in the sunny habitat contributed for an increase in the leaf thickness (Table 4). Leaves of *M.*
_stenostachya_ in the sun were thicker than leaves of plants in the shade. Nevertheless, leaves of plants in the sun presented cuticle and upper epidermis thicker compared to leaves of plants in the shade (Fig. 2, Tab. 4). The leaf mesophyll of _M. ibaguensis_ was thicker in the sun mainly because of the increased thickness of the palisade parenchyma which reflects increased cell number and length (Fig. 1). Nonetheless, in _M. stenostachya_ the increase in the thickness of the mesophyll was mainly influenced by the number of cell layers in the palisade parenchyma which increased three times (Fig. 2). However, the increased mesophyll thickness of this species in the sun was caused by either an increase in the palisade parenchyma or in the spongy parenchyma. Palisade parenchyma of _M. ibaguensis_ was significantly thicker in the sun habitat than in the shade habitat, while the thickness of the spongy parenchyma did not differ between plants in the sun and shade habitats (Table 4). The palisade parenchyma and spongy parenchyma of _M. stenostachya_ plants in the sun was significantly thicker than that of plants in the shade because of an increase in the number of cells, as well as increased cell width and length (Table 4). Cells of the spongy parenchyma of this species were larger and of irregular shape (due to branching). Besides, the distance between leaf veins was reduced forming cavities where the stomata are protected by trichomes (Fig. 2).

The two species are hypostomatous in both shade and sun habitats. The number of stomata per leaf area in plants in the shade habitat was significantly lower than in plants in the sun (Table 4). _Miconia ibaguensis_ and _M. stenostachya_ had trichomes only on the abaxial leaf surface, and plants in the sun of these two species had significantly higher trichome density than plants in the shade.
DISCUSSION

Sun-exposed plants of all two species had higher leaf thickness, density, and LSM, which is in harmony with several studies (e.g., Boardman, 1977; Witkowski and Lamont, 1991; Sims and Pearcy, 1992). Shade plants have showed thinner leaves, resulting in higher area but lower density and LSM (Corre, 1983).

In these species, LSM was positively correlated with leaf mass and leaf density in both habitats separated by light availability. Nonetheless, LSM was only positively correlated with leaf thickness under shade conditions. Variations in LSM of several plant species studied by Witkowski and Lamont (1991), and Garnier and Laurent (1994) resulted the variations in leaf density and/or thickness. Leaf density results from the increase of cell wall amount per unit volume (Garnier and Laurent, 1994). The plant species studied showed increased mesophyll cell size and amount which reflected in mesophyll thickness and density, therefore contributing to either an increase in the amount of the cellular walls or an increase in the percentage of carbon.

Leaf thickness is influenced by variations in palisade tissue (number of layers and cell length), number of layers and length of mesophyll, epidermis, hypodermis, and indumentum, as well as by increased cell size (Esau, 1977; Fahn and Cuttler, 1992; Garnier and Laurent, 1994, Witkowski and Lamont, 1991; Sims and Pearcy, 1992; Thompson et al. 1992). Ours results showed an increase in thickness of cuticle and upper epiderm of sun leaves for *M. stenostachya*, and only in thickness upper epiderm for *M. ibaguensis*. The increase both of the cuticle and upper epidermis thickness this species may have a protective role under high-light conditions. Carter (1991) argued that a second upper epidermal layer still may increase more the leaf reflectance; however an increase in thickness of cuticle and outer periclinal wall of epiderm cell as well as in height of cells us permit to think the some effect due to increase in the reflectance layer. Thus, the data presented showed that *M. stenostachya* more protection against light irradiation that *M. ibaguensis*.
*M. ibaguensis* and *M. stenostachya* showed an increase in the palisade parenchyma. Palisade parenchyma cells of *M. ibaguensis* and *M. stenostachya* sun-exposed plants were deeper and in the case of the latter it also had more layers. Thompson *et al.* (1992) discussed that high light irradiance induces the development of the mesophyll in the palisade and spongy parenchyma, while under low light irradiance leaf cells are smaller and densely packed. Moreover, palisade thickness may be a good predictor of maximum photosynthetic rate, but only on a species-specific basis (Strauss-Debenedetti and Berlyn, 1994). The size and quantity of cells may interfere in mesophyll resistance, therefore influencing CO₂ diffusion (Jurik *et al.*, 1982; Parkhurst and Mott, 1990; Syvertse *et al.*, 1995) and photosynthesis capacity per leaf area (Sims and Pearcy, 1992). However, the positive relationship between leaf thickness and increasing irradiance may be primarily associated to changes in structure than physiological changes, because anatomical adjustments may not always be coincident with changes in photosynthetic capacity within leaves (Chazdon and Kaufmann, 1993; Strauss-Debenedetti and Berlyn, 1994). *M. stenostachya* presented changes more drastic in thickness of leaf mesophyll because an increase of palis and spongy parenchyma, beyond the large gain of the carbon. This allow think in a strong relationship between structural changes and changes in photosynthesis for specie *M. stenostachya*.

Sun leaves of all species showed higher stomatal density than shade leaves. The increased number of stomata per unit area favours higher leaf conductance under high irradiance conditions (Mott *et al.*, 1982; Mott and Michaelson, 1991). Trichome density was also influenced by light. As expected, trichome density was higher in sun than in shaded of *M. ibaguensis*. Nevertheless, no statistically significant differences were found between sun and shaded *M. stenostachya*. The increase in trichome density plays an important role in water regulation through an increase in the boundary layer. Increase trichome density decrease the vapor pressure between the leaf tissues and the microclimate
just above the leaf lamina. Furthermore it reduces water loss (e.g., Gay and Hurd, 1975; Ehleringer and Mooney, 1978).

Given that the species studied here are endemic to the cerrado vegetation and primarily sun habitats (R. Goldenberg, pers. comm.), we postulate that shade has contributed to decrease of leaf thickness, and therefore to the decrease in leaf sclerophyll. The two sympatric species of cerrado studied presented numerous variations in their leaf traits which can have important physiological roles in relation to light. *M. stenostachya* was the most anatomically plastic species. Changes in structural traits are important as they allow the exploration of habitats with high spectrum of irradiance. Studies at the leaf level allow us to widen our understanding of plant adaptation to different habitats and ultimately may shed light on the differential distribution in heterogeneous habitats such as the cerrado.

Turner (1994a) has argued that the evolution of sclerophyll in some plant taxa may represent an important benefit which allowed for the exploration of new habitats and decrease herbivory. An interesting question to be pursued in these plant species is on the differential herbivory levels on plants of sun and shaded habitats, and whether light availability has influenced on plant metabolism and secondary chemistry and the effects they may have on herbivores. These questions shall be addressed in a near future.
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LITERATURE CITED


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<th>pH</th>
<th>Soil Relative Water (%)</th>
<th>Organic Matter (%)</th>
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<td>6.8 - 7.0</td>
<td>4.99 ± 0.01 - 4.95 ± 0.04</td>
<td>3.00 ± 0.08 - 3.00 ± 0.07</td>
<td>1.07 ± 0.00 - 0.18 ± 0.00</td>
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<td>1.70 - 2.40</td>
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<td>3.96 ± 0.09 - 4.35 ± 0.33</td>
<td>1.31 ± 0.03 - 1.13 ± 0.00</td>
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<tr>
<td>1.94 - 2.99</td>
<td>4.97 ± 0.01 - 4.92 ± 0.04</td>
<td>3.00 ± 0.08 - 3.00 ± 0.07</td>
<td>1.07 ± 0.00 - 0.18 ± 0.00</td>
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TABLE 1. Soil and environmental characteristics of habitats studied in Serra do Cipo, Brazil.

**Kipariss Forest**

**Cerrado**

**Trais**
<table>
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<th>Chemical Units</th>
<th>Structual Units</th>
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<tr>
<td><strong>Thickness (mm)</strong></td>
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<tr>
<td>132 ± 3</td>
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<td>780 ± 18</td>
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<td>404 ± 17</td>
<td>404 ± 17</td>
</tr>
<tr>
<td>2060 ± 76</td>
<td>2060 ± 76</td>
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</tbody>
</table>

TABLE 2. Leaf Traits (X ± SE) of Physcomitrella patens and M. Insignis (Metastomataceae) in sun and shaded habitats. (* p = < 0.05 and ** p = not statistically significant, LSW denotes least square means).
<table>
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<th>Sun</th>
<th>Shade</th>
<th>Sun</th>
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<td>0.538</td>
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<td>0.572</td>
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<td>0.150</td>
<td>0.187</td>
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<tr>
<th>Thickness</th>
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<tr>
<td>Shade</td>
<td>Sun</td>
<td>Shade</td>
<td>Sun</td>
<td></td>
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Letters indicate significant differences between habitats (Test 1, \( p > 0.05 \) and " = not statistically significant, different from Peaoniophyes (Lyttonia amplexicaulis) in sun and shaded habitats. \( * = p < 0.05 \) and various least signs of Peaoniophyes.}

**TABLE 3:** Linear (Pearson product moment) correlation between leaf specific mass (LSM) and various leaf traits of Peaoniophyes.
<table>
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<th>Trait</th>
<th>Value 1</th>
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<th>Value 3</th>
<th>Value 4</th>
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<td>36 = 1</td>
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<td>27 = 2</td>
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**Leaf Traits**

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* Significant
+ Not significant

**Note:** Significant level of Student t-test for comparison means each species. 

**Table 4:** Some morphological parameters, leaf stomatal density (stoma/μm²), and leaf thickness density (μm²).
FIGURES LEGENDS

FIGURE 1. A cross section of leaf of *Miconia ibaguensis* at sun habitat (A) and in shaded habitat (B). 1, cuticle; 2, epidermis; 3, palisade parenchyma; 4, spongy parenchyma; 5, stomata. Bar = 100 μm. (x 250)

FIGURE 2. A cross section of leaf of *Miconia stenostachya* at sun habitat (A) and in shaded habitat (B). 1, cuticle; 2, epidermis; 3, palisade parenchyma; 4, spongy parenchyma; 5, stomata; 6, trichomes. Bar = 100 μm. (x 250)
Cynipid Gall Growth Dynamics and Enemy Attack: Effects of Gall Size, Toughness, and Thickness

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ABSTRACT- Galling insects have developed many strategies to preclude or reduce the attack by natural enemies, such as an increased wall thickness early in the season, switching to larger and tougher walls later in the maturation stage. In this study, we observed the efficiency of each one of these parameters in reducing mortality of the leaf galling wasp Atrusca caprone Weld (Hymenoptera: Cynipidae), on Quercus turbinella Greene (Fagaccae), during the three months of gall development (June-August). Gall diameter and wall toughness increased from the first to the third month of the study (ANOVA, Diameter: F = 88.73, p < 0.0001; ANOVA, Toughness: F = 26.13, p < 0.0001). However, gall wall thickness increased from June to July, decreasing in August (ANOVA, F = 35.84, p < 0.0001). Gall survivorship was only 2% in June, increasing to 10% in July and to 29.3% in August. Multiple regression analyses showed that only gall wall toughness influenced gall susceptibility to parasitoid attack (r² = 0.52, F = 13.84, p < 0.01). Gall survivorship was very low in the first month due probably to low wall toughness, which led to a higher success of oviposition by parasitoids during this phase. These results suggest that the first month is critical to gall establishment, and the galls which are not parasitized at this stage are less likely to be attacked later.

KEY WORDS: Gall development, parasitoids, Atrusca caprone, window of vulnerability, Quercus turbinella
Dinâmica de Crescimento de um Cinipídio e Ataque por Inimigos Naturais: Efeitos do Tamanho, Dureza e Espessura da Galha.

RESUMO- Insetos galhadores desenvolveram várias estratégias para evitar ou reduzir o ataque por inimigos naturais, tais como maior espessura da parede no início de formação, e maior diâmetro e dureza da parede em estágios posteriores do desenvolvimento. Neste estudo, analisamos a eficiência de cada um desses parâmetros na redução da mortalidade das galhas de *Atrusca caprone* Weld (Hymenoptera: Cynipidae) em *Quercus turbinella* Greene (Fagaceae), durante os três meses de seu desenvolvimento (Junho-Agosto). O diâmetro e a dureza das galhas aumentaram do primeiro para o terceiro mês de estudo (ANOVA, diâmetro: $F = 88.73, p < 0.0001$; ANOVA, dureza: $F = 26.13, p < 0.0001$). Entretanto, a espessura das galhas apresentou um aumento de Junho para Julho, diminuindo de Julho para Agosto (ANOVA, $F = 35.84, p < 0.0001$). A análise de regressão linear múltipla mostrou que apenas a dureza das galhas influenciou a susceptibilidade das galhas ao ataque por parasitóides ($r^2 = 0.52, F = 13.84, p < 0.01, n = 15$). A sobrevivência das galhas foi elevada no primeiro mês, diminuindo com o tempo, provavelmente devido a menor dureza da parede. Estes resultados sugerem que o primeiro mês seja crítico para o estabelecimento das galhas, sendo que galhas não parasitadas neste estágio são menos suscetíveis a um ataque posterior.

The induction of galls by insects has been shown to be of adaptive nature. Gall formation may protect its inducers from harsh microenvironmental factors, such as dryness, and temperature (Price et al. 1987). In addition, galls can provide enemy-free space to the gall-inducer, by offering a protective refuge against predators and parasites (Askew 1961, Hodkinson 1984, Price et al. 1987, Price & Pschorr-Walker, 1988, Fernandes & Price 1992; but see Fernandes et al. 1987, Hawkins 1988).

Several factors may affect the rates of parasitism on gall-forming insects. Gall size may interfere with parasitoid oviposition success in an inverse relationship, since ovipositors of limited length are unable to reach the larvae inside the gall chamber (e.g., Weis & Abrahamson 1985, Rossi et al. 1992, Rossi & Stiling 1995). The toughness of gall tissue may also preclude parasitoid attack, if the gall wall is not easily penetrable (Cornell 1983, Craig et al. 1989). Finally, the thickness of the gall walls is also important to reduce parasitism rates, since the success of oviposition by a parasitoid is related to the length of the ovipositor and to the depth of the larvae in the gall (Askew 1961, Price 1972, Weis et al. 1985, see also Brandl & Vidal 1987).

Parasitoids may synchronize their activity pattern with gall development, by attacking early in the gall growing season (Askew 1975, Wiebes-Rijks 1982, Jones 1983, Schonrogge et al. 1996). This should be related to their ability to overcome gall size and toughness in time. With increasing age the gall tissue becomes harder and the gall larger, therefore precluding parasitism (Weis et al. 1985). In this way, a “window of vulnerability” (Cornell 1983) appears to exist early in the season, when the developing gall is smaller and softer. However, these early galls may preclude or decrease mortality by natural enemies if they have thicker walls.
which act as a barrier to the parasitoids' ovipositors. We postulate that galls may have different 'ontogenetic' barriers to avoid parasitoid attack, if their walls are thicker in the early season and harder and larger in the late season.

We tested this hypothesis observing the phenological development and the survivorship rates of a leaf galler, *Atrusca caprone* Weld (Hymenoptera: Cynipidae), on *Quercus turbinella* Greene (Fagaceae). This study aimed to answer the following questions: a) How does gall development affects gall toughness, gall size, and gall thickness of *A. caprone*? b) Which of these variables are more effective against the natural enemies of *A. caprone*?

**Material and Methods**

*Quercus turbinella* is widely shrub distributed in the chaparral vegetation of Arizona-USA (McDougall 1973). Galls were found throughout the distribution of the host plant, and were more abundant between 1,200 and 1,500 meters altitude (adjacent to highways I-17, and 89 A South) in northern Arizona.

The cynipid galls occurred on the abaxial leaf surface, were spherical, glabrous, and one-chambered with only one gall-making larva per chamber (Fernandes *et al.* 1990). Galls varied from pale yellow to red. Young galls are solid, but the centrally located larval chamber becomes separated from the gall walls during development. However, the larval chamber remains attached to the gall walls by fibers of conductive tissue during gall development (see Fernandes *et al.* 1990).

Galls were first observed at the beginning of June 1987, at the initial of their development, and by the end of September all of the galls were mature. As the induction of
new galls in a season are usually synchronized, we considered all galls as belonging to the 
same cohort. We randomly removed 100 galls in June, 50 galls in July and 75 galls in August, 
which were dissected and analyzed for survivorship, diameter, wall thickness, and wall 
toughness. Gall mortality was caused by several different species of hymenopteran 
parasitoids. Gall diameter was measured with a caliper (mm), while gall wall thickness was 
measured under a dissecting scope (mm). Gall wall toughness was obtained by using a 
Volander Texture Analyzer, which measured the force needed to push a needle probe 2 mm 
into the gall at a speed of 1 mm/s. The device was calibrated in “grams” of force; 
measurements were converted to newtons of force, using the conversion factor of 1 “gram-
force” = 9.80665 mn (Craig et al. 1990). All these parameters were compared between the 
three months using a one-way ANOVA and a Tukey test (Zar 1984).

We used linear regression analyses to verify the relationship between gall diameter 
and survivorship rates. Since there was no relationship between these variables ($r^2 = 0.005$, 
$F = 1.22, p = ns, n = 225$), we divided gall survivorship, thickness, and toughness in eight 
classes of diameter in each month. This procedure was conducted in order to transform gall 
survivorship from a binomial to a continuous variable. Data on gall survivorship were then 
arc sine-square-root transformed, and data on gall thickness and toughness were log 
transformed to meet normality (Zar 1984). We used stepwise multiple regression analysis to 
observe the influence of gall age, gall wall thickness, and toughness on the survivorship of A. 
cuprone galls (Zar 1984).
Results

Galls of *A. caprone* varied in diameter, wall thickness, and toughness during development (Fig. 1). On average, gall diameter and gall wall toughness were significantly higher at the end of maturation (August) (ANOVA and Tukey test, Table 1, Fig. 1). Thus, gall development influenced positively these variables. However, gall wall thickness showed a increase from June to July, decreasing from July to August, attaining a significantly lower average at the end of gall development (ANOVA and Tukey test, Table 1, Fig. 1).

Gall survivorship, on the other hand, increased with gall development (Table 1; Fig. 2). In June, survivorship rates were very low, with only 2% of the galls remaining alive, increasing to 10% in July and 29.3% in August. The stepwise multiple regression analyses showed that only gall wall toughness presented a significant positive relationship with gall survivorship ($r^2 = 0.52$, $F = 13.84$, $p < 0.01$, $n = 15$, Fig. 3). Therefore, all the other variables were excluded from the model, as they did not show significant relationships with gall survivorship ($p > 0.05$ for all). Therefore, the higher gall survivorship in the later stage of development may be related to an increase in the toughness of gall walls.

Discussion

The growth dynamics of *A. caprone* experienced a change from thicker and softer walls in the initial stage of development to thinner but harder walls later in the development. However, the higher gall wall thickness does not seem to be efficient to preclude parasitoid attack, since mortality of the earlier galls is almost 98%. Our results suggest that gall wall
toughness is more effective as a defense against natural enemies in A. caprone galls, assuming that parasitoid attacks are at similar rates over gall development. In fact, even longer ovipositors may generally be found broken off in many galls, if they are not strong enough to overcome gall wall toughness (see also Askew 1965). In addition, Craig et al. (1990) stated that larval inaccessibility (i.e., larval depth inside the gall) is less important than gall wall toughness in determining parasitism rates.

The existence of this window of vulnerability may decrease the range of resource availability, decreasing the efficiency of natural enemies (Craig et al. 1990). However, Schonrogge et al. (1996) suggested that parasitoids are morphologically, phenologically and/or physiologically well adapted to their host galls, being able to circumvent any protective function offered by the galls. Thus, gall wall toughness may diminish the parasitoid attack, but is far from precluding it completely (gall mortality, even in the third month, remains higher than 70%).

The higher gall mortality in the initial stage of development is probably due to a higher success of oviposition by natural enemies during this phase. This pattern was already observed in other systems (Wiebes-Rijks 1982, Craig et al. 1990, Shorthouse et al. 1990). Since gall wall thickness is not efficient in precluding parasitoid attack, and gall toughness is still low, this phase should be critical to gall establishment. The galls remaining alive in the second and third months of development have tougher walls, possibly excluding certain species of parasitoid with ovipositors of limited strength, and this factor seems to determine the vulnerability of the galls. In this way, if the larvae of galling insects escape detection
when galls are soft and within reach of parasitoids, they are protected once imbedded inside hard maturing galls.

We concluded that gall wall thickness of *A. caprone* was not sufficient to avoid the "window of vulnerability" in the initial phase of development. Thus, the mortality rates of the gall-maker are very high in this stage, probably due to a higher oviposition success by parasitoids. Gall wall toughness seems to limit larva susceptibility to parasitism and, as this parameter increased with gall age, galls in the late season are less likely to be affected by the pressures of natural enemies.
Acknowledgements

We are very grateful to D Yanega for his helpful comments on the manuscript and two anonymous reviewers that carefully reviewed and commented on drafts of this work.
Literature Cited


Table 1. One-way ANOVA comparison of variations on gall diameter, gall wall toughness, thickness and survivorship rates of galls of *Atrusca caprone* on *Quercus turbinella* between the three months of study.

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<td>Gall wall thickness</td>
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<td>&lt; 0.0001</td>
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<td>Gall survivorship</td>
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Figure Legends

Fig. 1. Average diameter, wall toughness, and wall thickness of the galls of *Atrusca caprone* on *Quercus turbinella* during three months of study. Statistically significant differences are represented by different letters above the bars (ANOVA and Tukey test, p < 0.05).

Fig. 2. Average mortality rates of the galls of *Atrusca caprone* on *Quercus turbinella* during three months of study. Statistically significant differences are represented by different letters above the bars (ANOVA and Tukey test, p < 0.05).

Fig. 3. Linear regression analyses showing the relationship between survivorship rates and wall toughness of *Atrusca caprone* galls ($r^2 = 0.52, y = 0.006x + 0.163$).
Preference of Four Neotropical Species of Galling Insects to Shoot Vigor

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Preferência de Quatro Espécies de Insetos Galhadores Neotropicais em Relação ao Vigor de Ramos.

RESUMO - A hipótese do vigor de plantas (HVP) prediz que plantas ou módulos de plantas mais vigorosos são preferencialmente selecionados por fêmeas de insetos galhadores como sítios de oviposição, pois aumentam a chance de sobrevivência da prole. A HVP foi testada para *Neopelma baccharidis* Buckhardt (Homoptera: Psyllidae) e *Rhousphondylia friburgensis* (Tavares) (Diptera: Cecidomyiidae) que causam galhas em *Baccharis dracunculifolia* D.C. (Asteraceae), e para duas espécies diferentes de Cecidomyiidae (Diptera) que provocam galhas em *Maytenus salicifolia* Reiss. (Celastraceae) e *Vernonia polyanthes* Less (Asteraceae). A abundância de galhas aumentou com o aumento do comprimento do ramo nas quatro espécies, como previsto pela HVP. Entretanto, ao considerarmos a taxa de ataque por unidade de ramo (cm), que inclui nas análises o efeito da disponibilidade de recursos por unidade de comprimento, o padrão de resposta dos quatro galhadores desapareceu. *R. friburgensis* e o cecidomiídeo que induz galhas em *M. salicifolia* não responderam ao vigor do ramo (*P* > 0,05), enquanto as outras espécies responderam diferencialmente. A abundância de galhas de *N. baccharidis* correlacionou-se negativamente com o aumento do comprimento do ramo (*y* = 0,185 - 0,007*x*; *r*² = 0,21; *F* = 6,013, *P* < 0,05), enquanto o número de galhas provocadas pelo cecidomiídeo em *V. polyanthes* correlacionou-se positivamente com o vigor do ramo (*y* = 0,09 + 0,002*x*; *r*² = 0,34; *F* = 6,157; *P* < 0,05). Portanto, apenas o padrão de ataque do cecidomiídeo galhador em *V. polyanthes* suportou a HVP.

PALAVRAS-CHAVE: Diptera, galhas, Homoptera, Insecta, interações inseto-planta.
ABSTRACT - The plant-vigor hypothesis (PVH) predicts that females of galling insects preferentially oviposit on the most vigorous plant or plant modules, where their offspring performance is highest. We tested the PVH on Neopelma baccharidis Buckhardt (Homoptera: Psyllidae) and Rhoasphondyliu friburgensis (Tavares) (Diptera: Cecidomyiidae) which induce galls on Baccharis dracunculifolia D.C. (Asteraceae), and on two different Cecidomyiidae (Diptera) species that induce galls on Maytenus salicifolia Reiss. (Celastraceae) and Vernonia polyanthes Less (Asteraceae), respectively. The abundance of galls induced by the four galling species increased with increasing shoot length, as predicted by the PVH. However, when we considered the rate of attack per shoot unit (cm), which includes in the analyses the effect of availability of resource per unit length, the response patterns of the four gallers disappeared. R. friburgensis and Cecidomyiidae species which cause galls on M. salicifolia did not respond to shoot vigor (P > 0.05) while the other species responded differentially. The abundance of N. baccharidis galls correlated negatively with shoot length (y = 0.185 - 0.007x, r² = 0.21, F = 6.013, P < 0.05) while the number of galls caused by Cecidomyiidae on V. polyanthes showed a positive relationship with shoot vigor (y = 0.09 + 0.002x, r² = 0.34, F = 6.157. P < 0.05). Hence, only the attack pattern of the Cecidomyiid galler on V. polyanthes corroborated the PVH.

KEY WORDS: Diptera, galls, Homoptera, Insecta, insect-plant interactions.
Studies on the effects of plant quality on the attack rates by herbivorous insects have shown contradictory results which have led to two major hypotheses. Many species show high preference and improved larval performance on stressed hosts, which resulted in the formulation of the "plant stress hypothesis" (PSH) (e.g., White 1969, 1976). It predicts that plants under abiotic stress become more suitable as food to herbivorous due to an increase in the availability of nutrients. In addition, stressed plants may synthesize less chemical defenses (Rhoades 1979, White 1984). Some studies support White's hypothesis (e.g., Waring & Cobb 1992, Bruyn 1995, Cobb et al. 1997). On the other hand, other studies have shown that several species of herbivorous insects respond positively to vigorously growing plants or plant parts (e.g., Price et al. 1990, Hunter & Price 1992, Preszler & Price 1995), which resulted in the "plant vigor hypothesis" (PVH) (Price 1991). Vigor is defined as any plant or plant module that grows rapidly and reaches a large size relative to the mean growth rate and size reached by the population of plants or plant modules. Price (1991) postulated that insect herbivores, whose larval development is associated with their host-plant growth processes, should prefer to attack the most vigorous plants or plant modules where subsequent larval performance is highest. The archetype herbivores with these characteristics are galling insects, whose association with host-plant vigor have important implications on their population dynamics (Preszler & Price 1995).

Price (1991) also suggested a solution for the divergence in the results of these two hypotheses, proposing an alternative view in which there is a continuum of strategies. This approach predicts that insect herbivores more specialized and intimately related with the growth processes of plant (latent species) tend to select shoots in one extreme of the continuum, hence characterizing the PVH. Other herbivores, notably those with oviposition and larval development spatially and temporally separated (eruptive species) tend to select modules in the other end of this continuum, characterizing the PSH.

Few studies on the role of plant vigor on insect herbivores have now been done in tropical region (e.g., Prada et al. 1995, Vieira et al. 1996, Cornelissen et al. 1997, Madeira et al. 1997, Faria et
al. 1997). Some of these studies corroborate the PVH, such as the work by Prada et al. (1997) in which they observed that fire induced higher production of flowers, resulting in a positive relationship between the number of herbivore insects per plant and the number of capitula per plant. Faria et al. (1997) also verified a positive relationship between attack by a Scarabaeidae beetle and shoots length in *Erythroxylum suberosum* Turcz. (Erythroxylaceae). Nevertheless, other studies have shown different results. Madeira et al. (1997) did not find any support for female preference for longer shoots, while Cornelissen et al. (1997) suggested idiosyncratic responses of the herbivores that attack shoots of *Bauhinia brevipes* Vog. (Leguminosae).

In this study, we evaluate the pattern of attack by four galling insects on three species of host plants, *Maytenus salicifolia* Reiss. (Celastraceae), *Baccharis dracunculifolia* D.C. (Asteraceae) and *Vernonia polyanthes* Less (Asteraceae). The study aims to answer the following questions: Are the longest shoots in the available shoot population of the three plant species the most attacked by gallers? Do the four galling species respond similarly to plant vigor?

**Material and Methods**

**Study Area.** This study was done in the Campus of the Federal University of Minas Gerais (19°52' S, 43°58' W), Belo Horizonte (MG) in southeastern Brazil. The campus is at 800 m above sea level and has a heterogeneous vegetation with native, introduced and ornamental species (Fernandes et al. 1988). The studied area has a marked dry period of 3 to 4 months with an average monthly precipitation of 50 mm and average temperature between 19°C and 21°C. The rainy season lasts 8 to 9 months and the average monthly precipitation is 300 mm with an average temperature of 23.9°C.
**Host Plants and Galling Insects.** An unidentified species of Cecidomyiidae (Diptera) induces galls on the central leaf vein of *M. salicifolia*. Galls are spheroid, brownish, glabrous, one-chambered, and have one larva per chamber. These galls are frequently observed on the host plant throughout the year.

*V. polyanthes* is a weedy species of cultivated and disturbed areas (Leitão Filho et al. 1972). Spheroid galls are formed on the central vein of its leaves by an unidentified species of Cecidomyiidae (Diptera). Galls are green, glabrous, one-chambered with one or two larvae per chamber and occur on the abaxial leaf surface, and very common in studied area.

Approximately 17 species of galling insects attack *B. druncunculifolia* (Fernandes et al. 1996). The host plant is a dioecious shrub which is widespread in Brazil. Two species of gallers were studied: *Neopelma baccharidis* Buckhardt (Homoptera: Psyllidae) is the most common galling insect on *B. druncunculifolia* which causes an elongated globular leaf gall (Lara & Fernandes 1994) and *Rhoasphondylia friburgensis* (Tavares) (Diptera: Cecidomyiidae) which produces globular, green and glabrous galls on the stems of the plant (Gagné 1994).

**Sampling and Statistical Analyses.** Random samples of 20 shoots were taken around the canopy on 10 individuals of each plant species between January and February of 1994. Shoots were placed in plastic bags and taken to the laboratory for measurements of shoot length (cm) and counts of the total number of galls. To answer how galling insects respond to plant vigor, shoots were grouped into size classes at 1 cm intervals (see Price 1991). The attack rates of the galling insects were obtained by two methods: the number of galls was divided by the number of shoots in each size class, which resulted in an estimate of the number of galls per shoot; and the number of galls was divided by shoot length in each size class, which resulted in number of galls per shoot unit (cm). The attack rates were also calculated as the number of galls per unit of shoot length (cm) in an attempt to eliminate the effect of the longest shoots having higher probability of being attacked. The data were analyzed by simple linear
regressions to test for the relationship between shoot length and number of galls per shoot, and between shoot length and number of galls per centimeter of the shoot.

Results

Longer shoots were less abundant than shorter shoots on the three plant species. However, high rates of attack by galling insects were always observed on the longest shoots (Fig. 1). The highest density of galls occurred on M. salicifolia with 10,090 galls per 1,000 shoots. N. baccaridis induced 570 galls/1,000 shoots, R. friburguensis induced 215 galls/1,000 shoots, while the unidentified species of cecidomyiid induced 2,695 galls/1,000 shoots on V. polyanthes.

Galling insects showed divergent responses to shoot length classes. The attack by R. friburguensis did not correlate with shoot length (y = 0.082 + 0.021x, r² = 0.12, F = 2.934, P > 0.05). On the other hand, the number of galls per shoot was positively correlated with shoot length in the other three galling species: N. baccaridis (y = 0.183 + 0.043x, r² = 0.52, F = 23.923, P < 0.05), cecidomyiid on V. polyanthes (y = -0.77 + 0.19x, r² = 0.86, F = 71.617, P < 0.05), and cecidomyiid on M. salicifolia (y = 2.42 + 0.67x, r² = 0.30, F = 5.059, P < 0.05) (Fig. 2). These results corroborate the plant vigor hypothesis.

However, when the attack rates were recalculated as the number of galls per unit of shoot length (cm), the patterns previously reported were modified (Fig. 3). The attack by N. baccaridis became negatively correlated with shoot length (y = 0.185 - 0.007x, r² = 0.21, F = 6.013, P < 0.05). The attack by the cecidomyiid on V. polyanthes became positively correlated with shoot length (y = 0.09 + 0.002x, r² = 0.34, F = 6.157, P < 0.05). The patterns of attack of R. friburguensis (y = 0.023, r² = 0.01, F = 0.038, P > 0.05) and that of the cecidomyiid on M. salicifolia (y = 1.13 - 0.008x, r² = 0.01, P > 0.05) did not show any relationship with shoot length. These results indicate that the plant vigor hypothesis was not supported for most insect species when we considered the attack rate per shoot unit,
that include in analyses the effect of resource availability per length unit.

**Discussion**

The distribution patterns of shoot sizes in the three species of plants corroborate many other studies (e.g., Craig *et al.* 1986, Craig *et al.* 1989), including tropical species (e.g., Cornellissen *et al.* 1997, Madeira *et al.* 1997) where the longest shoots are always rare in the population of shoots. The longest shoots also tended to be more attacked by galling insects than shortest shoots. In the tropics, Madeira *et al.* (1997) studying galling insect preference on *Baccharis concinna* Darroso (Asteraceae) observed that the herbivores preferred the most vigorous shoots.

However, the longest shoots have greater probability of being attacked than smaller shoots even if no selection is at work. Longer shoots offer more leaves and buds to be used by gallers than shorter shoots (Madeira *et al.* 1997). Furthermore, other variables such as the availability of sites for colonization and shoot age tend to produce greater attack frequencies in longer shoots (Karban 1987). Therefore, we argue that resource availability per shoot unit should be incorporated when testing the plant vigor hypothesis to avoid repetition in results of galling insects attacks. The grouping of shoot length into size classes may force the relationship where the longest shoots are always attacked due to chance alone (Cornellissen *et al.* 1997).

When we considered attack rate per shoot unit (cm), the four galling species did not respond similarly to plant vigor. Instead, each species responded differentially or did not respond at all to shoot vigor. Thus, the observed pattern which supported the vigor hypothesis disappeared after applying a correcting method. This work corroborates the study of Cornellissen *et al.* (1997) where the authors observed the existence of a continuum of responses by herbivores to plant and that herbivores may have idiosyncratic responses to plant quality even when feeding on the same host.
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Figure 1. Frequency distribution expressed as the percentage of total shoots (—) and percentage of shoots galled (♦—♦) in each shoot length class on A) B. dracunculifolia (Asteraceae) galled by R. friburgensis (Diptera: Cecidomyiidae); B) B. dracunculifolia (Asteraceae) galled by N. baccharidis (Homoptera: Psyllidae); C) V. polyanthes (Asteraceae) galled by Cecidomyiidae (Diptera) and D) M. salicifolia (Celastraceae) galled by Cecidomyiidae (Diptera).

Figure 2. Observed distribution of the number of galls per shoot on A) B. dracunculifolia (Asteraceae) galled by R. friburgensis (Diptera: Cecidomyiidae); B) B. dracunculifolia (Asteraceae) galled by N. baccharidis (Homoptera: Psyllidae); C) V. polyanthes (Asteraceae) galled by Cecidomyiidae (Diptera) and D) M. salicifolia (Celastraceae) galled by Cecidomyiidae (Diptera).

Figure 3. Observed distribution of the number of galls per unit of shoot length (cm) on A) B. dracunculifolia (Asteraceae) galled by R. friburgensis (Diptera: Cecidomyiidae); B) B. dracunculifolia (Asteraceae) galled by N. baccharidis (Homoptera: Psyllidae); C) V. polyanthes (Asteraceae) galled by Cecidomyiidae (Diptera) and D) M. salicifolia (Celastraceae) galled by Cecidomyiidae (Diptera).