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DE
PÓS-GRADUAÇÃO
I. B.

UNIVERSIDADE ESTADUAL DE CAMPINAS
INSTITUTO DE BIOLOGIA

ECOLOGIA DA POLINIZAÇÃO DE DUAS ESPÉCIES DE BROMÉLIAS DE MATA ATLÂNTICA NO ESTADO DE SÃO PAULO

Este exemplar corresponde à redação final
da tese defendida pelo(a) candidato (a)
MARIA BERNADETE FER-
REIRA CANELA .
e aprovada pela Comissão Julgadora.

Marlies Sazima

Maria Bernadete Ferreira Canela

Prof.ª Dr.ª Marlies Sazima
(orientadora)

Dissertação apresentada ao Instituto de Biologia da Universidade Estadual de Campinas, como parte dos requisitos necessários para a obtenção do título de Mestre em Biologia Vegetal.

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BANCA EXAMINADORA

1. Prof.ª Dr.ª Marlies Sazima ---------- Marlies Sazima

2. Prof.ª Dr.ª Tânia Wendt ---------- Tânia Wendt

3. Prof. Dr. Christian Westerkamp ----------

4. Prof. Dr. João Semir ----------

Tudo começou assim:

> "Não seja impaciente! Não tenha pressa em chegar ao fim. Deixe que o tempo amadureça os frutos, de modo que possa colhê-los adequadamente. Caminhe com segurança e constância, porque tudo nos chegará na hora exata e mais oportuna. Os frutos amadurecidos à força não são tão saborosos quanto os que amadurecem naturalmente. Saiba esperar com paciência e não desanime."

(n^0 236 de "Minutos de sabedoria", aberto ao acaso na primeira meia-hora de observação da tese na Praia da Fazenda).

"30/11/00, quinta. Acordei a noite toda com medo de perder a hora. Primeira observação às 04:00h, sozinha, na praia. Primeiro passo: comer muito pra ter a sensação de estar mais preparada pra enfrentar as coisas. Segundo: ir de uma vez! Era preciso, eu tinha que ir. E até que não foi tão difícil assim, logo clareou. O segredo é não hesitar!"

"13/12/00, quarta. Que barato, um grupo de adultos deficientes visuais passeando, brincando na praia. Eu reclamando de horas seguidas de observação e eles não podem ver nem um minuto das maravilhas que vejo todos os dias! Muitos deles não podem sequer ter a idéia de como é o brilho de um *Thalurania*, seus movimentos, o contraste das flores.....Sou uma pessoa privilegiada!"

("diário de campo")

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A querida e "ímpar" família CANELA: minha mãe ("Dona Iaiá") e seu belo sorriso, meu pai que infelizmente não pode estar neste momento, e meus fundamentais irmãos Antonio, João, Fate, Ana e Zé, OBRIGADA POR TUDO! Também incluo aqui a Lú e a Thalita!

A Marlies por sua orientação maternal insuperável, e ao Ivan pelo carinho e paciência em me ensinar a fotografar!

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"In order to understand the pollination ecology of a species it is necessary to live with its populations..."

Proctor & Yeo 1972

ÍNDICE

CAPÍTULO I. Polinização por beija-flores em *Aechmea pectinata* (Bromeliaceae) no litoral sudeste do Brasil.

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CAPÍTULO II. Florivoria por caranguejos *Armases angustipes* (Grapsidae) influi na visitação dos beija-flores em *Aechmea pectinata* (Bromeliaceae).

CAPÍTULO III. Ecologia da polinização de *Bromelia antiacantha* (Bromeliaceae) no litoral do sudeste brasileiro.

RESUMO

O objetivo desse estudo foi relacionar aspectos da fenologia, da morfologia e biologia floral bem como do sistema reprodutivo, com os visitantes florais e/ou polinizadores de duas espécies de bromélias, *Aechmea pectinata* e *Bromelia antiacantha,* que ocorrem em mata atlântica de baixada no Parque Estadual da Serra do Mar - Núcleo Picinguaba/São Paulo. Foram feitas observações diretas, análises das estruturas florais, medições da produção de néctar e experimentos sobre o sistema reprodutivo. As duas espécies apresentam características florais relacionadas à ornitofilia, tais como folhas avermelhadas, flores tubulares, antese diurna e néctar abundante. A produção de néctar foi maior nas primeiras horas da manhã, decrescendo no restante do dia em ambas as espécies. Os beija-flores *Thalurania glaucopis, Amazilia fimbriata* (Trochilinae) e *Ramphodon naevius* (Phaethornithinae) foram os principais polinizadores, visitando as inflorescências de *B. antiacantha* em rotas de forrageamento e, nas de *A. pectinata,* comportando-se habitualmente como territoriais. Esta diferença de comportamento provavelmente está relacionada a maior extensão do período de floração e distribuição mais agregada dos indivíduos de *A. pectinata,* em comparação com os de *B. antiacantha.* A abertura da corola de *B. antiacantha* favorece o acesso ao néctar e ao pólen por outros visitantes além dos beija-flores. Nesta espécie, foram também freqüentes as abelhas *Bombus morio* (Apidae) como polinizador efetivo, e *Trigona spinipes* (Apidae) como pilhadoras de pólen e néctar. Em *A. pectinata* foi encontrada relação positiva entre a produção de néctar e a visitação diária dos beija-flores, o que não ocorreu em *B. antiacantha*, provavelmente, devido à interferência das abelhas *T. spinipes,* que atacam e afugentam os beija-flores nas primeiras horas do dia. O caranguejo *Armases angustipes* (Grapsidae) foi registrado alimentando-se das estruturas reprodutivas de *A. pectinata* e com isso interferindo na visitação dos beija-flores, fato que pode afetar o sucesso reprodutivo desta planta. Ambas as espécies são dependentes de polinizador pois *A. pectinata* é completamente auto-incompatível e *B. antiacantha* é parcialmente auto-incompatível, mas não autógama. A formação de frutos está relacionada à distribuição espacial dos indivíduos de cada espécie de bromélia e às interações entre visitantes florais.

PALAVRAS-CHAVE: Bromeliaceae, biologia floral, polinização, reprodução, floresta atlântica.

ABSTRACT

The objective of this study was to relate aspects of the phenology, floral morphology and biology, and breeding system to the floral visitors and/or pollinators of the two bromeliad species, *Aechmea pectinata* and *Bromelia antiacantha* that occur in a submontane rainforest in southeastern Brazil. The pollination ecology of these species was studied through direct observation, analysis of the floral structures, measurement of nectar production and reproductive experiments. *A. pectinata* and *B. antiacantha* show some ornithophilous features such as reddish leaves, tubular-shaped flowers, diurnal anthesis, and abundant nectar. In both species, nectar production was greater early in the morning and diminished throughout the day. The hummingbirds *Thalurania glaucopis, Amazilia fimbriata* (Trochilinae) and *Ramphodon naevius* (Phaethornithinae) were the main pollinators of both bromeliad species. These birds exhibited a trapline foraging strategy on *B. antiacantha* inflorescences and mainly territorial behavior on *A. pectinata.* This difference is related to the longer flowering period and more aggregated distribution of the *A. pectinata* individuals as compared to *B. antiacantha.* In this latter bromeliad species, the corolla opening favors the access to nectar and pollen to visitors other than hummingbirds. Bees were also frequent in *B. antiacantha* flowers: *Bombus morio* (Apidae) acted as effective pollinator and *Trigona spinipes* (Apidae) as pollen and nectar thieve. *A. pectinata* presented a positive relation between nectar production and daily hummingbird visitation, which was not detected in *B. antiacantha*, probably due to interference of *T. spinipes* bees that attack and exclud the hummingbirds in the morning hours. The crab *Armases angustipes* (Grapsidae) was recorded feeding on the reproductive structures of *A. pectinata* flowers, thus inhibiting hummingbird visitation and probably interfered with the reproductive success of this bromeliad. Both species are pollinator dependent since *A. pectinata* is completely self-incompatible and *B. antiacantha* is partially self-incompatible, but is nonautogamous. Fruit set is related to the spatial distribution of the bromeliad individuals and to the interactions among floral visitors.

KEY-WORDS: Bromeliaceae, floral biology, pollination, reproduction, Atlantic Forest.

INTRODUÇÃO GERAL

A estrutura e o funcionamento dos ecossistemas estão relacionados, entre outras coisas, a diversas interações planta/animal tais como polinização, dispersão e predação. A polinização é um processo fundamental nas comunidades terrestres, pois constitui o primeiro passo na reprodução sexual das plantas e um pré-requisito essencial para o desenvolvimento de frutos e sementes (Kevan *et al.* 1990).

Muitas espécies de angiospermas dependem de animais para a polinização, estando a grande variedade de flores relacionada, em geral, com a diversidade morfológica e comportamental de seus visitantes (Waser 1983). O significado adaptativo desta variação está na atração do polinizador, na sua percepção do recurso floral e no transporte do pólen de modo preciso (Kevan 1983).

As plantas podem oferecer diferentes recursos florais nutritivos (p.e. pólen, néctar, óleo, exsudatos estigmáticos e tecidos florais) e não-nutritivos (resina, perfume), bem como fornecer locais para oviposição, abrigo e calor, a seus visitantes (Dafni 1992, Endress 1994). Os recursos fazem com que os visitantes sejam freqüentes e eficientes no transporte de pólen, atuando como polinizadores. O deslocamento direcional de pólen é favorecido pela capacidade dos animais de discriminarem as flores de acordo com características das estruturas relacionadas à atração, do período de antese e da oferta de recursos ("síndromes de polinização", ver Faegri & Pijl 1980). Diversos aspectos intrínsecos (p.e. fenologia, morfologia e biologia floral, sistema reprodutivo) e extrínsecos (interações entre visitantes, distribuição espacial dos indivíduos, fatores abióticos, etc) às plantas podem interferir nos processos de polinização, tanto no nível individual quanto populacional (Roubik 1989).

Ritmos fenológicos exercem influência nas relações planta/polinizador através de efeitos na abundância dos recursos (Opler *et al.* 1980), da mesma forma que podem ser determinados por essas relações (Morellato 1987) e influenciados por fatores abióticos dentro das limitações filogenéticas (ver Kochmer & Handel 1986). Em locais e/ou períodos diferentes pode haver competição entre as espécies de animais pelos recursos florais, bem como competição entre plantas pelo recurso polinizador (Stiles 1975, Waser 1978, Feinsinger *et al.* 1982, Fischer 1992). A competição por polinizadores pode atuar como força seletiva sobre os períodos de floração das plantas, por exemplo, através do deslocamento dos mesmos (Waser 1978, Feinsinger 1983), ou então a coexistência de espécies que usam o mesmo polinizador é favorecida pela sobreposição no uso de recursos (Stiles 1975, Heithaus 1979, Araújo *et al.* 1994).

A morfologia floral condiciona a possibilidade de visita legítima para determinados visitantes (Proctor & Yeo 1972). Em flores ornitófilas, por exemplo, variações em comprimento de corola e disposição das estruturas reprodutivas se refletem, respectivamente, na visitação por diferentes grupos de beija-flores de acordo com o comprimento do bico (Feinsinger & Colwell 1978) e na variação do local de deposição de pólen no corpo dessas aves (ver I. Sazima *et al.* 1995). Da mesma forma, o formato dessas flores ornitófilas pode limitar o acesso de insetos (Proctor & Yeo 1972, Faegri & Pijl 1980).

Um dos fatores que determinam o quanto um animal depende do recurso floral é a relação entre sua demanda de nutrientes e a quantidade de alimento que as flores oferecem (see Heinrich 1975). Esta relação pode influenciar a tendência das visitas durante a antese, os deslocamentos entre as flores e entre as plantas, pois se a oferta de recursos é a maneira pela qual as plantas atraem e mantém os polinizadores, é esperado que a visitação destes varie com a disponibilidade do recurso (ver Feinsinger 1976, Roubik 1989).

O transporte do pólen não necessariamente implica numa polinização eficiente. A "qualidade" do pólen transportado pode influir decisivamente no sucesso reprodutivo da progênie e a planta-mãe pode atuar limitando o acesso somente para o pólen mais adequado através de "barreiras" como a hercogamia, a dicogamia e mecanismos fisiológicos que caracterizam os sistemas genéticos de incompatibilidade (Faegri & Pijl 1980). Informações sobre a biologia reprodutiva são essenciais para a compreensão da dinâmica do fluxo gênico e do grau de variabilidade genética nas espécies vegetais (Bawa *et al.* 1985a,b; Proctor *et. al.* 1996; ver Lloyd 1992, Wendt *et al.* 2001, 2002).

Interações entre visitantes florais podem também interferir no sucesso reprodutivo de muitas espécies de plantas. Pilhadores de néctar e/ou pólen, bem como herbívoros que se alimentam de estruturas florais, podem reduzir a visitação dos polinizadores mais efetivos como resultado indireto de mudanças na disponibilidade de recursos e na exibição floral (Zammit & Hood 1986, Karban & Strauss 1993) ou, mais raramente, por inibição direta devido a sua presença e comportamento. Os efeitos desses florívoros, principalmente insetos, podem ser também através da perda de gametas por danos causados nas anteras e no ovário. Essas mudanças alteram as possibilidades das plantas serem visitadas com sucesso e comprometem a sua produção de sementes (Strauss 1997).

Estudos em biologia da polinização têm fornecido padrões e modelos para elucidar parte das questões evolutivas e ecológicas em comunidades (Heithaus 1974, Wolf & Hainsworth 1978, Bawa 1990), sendo a interação entre flores e polinizadores considerada como um forte componente de integração da biocenose (Vogel & Westerkamp 1991). O destino de muitas plantas nativas depende da preservação de suas relações com os polinizadores (Kearns & Inouye 1997), bem como da conservação das áreas naturais. O entendimento das relações planta/polinizador, além de fornecer conhecimento básico, pode contribuir para elucidar processos de regeneração, subsidiando o manejo adequado e a conservação de recursos florestais (Coimbra-Filho *et. al.* 1990, Joly *et al.* 1990).

A floresta atlântica, um dos ecossistemas mais ameaçados do mundo (Prance & Campbell 1988), estende-se por quase todo o litoral brasileiro, ocorrendo no estado de São Paulo a maior área contínua desse tipo de vegetação. A família Bromeliaceae constitui um componente significativo da sua flora, devido à ampla distribuição e riqueza de espécies (Reitz 1983). São plantas predominantemente neotropicais, compreendem cerca de 54 gêneros e aproximadamente 2900 espécies restritas ao novo Mundo, com exceção de uma espécie na África (Smith & Downs 1979, Luther & Sieff 1994). O Brasil abriga cerca de 40% das espécies, com vários gêneros endêmicos.

As bromélias possuem grande poder de adaptação, podendo ocupar diversos ambientes como o terrestre, o epifítico e o saxícola (Leme & Marigo 1993). Apresentam irradiação adaptativa ampla com relação aos seus polinizadores, tendo representantes entomófilos, ornitófilos e quiropterófilos (ver Vogel 1990, Kessler & Krömer 2000; p.e. Gardner 1986, Martinelli 1997, Sazima *et al.* 1999, Buzato *et al.* 2000, Wendt *et al.* 2001, 2002). No entanto, a polinização por animais vertebrados é predominante (Reitz 1983, Snow & Snow 1986, Sazima *et al.*1989, Araújo *et al.* 1994) e os beija-flores seriam os principais polinizadores da maioria das espécies de Bromeliaceae (McWilliams 1974, Sick 1984, Sazima *et al.* 2000).

Os beija-flores (Trochilidae) são aves restritas ao continente americano, distribuídas em cerca de 100 gêneros e 300 espécies (Tiebout 1993), sendo que quase um terço das espécies ocorre no Brasil (Grantsau 1988). Apresentam grande diversidade, diferindo quanto aos principais habitats de ocorrência, grupos de plantas que utilizam e modo de forrageamento (Stiles

1981). Constituem o grupo de aves mais especializado em dieta de néctar floral e, como possuem tamanho reduzido e limitada capacidade de estocar alimento, respondem rapidamente às mudanças na distribuição espacial e temporal do alimento no habitat (Stiles & Wolf 1970). A ampla sobreposição na distribuição das famílias Trochilidae e Bromeliaceae, somada à interdependência como "co-recursos", indicam evolução recíproca entre os beija-flores e as bromélias (Wolf *et al.* 1976, Sick 1984, Gentry & Dodson 1987).

Embora melitofilia seja rara em Bromeliaceae (Vogel 1990), existem registros para algumas espécies dessa família (ver Gardner 1986, Siqueira 1998, Kessler & Krömer 2000, Wendt *et al.* 2001, 2002) e, entre os insetos, as abelhas constituem um importante grupo de polizadores em grande parte das angiospermas (Bawa 1990).

Trabalhos enfocando a diversidade de Bromeliaceae e sua polinização são relativamente recentes no Brasil (Sazima *et al.* 1989, Fischer 1994, M. Sazima *et al.* 1995) e não muito abrangentes (Snow & Snow 1986, Bernardello *et al.* 1991, Sluys & Stotz 1995). Estudos detalhados sobre a biologia floral, a polinização e o sistema reprodutivo de espécies desta família são ainda escassos (Araújo *et al.* 1994, Martinelli 1997, Wendt *et al.* 2001, 2002).

O objetivo desse estudo foi relacionar aspectos do habitat e do hábito, da fenologia, da morfologia e biologia floral, e do sistema reprodutivo das bromélias *Aechmea pectinata* e *Bromelia antiacantha* com o espectro e a dinâmica de seus respectivos visitantes florais e/ou polinizadores em uma área de floresta atlântica no estado de São Paulo, sudeste do Brasil.

As espécies estudadas

Aechmea pectinata Baker e *Bromelia antiacantha* Bertoloni são abundantes em mata de baixada no Parque Estadual da Serra do Mar/Núcleo Picinguaba, São Paulo (Fig. 1). Suas inflorescências e/ou brácteas são bem evidentes e suas flores produzem néctar em quantidade (I. Sazima *et al.* 1995; M.B.F Canela & M. Sazima, *obs. pess.).* Além disso, indivíduos das duas espécies podem ocorrer próximos e apresentar sobreposição nos períodos de floração.

Aechmea pectinata apresenta distribuição irregular e descontínua do Rio de Janeiro a Santa Catarina (Reitz 1983, Wendt 1997). Ocorre na restinga, no mangue e em costão rochoso, como terrestre, epífita ou saxícola, e floresce de outubro a janeiro (Reitz 1983, Wendt 1997, M.B.F. Canela & M. Sazima *obs. pess.*). Para esta espécie, há estudos feitos em outras localidades do sudeste em relação a diversas características florais e registro de visitantes (Fischer 1994, I. Sazima *et al.* 1995, Buzato *et. al.* 2000). Porém, aspectos da biologia floral e o do sistema reprodutivo ainda não haviam sido explorados detalhadamente.

Bromelia antiacantha ocorre tanto em restinga como em floresta, do nível do mar até 1000 m de altitude, pelo sul e sudeste do Brasil (Smith & Downs 1979). Essa espécie é terrestre em mata, porém saxícola no costão, está distribuída principalmente em pequenos agrupamentos de 3-4 indivíduos, e floresce de dezembro a fevereiro com episódios de floração espaçados (ver Reitz 1983; M.B.F. Canela & M. Sazima, *obs. pess*). Apesar da ampla distribuição e de ser uma espécie visível e comum, pouco se conhece sobre sua biologia da polinização (vide Wolf 1970), provavelmente, pela dificuldade de acesso aos indivíduos (Fischer 1994) devido aos seus afiados espinhos foliares.

Área de estudo

A planície costeira de Picinguaba possui cerca de 8 km^2, situa-se no município de Ubatuba, litoral norte de São Paulo (23^{0}20'- 23^{0}22'S / 44^{0}48'- 44^{0}52'W), e faz parte da Unidade de Conservação do Parque Estadual da Serra do Mar, sendo uma das poucas unidades protegidas cujos limites se estendem até a orla marítima (Melo Neto 1992). Essa região se caracteriza pela ocorrência descontínua de pequenas baías e praias estreitas, intercaladas pelos avanços da Serra do Mar (Ponçano *et al.* 1981). O clima regional é do tipo tropical úmido, apresenta temperatura média acima de 18^{0}C e índice pluviométrico médio anual acima de 2200 mm, não havendo estação com déficit hídrico (Piccolo 1992, Oliveira *et al.* 1998, Sanchez *et al.* 1999). A vegetação é constituída de mosaicos (Garcia 1992) como mangue próximo ao estuário do rio Picinguaba, floresta densa e áreas de capoeira (Furlan *et al.* 1990). Essas diversificações se relacionam às variações fisiográficas, edáficas e de drenagens da planície. O acesso à região é feito pela Rodovia BR-101, que atravessa a planície estudada, sendo responsável por numerosas modificações no ambiente (Assis 1999).

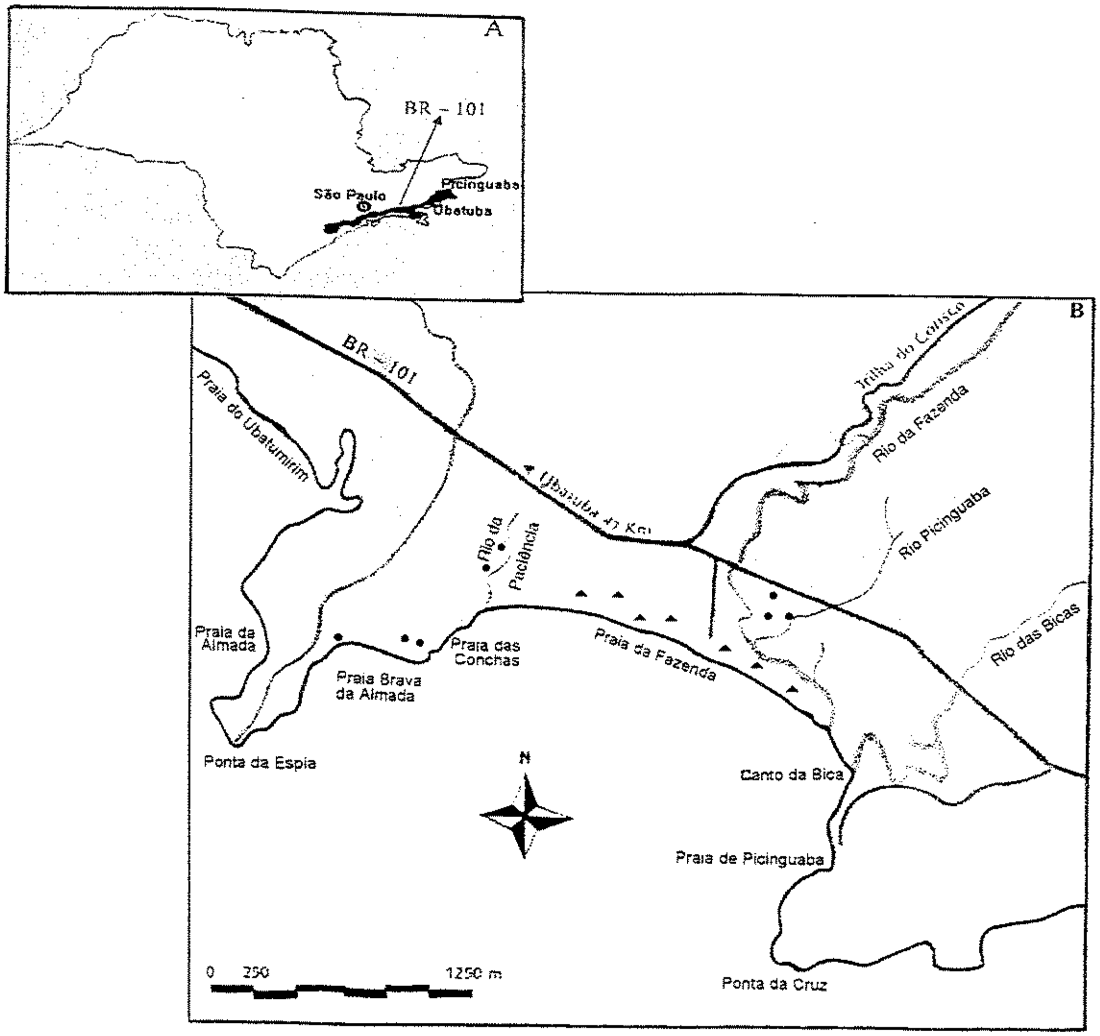

FIGURA 1. Localização da área de estudo, o Núcleo Picinguaba - Parque Estadual da Serra do Mar, no litoral norte de São Paulo (A) e localização das populações de *A. pectinata* (●) e *B. antiacantha* (▲) na área de estudo (B).

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CAPÍTULO I

POLINIZAÇÃO POR BEIJA-FLORES EM *AECHMEA PECTINATA* (BROMELIACEAE) NO LITORAL SUDESTE DO BRASIL

RESUMO

A biologia da polinização de *Aechmea pectinata* (Bromeliaceae) foi estudada numa floresta úmida de encosta do sudeste do Brasil. Os indivíduos dessa espécie crescem, geralmente, em grandes agrupamentos e florescem de outubro a janeiro, ocasião em que suas folhas tornam-se avermelhadas nas extremidades. Sua inflorescência é densa e apresenta de 1-15 flores/dia durante um período de 20 a 25 dias. As flores são alvo-esverdeadas, de formato tubular com abertura estreita e o estigma se localiza ligeiramente acima das anteras. A antese é diurna, inicia-se por volta das 04:00h e dura ca de 13 horas. Os maiores valores de volume e concentração de açúcares do néctar foram registrados entre 06:00h e 10:00h, decrescendo ao longo do dia. *Aechmea pectinata* apresenta características florais relacionadas à ornitofilia, como folhas avermelhadas, flores de formato tubular, néctar abundante, e odor pouco perceptível. Os beija-flores foram os principais polinizadores (ca. 91% das visitas), sendo mais freqüentes de manhã. O arranjo das estruturas florais favorece a deposição de pólen no bico dessas aves. A visitação pelos beija-flores se relacionou com a produção de néctar, sugerindo que a disponibilidade do recurso é importante para atrair e manter as visitas dessas aves às flores de *A. pectinata*. As abelhas tocam as estruturas reprodutivas enquanto retiram néctar e/ou pólen mas foram pouco freqüentes, atuando como polinizadores ocasionais. Caranguejos consomem estruturas reprodutivas florais, interferindo também na visitação dos beija-flores, o que provavelmente interfere na produção de frutos. *Aechmea pectinata* é auto-incompatível e, portanto, dependente de polinizador. A frutificação bem sucedida parece depender da distribuição espacial dos indivíduos dessa bromélia e das interações entre os visitantes florais, uma vez que fontes concentradas de néctar promovem territorialidade nos beija-flores e os indivíduos de *A. pectinata* nos agrupamentos são, provavelmente, clones.

PALAVRAS-CHAVE: *Aechmea pectinata*, beija-flores, polinização, produção de néctar, reprodução, floresta atlântica, sudeste do Brasil.

Hummingbird Pollination of *Aechmea pectinata* Baker (Bromeliaceae) in a Coastal Forest in southeastern Brazil. [1]

MARIA BERNADETE F. CANELA [2] and MARLIES SAZIMA[2]

The pollination biology of *Aechmea pectinata* was studied in a southeastern Brazil wet tropical forest. This species mainly has a clumped distribution and flowers from October to January. During this period, leaves become red. The inflorescence is dense and produces 1-15 flowers per day over a period of 20-25 days. The flowers are greenish-white, tubular-shaped with a narrow opening, and situate their stigma just above the anthers. Anthesis is diurnal beginning around 0400 hr and lasting for about 13 hours. The greatest nectar volume and sugar concentration occur between 0600-1000 hr, and decrease throughout the day. *Aechnmea pectinata* presents ornithophilous features, including red leaves, tubular flowers, abundant nectar, and a very faint odour. Hummingbirds were the main pollinators (90% of the visits), visiting inflorescences mainly in the morning. Arrangement of the floral structures favors pollen deposition on the hummingbird bill. Hummingbird visits followed the production of nectar, suggesting that availability of this resource is important to attract and maintain the visits of the birds. Bees make contact with reproductive structures while taking nectar and/or pollen, but were less frequent, acting as occasional pollinators. Crabs consumed reproductive structures, interfered with hummingbird visitation and probably affected fruit set. *Aechmea pectinata* is self-incompatible and therefore pollinator dependent. Flower clumps promote hummingbird territoriality, and *A. pectinata* aggregated individuals are likely to be clones. These facts suggest that successful fruit production of this bromeliad species depends on the spatial distribution of their individuals and interactions among floral visitors.

Key words: *Aechmea pectinata*, hummingbirds, nectar production, pollination, reproduction, submontane rainforest, southeastern Brazil.

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[2] Dept° de Botânica, IB/UNICAMP, C.P. 6109, 13090-970, Campinas/SP, Brazil.

INTRODUCTION

Several intrinsic (e.g. flowering phenology, floral morphology, resources availability) and extrinsic (such as spatial distribution of the plants and interactions among visitors) aspects to plants may influence the pollinator visitation and, consequently, interfere at the pollination process (see Proctor and Yeo, 1972; Feinsinger, 1976; Opler *et al.*, 1980; Karban and Strauss, 1993).

Hummingbirds are nectar feeding specialists (Brown and Brown, 1985), and have been assumed to be the major pollinators of several neotropical plants, among them, the bromeliads (McWilliams, 1974; Bawa, 1990; Sazima *et al.*, 2000). These plants constitute a large proportion of the nectar sources available to hummingbirds (Snow and Snow, 1986), and Sick (1984) suggested than the evolution among these birds and bromeliads is parallel. The most studies about ornithophily at Bromeliaceae species are recent (e.g. Araújo *et al.*, 1994; Sluys and Stotz, 1995; Sazima *et al.*, 1995, 1996; Martinelli, 1997; Buzato *et al.*, 2000).

This study sought to relate data on phenology, floral morphology, floral biology and breeding system with the composition and dynamics of the floral visitor and/or pollinator community of *Aechmea pectinata* Baker (Bromeliaceae) in a seasonally wet tropical forest in southeastern Brazil. This bromeliad species presents an irregular and discontinuous distribution along the south and southeastern Brazilian coast (Reitz, 1983; Wendt, 1997). It occurs in the "restinga" scrub, in the mangrove and on rocky shores, either as terrestrial, epiphytic or saxicolous plant, and grows mainly in assemblages of 10-15 individuals (Canela and Sazima, pers. obs.). Although cursory reports of the floral features of *A. pectinata* and its visitors were made by Snow and Snow (1986), Sazima *et al.* (1995) and Buzato *et al.* (2000), no detailed information about the floral biology and reproductive system of this species is available.

MATERIAL AND METHODS

Study site

This study was carried out in the Parque Estadual da Serra do Mar-Núcleo Picinguaba/SP, a submontane rainforest in southeastern Brazil ($23^0$22'S/$44^0$50'W). The climate is wet tropical ("Af."; see Köppen, 1948), with an annual rainfall of up to 2600 mm, an average annual temperature of 21^0C and there is no well defined dry-cold season, even during the so-called dry months, from May to September (data source: Instituto Agronômico de Campinas, Campinas, Brazil).

Procedure

Fieldwork was carried out during two consecutive flowering seasons of *Aechmea pectinata,* from Oct. 2000 to Jan. 2001 and from Dec. 2001 to Feb. 2002. Epiphytic, terrestrial and saxicolous individuals (n = 91) were sampled in the mangrove, in the "restinga" scrub and on rock outcrops. Inflorescences were observed *in situ* to determine the number of open flowers per day, features of anthesis, visitation frequency and foraging behaviour of floral visitors. Floral and vegetative structures related to attraction were also recorded. The internal length of the flowers was measured from the base of sepals to the tube opening ("effective length", defined by Wolf *et al.*, 1976).

Nectar sugar concentration (n = 20) was measured with a pocket refractometer and its volume (n = 50) with microliter syringes (Dafni, 1992). These measuring were made throughout anthesis, at two hours intervals, on previously bagged flowers. Accumulated nectar volume (n = 46) and its respective sugar concentration (n = 42) were also measured on bagged flowers, in the end of anthesis. Pollen viability (n = 10 flowers) was estimated by its cytoplasm stainability, using the aceto-carmine technique (Radford *et al.*, 1974). Stigmatic receptivity (n = 10 flowers) was tested using the H_2O_2 10V catalase activity method (Zeisler, 1938).

Breeding system was assessed by hand-pollination treatments on previously bagged flowers: manual self-pollination, cross-pollination (previously emasculated flowers) and autonomous self-pollination (bagged buds); flowers under natural conditions of pollination were marked as control (see Table 1). Fruit set for all treatments was determined approximately two months after pollination. Pistils of self- and cross-pollinated flowers (n = 5 each treatment) were fixed in FAA 50% after 12, 24, 36, 48 and 72 hours after pollination and analyzed under fluorescence microscopy for pollen tube growth (Martin, 1959).

Visitors were observed directly or through binoculars at 36 focal individuals from 0400 to 1800 hr (n = 16 for each two hours interval), totaling 112 hours in nineteen days. Floral visitors were photographed and videotaped. The identification of the hummingbird was made according to Ruschi (1992) and confirmed by a specialist. Hummingbird bill lengths were obtained from Grantsau (1989). Bees and crabs were also collected and identified by specialists.

Daily nectar production and hummingbird visitation were evaluated to normality by Kolmogorov-Smirnov test (BioEstat 2.0). As our data are non-parametric, the median (M) was calculated and variations were analyzed through box-plots graphs (Systat 8.0), Kruskall-Wallis test (H), Mann-Whitney test (U), Spearman correlation (R^2) and regression analysis (r) (BioEstat 2.0).

RESULTS

Phenology

Aechmea pectinata flowers continuously from late October to mid January, and fruiting occurs in February and March. During the period flowering, the leaves, in a dense funnelform rosette, have red coloration along the distal 1/3 of their length (Fig. 1). This coloration tends to disappear at the beginning of fruiting.

FIG. 1. An *Aechmea pectinata* individual with reddish leaf tips and bent inflorescence (photo center) in Picinguaba/SP.

Each individual of this bromeliad species has one strobiliform inflorescence, 10-15 cm long and 6-8 cm wide, bearing 150-250 flowers. During their development, each inflorescence opens 1-15 flowers per day in apical direction, over a period of 20 to 25 days. Usually, the inflorescence is erect, although bent inflorescences may occur in epiphytic (Fig 1) or saxicolous individuals.

Floral morphology and biology

Aechmea pectinata flowers are sessile, actinomorphic, tubular-shaped with a narrow opening, and the "effective length" of the floral tube is ~30 mm (Fig. 2). The flowers have densely serrate greenish floral bracts with an acuminate apex. Their sepals are connate for 2 mm, subovate, imbricate to the left and greenish white. Their petals are free, spatulate, imbricate to the right and yellowish white. Its lengths exceed the calyx approximately 10 mm (Fig. 2).

As the buds develop, the style lengthens and exceeds the stamens, which are adnate to petal base, juxtaposed and included in the flower (Fig. 2). The anthers have longitudinal dehiscence and are extrorse. Pollen is available from the first hours of anthesis and has high viability in this period (93.17%). The stigma is conical, has three spiraled lobes, and is located just above the anthers with its apex extending out of the corolla (Fig. 2). It is receptive during whole anthesis. The ovary is inferior, the nectary is septal and nectar accumulates in the base of the corolla tube (Fig. 2).

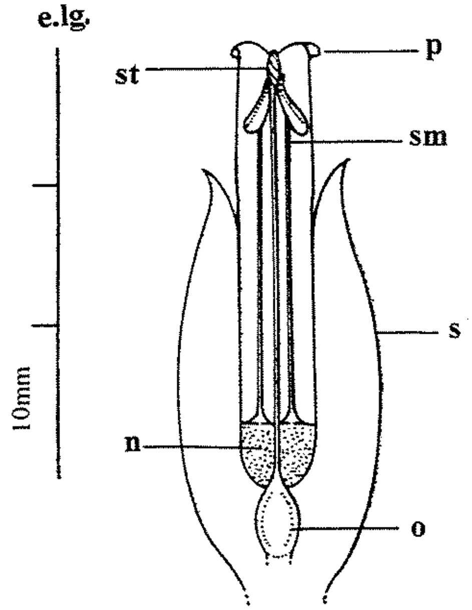

FIG. 2. Longitudinal section of *Aechmea pectinata* flower in anthesis, showing arrangement of the floral structures: stigma (st), petals (p), stamens (sm), sepals (s), ovary (o) and site where nectar accumulates (n). The effective length of the corolla ("e.lg.") is represented by the scale at left.

The anthesis of *A. pectinata* flowers is characterized by discrete movements of petal unrolling, separation and deflexion of the petal tips, resulting in approximately a 2 mm opening. This process lasts approximately from 0400 hr to 0600 hr, period in which the flowers present a slightly sweet, faint odour. Flowers last for approximately 13 hours and, after this period, the petals return their initial position, closing the flower.

Both nectar volume ($H = 134.00$, $P < 0.001$) and sugar concentration ($H = 80.41$, $P < 0.001$) of the flowers varied significantly throughout the day. This variation was most evident between the morning and afternoon periods (Fig. 3A and 3B). At the onset of anthesis (0400 hr), flowers do not contain nectar ($M = 0\mu l$, $n = 30$). Production of this resource begins soon after and reaches peaks between 0600 hr and 0800 hr ($M = 21.5\mu l$), after which it gradually decreases until late afternoon (Fig. 3A). Sugar concentration was also greatest in the early morning, from 0400 hr to 1000 hr (17.5-30.0%), decreasing to half its initial value between 1000 hr and 1200 hr, and continuing to decrease until late afternoon when it stabilizes (Fig. 3B). Nectar volume is correlated positively with sugar concentration ($r = 0.85$, $P < 0.01$). Nectar volume accumulated throughout the day ($M = 79.5\mu l$, $n = 46$) and the sum of the partial values ($M = 67.0\mu l$, $n = 43$) did not significantly differ ($U = 959.50$, $P > 0.05$), indicating that the nectar production is continuous and that nectar is not reabsorbed. Sugar concentration in accumulated nectar ($M = 26.7\%$, $n = 42$) was also similar (U=756.00, $P > 0.05$) to the concentration registered in the first hours of anthesis ($M = 25.1\%$, $n = 40$).

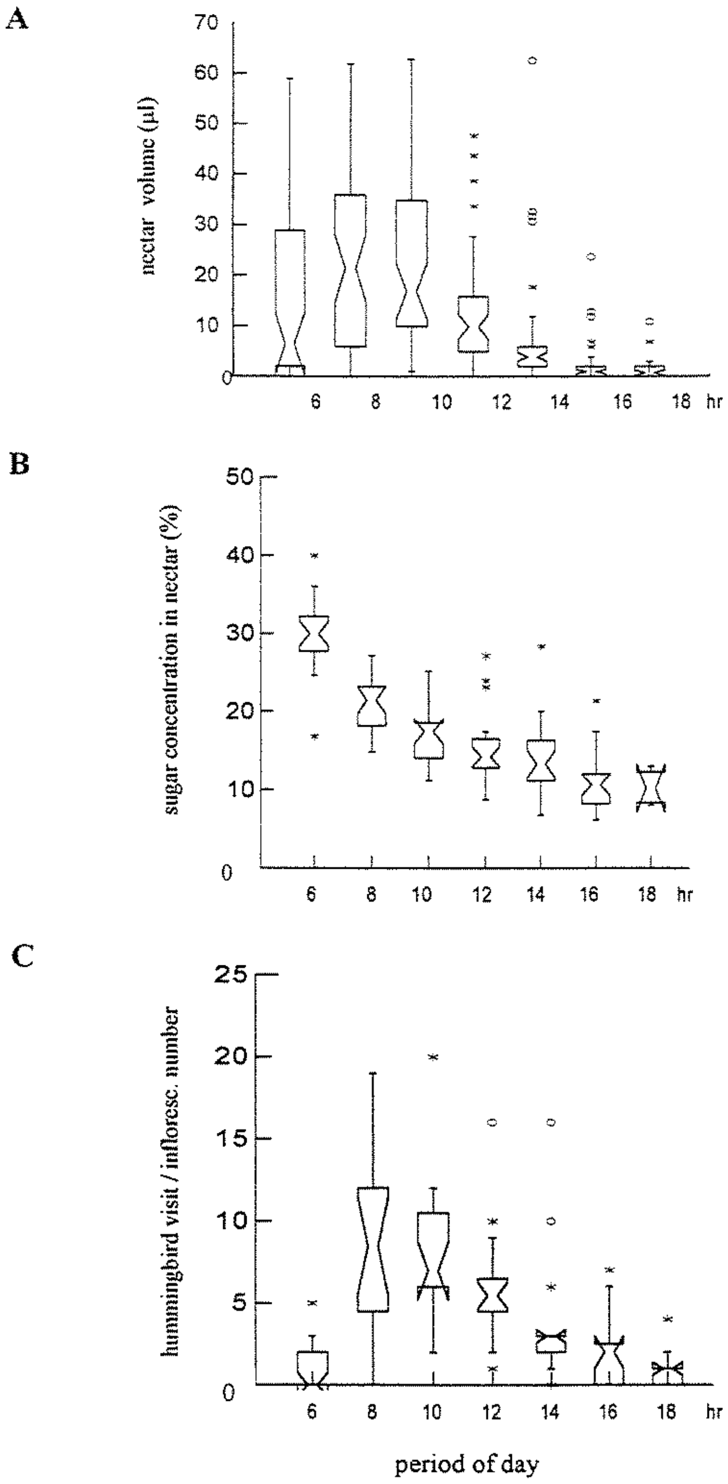

Fig. 3. Variation in nectar volume (A), sugar concentration in nectar (B), and number of hummingbird visits per *Aechmea pectinata* inflorescence (C) throughout the day in Picinguaba/SP. Boxes represent the inter quartile range; the center is the median. Interval between slanted lines around the median is the 95% confidence limit. Inferior and superior vertical lines represent total range of the distribution (25% and 75%). Extreme values are represented by (*), and outliers by (°). Overlap between confidence limit indicates no statistical difference.

Floral visitors

Out of the 535 visits registered to *A. pectinata* flowers, 489 were made by hummingbirds (91.4 %), 38 by bees (7.1 %) and only 8 visits by hesperids (1.5 %).

Between 0600 hr and 1000 hr occurred 55% of hummingbird visits ($\bar{X}$=3.8 visits/hour), the remainder occurring throughout the rest of the day at a diminishing frequency (Fig. 3C). This variation in the number of hummingbird visits throughout the day (H = 72.02, $P < 0.001$) is correlated with nectar production in the flowers, in relation to volume ($r^2 = 0.97$, $P < 0.001$; Fig. 4A) and sugar concentration in the nectar ($R^2 = 0.93$, $P < 0.005$; Fig. 4B).

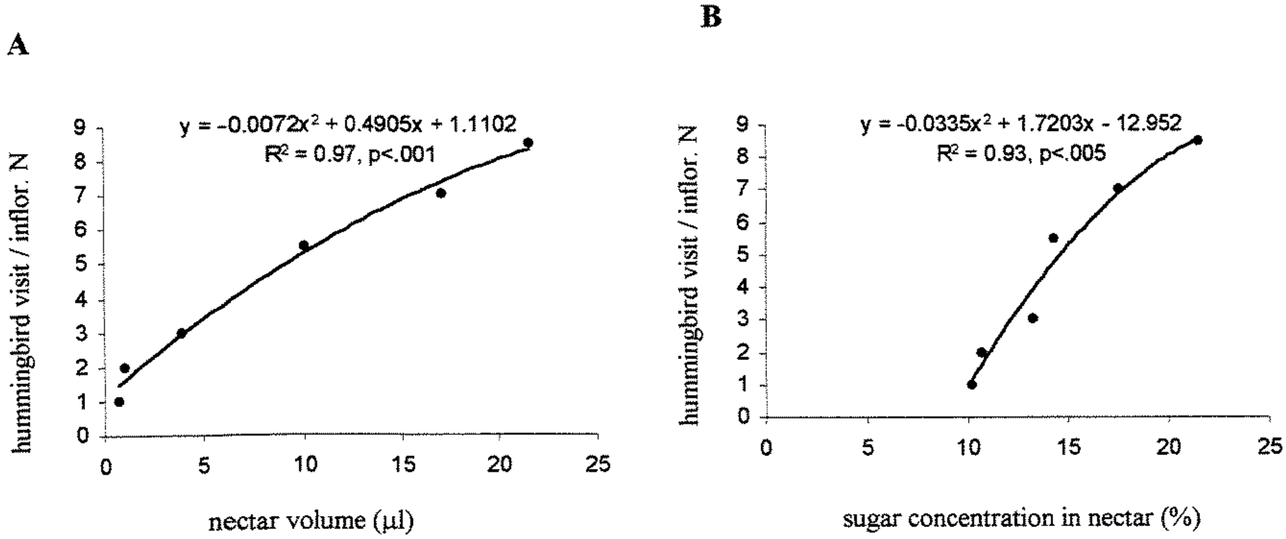

FIG. 4. Positive correlation between the number of hummingbird visits per inflorescence and nectar offered by *Aechmea pectinata* flowers: volume (A) and sugar concentration (B). The values of nectar production from 0400 hr to 0600 hr were excluded from this analysis as they correspond to a period of low activity of the hummingbirds.

Thalurania glaucopis Gmelin (Trochilinae) was the most frequent hummingbird, responsible for approximately 42% of the visits (*n* = 489), of which 83% were made by males (Fig. 5A). *Amazilia fimbriata* Elliot (Trochilinae) represented ~36% of the visits (Fig. 5B) and *Ramphodon naevius* Dummont (Phaethornithinae) ~20% (Fig. 5C). *Phaethornis ruber* Linné and *Melanotrochilus fuscus* Vieillot (Phaethornithinae) were rarely observed (only 1% of the visits).

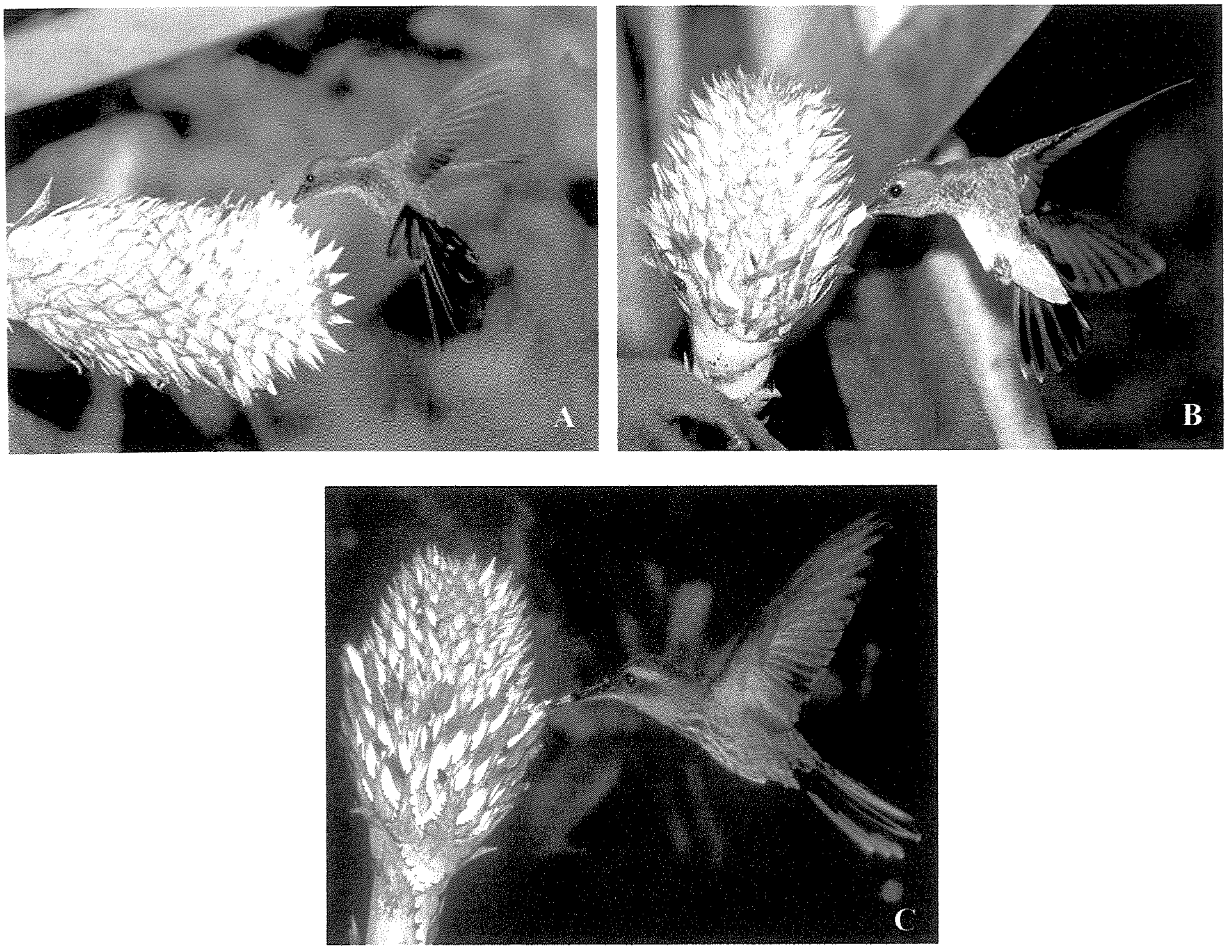

FIG. 5. The major visiting hummingbirds of *Aechmea pectinata*: *Thalurania glaucopis* male (A), and *Amazilia fimbriata* (B) in Picinguaba/SP; *Ramphodon naevius* (C) visiting *A. pectinata* in Caraguatatuba/SP (Photo: Ivan Sazima; note pollen load on bill tip).

Thalurania glaucopis and *Amazilia fimbriata* were more frequent at clumped individuals of *A. pectinata* than at isolated plants, often being found on the most evident inflorescences or with the greatest number of flowers. They visited every flower on each inflorescence before moving to other plants, sometimes returning to previous inflorescences after visiting the majority of flowering plants in the assemblage. Between visits, the hummingbirds commonly remained perched on nearby tree branches. *Thalurania glaucopis* (mainly males) and *A. fimbriata* frequently showed aggressive behavior and interacted agonistically with intruder hummingbirds, of other and same species, also excluding and chasing bees that approached the inflorescences. *R. naevius* (both males and females) visited *A. pectinata* inflorescences in their foraging routes, sometimes interacting agonistically with other visitors. Territory intruders were common, comprising mainly individuals of the three most common species. Rarely two hummingbird species simultaneously visited plants of the same assemblage.

Although periods of 30-40 min between visits were common, intervals were highly irregular. Longest intervals occurred mainly in the afternoon. Visit duration at each flower also varied from 1s to 10 s. When taking nectar, hummingbird species make contact with plant reproductive structures with their bills (Fig. 6C). Hummingbird visits to *A. pectinata* decreased when flowering declined, and with the onset of flowering of other Bromeliaceae and Heliconiaceae species in the study area.

Bombus morio and *Euglossa* cf. *safferina* (Bombinae, Apidae) bees visited *A. pectinata* flowers, but were little frequent (~7.0% of the visits). *Bombus morio,* comprising 87% of bee visits, made contact with the flowers` reproductive structures while taking nectar and collecting pollen, acting as occasional pollinators. *Euglossa* cf. *safferina* (~0.9% of the visits) may act in pollen transfer as it takes nectar and/or pollen, but this bee species visits few flowers and remainder for an long period of time on a single flower. *Trigona spinipes* (Meliponinae, Apidae) bees were not frequent at *A. pectinata* flowers, and only robbed nectar through holes at the corolla made by them.

Armases angustipes (Grapsidae) crabs were registered in 31.5% of the inflorescences of *A. pectinata*, 92% of which were located in clumps. Crabs consumed flower reproductive structures and inhibited 43% of the visit attempts made by hummingbirds (Canela and Sazima, unpubl. data; see cap. II).

Reproduction

The flowers of *A. pectinata* are hermaphroditic, homogamic and self-incompatible. In flowers fixed 12 hours after manual self-pollination, pollen grains germinated only on the stigma, and some pollen tubes showed evidence of incompatibility (see Murray, 1990), as curvature and thickening of the callose plugs on their extremities (Fig. 6A). Flowers fixed 48 hours after this treatment did not produce pollen tubes along the style. In the cross-pollination experiments, flowers fixed 12 hours after pollination showed high quantities of germinated pollen grains on the stigma and developed pollen tubes up to ~2/3 of the length of the style. After 24 hours fertilization has occurred (Fig. 6B). It was observed that under natural conditions fertilization occurred after a similar period (Fig. 6C).

The pollen tube results corroborated the pollination experiments, since none of the autonomously or manually self-pollinated flowers produced fruits, in contrast to the fruiting verified in 96% of the manually cross pollinated flowers and 56% of the flowers under natural conditions (Table 1).

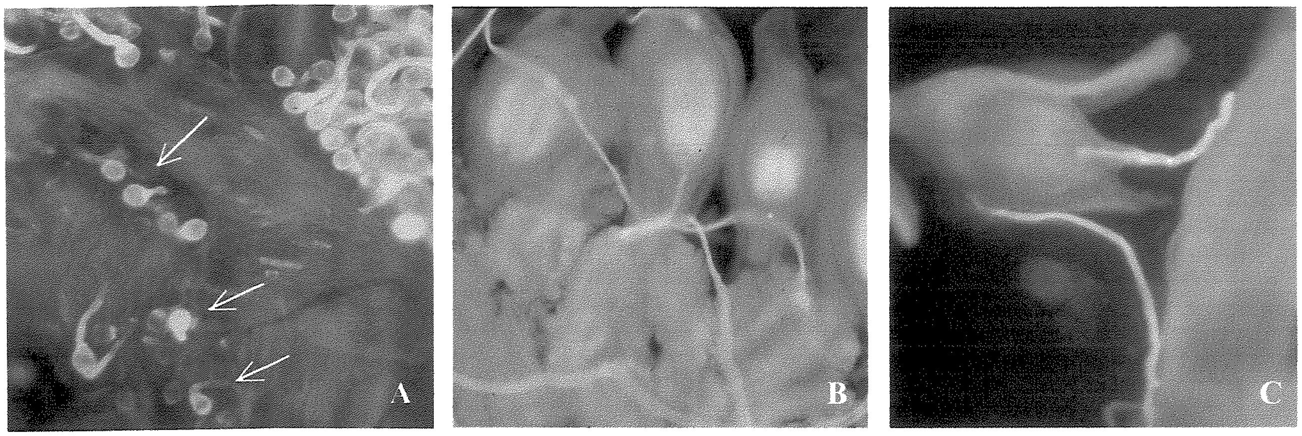

FIG. 6. Stigma of *Aechmea pectinata* flower fixed 12 hours after manual self-pollination (A). Arrows indicate signs of incompatibility as curvature and thickening of the callose deposit in the extremity of the pollen tubes; *A. pectinata* fecundated ovules in flowers fixed after 24 hours of cross pollination (B) and in flowers fixed 24 hours after pollination in natural conditions (C).

TABLE 1. Percentage of fruit-set from hand-pollinated, autonomously self-pollinated and under natural conditions *Aechmea pectinata* flowers. Figures in brackets are number of fruits/number of flowers, respectively.

Treatments	Percentage of fruit-set
Autonomous self-pollination	0 (0/171)
Manual self-pollination – same flower	0 (0/37)
Cross-pollination	96 (24/25)
Natural conditions (control)	56 (398/716)

Only 23% of the clumped individuals (*n* = 22) produced fruits, whereas most isolated individuals (88%, *n* = 8) set fruit. Fruits are highly apparent, reddish when mature and regularly distributed around the erect infructescences. In the bent infructescences, fruits mainly developed in parts of the inflorescence in which flowers were more exposed and visited by hummingbirds.

DISCUSSION

Aechmea pectinata blooms only once a year, and its flowering pattern at population level is considered annual following Newstrom *et al.* (1994). The individual flowering strategy, characterized by the continual opening of some flowers over an extended period, is defined as 'steady-state' by Gentry (1974). Well-defined and synchronized blooming periods, as demonstrated for *A. pectinata,* are common in Bromeliaceae and ornithophilous plants from other families (e.g. Araújo *et al.*, 1994; Sazima *et al.*, 1996; Martinelli, 1997; Buzato *et al.*, 2000), and indicate specialization for a given kind of pollinator (see Stiles, 1978; Fleming, 1982). Hummingbird behaviour is influenced by availability of floral resources, and hummingbirds have preference for plants that offer a regular and constant resource (Wolf *et al.*, 1976; Real and Rathcke, 1991).

This bromeliad species presents some floral characteristics related to ornithophily (see Faegri and Pijl, 1980), such as tubular-shaped flowers, diurnal anthesis, abundant nectar, and reddish leaf tips during flowering. Since flowers are inconspicuous (Percival, 1969; Stiles, 1981; Sazima *et al.*, 2000), this red coloration of the leaves is interpreted as part of the hummingbird attraction. Coloured leaves and bracts instead of flowers, which exert pollinator attraction, are common in various bromeliad species visited by hummingbirds (Araújo *et al.*, 1994; Martinelli, 1997; Sazima *et al.*, 2000).

The tubular shape and narrow opening of *A. pectinata* flowers (see Fig. 2) permit legitimate access to nectar by visitors with long and thin mouth parts, mainly hummingbirds, and exclude less specialized visitors (see Proctor and Yeo, 1972; Faegri and Pijl, 1980). The moderately long floral tube, approximately 30mm, allows the visits of both short-billed (Trochilinae, 11-24mm bill length) and long-billed (Phaethornithinae, 22-46mm bill length) hummingbirds (Feinsinger and Colwell, 1978). Other bromeliads, which have long corolla, are mainly visited by hummingbirds of the sub-family Phaethornithinae (Schoener, 1983; see also Araújo *et al.*, 1994; Sazima *et al.*, 1995, 1996; Buzato *et al.*, 2000).

In addition to corolla length and shape, the stamens that are juxtaposed and included in the corolla (Fig. 2) promote pollen deposition on the hummingbird' bill. This aspect is particularly frequent in Bromeliaceae (see Sazima et al. 1995, 1996; Buzato et al. 2000, Canela and Sazima, see cap. III), and probably is an efficient way of pollen transfer due to pollen of these plant species be somewhat sticky. Besides, the hummingbirds visit several flowers before cleaning its bills, although Dressler (1971) and Rose and Barthlott (1994) pointed out that a bill, is too smooth and cleaned before effecting pollination, and thus not well suited for pollen transport.

The half-day duration of *A. pectinata* flowers is also common to other bromeliad species (eg. Araújo *et al.*, 1994; Sluys and Stotz, 1995; Siqueira, 1998; Sluys *et al.*, 2001; Wendt *et al.*, 2002; see cap. III). This short period of anthesis is probably associated with the efficiency of pollinators, which may pollinate flowers in just a few visits (Ramirez *et al.*, 1990), or associated to homogamy, a characteristic also observed in *Bromelia antiacantha* Bertoloni (Canela and

Sazima, pers. obs.; see cap. III) and *Hohenbergia ridleyi* (Baker) Mez (Siqueira, 1998), but not commonly in all Bromeliaceae species (Martinelli, 1997).

Nectar volume and sugar concentration in *A. pectinata* flowers were similar to that registered for this species in other locations by Snow and Snow (1986), Sazima *et al.* (1995) and Buzato *et al.* (2000), and for ornithophilous species in general (Arizmendi and Ornelas, 1990; Sazima *et al.*, 1996; Locatelli and Machado, 1999; see cap. III). In addition, the major production of nectar early the day is consistent with the tendency of ornithophilous flowers (Feinsinger, 1976) and activity phases of birds (Sick, 1984). The positive correlation between nectar production and visitation of hummingbirds in *A. pectinata* suggests that both the quantity and quality of nectar are important factors in attracting and maintaining these bird visits (see Percival, 1969; Baker, 1975).

The territorial behaviour of hummingbirds during visits to *A. pectinata* flowers was probably favored by the clumped distribution of the individuals and prolonged flowering period of this bromeliad species. Aggregated individuals concentrate the nectar source, thereby reducing pollinator energetic costs for food search (Locatelli and Machado, 1999) and promoting territoriality among visiting hummingbirds (Feinsinger, 1978; Snow and Snow, 1986; Buzato *et al.*, 2000).

According to the roles of hummingbirds in the community defined by Feinsinger and Colwell (1978), *T. glaucopis* and *A. fimbriata* may be classified as territorial, although some individuals of these species frequently acted as territory parasites, i.e. hummingbirds that visit flowers defended by smaller territorialists, ignoring attempts to displace them. In addition, the same individual (male or female) may temporarily alternate between different types of feeding strategies, which have been observed in other studies (Locatelli and Machado, 1999; Buzato *et* *al.*, 2000). Although *R. naevius* may be regarded as a typical high-reward trapliner without extensive territorial behavior (cf. Stiles, 1975; Stiles and Freeman, 1993), it can behave aggressively along its routes excluding hummingbird intruders with which it comes across (see Sazima *et al.*, 1995). Phaethornithinae species ("hermits") are known to occasionally hold temporary flower-centered territories (Stiles 1975; Feinsinger and Colwell (1978), and this "patrolling" behaviour may be regarded as a specific resource defense (cf. Wolf *et al.*, 1976).

Aechmea pectinata is a self-incompatible species and, therefore, depends on a pollinator. Although most species in the Bromeliaceae are genetically self-compatible, several species depend on pollinators due to diverse floral mechanisms (dicogamy, hercogamy) hindering self-pollination (see Gardner, 1986[17]; Araújo *et al.*, 1994; Martinelli, 1997; Siqueira, 1998[45]; Wendt *et al.* 2001, 2002; cap. IIi).

The fact that several individuals of *A. pectinata* in large assemblages did not produce fruits in contrast to high fruit set at most isolated plants is probably related to aggregate distribution of the individuals of this bromeliad species and to territorial behavior of its hummingbirds. Territoriality prevents visits of trap-liner hummingbirds carrying pollen from distant plants and promotes geitonogamy because *A. pectinata* individuals in assemblages are genetically close (clones). As this species is self-incompatible, these aspects may reflect in low fruit set (see Feinsinger, 1978). Usually, isolated plants, albeit less attractive, have more chance to receive cross pollen (Janzen, 1971; Stiles, 1975).

The irregular intervals between hummingbird visits suggest that intruders ('territory-parasites', see Feinsinger and Colwell, 1978) were frequent, and sometimes not excluded by primary territory holders. Great sources of aggregated resources attract territory-parasites (Wolf and Stiles, 1970), and those hummingbirds that successfully manage to invade the territory have more possibilities to carry out crossed pollination in aggregated individuals. Therefore, intruder individuals of *T. glaucopis*, *A. fimbriata* and mainly *R. naevius* potentially play an important role in the fruit set of *Aechmea pectinata*.

In addition, florivory by crabs was common in *A. pectinata* individuals located in assemblages and possibly contributed to the lower fruit set in these individuals due to the consumption of reproductive structures and to the interference with the hummingbird visitation (see cap. II). Similar interference was reported for *Bromelia antiacantha* (Bomeliaceae), where *T. spinipes* bees, which are pollen/nectar robbers, attack and exclude visiting hummingbirds and probably interfered in fruit production under natural conditions (Canela and Sazima, pers. obs.; cap. III).

Aechmea pectinata, due to its high numbers of individuals and flowers during a long and continuous period in Picinguaba, represents a highly apparent floral resource for its visitors (see Stiles, 1975). Hummingbirds were the main pollinators of this species demonstrated by their behaviour of legitimate visitation on the flowers and the constancy of visit, whereas bees (sub-family Bombinae) were only occasional pollinators. The dependency on a pollinator for *A. pectinata* is correlated to characteristics that attract and maintain hummingbirds such as leaf coloration, floral morphology and nectar availability. However, a successful fruiting appears related to external factors, such as spatial distribution of its individuals, hummingbird community dynamics and interactions with other visitors.

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CAPÍTULO II

FLORIVORIA POR CARANGUEJOS *ARMASES ANGUSTIPES* (GRAPSIDAE) INFLUI NA VISITAÇÃO DOS BEIJA-FLORES EM *AECHMEA PECTINATA* (BROMELIACEAE)

RESUMO

A influência da florivoria por caranguejos nas visitas dos polinizadores de *Aechmea pectinata* (Bromeliaceae) foi estudada em 38 indivíduos dessa bromélia numa área de Mata Atlântica no sudeste do Brasil. *Aechmnea pectinata* ocorre no mangue, na restinga e no costão como epífita, terrestre ou saxícola. Floresce de outubro a fevereiro e sua densa inflorescência (150-250 flores) dura 20-25 dias. As flores, 1-15/dia, são de formato tubular e a antese se estende por ca. de 13 horas. A maior produção de néctar ocorre de manhã, período em que os beija-flores, seus principais polinizadores, são mais freqüentes. O caranguejo *Armases angustipes* (Grapsidae) foi registrado em 31.5% das inflorescências de *Aechmea pectinata*, sendo 50% desses casos de florivoria em indivíduos no mangue, 92% em indivíduos agrupados, e 67% dos indivíduos com caranguejos são epífitas. Os caranguejos, até três indivíduos por inflorescência, forrageavam das 0400-1800 h, mas principalmente de manhã, visitando várias flores. *Armases angustipes* utilizava, principalmente, flores em antese, e raramente botões e flores velhas. Durante as visitas, este caranguejo danificava as corolas e consumia apenas as estruturas reprodutivas. As visitas dos beija-flores ocorreram em apenas 57% de suas aproximações às inflorescências com caranguejos, e o número de flores visitadas pelos beija-flores foi reduzido em 70%. Dessa forma, a influência de *A. angustipes* no sucesso reprodutivo de *A. pectinata* pode ser direta pelo consumo de flores, e indireta devido à redução da visitação dos polinizadores.

PALAVRAS-CHAVE: Bromeliaceae, caranguejos bromelícolas, florivoria, beija-flores, sucesso de polinização, sudeste do Brasil, floresta atlântica.

Florivory by the crab *Armases angustipes* (Grapsidae) influences hummingbird visits to *Aechmea pectinata* Baker (Bromeliaceae).[1]

Maria Bernadete F. Canela[2] and Marlies Sazima[2]

ABSTRACT

The influence of florivory by the crab *Armases angustipes* (Grapsidae) on pollinators' visits to the inflorescences of *Aechmea pectinata* (Bromeliaceae) was studied in 38 plants in a submontane rainforest in southeastern Brazil. *A. pectinata* occurs in the mangrove, in the "restinga" scrub and on rocky shores, as either epiphytic, terrestrial or saxicolous plant. It blooms from October to February with a dense inflorescence (150-250 flowers) lasting 20-25 days. The flowers, 1-15/day, are tubular-shaped and anthesis lasts for about 13 hours. Nectar production is greatest in the morning. During this period visits of hummingbirds, the main pollinators, are most frequent. The crab *A. angustipes* was recorded on 31.5% *A. pectinata* inflorescences. Fifty percent of the florivory cases occurred in mangrove plants, 92% on aggregated individuals; 67% of the individuals with crabs were epiphytes. The crabs, up to three individuals per inflorescence, foraged from 0400 to 1800 h, but mainly in the morning, visiting several flowers on the same inflorescence. They used mainly newly-open flowers and were rarely seen handling buds or old flowers. *Armases angustipes* usually damaged the corolla and consumed only the reproductive structures. Hummingbird visits occurred in only 57% of their approaches to inflorescences bearing crabs. During these visits, the number of flowers visited by hummingbirds was reduced in about 70%. Thus, *A. angustipes* may affect the reproductive success of *A. pectinata* directly by consuming its flowers and/or indirectly by reducing pollinator visits.

Key words: Bromeliaceae; bromelicolous crab; florivory; hummingbirds; pollination success; southeastern Brazil; submontane rainforest.

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[1] Manuscrito a ser submetido para a revista *Biotropica*.
[2] Dept° de Botânica, IB/UNICAMP, C.P. 6109, 13090-970, Campinas/SP, Brazil.

Herbivores that feed upon floral structures may reduce the reproductive success of several plant species, either through the loss of gametes due to damages on anthers and ovary, or by hindering pollinator visits (Krupnick *et al.* 1999, Mothershead & Marquis 2000, Malo *et al.* 2001). Low visitation is caused either by changes in floral display and rewards (e.g. Zammit & Hood 1986, English-Loeb & Karban 1992, Karban & Strauss 1993, Cunningham 1995) reducing the attractiveness of flowers to pollinators (Schemske 1980, Roubik & Buckman 1984), or by the presence of herbivores that directly inhibit pollinators (Roubik 1982, Piratelli 1997).

Several crab species are been reported as herbivorous, feeding on leaves, stems, roots, seeds and seedlings (e.g. Capitoli *et al.* 1977, Hagen 1977, Garcia-Franco *et al.* 1991, Kneib *et al.* 1999, Sherman 2002). The first record of flowers as part of crabs diet was made by Fischer *et al.* (1997), which observed *Armases rubripes* Rathbun, 1917 (=*Metasesarma rubripes*) (Grapsidae) eating flowers of some bromeliad species in southeastern Brazil, among them *Aechmea pectinata* Baker (Bromeliaceae).

Armases angustipes Dana (Grapsidae) is habitually recorded in the water accumulated on the basal leaves of bromeliads in different habitats (Hagen 1977, Abele 1992), mainly in the marginal zones of mangrove swamps (see Anger *et al.* 1990). Sattler and Sattler (1965) analyzed stomach contents of this crab species, which contained chitinous parts of insects, detritus, plant material and many stellate trichomes, but no evidence of floral tissues.

The purpose of this study is to characterize the florivory by *Armases angustipes* and to verify its effect on the pollination success of *A. pectinata*.

STUDY SITE AND BROMELIAD SPECIES

Fieldwork was carried out in the Parque Estadual da Serra do Mar-Núcleo Picinguaba in São Paulo, a submontane rainforest of southeastern Brazil ($23^0 22$'S and $44^0 50$'W), with wet tropical climate ("Af."; see Köppen 1948) and annual rainfall up to 2600 mm. Average annual temperature is ca. 21^0C and there is no well defined dry-cold season, even during the so-called dry months, from May to September (data source: Instituto Agronômico de Campinas, IAC-SP).

The bromeliad *Aechmea pectinata* Baker commonly dwells in the mangrove areas, in "restinga" scrub and on rocky shores in Picinguaba, either as epiphytic, terrestrial and saxicolous plant. This bromeliad species blooms from October to February, showing red leaf tips during this period. The inflorescences bear 150-250 densely packed flowers for 20-25 days. The 1-15 flowers that open every day per inflorescence are greenish white and tubular-shaped. Anthesis begins at about 0400 h and lasts for ca.13 hours. Nectar production is highest in the morning when the hummingbirds *Thalurania glaucopis* Gmelin, *Amazilia fimbriata* Elliot and *Ramphodon naevius* Dumont (Trochilidae), its main pollinators, are most frequent. *A. pectinata* is self-incompatible and, thus, pollinator dependent (Canela & Sazima, unpublished data; see cap. I).

METHODS

From October 2000 to February 2001, 38 individuals of *A. pectinata* were sampled, 12 in the mangrove (ten epiphytic and two terrestrial individuals), 13 in the "restinga" scrub (nine epiphytic and four terrestrial) and 13 saxicolous individuals on rocks near the shore (Table 1). During 19 days, observations were made directly or through binoculars from early morning (0400 h) to late afternoon, totaling 112 hours (62 hours in the morning and 50 hours in the afternoon). We recorded the plant habitat, habit, daily number of open flowers per inflorescence, number of hummingbird visits per day, presence or absence of crabs, time of visits and behavior of both the birds and the crabs. Hummingbirds and crabs were photographed and videotaped during their visits to the flowers. Crab specimens were collected for identification and deposited as vouchers at the Museu de Zoologia, Universidade de São Paulo, Brazil (MZUSP 13820).

RESULTS

Armases angustipes foraged on flowers of *A. pectinata* (Fig. 1) during the flowering peak from November 2000 to mid-January 2001. In the beginning and end of the flowering season when the number of *A. pectinata* individuals with flowers was low, crabs were rarely recorded. Some individuals of other bromeliad species, namely *Aechmea distichantha* Lem., *Neoregelia johanis* (Car.) L.B. Sm. and *Aechmea nudicaulis* (L.) Griseb., flowered during the same period as *A. pectinata*, but no crabs were seen foraging on their flowers.

FIGURE 1. The grapsid crab *Armases angustipes* handling a flower of the bromeliad *Aechmea pectinata*.

The crab was recorded on 12 of the 38 sampled *A. pectinata* individuals (31.5%). Of these plants with crabs, six were in the mangrove (50%), three in the restinga scrub (25%) and three on the rocks near the shore (25%). Eight of the crab florivory occurrences (67%) took place on epiphytic individuals, three (25%) on saxicolous and only one (8.3%) on a terrestrial individual (Table 1).

TABLE 1. *Aechmea pectinata* with inflorescences in the three habitats, plant habit and number of inflorescences with and without the crab *Armases angustipes* in Picinguaba, Brazil.

	mangrove			"restinga"			rocky shore			
inflor.	E	T	S	E	T	S	E	T	S	total
with crabs	6	0	-	2	1	-	-	-	3	12
without crabs	4	2	-	7	3	-	-	-	10	26
total		12			13				13	38

Plant habit: E= epiphytic, T= terrestrial, S=saxicolous form.

Florivory was recorded on clumped, rather than isolated, individuals of *A. pectinata* (92%, *N* =12), and more frequently (83%) on inflorescences with more than five open flowers per day. Typically, one or two (rarely three) crabs were recorded per inflorescence at the same time, totaling 19 crabs during the study period. The frequency of *A. angustipes* on *A. pectinata* was 0.5 crabs/inflorescence.

Although crabs foraged from 0400 h to 1800 h, 80 percent of the flower feeding records (*N* = 20) occurred in the morning (Fig. 2). Crabs visited ca. 30 percent of the flowers on the same inflorescence per day, spending 10-30 min foraging on a given flower before moving to another. A visit to a given inflorescence could last up to two hours, and crabs could visit the same inflorescence up to three times a day. Some inflorescences were visited by crabs during consecutive days. When visiting a flower, the crab separated the sepals and petals with its chelas (Fig. 1), usually damaging these floral structures, and consumed only the stamens and stigma. The crabs used mainly newly-open flowers and rarely dealt with buds or old flowers.

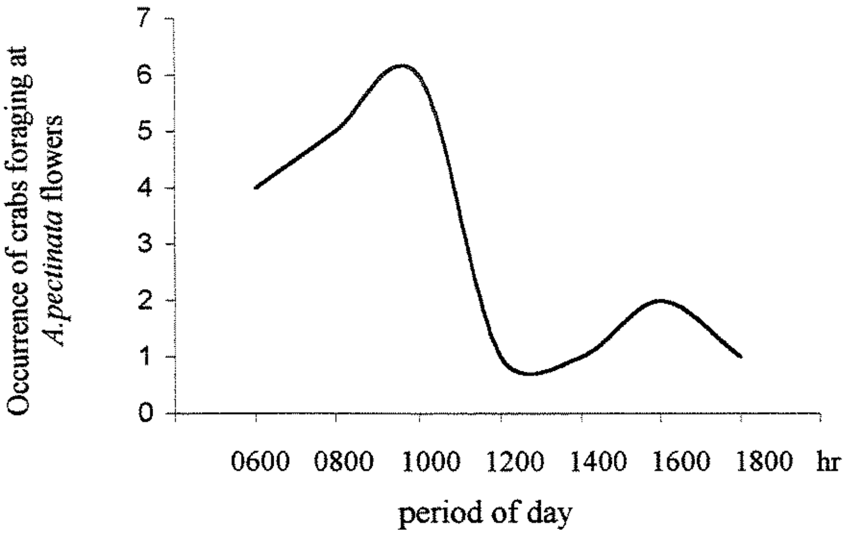

FIGURE 2. Records of crab foraging at *Aechmea pectinata* flowers throughout the day, in Picinguaba/SP.

Hummingbird approaches (N = 44) to *A. pectinata* plants bearing crabs (N = 12) were significantly reduced (X^2 =17.49, $P < 0.001$) compared to approaches (N = 423) to inflorescences without crabs (N=26) during the same period. Although the hummingbirds made 25 visits during the approaches to inflorescences with crabs, interrupted visits predominated at most inflorescences (Fig. 3). The number of interrupted visits (N=19, 43%) on inflorescences with crabs (see Fig. 4) was significantly greater (X^2 =81.20, $P < 0.001$) as compared to the number of interrupted visits (N =9, 2.1%) in inflorescences without crabs. When the hummingbirds visited inflorescences with crabs, 57% of the records, the number of flowers visited per inflorescence was reduced to approximately 70 percent and the visits were up to five times shorter.

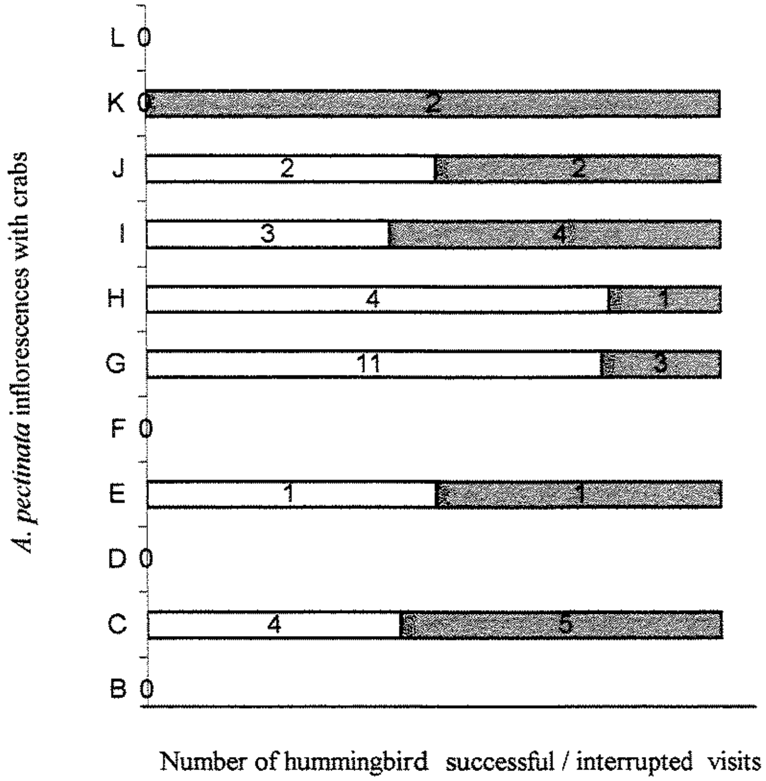

FIGURE 3. Diagram representing the number of successful (N =25; white bars) and interrupted (N =19; gray bars) visits of the hummingbirds at twelve *A. pectinata* inflorescences (A-L) bearing crabs in Picinguaba/SP. Number of approaches = 44.

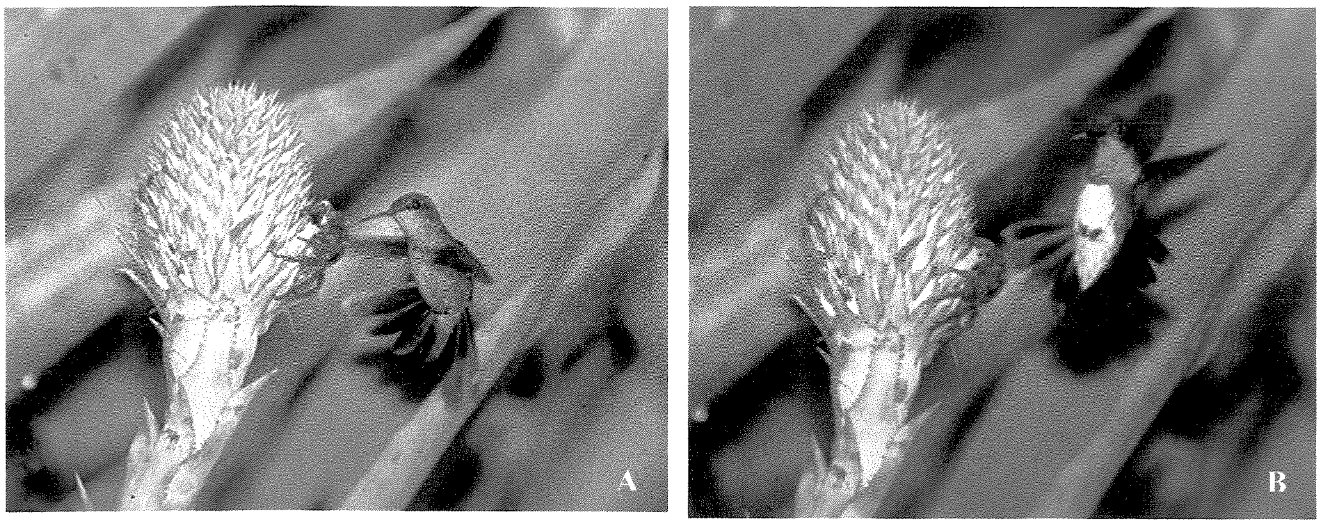

FIGURE 4. Interruption of (A) *Thalurania glaucopis* (female) and (B) *Amazilia fimbriata* visits to *Aechmea pectinata* inflorescences with *Armases angustipes*.

In inflorescences with only one crab foraging and during a short period, hummingbirds sometimes resumed their visits after the crab left the inflorescence (Fig. 5), a situation more frequent in the afternoon. On occasions, hummingbirds approached inflorescences with crab-damaged flowers but did not visit them. Five of the twelve inflorescences of *A. pectinata* visited by crabs (42%) set no fruits.

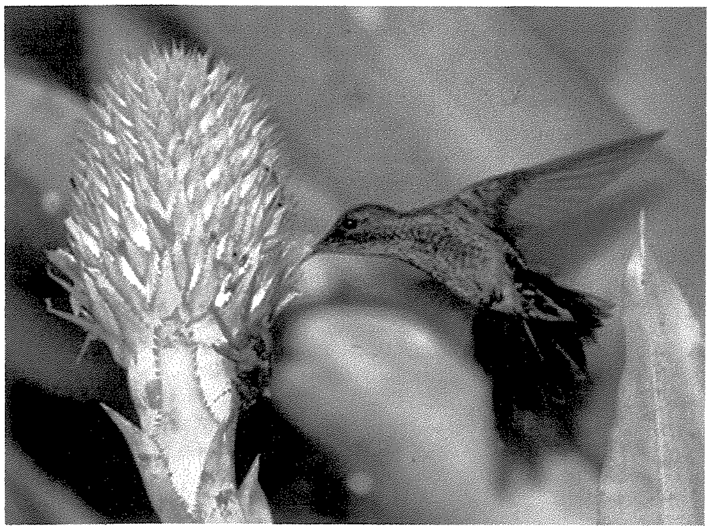

FIGURE 5. *Thalurania glaucopis* (male) visiting a flower of *Aechmea pectinata* when crab (lower right) moves from the inflorescence.

The hummingbird behaved in a different way in relation to inflorescences with crabs. Upon the first contact with such a situation, *R. naevius* usually discontinued visits to this particular inflorescence for that day. On the other hand, *A. fimbriata* and *T. glaucopis* (males) visited the inflorescences with crabs at least a few times before giving up. Agonistic interactions between crabs and hummingbirds were not recorded.

DISCUSSION

After first cursory report (Fischer *et al.* 1997), this study presents the first description of crab florivory in relation to pollinators, and comment on their consequences. Many species of grapsid crabs are known live and breed in several bromeliad species (McWilliams 1969, Hartnoll 1971, Abele 1972), but the use of bromeliad flowers in the diet of crabs was unrecorded. The use of different bromeliad species may indicate that Bromeliaceae play an important ecological role in grapsid crab community structure and dynamics.

Aechmea pectinata is an important feeding resource during its flowering season due to the high quantity of both individuals and flowers in Picinguaba. During the remaining part of the year, the crab *A. angustipes* likely feeds on other bromeliad with clustered flowers, like *Quesnelia arvensis* (Vell.) Mez, *Nidularium inocentii* Lem. and *Bromelia antiacantha* Bertoloni (see Fischer *et al.* 1997).

The frequency of *Armases angustipes* in our study (0.5 crabs/plant) is aproximately eight times greater than that recorded for *Armases rubripes* on *Aechmea pectinata* (0.06 crabs/plant) at the southernmost Ecological Station of Juréia (Fischer *et al.* 1997). This difference is likely explained by the smaller number of *A. pectinata* individuals and higher numbers of other flowering bromeliad species at this latter site (see Fischer *et al.* (1997).

The fact that crab florivory occurs mainly in clustered bromeliads and with a large number of flowers indicates that crabs are attracted by high flower density, in analogy to pollinating insects which concentrate their visits to plant clusters with high rewards (see Thomson 1981, Klinkhamer *et al.* 1989). Therefore, isolated individuals, plants blooming at the beginning or the end of the season, and those with few flowers likely are less attractive, and have a great chance of escaping from crab florivory.

Our observations on *A. angustipes* primarily foraging in the morning and using mainly newly-open flowers are consistent with those recorded for *A. rubripes* by Fischer *et al.* (1997). This may be related to the greater availability of pollen, a highly nutritional part of the flower (Stanley & Linskens 1974).

The low fruit set on some inflorescences of *A. pectinata* with presence of *A. angustipes* crabs may be a result of this crab interference on pollination. Consumption of stamens and stigma by the crabs directly affects the export and receipt of pollen, respectively. The damage caused to sepals and petals by florivore may interfere in flower attractiveness, thus resulting in diminished pollinator visitation rates in the damaged plants (see Lehtilä & Strauss 1997, Kudoh & Whigham 1998, Mothershead & Marquis 2000). Reduction of hummingbird visits to *A. pectinata* inflorescences with damaged flowers may result in an additional wastage of surviving gametes of the remaining intact flowers (see Armbruster 1988, Krupnick *et al.* 1999). These aspects may interfere with fruit set, as mentioned by Gross & Werner (1983), Bertness *et al.* (1987) and Cunningham (1995), mainly to self-incompatible species, as *A. pectinata.*

Based on consumption of floral structures and inhibition and/or reduction of hummingbird visitation rates, we suggest that the crabs interfere directly, as well as indirectly, with the reproductive success of *A. pectinata.* As a result, crab florivory may play an important role in the population and community dynamics of this bromeliad and act as a selective force in the evolution of some of its features. A careful long term study regarding the consequences of crab florivory is recommended.

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CAPÍTULO III

ECOLOGIA DA POLINIZAÇÃO DE *BROMELIA ANTIACANTHA* (BROMELIACEAE) NO LITORAL DO SUDESTE BRASILEIRO

RESUMO

A ecologia da polinização de *Bromelia antiacantha* (Bromeliaceae) foi investigada em uma área de restinga no sudeste do Brasil. Os indivíduos dessa espécie apresentam distribuição pouco agregada e florescem em episódios, principalmente, de dezembro a fevereiro, ocasião em que as folhas ao redor da inflorescência e brácteas apresentam coloração vermelha intensa. A inflorescência é paniculada (150-350 flores), abrindo de 10-35 flores por dia durante 4-5 dias. As flores são tubulares, as pétalas são de cor magenta com margens brancas e o estigma está localizado abaixo das anteras. A antese é diurna, iniciando-se por volta das 04:00 h e dura ca. 15 horas. Os maiores valores de volume e concentração de açúcares do néctar foram registrados entre 04:00-06:00 h, decrescendo em seguida e mantendo-se relativamente estáveis na maior parte do dia. Os principais polinizadores foram os beija-flores *Thalurania glaucopis, Amazilia fimbriata* e *Ramphodon naevius,* responsáveis por ca. 55% das visitas, sendo mais freqüentes no período da tarde. O arranjo das estruturas florais favorece a deposição de pólen no bico dessas aves. A coloração, o odor e a abertura do tubo da corola favorecem a visitação por abelhas. *Bombus morio e Euglossa* cf. *safferina* representaram 38% das visitas e atuaram também como polinizadores, sendo mais freqüentes nas primeiras horas da manhã, período em que a concentração do néctar é maior. Abelhas *Trigona spinipes* foram freqüentes mas agiram principalmente como pilhadores de pólen/néctar, além de agredirem e afugentarem os beija-flores. *Bromelia antiacantha* apresentou características florais relacionadas à ornitofilia, porém a visitação dos beija-flores não se relacionou positivamente com a produção diária de néctar, provavelmente, devido à interferência de *T. spinipes.* Essa espécie de bromélia é parcialmente auto-incompatível mas não autógama, e portanto, dependente de polinizador. A distribuição pouco agregada dos indivíduos de *B. antiacantha* promove o comportamento 'trap-line' dos beija-flores, e favorece a frutificação por xenogamia. A auto-polinização facultativa pode representar uma alternativa para a formação de frutos em indivíduos florescendo assincronicamente.

PALAVRAS-CHAVE: Bromelia antiacantha, beija-flores, abelhas, produção de néctar, reprodução, floresta atlântica, sudeste do Brasil.

Pollination Ecology of *Bromelia antiacantha* Bertoloni (Bromeliaceae) in Southeastern Brazil.[1]

Maria Bernadete Ferreira Canela[2] and Marlies Sazima[2]

Abstract: The pollination ecology of *B. antiacantha* was investigated in southeastern Brazil restinga. This species flowers from December to February. In this period the central leaves and bracts display a bright red color. The inflorescence is paniculate (150-350 flowers) with 10-35 flowers opening per day during 4-5 days. The flowers are tubular, dark Magenta with white margins, and have the stigma located below the anthers. Anthesis is diurnal, beginning around 04:00 h and lasting approximately 15 hours. The greatest nectar volume and sugar concentration occurred between 04:00-06:00 h; after this both decreased throughout the day. The hummingbirds *Thalurania glaucopis, Amazilia fimbriata* and *Ramphodon naevius* were the main pollinators (55% of the visits), visiting the inflorescences primarily in the afternoon. The arrangement of the floral structures favours pollen deposition on the hummingbird' bill. Corolla colour, odour and tube opening favour bee visitation. *Bombus morio* and *Euglossa* cf. *safferina* were responsible for approximately 38% of the visits, primarily in the morning when nectar sugar concentration is greatest, and acted as pollinators too. *Trigona spinipes* bees were frequent visitors to the flowers but acted predominantly as pollen/nectar thieves, excluding hummingbirds. *Bromelia antiacantha* displays ornithophilous features, however, hummingbird visitation did not follow nectar production. This was likely because of the interference of *T. spinipes* bees. This bromeliad species is partially self-incompatible but nonautogamous, and therefore, pollinator dependent. The scattered distribution of the individuals promotes 'traplining' behaviour of the hummingbirds, which in turn, favours fruit set through xenogamy. Facultative selfing is an alternative for individuals asynchronously flowering.

Key words: *B. antiacantha*, hummingbirds, bees, nectar production, reproduction, submontane rainforest, southeastern Brazil.

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[1] Manuscrito a ser submetido para a revista *Plant Biology*.

[2] Dept° de Botânica, IB/UNICAMP, C.P. 6109, 13090-970, Campinas/SP, Brazil.

Introduction

Floral characteristics (e.g. colour, shape, odour, resource availability), among the other aspects, may to determine the kind of pollinators, and their behaviour, in a given species (see Percival, 1969[30]; Baker, 1975[3]; Proctor and Yeo, 1972[32]; Faegri and Pijl, 1980[8]). Bromeliaceae shows ample adaptative radiation in the diversity of its pollinators (Vogel 1990[55]), but is among the few plant families in which pollination by vertebrates predominates over entomophily (Sazima et al., 1989[42]). The bromeliads represent one of the primary sources of nectar for hummingbirds, their major pollinators (see McWilliams, 1974[25] ; Snow and Snow, 1986[51]; Sazima et al., 1996[44]). Melittophily is not common in this plant family (Vogel, 1990[55]), however, there are some records of bee-pollinated bromeliad species (Ule, 1898[53]; Knuth, 1904[18]; Siqueira, 1998[47]; Wendt et al. 2001[56], 2002[57]). In addition, species with unspecific pollination, i.e. visited by hummingbirds as well as various insects and/or bats, has been recorded at Bromeliaceae and other tropical families (see Kessler and Krömer, 2000[17]).

The objective of this study was to relate aspects of phenology, floral morphology and biology, and breeding system to the spectrum and dynamics of the floral visitors and/or pollinators of *Bromelia antiacantha* Bertoloni (Bromeliaceae). This species is found in coastal "restinga" scrub and in semideciduous forest up to 1000m a.s.l. in south and southeastern Brazil (Smith and Downs, 1979[50]). Individuals occur as terrestrial plant in the "restinga" scrub, but some are found as saxicolous plant on rocky shores, and are distributed mainly in small assemblages of 3-4 plants (M. B. F. Canela and M. Sazima, pers. obs.). According to Reitz (1983[36]), there are multiple flowering periods throughout the year. In spite of wide distribution and abundance of *B. antiacantha*, however, little is known about its pollination biology (see Wolf, 1970[58]).

Material and methods

Study site

This study was carried out in the Parque Estadual da Serra do Mar-Núcleo Picinguaba/SP, a submontane wet tropical forest in southeastern Brazil ($23^0$22'S-$44^0$50'W) ("Af."; see Köppen, 1948[19]). Annual rainfall up to 2600 mm and average annual temperature about 21^0C define the forest. There is no well-defined dry-cold season, even during the so-called dry months, from May to September (data source: Instituto Agronômico de Campinas, IAC-SP, Brazil).

Procedure

Fieldwork was carried out during two *B. antiacantha* flowering seasons, from December 2000 to February 2001 and from January to February 2002, on 53 sampled individuals in the "restinga" scrub closest to the beach. Inflorescences were observed *in situ* to determine the number of flowers opening per day, features of anthesis, visit' frequency and foraging behaviour of the floral visitors. The floral parts and vegetative structures related to attraction were also studied. The internal length of flowers was measured from the free portion of the petals to the tube opening ("effective length", defined by Wolf et al., 1976[59]).

Nectar sugar concentration ($n = 20$) was measured with a pocket refractometer and its volume ($n = 20$) with microliter syringes (Dafni, 1992[6]). These measuring were made throughout anthesis, at intervals of two hours, on previously bagged flowers. Accumulated nectar volume ($n = 12$) and its respective sugar concentration ($n = 9$) were also measured on bagged flowers, in the end of anthesis. Pollen viability ($n = 10$ flowers) was estimated through cytoplasm stainability, using the aceto-carmine technique (Radford et al., 1974[33]). Stigmatic receptivity was tested using the H_2O_2 10V catalase activity method (Zeisler, 1938[60]).

The breeding system was assessed by hand-pollination treatments of previously bagged flowers: manual self-pollination, cross-pollination (previously emasculated flowers) and autonomous self-pollination (bagged buds); flowers under natural conditions of pollination were marked as control (see Table 1). Fruit set for all treatments was determined approximately one month after pollination. The self-compatibility index (SCI) was calculated by the ratio "fruit set of self-pollinated flowers/fruit set of cross-pollinated flowers", where values >0.75 indicate self-compatibility (Jacquemart, 1996[16]). Pistils of self- and cross-pollinated flowers (n = 5 each treatment) were fixed in FAA 50% after 12, 24, 36, 48 and 72 h of handling and analyzed under fluorescence microscopy to observe pollen tube growth (Martin, 1959[23]).

Visitors were observed directly or through binoculars at 21 focal individuals from 04:00 h to 180:0 h (n = 10 for each two hours interval), totaling 114 hours in fifteen days. Floral visitors were photographed and videotaped. Hummingbird identification was made according to Ruschi (1992[40]) and confirmed by a specialist. Hummingbird bill lengths were obtained from Grantsau (1989[13]). Bees were also collected and identified by specialists.

Daily nectar production and hummingbird visitation were evaluated to normality by Kolmogorov-Smirnov test (BioEstat 2.0). As our data are non-parametric, the median (M) was calculated and variations were analyzed through box-plots graphs (Systat 8.0), Kruskall-Wallis test (H), Mann-Whitney test (U), Spearman correlation (R^2) and regression analysis (r) (BioEstat 2.0).

Results and discussion

Phenology

Flowering of *Bromelia antiacantha* is characterized by spaced blooming episodes from December to January, but some individuals flower asynchronously. The flowering pattern of the population corresponds to the sub-annual type (see Newstron et al., 1994[28]). This species presents a great quantity of flowers for a few days, flowering pattern classified as 'big-bang' in relation to individual plants by Gentry (1974[14]). This strategy, uncommon in bromeliad species (e.g. Araújo et al., 1994[1]; Sazima et al., 1996[44]; Martinelli, 1997[24]; see cap. I), depends on the opportunistic behaviour of potential pollinators which may abandon their regular foraging patterns to take advantage of a conspicuous and munificent, if fleeting, source of nectar (Gentry, 1974[14]).

Bromelia antiacantha has a paniculate inflorescence, which is 50-80 cm long and bearing 150–350 flowers. Flowers open in different parts along the inflorescence and in variable number (10-35 flowers per day) during 4-5 days. Many buds, especially those of the apical and basal portions of the inflorescence, do not develop into flowers. Several species produce flowers in excess as compared to fruit set, and experimental studies indicate that floral abortion may be not a consequence of resource limitation, but is related to reproductive investment of the plant and to be genetically controlled (O' Brien and O' Brien, 1995[29]). The pattern of flower opening in this species differs from that of several bromeliads, where the flowers open from bottom to top on the inflorescence, and also occur at *Hohenbergia ridleyi* (Baker) Mez. and *Aechmea fulgens* Brongniart (see Siqueira, 1998[47]). These species have compound inflorescence, as well as *B. antiacantha*, and flower opening at random likely is associated with this fact.

During the flowering season, some leaves and bracts unfold from the inflorescence, leaving it well exposed. These leaves display an intense red coloration as well as the bracts in their distal parts (Fig. 1). This coloration, which slowly disappears at the beginning of fruiting, is interpreted as an attractive factor for pollinators (Stiles, 1981[52]), and also occurs in other ornithophilous bromeliad species (see Martinelli, 1997[24]; Sazima et al., 2000[45]; see cap. I).

Fig. 1 *Bromelia antiacantha*: flowering individual with red bracts and internal leaves set apart from the inflorescence, which becomes accessible to visitors, in Picinguaba/SP.

Floral morphology

Bromelia antiacantha flowers are short-pedicellate, actinomorphic, tubular, and concentrated in the axils of white scape-bracts along the length of main inflorescence. The sepals are free, oblong and pale green. The petals are connate for 3 mm, oblong, imbricate to the left, of dark Magenta colour with white margins. The contrasting colour of the petals (magenta/white) of this bromeliad species may be attractive for bees (see Percival, 1969[30]). The stamens are included in the corolla, juxtaposed and the filaments are adnate to the petals (Fig. **2**). The anthers are situated above the stigma ("herkogamy"; Fig. **2**), have longitudinal dehiscence and are extrorse. This stigma is trilobate, oblong and papillous, the nectary is septal, and nectar accumulates at the base of the corolla tube. The ovary is inferior and elongated (Fig. **2**).

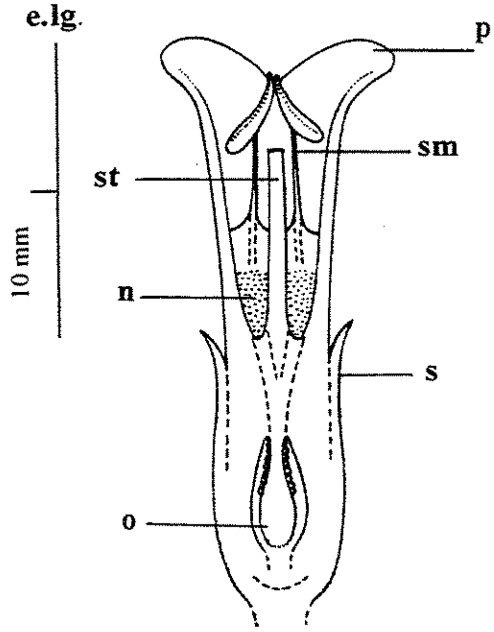

Fig. 2 Longitudinal section *Bromelia antiacantha* flower in anthesis, showing the floral elements disposition: petals (p), stamens (sm), stigma (st), sepals (s), ovary (o) and the site where nectar accumulates (n). The effective length of the corolla ("e.lg.") is represented by to scale at left.

The effective length of the floral tube is approximately 20 mm and the diameter of its opening varies from 5-8 mm. The relatively short floral tube allows visitations not only by long-billed hummingbirds (Phaethornithinae, 22-46 mm bill length) but also by long-billed species (Trochilinae, 11-24 mm bill length) (Schoener, 1983[46]; see also Sazima et al., 1996[44]; Buzato et al., 2000[5]; see cap. I). Wide opening of the corolla tube permits the legitimate access of visitors other than hummingbirds, including insects (Percival, 1969[30]).

Floral biology

The anthesis begins at around 04:00 h, and lasts approximately 15 hours. In the early morning, the petals begin to separate and the tips slowly curve outward, exposing the apical part of the anthers. At mid-afternoon, the petals begin a reverse movement and slowly spin clockwise. At approximately 19:30 h, the flowers are closed and their withering is accentuated. This short period of anthesis, about half-day, is similar to that reported for many Bromeliaceae species (e.g. Araújo et al., 1994[1]; Sluys and Stotz, 1995[49]; Siqueira, 1998[47]; Sluys et al., 2001[48]; Wendt et al., 2002[57]), and may be related to the pollinator' ability to transfer a sufficient amount pollen in one to a few visits (Ramirez et al., 1990[34]).

In the early morning, flowers of *B. antiacantha* present a strong, sweetish odour that diminishes throughout the day and may be an attractive element for bees (Roubik, 1989[38]), which were very frequent at this bromeliad species during the morning period. A similar early-morning odour has also been reported for *Hohenbergia ridleyi*, a melittophilous bromeliad species (Siqueira, 1998[47]).

Pollen is mainly available in the first hours of morning, period in which its viability is high (96%). The stigma is receptive during whole anthesis. *Bromelia antiacantha* is a homogamous species, as are *Aechmea pectinata* Baker (M.B.F. Canela and M.Sazima, *pers. obs.*; see cap. I) and *Hohenbergia ridleyi* (Siqueira, 1998[45]), which is not common in Bromeliaceae species (Martinelli, 1997[24]).

The major nectar production per *B. antiacantha* flower occurred in the early morning between 04:00-06:00 h. Its volume decreased by more than half by 08:00 h and remained stable from that time until approximately 16:00 h, when it began to decrease again (Fig. 3A). In addition, nectar is more concentrated in the early morning, and becomes diluted by 08:00 h, remaining stable from that time on throughout the rest of the day (Fig. 3B).

Statistical significant differences were found only between early morning and late afternoon for nectar volume ($H = 68.56$, $p < 0.001$), and between early morning and the rest of the day for sugar concentration in the nectar ($H = 68.67$, $p < 0.001$). These results support the idea that, despite its variation throughout the day, nectar production in ornithophilous flowers tends to be greater early in the day (see Feinsinger, 1976[9]).

The accumulated nectar volume during the day ($M = 73.0$µl, $n = 12$) and the sum of the partial values ($M = 74.5$µl, $n = 10$) did not significantly differ ($U = 58.00$, $p > 0.05$), demonstrating that nectar production is continuous and this resource is not reabsorbed. The sugar concentration in the accumulated nectar ($M = 31.6\%$, $n = 9$) was also similar ($U = 58.00$, $p > 0.05$) to the concentration registered in the first hours of anthesis ($M = 30.8\%$, $n = 37$). These findings are consistent with those found for *Aechmea pectinata* (Bromeliaceae) (Canela and Sazima, unpubl. data; cap. I). Nectar volume showed no relation to sugar concentration ($r = 0.68$, $p > 0.05$).

The following hummingbirds species visited *B. antiacantha* flowers: *Thalurania glaucopis* Gmelin, *Amazilia fimbriata* Elliot (Trochilinae), *Ramphodon naevius* Dummont, *Phaethornis ruber* Linné, *Phaethornis squalidus* Temminck and *Glaucis hirsuta* Gmelin (Phaethornithinae).

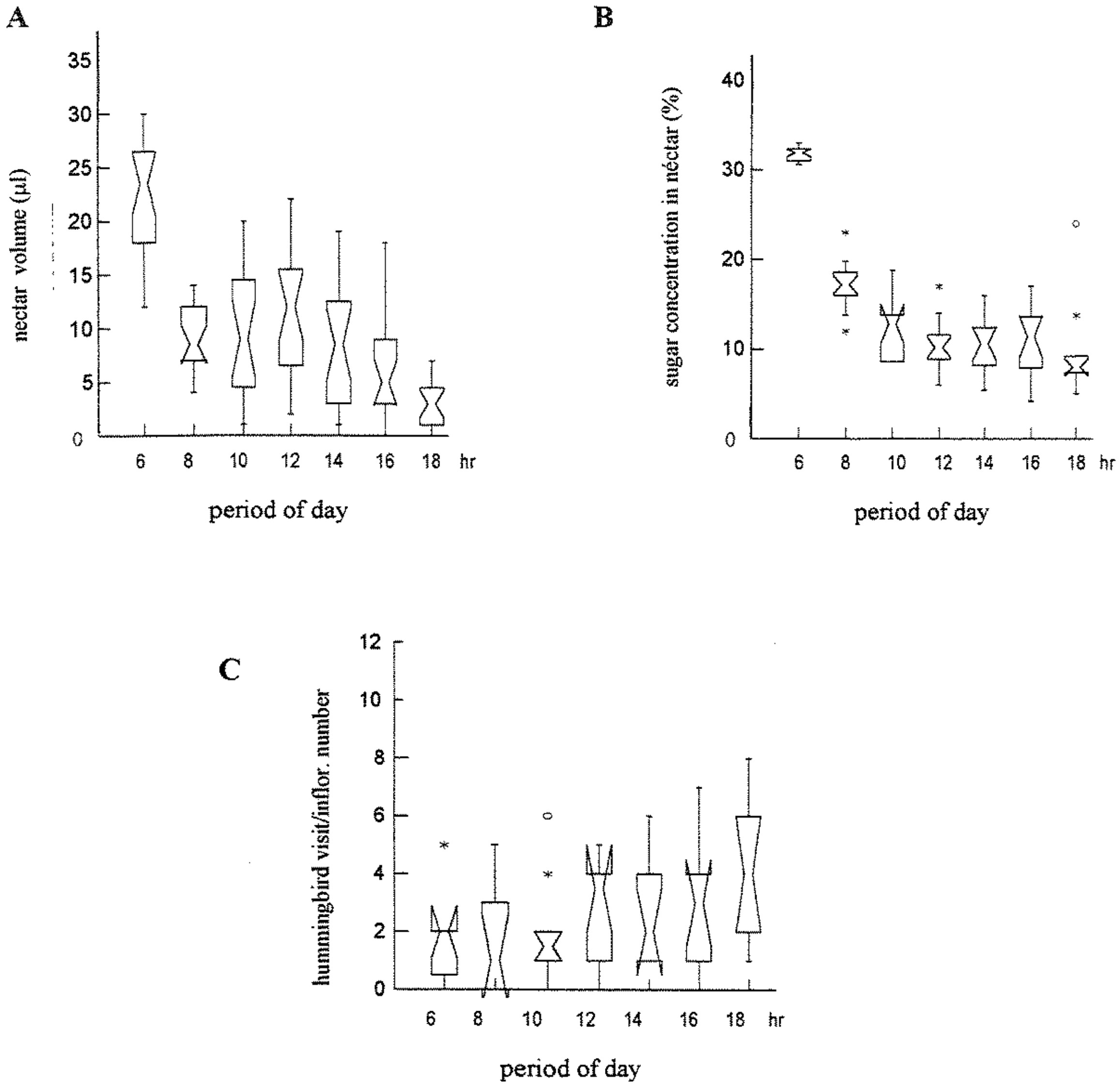

Fig. 3 Variation in (A) nectar volume, (B) sugar concentration in nectar, and (C) number of hummingbird visits per *Bromelia antiacantha*, throughout the day in Picinguaba/SP. Boxes represent the inter quartile range; the center is the median. Interval between slanted lines around the median is the 95% confidence limit. Inferior and superior vertical lines represent total range of the distribution (25% and 75%). Extreme values are represented by (*), and outliers by (°). Overlap between confidence limit indicates no statistical difference.

Thalurania glaucopis (34% of the visits) and *Amazilia fimbriata* (33%; Fig. **4A**) were the most frequent hummingbirds. Females were responsible for 67% of the visits made by *T. glaucopis*. Males and females of this species markedly differ in feeding strategies, and predominance of females visiting *B. antiacantha* inflorescences, likely, is related to low sugar concentration in the nectar of their flowers at most day time, since that interesting nectar sources are aggressively defended by males, and females are observed more often insect-foraging than taking nectar (see Snow and Snow, 1986[51]).

Ramphodon naevius was also common (24%), predominating in forest environments. *Phaethornis ruber*, comprising only 7 % of the visits, occurred in open areas. *Phaethornis squalidus* and *G. hirsuta* were only observed once each at *B. antiacantha*. Interestingly *P. squalidus* (Fig. **4B**), a hummingbird species commonly known in submontane forest (Ruschi, 1982[40]), had never been registered visiting flowers of this species or occurring in "restinga" scrub.

Fig. 4 (A) *Amazilia fimbriata* and (B) *Phaethornis squalidus* (single visit) at flowers in the upper part of the inflorescence of *Bromelia antiacantha*, Picinguaba/SP.

Hummingbirds commonly visited the same flower 2-3 times in a sequence, primarily in the upper portion of the inflorescence. Visits were very short in some flowers and longer in others, varying from 1-15 s. The juxtaposition of the stamens, an aspect common to other ornithophilous bromeliads, promotes pollen on the deposition hummingbirds' bill while they take nectar (see Sazima et al., 1995[43], 1996[44]; Buzato et al., 2000[5] ; Canela and Sazima, cap. I). Pollen deposition on the hummingbirds' bill in Bromeliaceae is an efficient way of pollen transfer, since in these plant species the pollen is somewhat sticky. In addition, the hummingbirds visit several flowers before cleaning its bills, although Dressler (1971[7]) and Rose and Barthlott (1994[39]) pointed out that a bill, is too smooth and cleaned before effecting pollination, and thus not well suited for pollen transport.

Thalurania glaucopis, A. fimbriata and *R. naevius* usually visited *B. antiacantha* inflorescences along their foraging routes, at irregular intervals, and occasionally interacted agonistically among them. These three species acted as 'low reward trap-liners', although *T. glaucopis* and *A. fimbriata* are typically territorial birds (see Feinsinger and Colwell, 1978[11]). This suggests that *B. antiacantha* was not a sufficiently stable food source over time and/or space to provide sufficient advantages to establish and defend territories (see Wolf, 1970[58]). The distribution of *B. antiacantha* individuals in small assemblages and flowering over a short period contributed to the predominance of the 'trapline' behavior, once small and scattered nectar sources tend to be explored in foraging routes (Snow and Snow, 1986[51]; Neill, 1987[27]).

The number of hummingbird visits (Fig. **3C**) showed no statistically significant difference throughout the day ($H = 12.45$, $p > 0.05$). Nevertheless, approximately 70% of these visits occurred from 10:00-18:00 h, with a peak of 2.1 visits/h between 16:00-18:00 h. In the afternoon, likely because of the smaller amount of nectar per flower, hummingbirds visited up to five times more flowers per inflorescence as compared to the morning period. After 18:00 h, flowers were almost completely closed and hummingbird visitation was diminished, accounting for only 4.5% of the visits.

Daily visitation by hummingbirds showed no relation to nectar volume ($R^2 = 0.13$, $p > 0.05$) and an inverse relation to sugar concentration in the nectar ($R^2 = 0.75$, $p < 0.05$; Fig. **5**), suggesting that, besides resource availability, other factors may have influenced bird visitation.

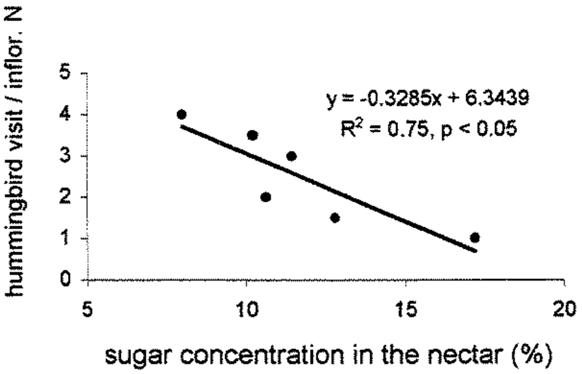

Fig 5 Inverse relation between the number of hummingbird visits per inflorescence and sugar concentration in nectar of *Bromelia antiacantha* flowers. Values from 04:00 h to 06:00 h were excluded from this analysis as they correspond to a low activity period of the hummingbirds.

In the early morning (06:00-10:00 h), hummingbirds made few visits. In the same period, *Trigona spinipes* (Meliponinae, Apidae) bees visited *B. antiacantha* flowers entering the corolla tube and thieved much of the pollen. Later, they robbed nectar through holes made by them in the corolla base. Hummingbirds that approached to the inflorescences were commonly attacked by the numerous bees (10 to 15 individuals per inflorescence). The birds gave up the visits in

48% of the approaches made between 06:00-10:00 h (n = 63, 10 plants), and reduced the number of flowers visited by approximately 75%. Hummingbirds resumed visits to the whole inflorescence between 10:00 h and 11:00 h, when bee density diminished.

Trigona spinipes individuals spent a long time in the same flower or inflorescence, rarely moving between different *B. antiacantha* plants. Similar behaviour of these bees was observed by Wendt et al. (2001[57]) at *Pitcairnia* (Bromeliaceae) individuals. The low mobility of these bees is a characteristic that leads Bawa (1980[4]) to classify them as "low quality pollinators" because mainly promote self-pollination/geitonogamy.

Trigona species affect pollinator visits both directly, through aggressive interactions, and indirectly through the reduction of resources (see Hubbell and Johnson, 1978[15]; Renner, 1983[36]; Roubik, 1982[37], 1989[38]; Piratelli, 1997[31]; Barbosa, 1999[2]). Although there is no quantitative data in relation to the influence of *T. spinipes* over the reproductive success of *B. antiacantha*, these bees may have contributed to the low fruit set (Table 1) under natural conditions (see Sazima and Sazima, 1989[41]). A similar interference was registered in *Aechmea pectinata* (Bromeliaceae), in which crabs consumed floral reproductive structures and intimidated visiting hummingbirds, which avoided the inflorescences with crab presence (Canela and Sazima, unpubl. data; see cap. II).

Bombus morio and *Euglossa* cf. *safferina* (Bombinae, Apidae) bees were also frequent (38% of visits), predominantly in the early morning (06:00-10:00 h) when sugar concentration in the nectar is greater. High values of sugar concentration in the nectar are characteristic of melittophilous flowers (Baker, 1975[4]; Faegri and Pijl, 1980[12]; Vogel, 1983[53]) as demonstrated in Bromeliacae *Hohenbergia ridleyi* (Siqueira, 1998[47]).

Bombus morio was responsible for 96% of the bee visits, and visited from the early morning until late afternoon, only reducing visits during the hottest hours of the day (12:00-14:00 h). When taking nectar, pollen was deposited on the bee' forehead. Individuals of *B. morio* used to visit flowers of several inflorescences, i.e. in a 'trapline' fashion, therefore promoting cross-pollination and acting as effective pollinator. Aggressive interactions were frequently observed among *B. morio* individuals, and occasionally these bees avoided flowers with *T. spinipes*. *Euglossa* cf. *safferina*, on the other hand, accounted for only 3.7% of the visits, taking nectar and/or collecting pollen, and thus acts as an occasional pollinator of *B. antiacantha.*

Similar to *B. antiacantha, Vriesea jonghei* (K. Koch) E. Morren (Bromeliaceae) is regularly visited by hummingbirds but does not seem to be exclusively adapted for pollination by these birds. It has an open, trumpet-shaped corolla tube, where insects can enter freely, and its flowers are consistently visited by *Trigona* bees that likely act as pollinators (Snow and Snow, 1986[51]). Three *Pitcairnia* species (see Wendt et al., 2001[57], 2002[58]) and *Hohenbergia ridleyi* (see Siqueira, 1998[47]), with tubular flowers and large openings, are also frequently visited/pollinated by different bee species.

Hesperids (moths and butterflies) visited few flowers on each inflorescence, spending little time in each flower and occasionally returning to the same flower. Hawk moths (Sphingidae) were registered in about 43% of the plants between 04:00-06:00 h, but represented only 0.8% of the visits, and no pollen transport was observed. Hesperids were also recorded at *Pitcairnia* species (Wendt et al., 2001[57]) and *H. ridleyi* (Siqueira, 1998[47]) with similar behaviour to that described on *B. antiacantha*. Wasps were frequently observed visiting *B. antiacantha* flowers in search of oviposition sites. Fruits situated at the base of inflorescences often contained wasp larvae, and consequently did not develop further. The rare hummingbird visitation in the lower portions of inflorescences is likely related to this parasitism, contributing to reduced fruit set too.

Reproduction

Bromelia antiacantha flowers are hermaphrodite and predominantly xenogamic, since about 92% of the cross-pollinated flowers produced fruits, as compared to fruit set at 14% of the manually self-pollinated flowers (Table **1**). In spite of this facultative selfing, fruit set does not occur through autonomous self-pollination (Table **1**). Under natural conditions, fruit set occurred in 50% of the flowers (Table **1**). The fruits developed under natural conditions were usually situated at the upper portion of the inflorescences, which is less parasitized by wasps and most visited by hummingbirds.

In the self-pollinated flowers fixed after 48 hours, pollen grains germinated on the stigma and presented short tubes, some of which showed evidence of incompatibility (see Murray, 1990[26]) as callose plugs in the tips (Fig. **6A**). 72 hours after self-pollination some tubes developed in the style and reached the ovary, although no fertilization occurred. Nevertheless, considering that fruits were set in about 15% of the manually self-pollinated flowers, fertilization must occur more than 72 hours after self-pollination. In cross-pollinated flowers, pollen grains germinated in the stigma 24 hours after pollination, more rapidly and intensely than in self-pollinated flowers. Approximately 48 hours after cross-pollination, pollen tubes developed in quantity along the style and reached the ovary; after 72 hours there were some fertilized ovules (Fig. **6B**). Flowers in natural conditions presented pollination results similar to those observed for manual cross-pollinated.

B. antiacantha is considered partially self-incompatible (SCI = 0.15) because the Self-incompatible Index is < 0.75, and also produce some fruits after manual self-pollination (see Lloyd and Schoen, 1992[22]). As this species has herkogamic flowers and is nonautogamous, it is pollinator dependent. Self-incompatibility is not common at Bromeliaceae, however, several species of this family require agents for pollen transfer, even in the case of self-pollination (see Gardner, 1986[12]; Araújo et al., 1994[1]; Martinelli, 1997[24]; Siqueira, 1998[47]; Wendt et al., 2001[57], 2002[58]). Variance in pollen tube formation and time until fertilization between self-pollen and crossed-pollen is also verified for some bromeliad species, and this condition suggests that exist a competition among pollen grains under natural conditions (see Lloyd and Schoen, 1992[22]; Martinelli, 1997[47]).

Table 1 - Percentage of fruit-set from hand-pollinated treatments, autonomous self-pollination and under natural conditions flowers (control) of *Bromelia antiacantha*. Figures in brackets indicate number of respective fruits/flowers.

Treatments	Percentage of fruit-set	
Autonomous self-pollination	0	(0/896)
Manual self-pollination – same flower	14	(4/28)
Cross-pollination	92	(22/24)
Natural conditions (control)	50	(662/1320)

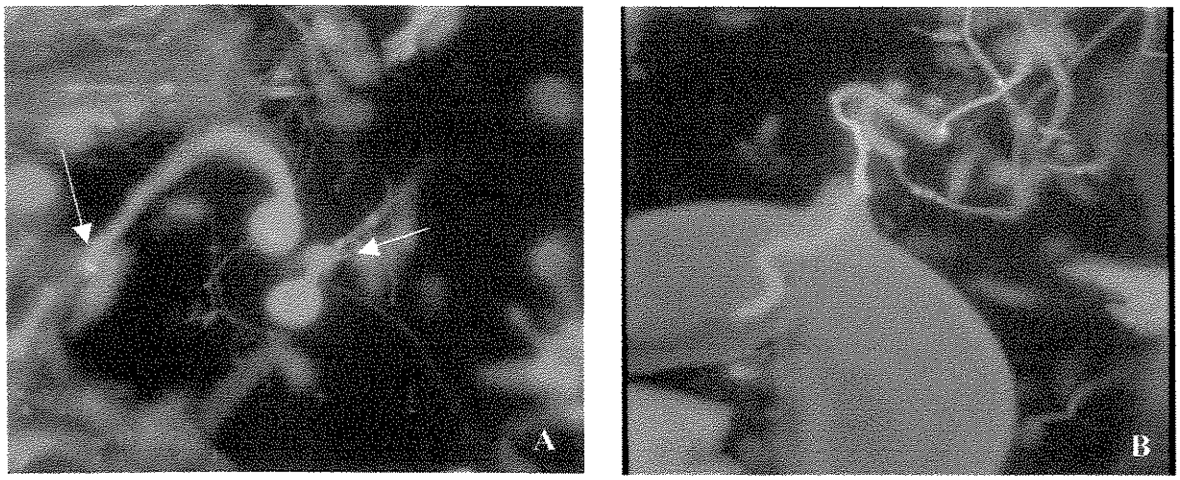

Fig. 6 (A) Stigma of *Bromelia antiacantha* flower fixed 72 hours after self-pollination Arrows indicate evidence of incompatibility as callose plugs in the pollen tube tips; (B) fertilized ovule in a *B. antiacantha* flower fixed 72 hours after cross-pollination.

Bromelia antiacantha is pollinator dependent and displays floral characteristics related to ornithophily. Hummingbirds are its main pollinators due to visitation frequency and 'trap-line' foraging. This behaviour, associated to distribution of *B. antiacantha* flowering individuals in small assemblages, promotes cross-pollination (Feinsinger, 1978[10]). Nevertheless, corolla colour and morphology, odour and concentrated nectar in the early morning admit visits by bees (Percival, 1969[30]; Roubik, 1989[38]), which are considered important pollinators too. *Trigona spinipes* bees, in spite of interfering with hummingbird visitations, display low mobility and may mainly carry out self-pollination. In this case, and in asynchronic flowering episodes, delayed selfing may represent an alternative for fruit production in *B. antiacantha* (see Lloyd, 1992[21]; Locatelli and Machado, 1999[20]; Wendt et al., 2002[58]).

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CONSIDERAÇÕES FINAIS E CONCLUSÕES

Aechmea pectinata e *Bromelia antiacantha* apresentam algumas características florais relacionadas à ornitofilia (Faegri & Pijl 1980), tais como folhas vermelhas, flores tubulares, antese diurna e néctar abundante. Pela constância e comportamento durante as visitas, os beija-flores foram os principais polinizadores nas duas espécies.

Aechmea pectinata apresenta padrão de floração anual e estratégia individual de floração caracterizada pela abertura de algumas flores durante um longo período, ("steady state"), enquanto em *B. antiacantha* a floração da população é sub-anual e cada indivíduo apresenta grande quantidade de flores durante poucos dias ("big bang") (Gentry 1974, Newstrom *et al.* 1994). Aspectos fenológicos podem ser relacionados ao espectro e comportamento dos polinizadores (Opler *et al.* 1980, Morellato 1987). Períodos de floração bem definidos e sincronizados indicam plantas especializadas num certo tipo de polinizador (Stiles 1978, Fleming 1982) como os beija-flores, que são frequentemente territoriais em plantas com oferecimento regular e constante de recursos (ver Wolf *et al.* 1976, Real & Rathcke 1991, Buzato *et. al.* 2000). O padrão explosivo de floração é associado ao comportamento oportunista de polinizadores em fontes de néctar temporárias (Gentry 1974), como beija-flores "trap-liners" e abelhas.

Apesar de certa sobreposição no período de floração de *A. pectinata* e *B. antiacantha* durante o estudo, indivíduos próximos das duas espécies floresceram assincronicamente, diferindo do verificado em anos anteriores (Postch, com. pess.; M.B. F. Canela, obs. pess). A coexistência de espécies simpátricas que utilizam polinizadores em comum pode ser permitida pela partilha do recurso (Stiles 1975, Heithaus 1974, 1979; Araújo *et. al.*1994), ou por separação temporal de floração. Nossos resultados sugerem que eventos sucessivos de sobreposição espacial e temporal de floração poderiam estar conduzindo a deslocamentos dos períodos de floração das duas espécies devido às pressões de competição entre plantas pelo mesmo polinizador (ver Waser 1978, Feinsinger 1983). Esse fato pode ser exemplificado pelos picos de floração de *A. pectinata* e *B. antiacantha* em épocas diferentes, e pelo florescimento de diversos indivíduos distantes entre si de ambas as espécies durante o mesmo período.

Em *B. antiacantha* foram freqüentes visitas por abelhas, atuando também como polinizadores, principalmente no começo do dia. A ampla abertura do tubo da corola dessa espécie favorece visita legítima de diversos visitantes além dos beija-flores. Suas flores apresentam uma coloração contrastante (magenta/branco), um forte odor adocicado e alta concentração de açúcares no néctar nas primeiras horas da manhã, aspectos importantes na visitação por abelhas (ver Percival 1969). Em *A. pectinata*, as flores são inconspícuas, sem odor perceptível e o tubo da corola é estreitado no ápice, limitando a utilização de pólen e néctar por certas abelhas como, por exemplo, *Trigona spinipes*.

O volume e a concentração de açúcares do néctar nas flores de *A. pectinata* e *B. antiacantha*, de forma geral, foram semelhantes aos registrados para espécies ornitófilas de Bromeliaceae e outras famílias vegetais (Snow & Snow 1986, Arizmendi & Ornelas 1990, Sazima *et. al.* 1995, Locatelli & Machado 1999, Buzato *et al.* 2000). Apesar da tendência de maior produção de néctar nas primeiras horas do dia nas duas espécies, como verificado para a maioria das espécies polinizadas por beija-flores (Feinsinger 1976), os valores encontrados nesse estudo foram muito variáveis entre flores de um mesmo indivíduo e entre indivíduos (dados não paramétricos). A produção de néctar numa determinada espécie pode variar em função da posição das flores na planta, da idade e do estado nutricional desta planta, e em relação a aspectos do ambiente como incidência da radiação solar, temperatura do ar, umidade relativa e do solo, entre outros fatores (Percival 1969). Os beija-flores, em função dessa variação e de suas necessidades energéticas, visitariam muitas flores/planta e um número grande de indivíduos (ver Feinsinger 1978), aumentando as chances de *A. pectinata* e *B. antiacantha* serem polinizadas.

Embora na maioria das flores ornitófilas a deposição do pólen ocorra na cabeça, na garganta ou no peito dos beija-flores, pólen no bico dessas aves é comum em flores tubulares com estruturas reprodutivas inclusas na corola (see Rose & Barthlott 1994, Sazima *et al.* 1996), como é o caso de *A. pectinata* e *B. antiacnatha*. Para que a polinização seja eficiente, o pólen precisa ser mantido no corpo das aves até o contato com o estigma em outras flores. O transporte seguro de pólen no bico é bastante discutível, principalmente se este é pulverulento, uma vez que os beija-flores procuram se limpar do pólen (Dessler 1971). Há forte relação entre pólen claro, brilhante e flores polinizadas por abelhas, e pólen de cores mais escuras em flores ornitófilas de Orchidaceae (Dressler 1971) e Cactaceae (Rose & Barthlott 1994). Uma coloração "críptica" do pólen reduziria o contraste entre a cor do pólen e do bico, evitando que as aves se limpem freqüentemente antes de realizarem a polinização (Dressler 1971, Rose & Barthlott 1994). Outra "solução" seria a deposição de pólen não apenas no bico, mas principalmente na fronte dos beija-flores, o que é mais provável de ocorrer naqueles de bico curto. Apesar da visitação de beija-flores da sub-família Trochilinae em *A. pectinata* e *B. antiacnatha*, a deposição de pólen ocorre apenas no bico em todos os beija-flores visitantes das duas espécies. No entanto, o pólen dessas duas espécies de bromélia é pegajoso, e os beija-flores, de maneira geral, pousam para se limparem somente após várias visitas consecutivas às flores.

A sobreposição no uso de espécies ornitófilas por Phaethornithinae e Trochilinae é raramente encontrada nos neotrópicos, onde existem conjuntos bem caracterizados de flores utilizadas por cada sub-família (Murray *et al.* 1997). Essa sobreposição pode ser explicada pelas similaridades florais entre as duas espécies, como por exemplo, o comprimento da corola e a produção de néctar (ver Buzato *et al.* 2000). No entanto, embora as espécies de Trochilidae visitantes nas duas espécies de bromélias tenham sido as mesmas, *Thalurania glaucopis, Amazilia fimbriata* e *Ramphodon naevius,* elas diferiram em comportamento de forrageio e na freqüência das visitas. Em *A. pectinata* as duas primeiras espécies comportaram-se principalmente como territoriais, fato provavelmente relacionado à distribuição agregada e ao longo período de floração de seus indivíduos, uma vez que representam uma oferta de alimento abundante e contínua que promove territorialidade (Buzato *et al.* 2000). Em *B. antiacantha*, de forma geral, os beija-flores visitaram as inflorescências em rondas de forrageamento. A distribuição pouco agregada dos indivíduos dessa espécie, bem como o curto período de floração, contribuem para a predominância desse tipo de comportamento (Neill 1987).

Thalurania glaucopis foi o beija-flor mais freqüente nas duas espécies, no entanto, em *A. pectinata* a maior parte das visitas foi feita pelo macho e, em *B. antiacantha,* pela fêmea. Esse resultado provavelmente se deve às diferenças de comportamento alimentar entre os sexos e à relação distribuição do recurso/estratégia de forrageio discutida anteriormente. Os machos de *T. glaucopis* são conhecidamente territoriais e muito agressivos - inclusive com relação às suas próprias fêmeas - concentrando suas visitas em grandes manchas de recursos como ocorre com *A. pectinata.* Uma vez que em *B. antiacantha* o recurso é espalhado, são as fêmeas que o utilizam mais freqüentemente enquanto os machos forrageiam em fontes de néctar mais vantajosas, inclusive pela relativamente baixa concentração de açúcares no néctar na maior parte do dia (ver Snow & Snow 1986).

Diferentes interações entre os visitantes florais foram relevantes nas duas espécies, influenciando a visitação dos polinizadores. Em *Aechmea pectinata,* embora o caranguejo *Armases angustipes* tenha interferido na atividade dos beija-flores em 1/3 das plantas, no nível populacional os efeitos não foram muito evidentes, sendo verificada uma relação positiva entre a produção de néctar e a visitação diária dos beija-flores, indicando que a quantidade e a qualidade do néctar são importantes para atrair e manter as visitas dessas aves (ver Percival 1969, Baker 1975). Em *B. antiacantha* essa correspondência não foi encontrada, provavelmente, devido à interferência das abelhas *Trigona spinipes*, que além de pilhadoras de pólen/néctar, são agressivas em relação aos beija-flores e outras abelhas (Hubbell & Johnson 1978, Inouye 1980, Renner 1983, Roubik 1989), e foram muito freqüentes em todos os indivíduos de *B. antiacantha* ao longo do estudo, permanecendo muito tempo nas mesmas flores. Por outro lado, embora essas abelhas sejam "polinizadores de baixa-qualidade" segundo Bawa (1990), podem realizar principalmente autopolinizações em *B. antiacantha,* que é uma espécie parcialmente auto-incompatível. Em *A. pectinata* os caranguejos, além de dificilmente realizarem polinização, destroem as estruturas reprodutivas das flores, e assim, comprometem a produção de frutos.

Como *B. antiacantha* é parcialmente auto-incompatível, mas não autógama, e *A. pectinata* é completamente auto-incompatível, ambas as espécies são dependentes de agentes para a polinização, aspecto que se relaciona com as estratégias que as duas espécies apresentam para atrair e manter os beija-flores. O comportamento territorial dessas aves em *A. pectinata* promove geitonogamia em boa parte das plantas agrupadas (possivelmente clones), enquanto que em *B. antiacantha* a distribuição espaçada dos indivíduos promove o comportamento "trap-line" dos beija-flores, favorecendo a xenogamia (ver Feinsinger 1978). A autopolinização facultativa em *B. antiacantha* representa uma alternativa para a frutificação, por exemplo, em indivíduos florescendo assincronicamente. A formação de frutos parece condicionada às interações entre os visitantes florais (caranguejos, beija-flores, abelhas) e à distribuição espacial dos indivíduos em cada espécie.

Aechmea pectinata e *Bromelia antiacantha* representam expressivas fontes de recurso alimentar para os beija-flores em Picinguaba, em função do número de indivíduos, da oferta de néctar e da extensão dos períodos em que florescem. Apresentam características em comum e pecularidades com relação ao habitat e hábito, à fenologia, à morfologia e à biologia floral, ao sistema reprodutivo e aos visitantes florais, aspectos que influem conjuntamente no espectro e na dinâmica de seus polinizadores.

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"What escapes the eyes, however, is a much more insidious kind of extinction: the extinction of ecological interactions."

Janzen, 1974