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THAMIRES OLIVEIRA REIS

Biologia floral de *Serjania paucidentata* DC. (SAPINDACEAE)

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Dissertação apresentada à Universidade Federal Rural da Amazônia e ao Museu Paraense Emílio Goeldi como parte das exigências do Programa de Pós-Graduação em Ciências Biológicas - Botânica Tropical para obtenção de grau de mestre em Botânica.

Área de Concentração: Morfologia e Sistemática Vegetal ou de Fungos.

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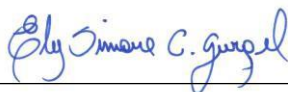
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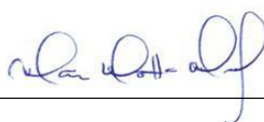
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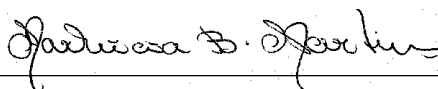
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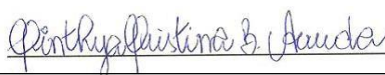
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À minha família, em especial à minha sobrinha Ana Cecília!

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“Na natureza, nada existe sozinho”

Rachel Carson

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RESUMO

Serjania paucidentata DC (Sapindaceae) é uma liana nativa do Brasil, frequente em áreas de borda florestal, capaz de colonizar áreas degradadas, colaborando nas etapas iniciais da restauração florestal. Este estudo descreve aspectos da biologia floral de *S. paucidentata* em populações naturais ocorrentes em áreas de restauração florestal em Paragominas, Pará, Brasil. A morfologia e o comportamento floral foram acessados em 16 plantas. Flores marcadas de polinização aberta foram observadas da pré-antese até três dias após antese, a fim de caracterizar a longevidade e a disponibilidade dos recursos aos polinizadores. O tamanho e aspecto dos verticilos nos morfo florais foram registrados com o auxílio de esteromicroscópio e microscópio eletrônico de varredura, e comparados por Análise de Variância, seguida do teste Tukey. Testou-se no campo, em diferentes morfo e idades florais, a receptividade estigmática com uma solução aquosa de peróxido de hidrogênio; a concentração de açúcar (% brix) e o volume (μ l) de néctar com auxílio de refratômetro portátil; e a presença dos osmóforos com solução de vermelho neutro. Os resultados mostram que *S. paucidentata* têm flores inconspícuas (4-5 mm), brancas, funcionalmente unissexuais, zigomorfas, nectaríferas e odoríferas. A antese inicia às 3:00 horas e senescência após 12 horas. No período do estudo, os tirso dos ramos marcados tiveram uma sequência temporal de apresentação de flores estaminadas-pistiladas- estaminadas, com não sobreposição de apresentação entre os morfos. As flores estaminadas têm gineceu rudimentar não funcional, e as flores morfologicamente bissexuadas são funcionalmente pistiladas com estames de anteras indeiscentes. As flores são tetrâmeras. As sépalas trimorfas e pétalas dimorfas. Os quatro apêndices das pétalas são convergentes pela margem pilosa e formam um pseudotubo floral, onde o néctar acumula, e possuem cristas amarelas que funcionam como guia nectarífero. Em ambos morfo-florais as estruturas reprodutivas são deslocadas para a porção anterior do receptáculo floral, e curvadas em direção às cristas dos apêndices das pétalas. Registrou-se a produção do néctar (0,6-1,2 μ l) desde a antese até o terceiro dia floral, sendo maior no primeiro dia, com uma concentração de açúcar entre 40-60%. Os osmóforos estão presentes principalmente no estigma das flores pistiladas e nas anteras e nas cristas das pétalas das flores estaminadas. No horário das 12:00 horas, o odor floral é suave, agradável, perceptível, quando se registrou uma abundante e diversa visitação de abelhas, mariposas, moscas, besouros, borboletas, vespas e beija-flores. Conclui-se que esta espécie tem uma aperfeiçoada e complexa apresentação floral, exhibe dimorfismo sexual do tipo andromonoico, porém funcionalmente monoico, com apresentação alternada dos morfos florais nos ramos e indivíduos estudados, indicativo do raro fenômeno da duodicogamia, que envolve fases sexuais alternadas dentro de um indivíduo.

Palavras chave: Monoícia. Duodicogamia. Nectários. Fenofases florais. Visitantes florais

ABSTRACT

Serjania paucidentata DC (Sapindaceae) is a liana native to Brazil, often found in forest edge habitats, and able to colonize degraded areas, making it an important species in the initial stages of forest restoration. This study describes aspects of the floral biology of *S. paucidentata* using natural populations in post-mining forest restoration areas in Paragominas, Pará State, Brazil. Morphology and floral behavior were assessed on 16 individual plants. Marked open-pollinated flowers were observed from pre-anthesis to three days after anthesis, in order to characterize longevity and resource availability to pollinators. The size and appearance of the whorls in the floral morphs were recorded with the aid of a stereomicroscope and scanning electron microscope, and compared using Analysis of Variance, followed by the Tukey test. Stigmatic receptivity with an aqueous solution of hydrogen peroxide, sugar concentration (% brix) and nectar volume (μl) with the aid of a portable refractometer, and the presence of osmophores with neutral red solution, were tested in the field at different flower morphs and ages. The results show that *S. paucidentata* has inconspicuous (4-5 mm), white, functionally unisexual, zygomorphic, nectariferous and odoriferous flowers. Anthesis begins at 3:00 a.m. with newly opened flowers senescing after 12 hours. During the study period, the thyrses of the marked branches had a temporal sequence of presentation of staminate-pistillate-staminate flowers, with no overlap of presentation between the morphs. Staminate flowers have rudimentary non-functional gynoecium, and morphologically bisexual flowers are functionally pistillate with indehiscent anther stamens. The flowers are tetrameres. The sepals are trimorphic and petals are dimorphic. The four petal appendages converge along the villose margin and form a floral pseudotube, where nectar accumulates, and have yellow crests that function as a nectar guide. In both floral-morphs, the reproductive structures are dislodged to the anterior part of the receptacle, and curved towards the appendage crests. Nectar production (0.6-1.2 μl) was recorded from anthesis to the third floral day, and was highest on the first day, with a sugar concentration between 40-60%. Osmophores are present mainly in the stigma of pistillate flowers and in the anthers and crests of petals of staminate flowers. At 12:00 a.m. the floral odor is soft, pleasant, noticeable, when there was an abundant and diverse visitation of bees, moths, flies, beetles, butterflies, wasps and hummingbirds. It was concluded that this species has a conspicuous and complex floral display, exhibits sexual dimorphism of the andromonoecious type, but functionally monoecious, with alternating presentation of floral morphs in the branches and individuals studied, indicative of the rare phenomenon of duodichogamy, which involves alternating sexual phases within of an individual.

Keywords: Monoecious. Duodichogamy. Nectary. Floral phenofases. Floral visitors

1 CONTEXTUALIZAÇÃO

Este trabalho faz parte do projeto “Como as interações ecológicas influenciam as atividades de mineração e seus esforços de restauração ambiental pós-mineração no município de Paragominas, área degradada da Floresta Amazônica Brasileira” desenvolvido pelo Museu Paraense Emílio Goeldi em parceria com a Companhia Mineradora de Bauxita Norsk Hydro do estado do Pará e a Universidade de Oslo da Noruega (Consórcio Brasil-Noruega - *Biodiversity Research Consortium - BRC*), cujo objetivo é determinar o efeito das atividades da mineração sobre as redes de interações entre plantas e animais e dar suporte à Companhia Hydro na escolha das estratégias de compensação e mitigação dos impactos de suas atividades, através da restauração ecológica das áreas mineradas. O projeto apresenta três enfoques de pesquisa: herbivoria, dispersão de sementes e polinização, no qual este estudo está inserido.

A liana *Serjania paucidentata* DC, uma Sapindaceae nativa do Brasil (FLORA DO BRASIL, 2020), foi escolhida para estudos de biologia floral após ter sido observada em área sob processo de restauração ambiental pós-mineração de bauxita, a pleno sol e ocupando as bordas da floresta adjacente. Ocorre em agrupamentos de indivíduos cujo os ramos entrelaçam entre si, frequentemente presos uns aos outros por gavinhas caulinares, formando extensos emaranhados (ou “moitas”), o que dificulta ou impossibilita a quantificação dos indivíduos em cada agrupamento.

De hábito pioneiro, as suas folhas recobrem o solo, contribuindo para a serapilheira, o que favorece os estágios iniciais da sucessão florestal e, conseqüentemente, com a recuperação da biomassa nessas áreas (SILVA; CORREA, 2019).

As suas flores de odor adocicado e com quatro discos nectaríferos (BARROSO *et al.* 1991; PEREIRA, 2014) atraem uma variedade de visitantes ao longo do dia, o que pode contribuir com a rede de interações biológicas planta-polinizador na área em restauração.

As lianas são propícias a se estabelecerem em áreas fragmentadas, com grande disponibilidade de luz, ocupando principalmente a borda da floresta (LAURANCE *et al.* 2001), onde servem de recursos alimentares para frugívoros e herbívoros (ARROYO-RODRÍGUEZ *et al.* 2015; MARTINS, 2009). Além disso, são utilizadas como suporte para a locomoção e/ou habitat para primatas (MADDEN *et al.* 2010; VIDAL; CINTRA, 2006; YOULATOS, 1999) e pequenos animais (JUNIOR; LEITE, 2007) e, contribuem com a diversidade dos polinizadores (MORELLATO, 1991) que, no caso dos fragmentos florestais,

o empobrecimento destes ou dos sistemas sexuais levam a alterações na produção de frutos e sementes e, conseqüentemente, no processo de regeneração natural, assim como modificam o fluxo gênico nas populações vegetais, com conseqüências desconhecidas a longo prazo (ENGEL; FONSECA; OLIVEIRA, 1998).

Melo & Reis (2007), destacam a importância de várias espécies do gênero *Serjania* como poleiros artificiais vivos que auxiliam no processo de restauração pela atração de polinizadores. Conhecer a biologia reprodutiva da liana *S. paucidentata* é importante para ajudar a determinar o seu potencial de contribuição ao processo de restauração em relação a sustentação das redes de polinização já que é uma espécie onde se verifica uma grande atratividade de visitantes florais, os quais podem ter importância na restauração ambiental.

Neste contexto desenvolveram-se as investigações sobre os aspectos da morfologia e biologia floral e da diversidade dos visitantes florais de populações naturais de *S. paucidentata* em área antropizada.

1.1 Referencial teórico

1.1.1 A família Sapindaceae

Sapindaceae é uma família monofilética, pertencente à ordem Sapindales (APG IV, 2016; BUERKI *et al.* 2010; GADEK *et al.* 1996) e composta por 144 gêneros e 1900 espécies (ACEVEDO-RODRÍGUEZ *et al.* 2017) de árvores, arbustos e trepadeiras herbáceas ou lenhosas presentes em regiões tropicais e subtropicais (ACEVEDO-RODRÍGUEZ *et al.* 2010; BARBOSA *et al.* 2013; FRAZÃO; SOMNER, 2016; METCALFE; CHALCK, 1950). Dentre elas, 418 espécies e 28 gêneros se encontram no Brasil (SOMNER *et al.* 2015), distribuídas entre quatro subfamílias: Dodonaeoideae, Hippocastanoideae, Sapindoideae e Xanthoceroideae (BUERKI *et al.* 2009).

As trepadeiras de Sapindaceae apresentam um par de gavinhas na base da raque; flores tetrâmeras ou pentâmeras, actinomorfas ou zigomorfas; nectários extra estaminais; fruto do tipo cápsula loculicida ou septífraga, baga, esquizocarpo com mericarpos alados, cocos drupáceos; sementes com ou sem excrescência (PEREIRA *et al.* 2016).

Sapindaceae possui espécies importantes como flora apícola (ALVES, 2013; GUARIM NETO; SANTANA; SILVA, 2000; MELO, 2008), na restauração ambiental (MELO; REIS, 2007) e com propriedades medicinais, ornamentais, econômicas, industriais

(GUARIM NETO; SANTANA; SILVA, 2000) e alimentares, com frequente utilização das raízes, folhas, frutos, sementes, madeira, casca, caule e árvore (GUARIM NETO; SANTANA; SILVA, 2000; MARTINS, 2009).

Dentre as espécies mais conhecidas na família, está a espécie nativa da Amazônia *Paullinia cupana* Kunth, popularmente denominada “guaraná” (PRANCE, 1997). Seus frutos e sementes têm usos medicinal, artesanal e como refrescos (GUARIM NETO; SANTANA; SILVA, 2000), especialmente na fabricação de refrigerantes (ACEVEDO-RODRÍGUEZ *et al.* 2010; PRANCE, 1997). O fruto também faz parte da dieta dos pássaros, que ingerem a polpa e dispersam as sementes pela floresta (PRANCE, 1997).

1.1.2 Biologia Floral e Polinização em Sapindaceae

As flores de Sapindaceae são pequenas, variando de 2,5 a 9 mm (PEREIRA *et al.* 2016), organizadas em inflorescências racemiformes terminais ou axiliares, ou em panículas axilares ou terminais (ACEVEDO-RODRÍGUEZ *et al.* 2010; PEREIRA *et al.* 2016). As flores são actinomorfas ou zigomorfas, bissexuais ou funcionalmente unissexuais, com sépalas e pétalas tetrâmeras ou pentâmeras; ovário dicarpelar, tricarpelar ou pluricarpelar e estigma inteiro, bifido ou trifido (ACEVEDO-RODRÍGUEZ *et al.* 2010; BARBOSA *et al.* 2013; LIMA; SOMNER; GIULIETTI, 2016; PEREIRA *et al.* 2016; WERYSZKO-CHMIELEWSKA; SULBORSKA, 2011).

Estudos reprodutivos realizados na família mostram variações em seus sistemas sexuais. Lenza e Ferreira (2000), ao estudar a biologia reprodutiva de *Serjania erecta* Radlk em uma vegetação de Cerrado no Brasil, identificaram a monoiccia (os órgãos reprodutores de ambos os sexos podem ser observados no mesmo indivíduo) na espécie. Entretanto, devido a fatores reprodutivos peculiares, ela pode apresentar dioica temporal.

O caráter monoico também é relatado em *Koelreuteria elegans* (Seem.) A.C. Sm. subsp. *formosana* (Hayata) (AVALOS *et al.* 2019), *P. weinmanniifolia* Mart (LIMA; SOMNER; GIULIETTI, 2016), *Xanthoceras sorbifolium* Bunge (ZHOU *et al.* 2019) e em espécies de *Acer*, como: *A. elegantulum* W.P. Fang & P.L. Chiu, *A. oblongum* Wall. ex DC, *A. pictum* subsp. *mono*, (Maxim.) H. Ohashi, *A. pseudoplatanus* L e *A. saccharinum* L (ACEVEDO-RODRÍGUEZ *et al.* 2010; AVALOS *et al.* 2019; ROSADO; VERA-VÉLEZ; COTA-SÁNCHEZ, 2018; SHANG; LUO; BAI, 2012; TAL, 2009).

O gênero *Acer* também pode apresentar espécies andromonoicas (presença de flores masculinas e hermafroditas no mesmo indivíduo) e dioicas (ocorrência de órgãos reprodutores

masculinos e femininos em indivíduos diferentes), como foi constatado por Rosado, Vera-Vélez e Cota-Sánchez (2018) nas espécies *A. ginnala* Maxim, *A. tataricum* L, no híbrido *A. ginnala* x *tataricum* L e *A. negundo* L. Outro sistema sexual observado na família é a androdioicia (flores masculinas e bissexuais em indivíduos distintos), identificada em *Nephelium lappaceum* L (GEORGE, 2019).

A estratégia sexual temporal, denominada duodicogamia, também pode ocorrer dentro de Sapindaceae, como observado nos gêneros *Acer* L., *Allophylus* L., *Cupania* L., *Dipteronia* Oliv., *Koelreuteria* Laxm., *Litchi* Sonn., *Sapindus* L., *Serjania* Mill, *Talisia* Aubl (ACEVEDO-RODRÍGUEZ *et al.* 2010; AVALOS *et al.* 2019; SHANG; LUO; BAI, 2012; YADAV; PANDEY; BHATNAGAR, 2016, 2019) e *Paullinia* (LIMA; SOMNER; GIULIETTI, 2016). Este tipo de estratégia constitui no aparecimento sequencial de três fases florais dentro de um indivíduo, geralmente com um padrão de floração masculino-feminino-masculino (FIELD; BARRETT, 2012; SATO, 2002; TAL, 2009) e mais raramente feminino-masculino-feminino (AVALOS *et al.* 2019; TAL, 2009) e, ainda feminino-masculino-masculino (TAL, 2009).

Flores pistiladas e estaminadas podem ser observadas no mesmo indivíduo ou na mesma inflorescência (LENZA; FERREIRA, 2000; LUO *et al.* 2017; ROSADO; VERA-VÉLEZ; COTA-SÁNCHEZ, 2018), mas não abrem no mesmo dia (LENZA; FERREIRA, 2000). As flores abrem normalmente pela manhã (AVALOS *et al.* 2019; GEORGE, 2019; LIMA; SOMNER; GIULIETTI, 2016; OLIVEIRA; CARVALHO; AONA-PINHEIRO, 2013), apresentam glândulas odoríferas (AVALOS *et al.* 2019; GEORGE, 2019) e apêndices petalóides com cristas amarelas, que funcionam como guias nectaríferos e se posicionam de modo a conterem o néctar (BARROSO *et al.* 2001) e que, por sua vez promovem a interação planta-animal (ACEVEDO-RODRIGUEZ, 1993; BARROSO *et al.* 2001).

O pólen e o néctar são as principais recompensas florais observadas em espécies de Sapindaceae (AVALOS *et al.* 2019; GEORGE, 2019; LENZA; FERREIRA, 2000; LIMA; SOMNER; GIULIETTI, 2016; OLIVEIRA; CARVALHO; AONA-PINHEIRO, 2013; ROY; PANDEY; BHATNAGAR, 2017). Em flores pistiladas, o néctar é o principal recurso oferecido, uma vez que, apesar de se registrar estames, as anteras são indeiscentes (AVALOS *et al.* 2019; GEORGE, 2019; LUO *et al.* 2017; SHANG; LUO; BAI, 2012; YADAV; PANDEY; BHATNAGAR, 2016, 2019). Nas flores estaminadas, verifica-se tanto a presença do pólen quanto do néctar. As suas anteras deiscentes expõem os grãos de pólen viáveis (AVALOS *et al.* 2019; GEORGE, 2019; LIMA; SOMNER; GIULIETTI, 2016; YADAV; PANDEY; BHATNAGAR, 2016, 2019).

Os visitantes florais são bastante diversificados. As flores são visitadas por moscas (ACEVEDO-RODRIGUEZ, 1993; AVALOS *et al.* 2019; GEORGE, 2019); mariposas, vespas, besouros (ACEVEDO-RODRIGUEZ, 1993; ALVES *et al.* 2014; ROY; PANDEY; BHATNAGAR, 2017), borboletas (ACEVEDO-RODRIGUEZ, 1993; GEORGE, 2019), formigas (ALVES *et al.* 2014), joaninhas (ROY; PANDEY; BHATNAGAR, 2017), a espécie de ave *Coereba flaveola* L (LENZA; FERREIRA, 2000) e abelhas (ACEVEDO-RODRIGUEZ, 1993; AVALOS *et al.* 2019; GEORGE, 2019; MORELLATO, 1991).

1.1.3 O gênero e a espécie

Serjania Mill é o gênero de maior representatividade dentro da tribo Paullinieae (Kunth) com 230 espécies de trepadeiras nativas da América Tropical e Subtropical (ACEVEDO-RODRÍGUEZ *et al.* 2010; BUERKI *et al.* 2009), ocorrentes na Caatinga, Cerrado, Campo Rupestre, Floresta de Galeria, Restinga, Savanas, Florestas de Terra Firme e de Várzea e, áreas perturbadas (ACEVEDO-RODRIGUEZ, 1993).

Serjania possui botões florais pistilados e estaminados na mesma inflorescência (BARROSO *et al.* 1991). Entretanto, o número de estudos ainda reduzido, não evidenciam as diferenças morfológicas entre os tipos sexuais florais (LENZA; FERREIRA, 2000; SILVA, 2009).

Os caracteres vegetativos são bastante considerados em estudos taxonômicos do gênero, onde os órgãos vegetais utilizados são caule (BARBOSA; COELHO; VIANA, 2018; SPRENGEL-LIMA; REZENDE, 2013), folhas e raque (ACEVEDO-RODRIGUEZ, 1993; FRAZÃO; SOMNER, 2016; PEREIRA, 2014; PEREIRA *et al.* 2016; SOMNER; FERRUCCI, 2009).

A sistemática do grupo também tem como caráter de importância a morfologia dos frutos esquizocárpicos com três mericarpos alados e parte seminífera distal (ACEVEDO-RODRIGUEZ, 1993; ACEVEDO-RODRÍGUEZ *et al.* 2017; BARBOSA; COELHO; VIANA, 2018; BARROSO *et al.* 1991), que podem ser dispersos pelo vento ou pela água (ACEVEDO-RODRIGUEZ, 1993; SILVA, 2009).

As peças florais também apresentam importância taxonômica em *Serjania* (ACEVEDO-RODRIGUEZ, 1993; BARBOSA; COELHO; VIANA, 2018; PEREIRA *et al.* 2016; SOMNER; FERRUCCI, 2009), tais como estames heterodínamos e pólen triangular (ACEVEDO-RODRÍGUEZ *et al.* 2017)

Em Somner e Ferrucci (2009) as sépalas e pétalas foram usadas na distinção taxonômica em *Serjania*, pela presença ou ausência de tricomas no cálice, pelo tipo de indumento, ou ainda pelo formato da crista observado nos apêndices das pétalas.

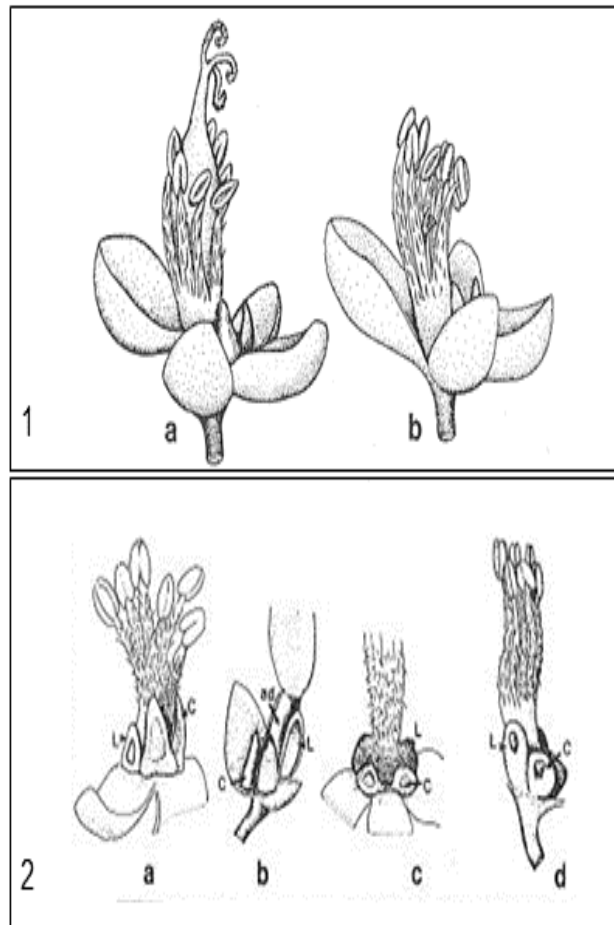
A separação quase total dos limbos ventral e dorsal das pétalas ocorre em *Nephelium*, *Blighia*, *Serjania* e gêneros afins, sendo que em *Serjania* juntamente com *Pancovia* e *Radlkofera* ocorrem as variações mais aperfeiçoadas e complicadas de ornamentação das pétalas (BARROSO *et al.* 1991).

Barroso *et al.* (1991) informa que “as pétalas desse tipo têm as porções dorsal e ventral distintamente separadas, ligadas apenas em uma pequena porção mediana, mantendo-se, porém, os bordos livres entre si”. Os autores também destacam que “o ápice do limbo ventral tem forma de coifa, com extremidade inclinada para baixo “[...] sobre o ápice dessa coifa assenta-se a giba, ou crista, que se distingue pela espessura maior e pelo colorido amarelo [...]”.

Além disso, em *Serjania* e gêneros afins, as pétalas são dimorfas: duas com limbo ventral do tipo simétrico e duas com o tipo assimétrico, nestes, a giba reduz a uma pequena saliência (BARROSO *et al.* 1991). As flores de *Serjania* são funcionalmente unissexuais, apesar das pistiladas apresentarem estames com anteras indeiscentes, e as estaminadas um pistilo rudimentar (ACEVEDO-RODRIGUEZ, 1993) (Figura 1; 2a-d) e são providas de evidentes discos nectaríferos com quatro glândulas (figura 1; 1a e b) (ACEVEDO-RODRIGUEZ, 1993; SOLÍS *et al.* 2017).

A espécie *S. paucidentata* DC é conhecida como cipó cururu ou cipó de pesca (BAKSH-COMEAU *et al.* 2016; PEREIRA *et al.* 2016), pois suas folhas são usadas como veneno para peixes (PRANCE, 1997). É encontrada em bordas de floresta (BAKSH-COMEAU *et al.* 2016), matas ciliares, cerrado, áreas perturbadas, florestas de terra firme (ACEVEDO-RODRIGUEZ, 1993) e de várzea (ACEVEDO-RODRIGUEZ, 1993; MAUÉS *et al.* 2011).

Figura 1 Flores pistiladas (1a) com anteras indeiscentes e flores estaminadas (1b) com pistilo rudimentar; 2. Discos nectaríferos em *Serjania* Mill



Fonte: ACEVEDO-RODRIGUEZ (1993).

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2 FLORAL BIOLOGY OF A NATIVE LIANA *Serjania paucidentata* DC. (SAPINDACEAE), IN A BAUXITE POST-MINING RESTORATION AREAS IN THE EASTERN BRAZILIAN AMAZON

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2.1 Introduction

The cururu vine *Serjania paucidentata* (Sapindaceae) DC, also known as the fishing vine, is a liana native to Brazil (Flora do Brasil 2020), belonging to the tribe Paullinieae (Baksh-Comeau et al. 2016; Buerki 2009; Pereira et al. 2016). The vine inhabits the forest edge, gallery forest, savannas, disturbed vegetation, terra-firme forest and varzea forest (Acevedo-Rodriguez 1993; Baksh-Comeau et al. 2016; Maués et al. 2011).

The species *S. paucidentata* plays an important role in human-altered ecosystems in the Amazon region, due to its capacity to thrive under harsh conditions, in nutrient-poor soils areas (Rodrigues et al. 2003), and with high temperatures (Bastos et al. 2005). In addition, the presence of samarid fruits, with winged mericarps favor wind dispersal (Barbosa et al. 2013; Pereira 2014; Pereira et al. 2016), which can contribute to rapid colonization of degraded environments.

Lianas are well adapted to fragmented tropical habitats, such as the forest edge, thriving under greater light availability (Laurance et al. 2001). They represent a significant portion of the floral diversity found in tropical forests (Morellato 1991; Polisel 2017), including the megadiverse Sapindaceae family (Morellato 1991; Nabe-Nielsen 2001).

The Sapindaceae family comprises about 144 genera and 1900 species of trees, shrubs and vines (Acevedo-Rodruiguez et al. 2017). Among species, monoecy is the most common

sexual system (Acevedo-Rodríguez et al. 2010; Luo et al. 2017; Rosado, Vera-Vélez and Cota-Sánchez 2018; Yadav, Pandey and Bhatnagar 2016, 2019; Zhou et al. 2019).

In the Sapindaceae, the staminate flowers present rudimentary pistils that are non-functional (Rosado, Vera-Vélez and Cota-Sánchez 2018). Morphologically perfect flowers (also called hermaphrodite or bisexual) have indehiscent anthers (Acevedo-Rodríguez 1993; Avalos et al. 2019; George 2019; Luo et al. 2017; Shang, Luo and Bai 2012; Yadav, Pandey and Bhatnagar 2016, 2019), that contain unviable pollen grains (Lima, Somner and Giulietti 2016); therefore, they are functionally pistillate (Acevedo-Rodríguez et al. 2010; Avalos et al. 2019; Solís et al. 2017; Zini, Solís and Ferrucci 2014).

In addition, a temporal sexual strategy called duodicogamy can also occur in the Sapindaceae, such as in: *Acer* L., *Allophylus* L., *Cupania* L., *Dipteronia* Oliv., *Koelreuteria* Laxm., *Litchi* Sonn., *Sapindus* L., *Serjania* Mill, *Talisia* Aubl. (Acevedo-Rodríguez et al. 2010; Avalos et al. 2019; Shang, Luo and Bai 2012; Yadav, Pandey and Bhatnagar 2016, 2019) e *Paullinia* (Lima, Somner and Giulietti 2016). This constitutes the sequential appearance of three floral phases within an individual, usually with a male-female-male flowering pattern (Field and Barrett 2012; Luo, Zhang and Renner 2007; Sato 2002; Snyder and Richards 2005; Tal 2009) and more rarely female-male-female (Avalos et al. 2019; Tal 2009) and, rarer still, female-male-male (Tal 2009).

Pollen and nectar are the main floral rewards observed in Sapindaceae (Avalos et al. 2019; George 2019; Lenza and Ferreira 2000; Yadav, Pandey and Bhatnagar 2016, 2019), and are attractive to a variety of floral visitors, such as flies, moths, wasps, beetles, butterflies, ants, birds, and bees (Acevedo-Rodríguez 1993; Alves et al. 2014; Avalos et al. 2019; George 2019; Lenza and Ferreira 2000; Morellato 1991).

Several studies of reproductive biology in Sapindaceae have already been developed, however they are still absent for *S. paucidentata*. They have nectariferous discs (Pereira 2014) that can be attractive to visitors (Agostini, Lopes and Machado 2014) and consequently be involved with reproduction.

Reproductive flowering studies involve phenology, floral biology, pollination biology and breeding systems (Tandon, Shivanna and Moham Ram 2003). These studies are important to understand developmental processes, contributing to species' maintenance, management, conservation, and more broadly, ecosystem regeneration (Moza and Bhatnagar 2007).

The objectives of this study are to: (1) describe the floral biology of *S. paucidentata* (2) characterize the morphology of the flowers and inflorescences of the species; (3)

characterize the floral behavior regarding the supply of resources to pollinators and distinguish taxonomic groups of visiting insects of *S. paucidentata*.

2.2 Material and Methods

2.2.1 Study area

This study was conducted from November 2018 to December 2019 in the area of the Hydro Bauxite Mining Company, located 70 km from the city of Paragominas, northeast Pará state (S03°15'38" W47°43'28"). The details of the floral biology study were carried out during three expeditions of 10 to 15 days, which took place in November 2018, September and November 2019.

The vegetation around the forest edge at the field site has a high diversity of plant species, mainly trees, native to Brazil, with a great abundance of *Rinorea flavescens* (Aubl.) Kuntze, *Inga laurina* (Sw.) Willd, *Bauhinia rutilans* Spruce ex Benth; *Sagotia racemosa* Baill, *Chrysophyllum amazonicum* T.D. Penn (Silva and Correa 2019).

The local climate is humid tropical, with an annual average precipitation of 1742.9 mm, temperature and relative humidity of 26.3° C and 81%, respectively (Bastos et al. 2005). The wettest period comprises the months of January to March, while the driest period is from July to August (Carvalho, Costa and Oliveira 2005). Soils are Yellow Oxisols; Yellow Ultisols; Plinthosols, Gleissolos and Neosols (Rodrigues et al. 2003). Although the Hydro Bauxite Mining Company's soil has high cation exchange capacity (CEC), it is acidic and saturated in aluminum (Pereira and Souza 2019).

This work was part of a multidisciplinary project, developed by the Museu Paraense Emílio Goeldi in partnership with the Norsk Hydro Bauxite Mining Company in Pará state and the University of Oslo in Norway, which aims to understand the role of ecological interactions in post-mining restoration processes.

2.2.2 Study species

The caruru vine *Serjania paucidentata* is found in forest edge (Baksh-Comeau 2016), with individuals growing in large aggregations, with their branches intertwined forming large populations, which can climb over other trees and vines, using them as support, or cover the soil in bauxite post-mining natural regeneration areas of Hydro Paragominas (Fig 1a and 1b).



Figure 1 Population of *Serjania paucidentata* in Brazilian eastern Amazon, Paragominas, Pará, Brazil: a) horizontal landscape view of the forest edge area highlighting the arboreal vegetation structure near the impacted area; b) detail of pioneer habit of the species covering the soil in bauxite post-mining restoration areas; c) marked and bagged inflorescences for the experiments; d) Thyrses-type inflorescences with multi-flowering cincinnus.

Voucher specimens of *S. paucidentata* were deposited in the herbarium João Murça Pires (MG) of the Museum Paraense Emílio Goeldi (MPEG) and in the herbarium of Embrapa Amazônia Oriental (IAN) Belém, Pará, Brazil (Number MG: 239506 to 239507, 239513 to 239516 and number IAN: 197766, 197769 to 197774).

2.2.3 Reproductive phenology

To characterize the flowering and fruiting period of the species, in addition to expeditions to collect detailed information on floral biology, monthly expeditions during one year to the study area were carried out, between November 2018 and November 2019, when the presence or absence of flowering and fruiting events in *S. paucidentata* plants were registered.

2.2.4 Floral Biology

2.2.4.1 Morphological and morphometric analysis

The staminate (n=20) and pistillate (n=20) flowers were collected and preserved in 70% ethyl alcohol for morphological and morphometric analysis, and also fixed in Formalin Acetic Acid and Ethanol (FAA 70%) for 24 hours and preserved in 70% ethyl alcohol (Johansen 1940) for observation in Scanning Electron Microscope.

Samples of ten flowers were dried at critical point and covered with a thin layer of gold (Robards 1978) before the nectaries were examined with a Scanning Electron Microscope (Tescan Mira 3 Microscopy) in the laboratory of scanning electron microscopy of the Museu Paraense Emílio Goeldi, Belém, Pará, Brazil.

To verify morphological differences between staminate flowers at the beginning and end of the reproductive season (Yadav, Pandey and Bhatnagar 2016), samples of this floral type were collected in September and November, the beginning and end of population flowering in the studied area.

In addition, pistillate flowers collected in November were also compared with staminate flowers collected in September and November. Measured flowers (10 staminate for september, 10 staminate for November, and 20 pistillate) were selected from sampled inflorescences and individuals.

We measured filament length, sepals, petals, and appendage length/width (Fig 2, and Fig 3), with a reading scale ruler directly from structures photographed with a digital camera mounted on a stereoscopic microscope (stereo-microscope Leica, software LAS V4.12).

To verify the intra-floral variation of sepals, petals, and appendages, we performed Analysis of Variance (ANOVA) models, with the posthoc Tukey test to significative of included parameters. We then verified morphological differences between staminate flowers at the beginning and end of the reproductive season (Yadav, Pandey and Bhatnagar 2016), as well as differences in pistillate flowers. To this, we ran three Principal Components Analyses (PCA) with morphometric data of each structure: (i) petal length and width, (ii) sepal length and width, and (iii) appendage length and width. To determine significant differences among flowers groups, we ran an ANOVA with the first two principal components of the PCA. All presented analyses and graphs were produced using R software (VERSION 4.1) (R Core Team, 2022).

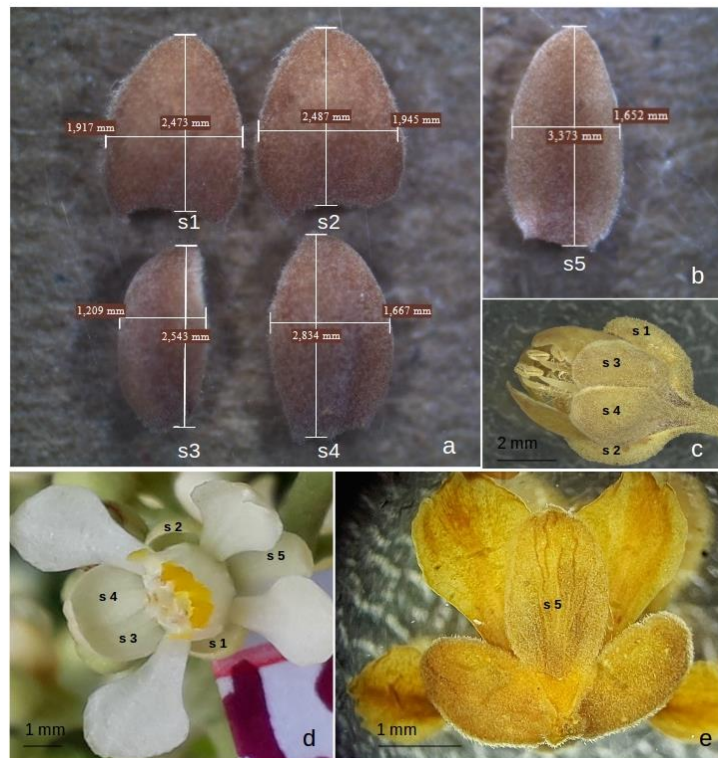


Figure 2 *Serjania paucidentata* DC (Sapindaceae). Morphometric analysis of sepals: a) external lateral sepals (s₁ and s₂) and anterior emarginate inner sepal (s₃ and s₄); b) posterior inner sepal (s₅); c) sepals arrangement (s₁ to s₄); d) sepals arrangement (s₁ to s₅); e) location of posterior inner sepal

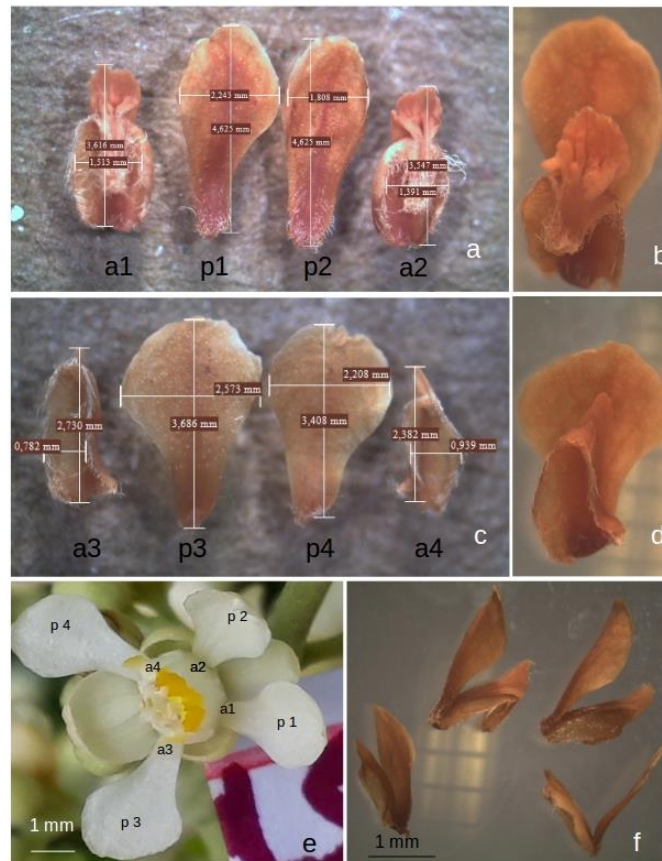


Figure 3 *Serjania paucidentata* DC (Sapindaceae). Morphometric analysis of petals: a) posterior petals (p₁ and p₂) and respective appendage (a₁ and a₂); b) posterior petal detail, showing appendage with crest at the apex; c) lateral petals (p₃, and p₄) and respective appendage (a₃ and a₄); d) lateral petal detail, showing appendage with crest at the apex; e) petals and appendages arrangement (p₁ to p₄ and a₁ to a₄); f) adnate appendages to posterior and lateral petals details.

2.2.4.2 Floral phenophases and stigma receptivity

Floral morphology and floral biology of *S. paucidentata* were assessed on 16 plants each separated by at least 100 m. Marked flowers from open pollination were observed from pre-anthesis to three days after anthesis to characterize: 1) longevity, 2) floral resources and attractants, 3) petals and sepals positioning, 4) style growth, and 5) stigmatic lobes distention.

We evaluated the receptivity of the stigma on tagged and bagged pistillate flowers using the rapid drop hydrogen peroxide test (H₂O₂) at 3% (Dafni et al. 2005). To accomplish this, we applied 10µL of H₂O₂ on the stigma surface with a micropipette (Micropipette 1–10

μL), after which observations were carried out with the aid of a stereomicroscope. We evaluated stigmas every three hours ($n=3$ plants; 3 flowers/plant), after the beginning of anthesis at 3:00, 6:00, 9:00, 12:00, 15:00 and 18:00) on the first day of anthesis, and at 03:00 and 6:00 in the second day.

2.2.4.3 Nectar presentation

Nectar sugar concentration (% brix) and volume (μl) from marked and bagged flowers (staminate and pistillate) (Fig 1c) was recorded at five intervals (3:00, 6:00, 9:00, 12:00, 15:00) on the first day of the anthesis, and at two intervals (9:00 and 12:00) on the third day, on three plants (4 flower/time/plant; 45 flowers in total), with the aid of glass microcapillaries (1 μl) and hand-held refractometer, with the nectar collected from a newly detached flower.

2.2.4.4 Location of the osmophores

To ascertain the activity of floral secreting glands (osmophores), we detached open staminate and pistillate flowers ($n= 2$ plants; 2 flowers/plant/sex flower) and immersed them in an aqueous neutral red solution (0.1%, distilled water) (Vogel, 1962 apud Dafni et al. 2005). Flowers were stained for exactly 60 min, after which, flowers were rinsed with distilled water and photographed using a stereomicroscope.

2.2.5 Floral visitors

Insect flower visitors (total $N=168$ insects) were collected with entomological net soon after anthesis until the beginning of flower senescence, at the following times: 4:00, 5:00, 6:00, 7:00, 8:00, 9:00, 10:00, 11:00 and 14:00, 16:00 (on aggregations of five plants; for 10 minutes/agregation/two collectors) in November 2018.

Sampled specimens were stored individually and killed in eppendorf flasks containing a cotton swab soaked in Ethyl Acetate.

All sampled insects were sent to the Entomological Laboratory of the Embrapa Amazônia Oriental, where they were initially kept in the freezer and then were sorted, mounted on entomological pins, labeled, quantified and where they are deposited. Identification keys and specialist consultations were used for taxonomic identification of the species.

2.3 Results

2.3.1 Reproductive phenology

The vegetative growth period of *S. paucidentata* occurred between the months of March and July. The flowering period began in mid-August and lasted until December, with September to October being the period in which the largest number of flowering individuals (> 80%) was observed. The fruits began their development in October, and dispersed seeds in December to February. The fruit is dry, indehiscent and schizocarpic with three winged mericarps.

2.3.2 Floral Biology

2.3.2.1 Morphological and morphometric analysis

S. paucidentata has thyrses-type inflorescences, with multi-flowering cincinnus (Fig. 1c, d).

Each thyrses has an average length of 19 cm ($\pm 3,5$ cm; n=30 thyrses), with 32 buds (± 12 buds; n=30), and 16 open flowers per day (± 6 flowers; n=30). At the base of the inflorescence a pair of tendrils can be seen.

Pistillate and staminate flowers can occur on the same inflorescence, but the individuals studied had a sequence of staminate-pistillate-staminate flowers on the marked branches, with the pistillate phase lasting between one to three days, whereas the staminate phase was much longer, typically lasting more than five days.

Pistillate and staminate flowers are inconspicuous (4 to 6 mm in length and width, n=40 flowers), functionally unisexual, zygomorphic, and scented.

The calyx of pistillate and staminate flowers is tetramerous, formed by outer and inner sepals. The two outer lateral sepals (Fig. 2a s₁ and s₂) are light green, cucullate and smaller ($2\pm 0,3$ mm in length, n=40 flowers) than the inner ones. The inner sepals are white and are located on the anterior and posterior part of the flower. The anterior emarginate inner sepals ($2,8\pm 0,3$ mm in length, n=40 flowers) are cucullate, connate at the base and bifurcated at the top, which makes the calyx tetramer (Fig. 2a s₃ and s₄). The posterior inner sepal ($3\pm 0,4$ mm in length, n=40 flowers) is elliptical and with a slightly truncated base (Fig. 2b).

The pistillate and staminate flowers have white tetramerous corolla, formed by two posterior ($4\pm 0,4$ mm in length, n=40 flowers) and two lateral ($4\pm 0,4$ mm in length, n=40

flowers) infundibuliform petals (Fig. 3a, c, e). Petals of this type have distinctly separated dorsal and ventral limbs, connected only in a small proximal median portion, keeping the edges free from each other (Fig. 3b, d, f). The apex of the ventral limb has the shape of a hood, with an extremity sloping downwards. At the apex of this hood sits the crest, which is greater thickness and yellow in color (Fig. 3b, d).

In *S. paucidentata* the petals are dimorphic, two with ventral limb of the asymmetrical type with a more developed crest (Fig. 3b) and two with the symmetrical type with reduced crest (Fig. 3d).

Analyses of morphometric differentiation revealed the biggest morphological differences were between staminate and pistillate flowers. The largest portion of the variation was explained by the x-axis (PC1), and associated with the sepal group. That is, the morphometric variation that separated the three groups (pistillate, staminate September and staminate November) was more determined by the morphometry of the sepals than that of the petals or appendages (Fig. 4).

Similarly, the only morphometric grouping that distinguished flowers collected in September and November were the sepals. That is, November and September staminate flowers presented different sepal structures, with November staminate sepals being more similar to pistillate sepals. The sepals of September are bigger than those of staminate flowers collected in November (Fig. 5).

The staminate flowers have androecium with eight heterodynamous stamens, five long ($2\pm 0,4\text{mm}$, $n=40$ flowers) and three short ($1,7\pm 0,2\text{mm}$, $n=40$ flowers); the anthers ($0,5\pm 0,08\text{mm}$, $n=40$ flowers) are dehiscent, biteca, rimose and with pubescent filiform filament and dorsifix insertion. Staminate flowers have a vestigial pistil ($0,7\pm 0,12\text{mm}$, $n=20$).

The pistillate flowers have heterodynamous stamens, bitecal and indehiscent anthers with dorsifix insertion, which can be considered staminodes. The gynoecium is tricarpelar, with superior ovary ($1,9\pm 0,2\text{mm}$, $n=20$), trilocular, uniovular, axial placentation and trifid style ($0,7\pm 0,1$; $n=20$).

In both flower morphs, the reproductive structures are displaced to the anterior portion of the floral receptacle and curved towards the crests of the petal appendages (Fig. 6c).

The nectaries of pistillate and staminate flowers are extrastaminal, yellow-green and four orbicular discs (Fig., 6c, d, f, g, h). We found open stomata on the upper part of the nectary disc with contents, probably nectar (Fig. 6h), and tector trichomes at the base and junction of the nectary.

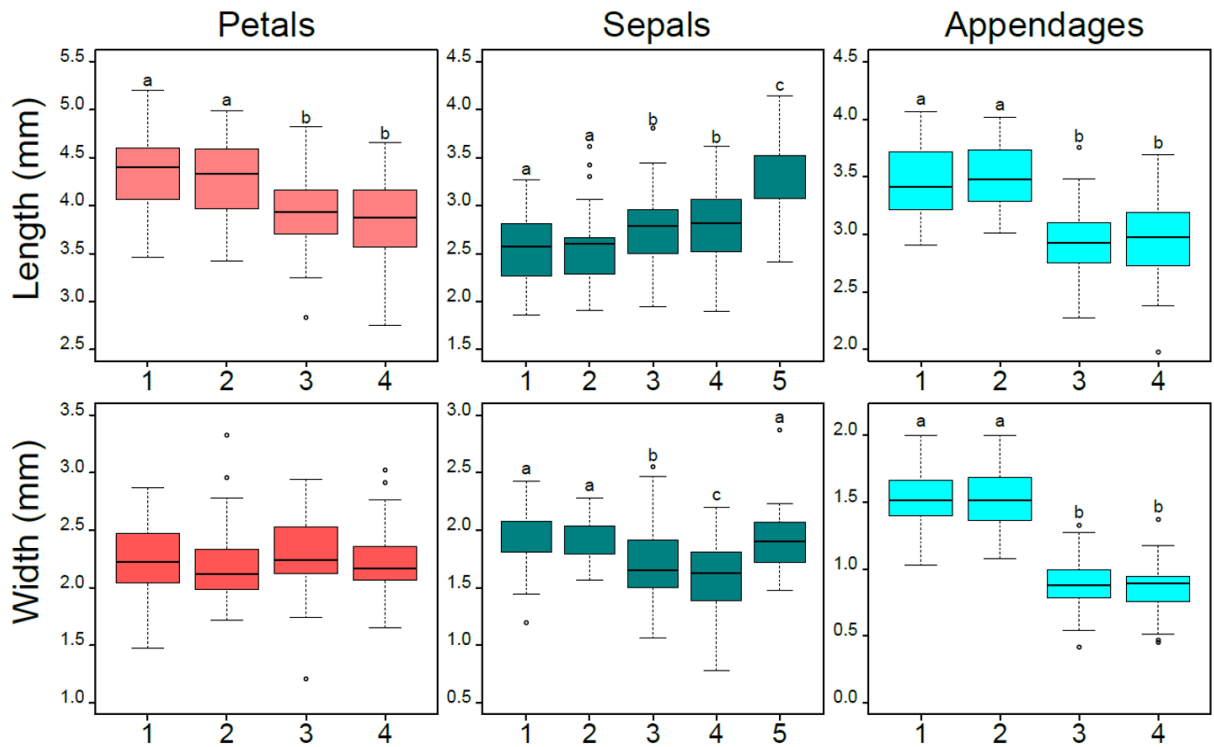


Figure 4 *Serjania paucidentata* DC (Sapindaceae). Intra-floral variation of structures of petals, sepals and appendages in Paragominas, Pará. The numbers (1 to 5) represent the position of floral whorls (see Fig 3 for more details of whorls)

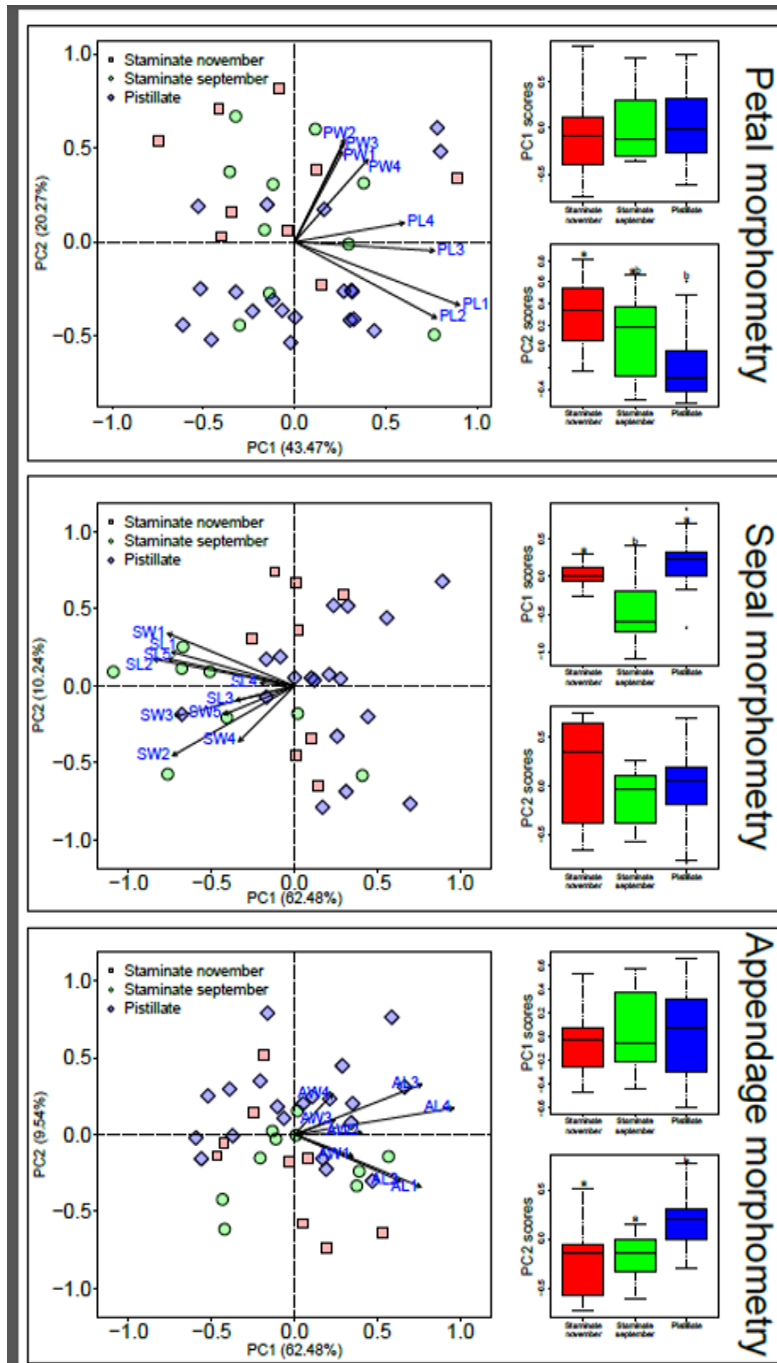


Figure 5 *Serjania paucidentata* DC (Sapindaceae) Morphological inter-floral differences between staminate flowers at the beginning september and end november of the reproductive season and pistillate flowers

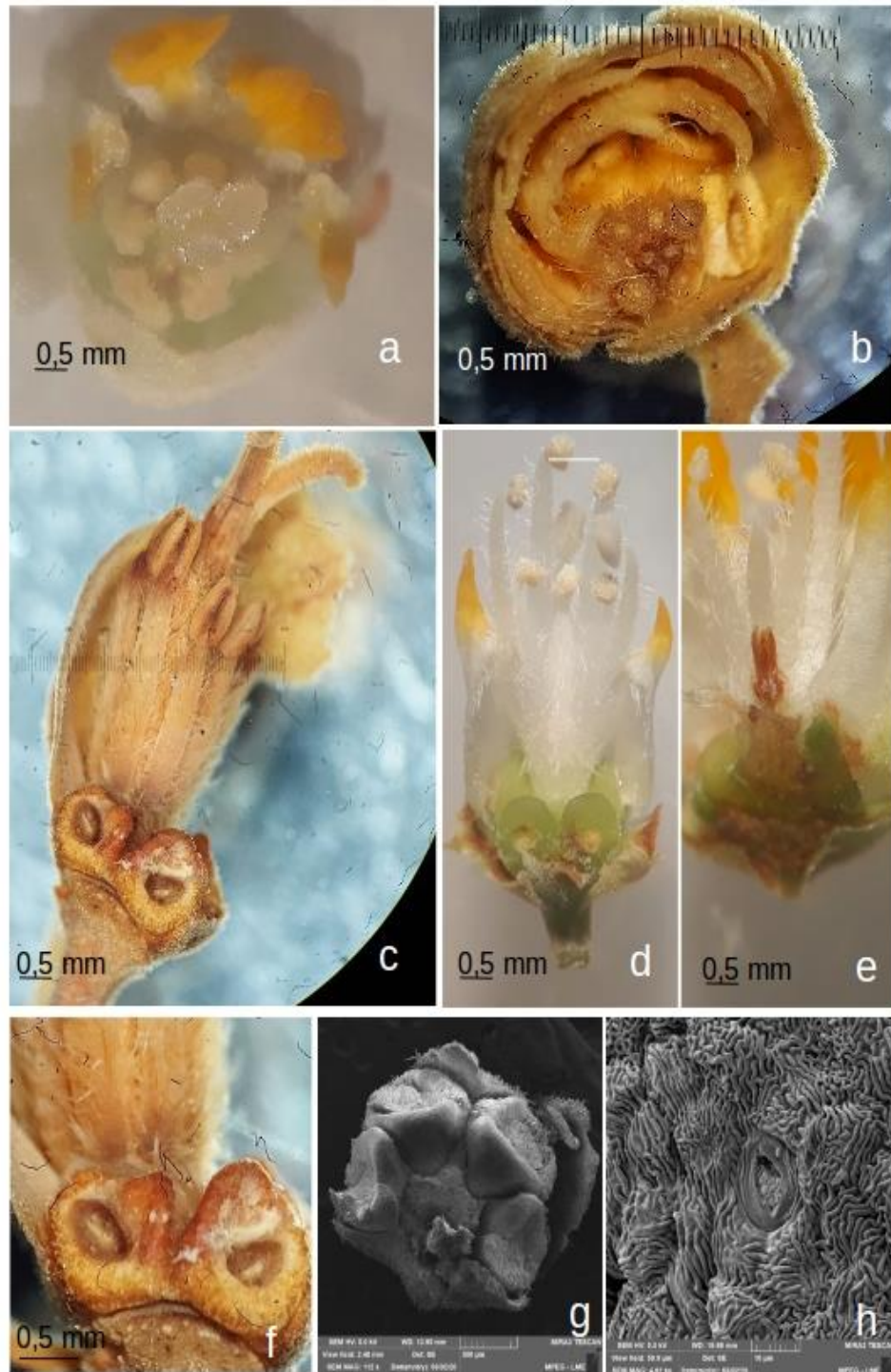


Figure 6 Extrastaminal nectaries of *Serjania paucidentata*: a-b) frontal view of the pistillate flower, showing the intrafloral space between stamens and petals, where the nectaries accumulate nectar; c) side view of the pistillate flower, showing the flower's zygomorphic symmetry; d) color nectary detail; e) vestigial pistil located between the stamens; f) view of a lateral (left) and posterior (right) nectary lobe; g-h) photomicrography in scanning electron

microscopy showing four nectariferous lobes, two bigger (posterior lobes) and two smaller (lateral lobes) (g) and open stomata in the upper part of the nectary (h)

2.3.2.2 Floral phenophases and stigma receptivity

The species has two types of flowers in the same tyrsos and the floral phenophases are represented (Fig. 7, 8 and 9). We observed alternating presentation of floral morphs in the branches and individuals studied, indicative of the rare phenomenon of duodichogamy, which involves alternating sexual phases within of an individual. The duration of each reproductive phase at the individual level has not yet been investigated.

Flower buds of both floral types open around 03:00 (Figs. 7, 1a-b and 8, 1a-c). Staminate (Fig. 7, 2a-b) and pistillate (Fig. 8, 2a-c) flowers are fully open at 06:00. Sepals and petals begin closing movement at 12:00 (Fig. 7, 4a-b and 8, 4a-c). Flowers show a more evident closing senescence movement around 15:00 (Fig. 7). The petals and sepals are fully closed at 18:00 (Fig. 7 and 8).

Staminate flowers on the second day post-anthesis close completely, but their anthers continue to release pollen grains and producing nectar (Fig. 9). Pistillate flowers on the second day produce nectar and have receptive stigma at 03:00 (Fig. 10).



Figure 7 Floral phenophases of the first day-old staminate flowers of *Serjania paucidentata*: 1a-b) floral anthesis at 3:00; 2a-b) open flowers showing details of anthers with pollen at 6:00; 3a-b) fragrant flowers with petals and sepals fully distended with abundant nectar and pollen at 09:00; 4a-b) flowers with pollen and a change in the position of the petals and sepals, which initiates the closing movement by senescence at 12:00; 5a-b) flowers with pollen and an evident closing movement by senescence at 15:00; 6a-b) Fully closed flowers with pollen at 18:00



Figure 8 Floral phenophases of one day-old pistillate flowers of *Serjania paucidentata*: 1a-c) floral anthesis at 3:00; 2a-c) open flowers showing details of the position of whorls, hyaline stigmas and indehiscent anthers, and stigmatic receptivity at 6:00; 3a-d) fully open flowers, distended and receptive stigmas and indehiscent anthers at 09:00; 4a-c) flowers with brown anthers, receptive stigma and initial closing movement by senescence at 12:00; 5a-c) flowers with distended and receptive stigmas and evident closing movement by senescence at 15:00; 6a-c) flowers with petals and sepals closing, brown anthers and receptive stigma at 18:00

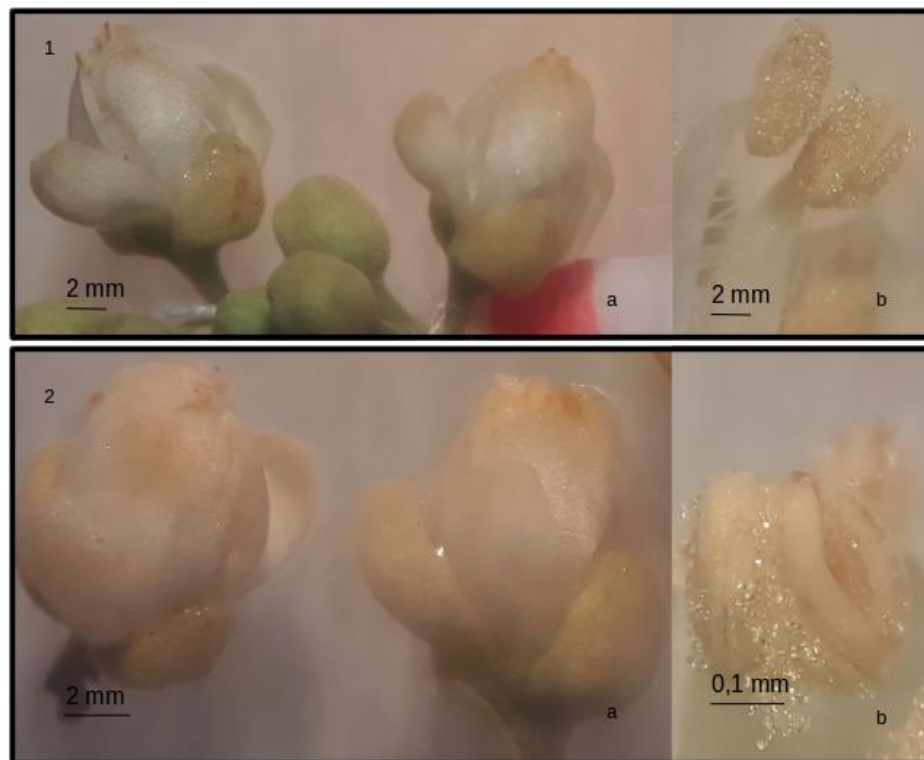


Figure 9 Floral phenophases of the staminate flowers of *Serjania paucidentata* on the second day following anthesis: 1a-b) fully closed flowers, anthers releasing pollen grains at 03:00; 2a-b) flowers completely closed and anther details with pollen grains at 06:00.



Figure 10 Floral phenophases of the pistillate flower of *Serjania paucidentata* on the second day old: 1a-d) The petals and sepals are completely closed at 03:00, but they produce nectar and have receptive stigmas; 2a-b) senescent flowers, showing the distended stigma; 3a-b) flowers on second and third day following anthesis.

2.3.2.3 Nectar presentation

On the first day of anthesis, staminate flowers had the highest nectar production at 15:00 ($1.23 \pm 0.68 \mu\text{l}$; $n = 3$ plants; 4 flowers/plant), while for pistillate flowers it was at 9:00 ($0.63 \pm 0.13 \mu\text{l}$; $n = 4$ flowers/3 plants). On the second and third days (at 9:00) we recorded a nectar production between 0.2 and 0.5 μl in the evaluated pistillate and staminate flowers ($n=8$). The average sugar concentration of the nectar was 40% (°Brix) in pistil flowers and 60% (°Brix) in staminate flowers.

2.3.2.4 Location of the osmophores

The sweet odor of both floral types was perceptible at 7:00, with greater intensity at 12:00. In staminate flowers, osmophores were located in the anthers and crests of the petals, and in pistillates were mainly present on the stigma.

2.3.3 Floral visitors

We identified six orders of insects visiting the flowers of *S. paucidentata* (Fig. 11), with the order Hymenoptera being the most represented. Among the Hymenoptera, the most prominent families were Vespidae and Apidae (Fig.12), with a high frequency of visitors in the morning (Fig. 13).

Insects interact with all morphs and reproductive organs of flowers (Fig. 14a). Insects, when visiting the flowers, contacted the reproductive whorls due to their positioning, following the signaling and odor of the flower's modified petals and sepals (Fig. 14 c-f). We also observed the presence of hummingbirds visiting *S. paucidentata* flowers in the morning and afternoon.

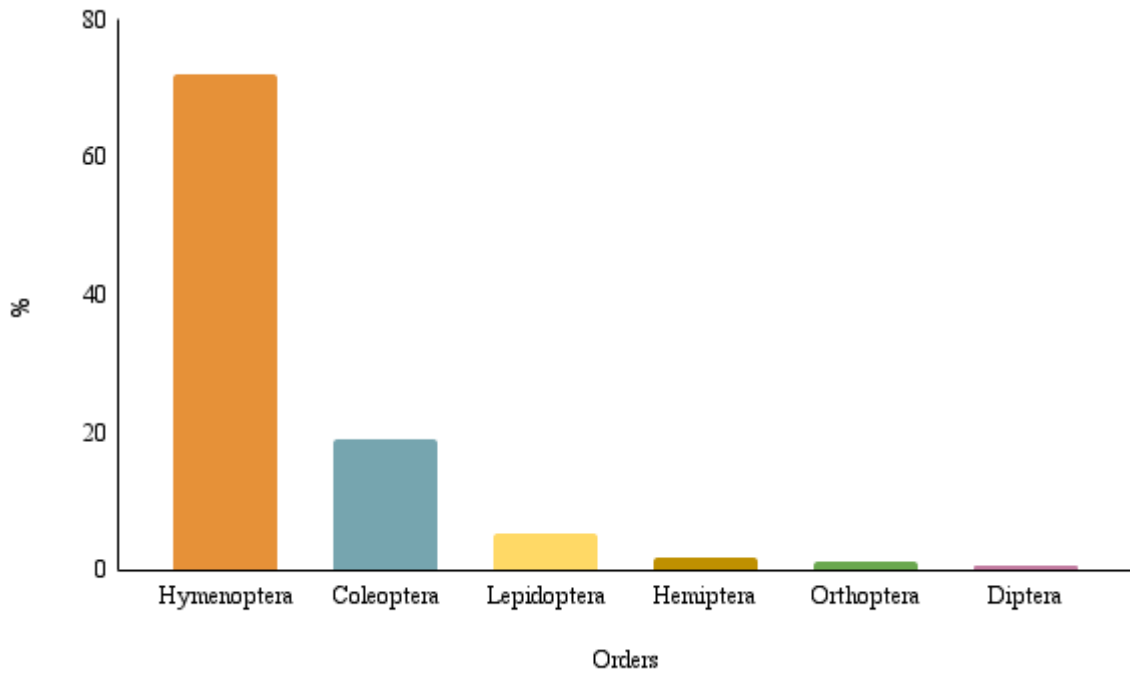


Figure 11 Relative frequency of floral visitors orders (total N=168 insects) in *Serjania paucidentata* in a forest edge area, Paragominas, Pará.

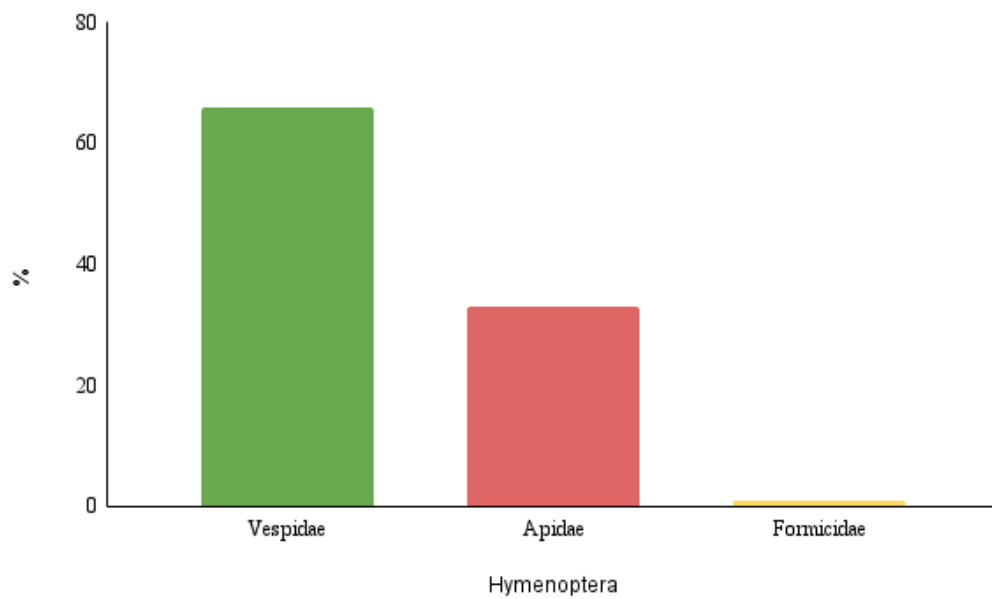


Figure 12 Relative frequency of floral visitors Hymenoptera collected (total N=121 insects) in flowers of *Serjania paucidentata*. Paragominas, Pará.

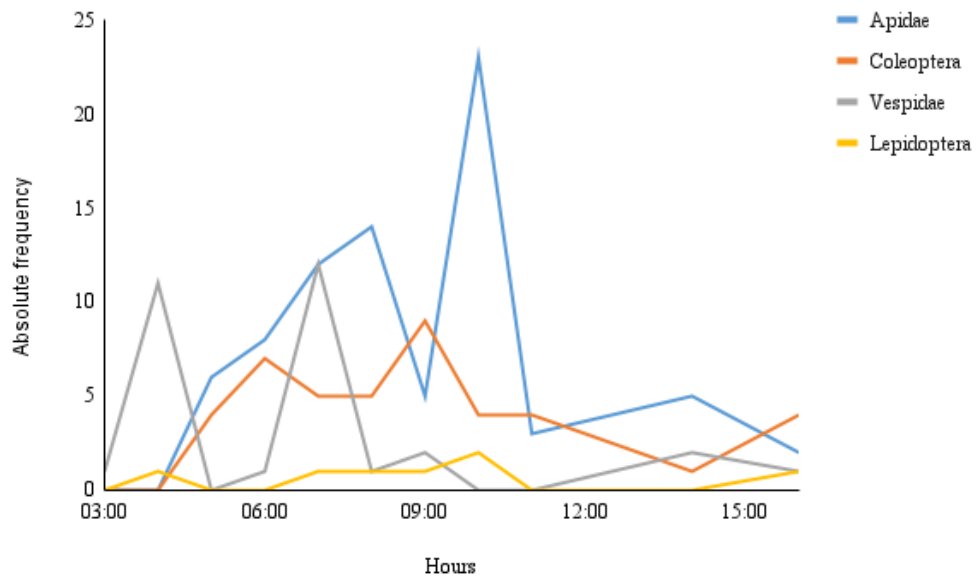


Figure 13 Absolute frequency of number of floral visitors in *Serjania paucidentata* throughout the day. Paragominas, Pará.



Figure 14 Positioning of petals (p₁ to p₄), sepals (s₁ to s₅) and appendage (a₁ to a₄): a-b) floral visiting insects showing their interaction with the floral whorls of *Serjania paucidentata* c-f). Paragominas, Pará.

2.4 Discussion

This study showed that *S. paucidentata* is a monoecious species. This sexual system is frequent in the sapindales (Gupta, Shivanna and Mohan Ram 1996; Lee, Kang and Park 2018; Pérez, Herrero and Hormaza 2019; Tavares et al. 2020), and in the family Sapindaceae (Lima, Somner and Giulietti 2016; Yadav, Pandey and Bhatnaga 2016; Luo et al. 2017; Wang et al. 2017; Rosado, Vera-Velez and Cota-Sanchez 2018; Zhou et al. 2019).

Additionally, we observed cycles of staminate-pistillate-staminate flowers in all tyrese and branches analysed within an individual, which may indicate the existence of a rare temporal sexual strategy, duodichogamy, which involves three alternating sexual phases within individuals. The duration of each reproductive phase at the individual level has not yet been investigated.

Monoecy, whether associated with dichogamic, heterodichogamic or duodicogamic temporal distribution patterns of flower morphs, is an important plant crossing strategy, because it reduces self-pollination and favors cross-pollination (Avalos et al. 2019; Lima, Somner and Giulietti 2016; Sato 2002).

Dichogamy might be selected through male fitness, rather than female fitness as a mechanism to reduce sexual interference (Routley and Husband 2003), thus maintaining the pollination accuracy.

Dai and Galloway (2011), according to experimental evidence with a dichogamous and hercogamic species, argue that the lack of difference in female fitness under varied levels of sexual interference indicates that male function is more likely to play a role in shaping floral traits that reduce sexual interference.

The extra-staminal floral nectary observed in *S. paucidentata* is common in other species of Sapindaceae (Avalos et al. 2019; Solís et al. 2017). Consisting mainly of carbohydrates (Nicolson and Thornburg 2007; Nepi et al. 2009; Demarco 2017; Antón, Komóm-Janczara and Denisow 2017; Chwil, Kostryco and Matraszek-Gawron 2019), floral nectar is an offered reward to animals (Agostini, Lopes and Machado 2014).

In relation to the supply of nectar in *S. paucidentata* flowers, our data show that this species exhibits highly elaborate and zygomorphic flowers, with four petal appendages that act as signaling structure for insect visitors, and converge along the villose margin forming a floral pseudotube, where nectar accumulates, preserving its quality. The yellow crests in the petal appendages may function as a nectar guide, as described by Lima, Somner and Giulietti (2016) for the specie *Paullinia weinmanniifolia* Mart.

In this study, many insects were observed visiting the flowers of *S. paucidentata*, mainly insects of the Coleoptera, Hymenoptera and Lepidoptera orders. The frequency of insect visitation can be defined by quantity of amino acids present in the nectar (Antoń, Komoń-Janczara and Denisow 2017; Nicolson and Thornburg 2007) and by the large supply of pollen from the more abundant staminate flowers, as individual plants offer pollen for longer periods in the studied aggregations of this species.

Monoecy, duodichogamy, the formation of extensive groups of individuals of *S. paucidentata*, which increases the proximity of flowers from different individuals, is a feature that allows the offer of pollen and nectar in different time periods for pollinators and ensures efficiency of cross-pollination. This, added to the fact that the species is a pioneer plant and very abundant at the bauxite post-mining restoration areas, make *S. paucidentata* a potential key species for the initial phases of the restoration process.

This activity will support the palynology team by providing specimens (insects) for analysis of the pollen grains adhered to the surface of the body of the insects, for future pollination networks studies.

2.5 Conclusion

We conclude that this species has an extensive and complex floral display, exhibits sexual dimorphism of the andromonoecious type, but is functionally monoecious, with the rare reproductive phenomenon, duodicogamy, which involves alternating sexual phases within of an individual.

Authors' contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Thamires Oliveira Reis, Marivana Borges Silva, Ely Simone Cajueiro Gurgel and Ana Cristina Andrade de Aguiar Dias. The first draft of the manuscript was written by Thamires Oliveira Reis and Marivana Borges Silva, and all authors

commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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