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Plant anatomy: history and future directions

Leaf traits and herbivory in a resin-producing plant species growing in floodable and non-floodable areas of the pre-Amazonian white-sand forest

Maria Ivanilde de Araújo Rodrigues[1,2], *Elza Maria Guimarães Santos*[1,3], *Juan de Nicolai*[1,4]
& *Tatiane Maria Rodrigues*[1,5,6]

Abstract

Plant species in the white-sandy forests are subject to unstable soils, high salinity, luminosity, extreme temperatures, and flooding caused by tidal cycles. *Protium heptaphyllum*, a tree species in the Burseraceae family known for its resin production, occurs in both floodable and non-floodable areas. We investigated differences in the accumulated herbivory indexes in leaves during the leaflet lifespan and correlated these data with leaf morphoanatomical traits in plants from floodable and non-floodable areas. Samples of young and mature leaves were processed using standard plant anatomy techniques. The percentage of leaf area consumed by herbivores and quantitative morphoanatomical data were subjected to MANOVA and ANOVA. Herbivory indexes of young and mature leaves were similar between plants from floodable and non-floodable areas. The morphoanatomical features of young leaves were also similar in plants from both areas. However, mature leaves from individuals in the floodable area exhibited longer leaflets and a higher abundance of wider secretory canals compared to plants from the non-floodable area. We suggest that most leaf consumption by herbivores occurs during the early stages of leaf development when there are fewer chemical defenses, and the leaflets are more tender.

Key words: anatomy, “breu-branco”, flooding, leaf, herbivory, restinga.

Resumo

As espécies vegetais das restingas estão sujeitas a solos instáveis, alta salinidade e luminosidade, temperaturas extremas e inundações causadas pelos ciclos das marés. *Protium heptaphyllum*, uma espécie arbórea de Burseraceae conhecida pela produção de resina, ocorre em áreas inundáveis e não inundáveis. Nós investigamos a ocorrência de diferenças nos índices de herbivoria acumulada durante o desenvolvimento dos folíolos e correlacionamos esses dados com as características morfoanatômicas das folhas em plantas de áreas inundáveis e não inundáveis. Amostras de folhas jovens e maduras foram processadas conforme técnicas usuais em anatomia vegetal. A porcentagem de área foliar consumida pelos herbívoros e os dados morfoanatômicos quantitativos foram submetidos à MANOVA e à ANOVA. Os índices de herbivoria de folhas jovens e maduras foram semelhantes entre plantas de áreas inundáveis e não inundáveis. As características morfoanatômicas das folhas jovens também foram semelhantes nas plantas de ambas as áreas. Entretanto, folhas maduras de indivíduos da área inundável exibiram folíolos mais longos e canais secretores mais abundantes e amplos em comparação às plantas da área não inundável. Sugerimos que a maior parte do consumo de folhas pelos herbívoros ocorre durante os estágios iniciais de desenvolvimento das folhas, quando há menor defesa química e os folíolos são mais tenros.

Palavras-chave: anatomia, breu-branco, inundação, folha, herbivoria, restinga.

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[1] Universidade Estadual Paulista - UNESP, Instituto de Biociências de Botucatu - IBB, Botucatu, SP, Brasil.

[2] Universidade Estadual do Maranhão - UEMA, Centro de Educação, Ciências Exatas e Naturais, Depto. Biologia, São Luís, MA, Brasil. ORCID: <https://orcid.org/0000-0002-1463-1976>.

[3] ORCID: <https://orcid.org/0000-0002-1006-357X>. [4] ORCID: <https://orcid.org/0000-0002-3366-1177>. [5] ORCID: <https://orcid.org/0000-0001-6473-1230>.

[6] Author for correspondence: tatiane.rodrigues@unesp.br

Introduction

Plant physical, chemical, and phenological traits play a pivotal role in determining the extent of herbivore damage to leaves (Coley & Barone 1996; Cárdenas *et al.* 2014). These traits often act as defense mechanisms, enhancing the plant's fitness by reducing the likelihood of herbivore discovery or deterring feeding once discovered (Fox 1981). One such defense mechanism involves the production of resin, known for its anti-herbivore properties (Fernandes 1994; Langenheim 2003).

Resin is produced and stored in secretory spaces, such as secretory cavities and canals, within the stems and leaves of many plant species (Fahn 1979). When the leaves of resin-producing plants are damaged, copious amounts of fluid typically flow from the injured tissues (Becerra *et al.* 2001). This resin may contain herbivore antifeedants, repellents, and toxins, such as terpenes (Raffa 1991; Evans *et al.* 2000), catechols, and flavonoids (Joel 1980; Furth & Young 1988; Vencl & Morton 1998). Furthermore, in addition to its toxicity, resin may pose a mechanical threat to insects, as it crystallizes and can ensnare insects and pathogens (Becerra *et al.* 2001; Langenheim 2003). However, specialized vein-cutting insects have evolved mechanisms to deactivate these secretory canals (Becerra 1994).

Abiotic factors significantly influence the phenotypic plasticity of plant species, affecting their physiological and morphological traits, including the development and function of secretory systems (Rodrigues *et al.* 2014). Consequently, these structural and functional changes, driven by environmental abiotic factors, can indirectly impact plant-animal interactions, including herbivory (Langenheim 2003). For instance, soil flooding, even if temporary, can trigger various morphoanatomical responses in plant bodies. The nature of these structural alterations varies depending on the flooding tolerance of each plant species (Kozlowski 1997). Previous studies have shown that the number of terpene secretory spaces in plant tissues can increase (Yamamoto *et al.* 1987) or decrease (Medri *et al.* 2007) in response to flooding. Additionally, environmental factors like temperature and moisture availability can influence both the total resin quantity and its exudation pressure (Langenheim 2003).

Coastal pre-Amazonian white-sand forests present an intriguing study system for investigating the role of flooding in shaping leaf traits and herbivory along an environmental gradient. In this environment, plant species located at sea level experience tidal cycles, submerging a portion of their vegetative bodies during high tide. In contrast, plant species in higher regions are not directly influenced by tidal flooding but face the same challenging environmental conditions, such as intense sunlight and physiological stress from saline aerosols (Scarano 2002, 2009). *Protium heptaphyllum* (Aubl.) March. (Burseraceae), a resin-producing plant, thrives in white-sand forests, occupying both higher, non-floodable areas and lower areas naturally inundated by tidal pulses (personal observation). This unique distribution allows for a direct comparison of the effects of flooding on various morphological and ecological parameters.

While studies linking herbivory to plant leaf traits often consider mechanical characteristics (see Caldwell *et al.* 2016, for examples), they frequently overlook the connection between these characteristics and underlying anatomical traits. Only a limited number of studies explore anatomical leaf traits and their significance in plant-herbivore interactions (Hagen & Chabot 1986). Yet, the relationship between the development of secretory structures and the incidence of herbivory remains an underexplored area of research, despite its relevance to the interface between plants and their herbivores. Therefore, our study aimed to consolidate information on the anatomy of resin-secreting canals and herbivory levels in *P. heptaphyllum* individuals across floodable and non-floodable environments.

Material and Methods

Study site

This study was conducted on Itaputiua Island (02°25'S, 44°03'W), being part of the Doctoral thesis of M.I.A. Rodrigues at the graduate program in Biological Sciences (Botany), in the Institute of Biosciences of Botucatu, São Paulo State University (UNESP). The Itaputiua Island is situated in Raposa City, within the metropolitan region of São Luís, in the mesoregion of northern Maranhão state, Brazil. It spans approximately 80 hectares and falls within the Aw climate classification, characterized by tropical conditions with a dry season between the equatorial and tropical patterns (Köppen 1948). Temperatures remain consistently high year-round, ranging from 18 °C to 28 °C. The climate features two distinct seasons: a rainy season (from January to June) and a dry season (from July to December). The average annual rainfall in the region is approximately 2,100 mm (Santos *et al.* 2011).

The study areas were within a white-sand forest, located between mangrove and dry land. These areas were divided into two distinct landscape units, each covering approximately 4,000 square meters:

a) Floodable area (Fig. 1a): this transitional environment occupies lower topography, approximately 10 meters above sea level, and is bordered by mangrove vegetation. It is characterized by the prevalence of plant species such as *Conocarpus erectus* L. and *Avicennia schaueriana* Stapf and Leechman. During high tide, the water level reaches the base of *P. heptaphyllum* stems, which occurs at least twice daily and lasts about four hours. During extreme syzygy tides, with variations exceeding seven meters, the water level can reach 15–20 cm at the height of the trunks of *P. heptaphyllum* individuals located in the border zone.

b) Non-floodable area (Fig. 1b): this environment is situated on the highest part of the island, approximately 17 meters above sea level and roughly 60 meters from the floodable area. Here, *P. heptaphyllum* plants dominate the upper canopy alongside other tree species. Although these plants are not subject to flooding, they are exposed to the effects of marine sprays.

In each of these areas, ten adult *P. heptaphyllum* individuals (n = 10) with similar sizes and characteristics were selected for morphoanatomical and herbivory studies, totaling 20 plants.

Plant species

Protium heptaphyllum (Aubl.) March. (Burseraceae), commonly known as “améscla”, “almecega”, or “breu-branco” (Corrêa & Pena 1984), is a significant producer of resin used in varnish, cosmetics, and medicines known for their analgesic, healing, and expectorant properties (Maia *et al.* 2001). This species is native to South America (Corrêa & Pena 1984) and thrives in various environments, including rainforests, savannas, white-sand forests, and riparian forests (Souza & Lorenzi 2008). *Protium heptaphyllum* can adapt to varying abiotic conditions, including floodable and non-floodable soils, which can be clayey or sandy (Maia *et al.* 2001; Bandeira *et al.* 2002; Citó *et al.* 2006; Souza & Lorenzi 2008). Its distribution ranges from latitudes with equatorial climates to those with tropical seasonal wet-dry climates (Mendonça & Danni-Oliveira 2007).

Voucher specimens were deposited in the Herbarium Irina Delanova Gemtchújnicov (BOTU) and registered under numbers 30230; 30231 and 30232. Plant identification was confirmed by Dr. Douglas Daly (New York Botanical Garden, USA), a specialist in the Burseraceae family.

Measurements of abiotic factors

Air temperature (°C) and relative humidity (%) were recorded in both study areas using a digital thermo-hygrometer (Minipa, MT 240). Light intensity was measured using a digital luxmeter (Lux Meter, Icel LD-511), with the equipment placed near the branches selected for morphoanatomical and herbivory studies. These measurements were taken at ten points within each area at 1:00 p.m. over two consecutive days.

Soil samples were collected near each *P. heptaphyllum* plant in both areas, totaling 20 samples. Samples were collected approximately 1 meter away from the plant trunks and at a soil depth of 20 cm using an auger. Soil physical and chemical analyses were conducted in the Laboratory of Soil Physics at Maranhão State University, following the protocol described in Donagema *et al.* (2011).

Morphoanatomical studies

Leaves were collected from branches located in the basal and peripheral portions of the crown of ten plants in each area. Leaves from the first node (young leaves) and the fourth node (mature non-senescent leaves) of each branch were sampled. The length of the median leaflets of each leaf was measured using a ruler.

For anatomical studies, samples excised from the median region of the median leaflet were fixed using FAA 50 (formalin: acetic acid: alcohol 50%) (Johansen 1940), dehydrated in an ethanol series, embedded in methacrylate resin (Gerrits 1991), and sectioned using a semi-automatic rotary microtome (Leica RM 2148). Cross-sections (5µm thickness) were stained with toluidine blue O at 0.05% pH 4.7 (O’Brien *et al.* 1964), and permanent slides were prepared using synthetic resin. The material was examined under an Olympus BX 41 microscope, and relevant results were documented with a digital camera. Quantitative anatomical analyses were performed to measure leaflet thickness, the number and lumen area of resin canals in the midrib, using Olympus Cell B -Imaging Software for Life Science Microscopy.

Leaf herbivory

Herbivory levels were assessed in mature leaflets collected from branches growing in the basal periphery of each individual’s crown, facing North, South, East, and West. Herbivory

Figure 1 – a-b. Study sites in a white-sand forest in Itaputiua island, Maranhão state, Brazil showing (a) floodable area during full tide and (b) non-floodable area.

was quantified in 10 leaflets in each direction, totaling 40 leaflets per individual plant. Collected leaflets were positioned on millimeter paper and photographed. The percentage area of leaflets consumed by herbivores was estimated using image editing software (Photoshop 10.0).

Statistical analysis

A preliminary two-way ANOVA was conducted to examine whether herbivory intensity varied based on leaf position within the plant (cardinal points) in both floodable and non-floodable environments. Leaf position within the plant's crown and environmental factors were considered explanatory variables, while the percentage of leaflet area consumed by herbivores served as the response variable.

A MANOVA was performed to assess whether leaf traits and herbivory levels differed between plants in floodable and non-floodable areas. This analysis included all quantitative variables measured in young and mature leaflets.

Results

Environmental features of the studied areas

The environmental conditions, including light intensity, air temperature, and relative air humidity, were found to be very similar in both floodable and non-floodable areas (Tab. 1).

In both areas, the soil exhibited a sandy texture with a higher proportion of fine sand and high acidity. The base saturation indicated dystrophic soil characteristics in both environments (Tab. 2).

Morphoanatomical leaf traits

Plants in floodable areas displayed longer mature leaflets compared to those in non-floodable areas (Tab. 3).

The young and mature leaves of *P. heptaphyllum* exhibited general histological features common to individuals from both areas. These leaves were hypostomatic, heterobaric, and displayed dorsiventral mesophyll (Fig. 2a-b). Secretory canals of varying sizes were observed in the phloem of

Table 1 – Microclimatic variables in floodable and non-floodable environments of coastal pre-Amazonian white-sand forest in Maranhão, Brazil. Mean values ± standard deviation (n = 10 plants/ environment).

Microclimatic features	Floodable environment	Non-floodable environment	T	*p*
Temperature (ºC)	31.50 ± 1.51	32.10 ± 1.45	0.91	0.38
Relative humidity (%)	73.00 ± 3.40	73.80 ± 3.68	0.51	0.62
Luminosity (x10 lux)	302.70 ± 73.79	308.20 ± 78.03	0.16	0.87

Table 2 – Chemical soil composition in floodable and non-floodable environments of coastal pre-Amazonian white-sand forest in Maranhão, Brazil. Mean values ± standard deviation (n = 10 samples/ environment).

Soil features	Floodable environment	Non-floodable environment	T	*p*
OM (g/dm^3)	21.5 ± 12.38	22.2 ± 15.2	0.08	0.93
pH ($CaCl_2$)	3.58 ± 0.35	3.48 ± 0.42	0.59	0.55
P (mg/dm^3)	2.0 ± 0.94	1.7 ± 0.67	0.72	0.47
K^+ (mmol$_c$/dm^3)	1.78 ± 3.66	0.68 ± 0.21	0.73	0.48
Ca^{++} (mmol$_c$/dm^3)	5.1 ± 3.34	4.3 ± 2.79	0.15	0.88
Mg^{++} (mmol$_c$/dm^3)	4.8 ± 4.66	3.1 ± 1.28	0.01	0.98
Na^{++} (mmol$_c$/dm^3)	3.18 ± 6.96	0.99 ± 0.22	0.93	0.37
SB (mmol$_c$/dm^3)	14.85 ± 11.88	9.08 ± 2.82	0.65	0.52
V (%)	19.92 ± 15.44	15.38 ± 7.18	0.19	0.85

Note: OM = Organic matter content; SB = sum of bases (Ca^{++} + Mg^{++} + K^+ + Na^{++}); V = base saturation.

Table 3 – Morphological and anatomical variables and herbivory of leaflets of *Protium heptaphyllum* (Burseraceae) plants growing in coastal pre-Amazonian white-sand forest. (Mean values ± standard-deviation, n = 10 plants per environment).

Morphological and anatomical features	Leaflet stage	Floodable environment	Non-floodable environment	F	*p*
Leaflet length (cm)	young	6.8 ± 2.1	5.8 ± 1,8	1.315	0.267
	mature	8.9 ± 1.4	6.6 ± 0.9	18.663	< 0.001
Leaflet thickness (µm)	young	145.0 ± 23.9	130.4 ± 27.9	1.583	0.224
	mature	169.6 ± 26.6	163.1 ± 18.5	0.407	0.532
Lumen area of the secretory canals (µm²)	young	615.0 ± 266.9	823.2 ± 191.2	4.019	0.060
	mature	1257.0 ± 472.6	883.4 ± 196.4	5.329	0.033
Number of secretory canals	young	6.4 ± 1.1	7.4 ± 2.4	1.480	0.239
	mature	8.0 ± 1.4	6.7 ± 1.2	5.053	0.037
Herbivory (%)	-	11.1 ± 4.5	12.4 ± 2.4	0.601	0.448

vascular bundles, embedded in the mesophyll (Fig. 2a-b), as well as in the midrib (Figs. 2c-d; 3a). These secretory canals consisted of uniseriate secretory epithelium and a lumen where secretion accumulated (Fig. 3b). In the midrib, the secretory canals were notably voluminous (Figs. 2c-d; 3a-b).

Mature leaves from plants in the floodable area (Fig. 2c) displayed a higher number of secretory canals in the midrib, with wider lumens compared to mature leaves of plants in the non-floodable area (Fig. 2d; Tab. 3). In young leaves, the analyzed characteristics did not differ significantly between plants from floodable and non-floodable areas (Tab. 3).

Leaf herbivory

The position of leaves within the plant (cardinal points) did not have a significant effect on herbivory intensity, whether in the floodable or non-floodable environments. Consequently, we pooled all sampled leaflets from the four cardinal points together (n = 40 leaflets per plant) for further analysis.

A MANOVA test revealed significant differences between individuals growing in floodable and non-floodable areas (Pillai's trace = 0.763; F = 3.578; p = 0.0298). However, when we compared each variable individually between floodable and non-floodable environments, we found that the percentage of leaflet area consumed by herbivores and all leaf traits of young leaflets did not differ significantly.

Discussion

This study was conducted in two closely situated coastal areas, which exhibited strikingly similar abiotic conditions, including light incidence, temperature, air humidity, and soil chemical composition. Notably, flooding appeared to be the primary abiotic distinction experienced by plants in these two environments. In the floodable environment, individuals displayed longer leaflets compared to those in the non-floodable area. Given the careful standardization of leaf collection under similar light conditions, it is reasonable to suggest that these differences in leaflet length may be linked to the occurrence of flooding. The increased length of leaf components is a common feature observed in plants inhabiting flooded environments (Insausti *et al.* 2001; Mollard *et al.* 2008, 2010) and may be associated with elevated expansin enzyme activity, which promotes cell wall loosening (Vriezen *et al.* 2000). This loosening is induced by the higher concentration of ethylene under such conditions (Heydarian *et al.* 2010).

Conversely, the absence of variations in leaflet thickness among individuals from both environments is a noteworthy finding in our study. According to Mommer *et al.* (2007), the lack of plasticity in leaf thickness in plants that tolerate flooding may indicate inherent adaptations to the aquatic environment. Indeed, Santos *et al.* (2012) demonstrated that young *P. heptaphyllum* plants exhibit physiological traits indicating tolerance to temporary flooding, including a decrease in liquid photosynthesis and stomatal conductance, as well as an increase in leaf and stem mass in flooding conditions.

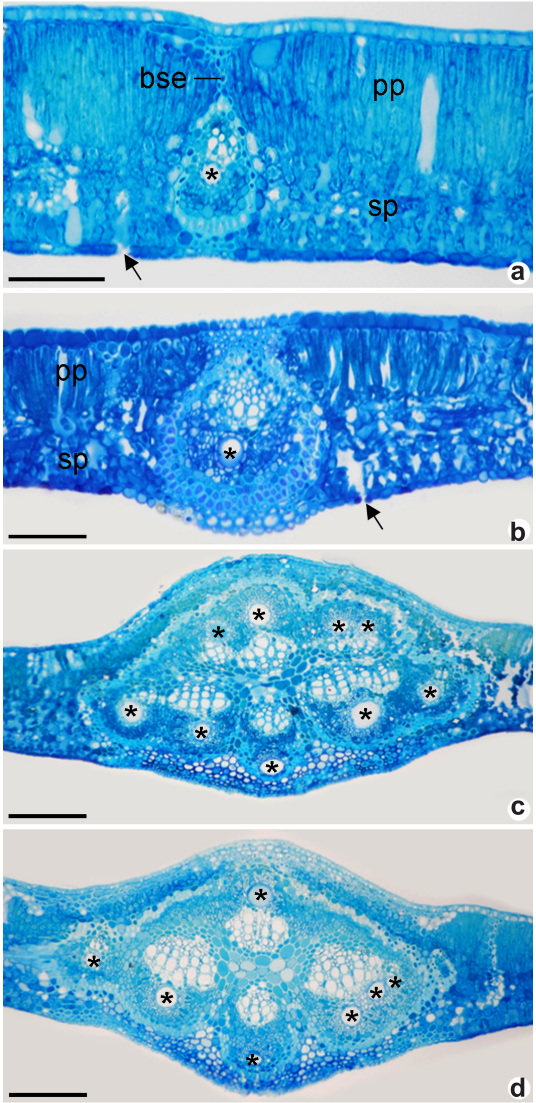

Figure 2 – a-d. Photomicrographies of *Protium heptaphyllum* leaflet blade in cross sections – a-b. general view of intercostal areas showing uniseriate epidermis with stomata (arrows) in the abaxial leaf side, mesophyll with palisade (pp) and spongy (sp) parenchyma, and secretory canals (*) in the phloem of tertiary (a) and secondary (b) order veins (bse = bundle sheath extension); c-d. leaflet midrib of plants from the floodable (c) and non-floodable (d) areas exhibiting secretory canals (*) in the phloem. Scale bars: a, b = 100 µm; c, d = 150 µm.

Although the presence of resin canals is a constitutive feature of *P. heptaphyllum* (Palermo *et al.* 2018), flooding appears to induce changes in the developmental aspects of the secretory system in mature leaves. In the floodable area, we observed a greater abundance and larger size of resin canals in mature *P. heptaphyllum* leaves, which likely leads to increased resin production and storage. Similar studies have demonstrated an increased number of secretory spaces in plants subjected to flooding (Yamamoto *et al.* 1987). This phenomenon may result from the temporary reduction in oxygen levels in the soil, directly affecting metabolic processes (Kozlowski 1997) and inducing increased ethylene production (Taiz & Zeiger 2004). Ethylene is known to stimulate the production of additional secretory canals in various plants (Fahn 1988; Tomás *et al.* 1993; Hudgins & Franceschi 2004). The role ethylene in inducing the synthesis of digestive enzymes involved in dissolving cell wall components, thereby creating

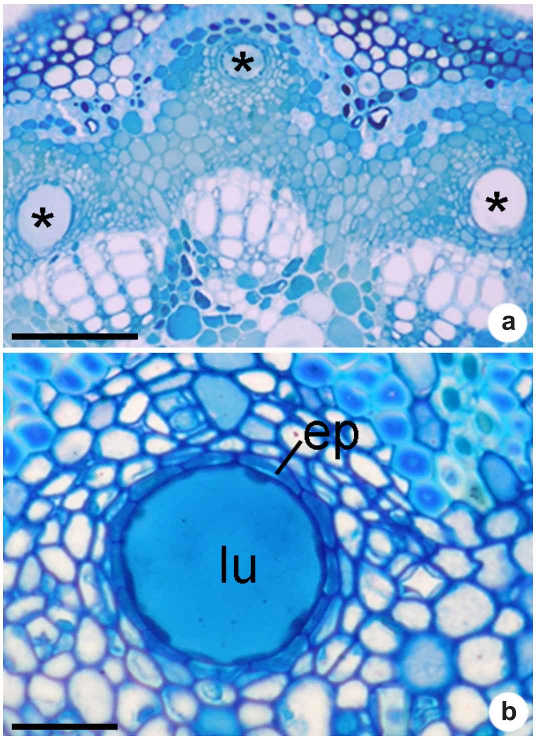

Figure 3 – a-b. Photomicrographies of *Protium heptaphyllum* leaflet blade in cross sections – a. secretory canals (*) immersed in the phloem of the midrib; b. detail showing secretory canal constituted by uniseriated epithelium (ep) and lumen (lu). Scale bars: a = 100 µm; b = 50 µm.

cell spacing (Fagan *et al.* 2015), may explain the wider lumens observed in the secretory canals of flooded plants.

Surprisingly, our results showed no significant differences in herbivory when comparing plants from the two environments, despite the longer mature leaflets and more developed secretory systems in the flooded environment. This observation may be attributed to the preference of herbivores for young leaves over mature ones, with the majority of damage typically occurring during the first month of leaf lifespan (Aide 1993). During this critical period, our study system showed similar resin canal characteristics in both environments. Moreover, specialized herbivores in the Burseraceae family, such as some insects, possess the ability to neutralize plant defensive mechanisms, including resin-based deterrents (Becerra 2003). *Protium* species contain a variety of secondary compounds that may account for 20 to 30% of their dry mass, suggesting that chemical anti-herbivore defense represents a significant energy investment in these species (Fine *et al.* 2013). The resin of *P. heptaphyllum* predominantly comprises mono- and sesquiterpenes (Siani *et al.* 1999; Maia *et al.* 2000; Bandeira *et al.* 2001), including triterpenes from the α-amyrin (ursane) and β-amyrin (oleane) series (Lima *et al.* 2016), known for their insect-deterring properties (Ahmed *et al.* 2017). Mono- and sesquiterpenes, such as myrcene and ß-caryophyllene, are major chemical compounds found in the leaves of this species (Bandeira *et al.* 2001). The physical and defensive characteristics of resin may be determined by the proportion of volatile (mono- and sesquiterpenes) and non-volatile compounds (di- and triterpenoids or phenolic compounds). The latter are responsible for resin viscosity and crystallization rate (Langenheim 2003). This combination of ecological and anatomical characteristics likely contributes to the establishment of interactions with more specialized herbivores that can overcome plant defense mechanisms.

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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