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What's on the Menu? Floral Exudate Composition in Areas Subjected to Different Levels of Abiotic Severity.

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A B S T R A C T

The allocation of resources in floral exudate composition represents a balance between the energy cost to the plant and the reward offered to pollinators. For instance, carbohydrates, while providing a lower reward to pollinators, impose a reduced energy cost on the plant compared to lipid production. In this study, we propose that the allocation of resources by plants and communities between carbohydrates and lipids may vary across environmental gradients. In resource-limited communities, plants tend to allocate fewer resources to higher-cost compounds in floral exudates. Understanding this composition is crucial for revealing pollinator behavior and its relationship with the environment, which may help predict behavioral changes in response to climate shifts. In this study, we characterized the composition of floral exudates across three locations along a gradient of water availability. Our results allow us to refute the hypothesis that plants in water-scarce environments are forced to allocate fewer resources to pollinator rewards, suggesting instead that increased competition among pollinators may play a more significant role. Additionally, our findings highlight the prevalence of pectins in floral exudates under drier conditions, supporting the hypothesis that these compounds are necessary to prevent exudate crystallization in arid environments.

Keywords: Caatinga - Cerrado – Floral resources – Montane evergreen forest - Secretory structures.

Qual o cardápio? Composição do exsudato floral em áreas sujeitas a diferentes níveis de severidade abiótica.

R E S U M O

A alocação de recursos na composição do exsudato floral representa um equilíbrio entre o custo energético para a planta e a recompensa oferecida aos polinizadores. Por exemplo, carboidratos, embora proporcionem uma recompensa menor aos polinizadores, têm um custo energético reduzido para a planta em comparação com a produção de lipídios. No presente estudo, propomos que a composição dos recursos produzidos pelas plantas e comunidades entre carboidratos e lipídios podem variar ao longo de gradientes ambientais, sendo que em comunidades com recursos limitados, as plantas tendem a destinar menos recursos para compostos de alto custo nos exsudatos florais. Compreender essa composição é crucial para desvendar o comportamento dos polinizadores e como ele se relaciona com o ambiente, o que pode ajudar a prever mudanças comportamentais em resposta às alterações climáticas. Neste estudo, caracterizamos a composição dos exsudatos florais em três localidades ao longo de um gradiente de disponibilidade hídrica. Nossos resultados nos permitem refutar a

hipótese de que ambientes com menor disponibilidade de água forçam as plantas a produzir recursos menos custosos para a recompensa dos polinizadores, sugerindo, em vez disso, que o aumento da competição entre polinizadores pode desempenhar um papel mais significativo. Além disso, nossos achados destacam a prevalência de pectinas nos exsudatos florais em condições mais secas, corroborando a hipótese de que esses compostos são necessários para prevenir a cristalização dos exsudatos florais em ambientes áridos.
Palavras-Chave: Caatinga, Cerrado, Estruturas secretoras, Floresta sempre-verde montanhosa, Recursos florais.

Introduction

Nectar is a sugary rich solution secreted by nectaries, and is one of several types of floral exudates (Fahn, 1979; Bentley and Elias, 1983; Roshchina and Roshchina, 1993; Nicolson et al., 2007; Heil, 2011; Silva et al., 2024). Floral exudates are substances released by plants that are usually involved in the attraction of pollinators, therefore, playing a vital role in plant-pollinator ecology (Nicolson, 2022; Venjakob et al., 2022). Specialized pollinators, such as oil bees, depend on floral oils, while many other insects visit flowers in search of nectar, which is more readily available and less costly for plants to produce (Pyke and Ren, 2023; Balbuena et al., 2024).

The chemical composition of nectar, predominantly made up of sugars such as sucrose, glucose and fructose, provides a rapidly metabolized energy source for pollinators, while oils, rich in lipids, offer more concentrated energy but with a higher metabolic cost (Schmitt et al., 2021; Gill and Walters, 2023). The diversity regarding the types of floral exudates reflect the adaptive strategies of plants to attract different types of pollinators and maximize reproduction (Venjakob et al., 2022; Wang et al., 2022).

While nectar is widely studied due to its primary function in pollination, other floral secretions, such as floral oils, are equally important, although less discussed (Nicolson et al., 2007; Heil, 2011; Liu et al., 2024). These oils are released by elaiophores and provide a valuable energy source for certain pollinators (Stephan Vogel, 1989; Alves-dos-Santos et al., 2007). Studying how these exudates are produced and how they vary in response to environmental conditions is essential to understanding plant-pollinator interactions and their responses to climate change.

The sugars and polysaccharides that compose floral nectar emerge from two main processes: sugars may either be uploaded (i) direct translocation from the phloem; or (ii) from starch grains that are hydrolyzed into less complex carbohydrates during secretion (Pacini et al., 2003; Kram and Carter, 2009; Heil, 2011; Liu et al., 2024). While nectar originates from phloem sap, it undergoes modifications before being secreted, resulting in a distinct final composition (Heil, 2011). These changes are influenced by factors such as osmosis and the plant's water balance (Pacini et al., 2003; Kram and Carter, 2009). However, we can generalize and say that there are no major differences between the resultant nectar sugars as they belong to the same chemical group, that is, carbohydrates.

A second class of floral resources differ strikingly from nectars in their high oil quantity and are secreted by glands called elaiophores (Stefan Vogel, 1969; Simpson and Neff, 1981; Buchmann, 1987; Possobom and Machado, 2017). Elaiophores secrete a mixture of nonvolatile and essential oils that serve as odor attractants, but here we use the term oils for only nonvolatile oily flower exudates (Simpson and Neff, 1981). Such floral oils have a high energy value, with up to eight times the calorific value of nectar and are thus of greater nutritional interest to pollinators (Stephan Vogel, 1989; Alves-dos-Santos et al., 2007).

Paul and Eastmond (2020) point out that the energy density of lipids are more than twice that of carbohydrates. The production of lipids depends on biochemical pathways with higher energy costs than those used to produce carbohydrates (Sangwan et al., 2001; Buchanan et al., 2015; Paul and Eastmond, 2020), thus the energy required to produce floral oils is higher than that needed to produce nectar (Paul and Eastmond, 2020).

Although the main constituents of floral nectars and floral oils are sugars and oils, respectively, both types of floral resources may contain other chemical constituents (Kevan, 1976; Thorp et al., 1976; Baker, 1977; Fahn, 1979; Bentley and Elias, 1983; Bernardello et al., 1999; Weber et al., 2019; Önder et al., 2023). These constituents include proteins, amino acids, carbohydrates, phenolic compounds, and terpenes (Roshchina and Roshchina, 1993; Nicolson et al., 2007; Possobom and Machado, 2017).

Environmental constraints on organisms have been a main focus of research directed at understanding the complexity of interactions found in ecosystems (Boulangeat et al., 2012; Aleixo et al., 2017). With respect to floral exudates, a

number of recent studies have quantified changes in exudate composition in floral secretions in relation to environment (Buchmann, 1987; Roshchina and Roshchina, 1993; Bernardello et al., 1999; Nicolson et al., 2007; Devoto et al., 2006; Cosacov et al., 2012; Ferreiro et al., 2015; Mittelbach et al., 2015; Roy et al., 2017; Domingos-Melo et al., 2020; Saddhe et al., 2021). Research has shown that temperature, salinity, soil nutrients, light, and water, may increase or decrease the volume of secreted floral exudates or even the amounts of certain nectar constituents (Schneider and McNally, 1992; Pacini et al., 2003; Galetto and Bernardello, 2004; Brandenburg et al., 2009; Weryszko-Chmielewska and Chwil, 2016; Aleixo et al., 2017; Graves et al., 2017; Saddhe et al., 2021).

The main question that arises is how plants and plant communities alter their floral secretions in response to environmental stress, especially in relation to water availability. Given the increase in extreme weather events and the progression of global climate change, it is crucial to understand how variability in exudate production affects plant-pollinator interactions and, consequently, plant reproduction and community structuring (Wei et al., 2021; Katumo et al., 2022). Since pollinators depend on exudates for their survival and reproduction, changes in the quality and quantity of these resources can have significant implications for pollinator populations and the maintenance of biodiversity (Wei et al., 2021).

Such a question is especially relevant in light of recent studies demonstrating changes in plant-pollinator interactions in environments subject to climatic stresses (Saddhe et al., 2021; Wei et al., 2021; Katumo et al., 2022). If plants in dry regions secrete compounds that are less caloric and easier to produce, such as nectar sugars, they may be compromising the survival of pollinators that depend on lipids for their reproduction. In regions where water availability is greater, there may be a greater production of floral oils, attracting specialized pollinators. However, climate change and the consequent redistribution of pollinators may disrupt these interactions, resulting in significant ecological impacts.

Previous studies (Machado and Lopes, 2004) have characterized floral exudates to allow comparisons among tropical regions. However, floral exudates were only characterized as nectars, oils, or pollens. More detailed characterization of the chemical composition of these exudates was not carried out (e.g. the presence or absence of sugars, proteins, carbohydrates, phenolic compounds, or lipids). Given climate change, it is important to know how the floral exudates produced in a plant community relate to abiotic factors such as the water availability. Is there a correlation between the chemical nature of the floral nectar/oil constituents and the severity of water stress? Understanding how plants and communities alter their floral exudates in response to water stress may help explain the foraging behavior of flower visitors and predict how this may change with changing climates.

Based on the above, the central hypothesis of this study is that the composition of floral exudates varies according to the availability of water in the environment. We expect that less costly to produce compounds but less calorific (*i.e.*, energy rich) such as sugars will be offered to floral visitors where water availability is low. In contrast, where water is more abundant flowers may offer more calorific but more costly to produce compounds such as oils. The present study therefore aimed to characterize the composition of floral exudates in communities undergoing different degrees of water stress.

Material and methods

Study site locations and soils

As a whole, the Brazilian semi-arid region occupies ~700,000 – 800,000 km^2 in Northeastern Brazil (Souza et al., 1992). The climate is predominantly hot and dry, with temperatures throughout the year around 26ºC, which result in high annual potential evapotranspiration (1,500 to 2,000 mm/year) (Reddy, 1983; Sampaio, 1995). The high evapotranspiration together with low rainfall (~400 and 800 mm/year) results in high water deficits which is aggravated by the erratic rainfall season (concentrated in 3 to 4 months) as rains are irregularly distributed even during the rainy season (Reddy, 1983; Souza et al., 1992)

Our study area is a region of complex altitudinal gradients and geomorphological differences spanning Ceará and Piaui States of Brazil (Zanella, 2005; Araújo et al., 2017; Oliveira et al., 2017) (Figure 1A). This region is a patchwork of vegetation types including savanna-steppe, savanna, and montane evergreen forest (Rodriguez et al., 2017). Within this region, our three study sites are representative of these three vegetation types.

The Estação Ecológica de Aiuaba (6º36'– 6º44'S and 40º07'– 40º19W, ~11,750 ha), here in referred as the Caatinga site (Figure 1B), is

predominantly composed of a savanna-steppe kind of vegetation also known in Brazil as the Caatinga (Medeiros and Araújo, 2013; Araújo et al., 2017). Unlike true savannas, savanna-steppe vegetation is not naturally subjected to fire and has fewer grasses than typical savannas. The protected area including the Caatinga site has a well-preserved central core and ~80% of its total area is covered by native natural vegetation (Araújo et al., 2017). The predominant soil type is a dystrophic red-yellow latosol, which has a good water storage capacity (Jacomine et al., 1973; Marques et al., 2014).

The Parque Nacional de Sete Cidades (04°05'–04°15'S and 41°30'–41°45'W, ~6,200 ha) is referred to here in as the Cerrado site (Figure 1C, D) and is composed mainly of savanna vegetation (known in Brazil as Cerrado *sensu stricto*) (Rocha and Prudente, 2010; Araújo et al., 2017; Oliveira et al., 2017). Three classes of soils associated with the cerrado are found in the park (Motta et al., 2002; Marques et al., 2014): (i) oxisols – deep soils with good water storage and sandy or loam-sandy texture; (ii) plinthossols – shallow mineral soils with a sandy-loam texture, occurring in situations of temporary flooding and with limited water permeability; and (iii) litholic neossols – shallow, partially weathered soils with stones and gravel.

The Parque Nacional de Ubajara (3º48'–03º58'S and 40º52'–40º55'W, ~6,250 ha) is referred to herein as the Montane Evergreen Forest site (Figure 1E). It includes a narrow strip of seasonal evergreen forest, locally known as humid montane forest. About ~90% of its vegetation cover is well-preserved (Araújo et al., 2017). Three types of soils are predominantly: oxisol dystrophic red-yellow, podzolic eutrophic and litholic soils, being oxisol dystrophic, with good drainage and good water storage present in the collection area (IBDF, 1981).

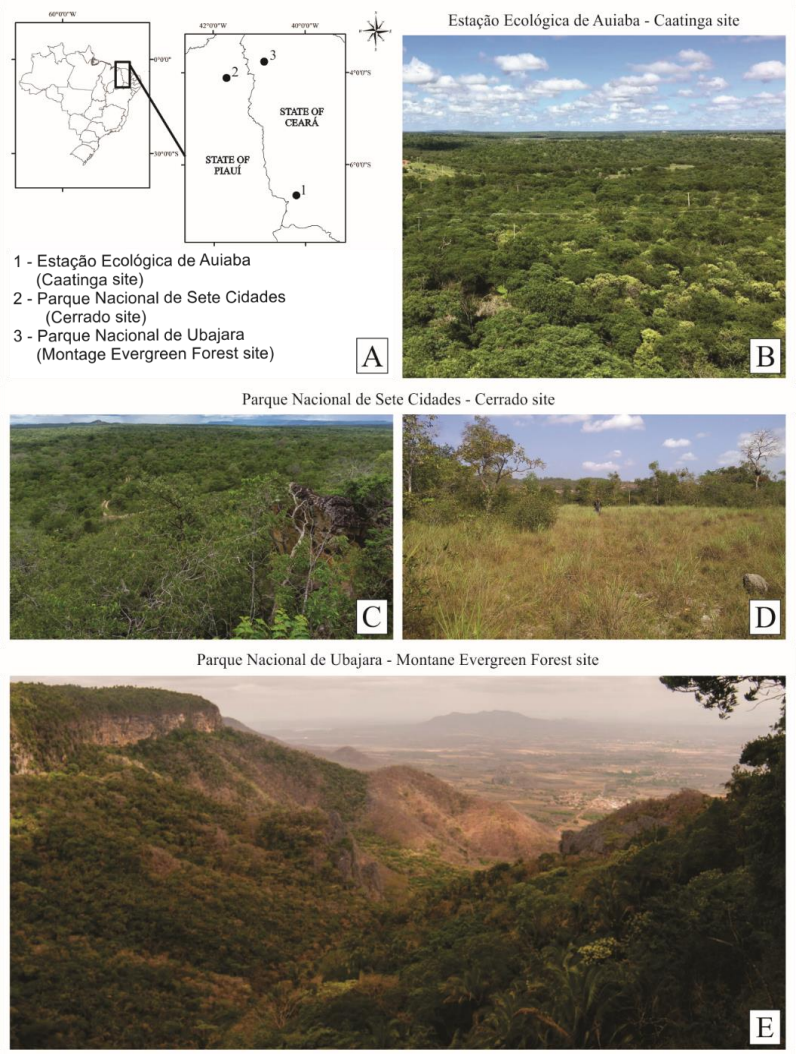

Figure 1. Characterization of the study areas during the rainy season. (A) Location of the three the study area is located in Northeast Brazil, in the States of Ceará and Piauí. (B) Caatinga site at the Estação Ecológica de Auiaba. (C, D) Cerrado site at Parque Nacional de Sete Cidades. (E) Montane Evergreen Forest at the Parque Nacional de Ubajara.

Characterization of water availability

Climatic data were collected from the Fundação Cearense de Meteorologia e Recursos Hídricos (FUNCEME, 2018), the Instituto Nacional de Meteorologia (INMET, 2020) and Climate-data.org (2019). We used the *climatol* package in R (R Development Core Team, version 2.15) to produce Walter and Lieth climatic diagrams (Walter and Lieth, 1967) based upon a historical series (1976 to 2018) of rainfall and temperature. For the Estação Ecológica de Aiuaba and Parque Nacional de Ubajara, data (i.e. precipitation and temperature) were available for the municipalities where the park are located (Aiuaba and Ubajara, respectively), while for the Parque Nacional de Sete Cidades data from the nearest city was used, Piripiri (Piauí State) located ~20km away from the park.

Walter and Lieth climatic diagrams are based on maximum, minimum and absolute minimum temperature and the averages of monthly rainfall totals, these factors are considered the most important and their graphical representation facilitates the understanding of climatic variations over the year (Walter and Lieth, 1967). Through visualizing climate diagrams for the three areas, it was possible to characterize the annual periods of rain and drought.

Study site climates

In the Caatinga site, the average annual rainfall is 559 mm and the average annual temperature is 25°C (Figure 2A). The rainy season begins in late December and extends until May (Figure 2A). The Caatinga site has the longest dry period of the three study sites; August is the driest the month of the year (Figure 2A).

In the Cerrado site, rains were concentrated in the period ranging from the end of December to the beginning of June, with average precipitation and temperature of 1273 mm and 27 ° C, respectively (Figure 2B). September is the month with the strongest water deficit, but the dry season is shorter than at the Caatinga site (Figure 2B).

The Montane Evergreen Forest site has the highest average annual precipitation and lowest average temperature, 1459 mm and 21ºC, respectively (Figure 2C). The rainy season is from December to mid-July (Figure 2C). September is also the driest month in the the Montane Evergreen Forest site; however, this site has the shortest dry season of the three study sites (Figure 2C).

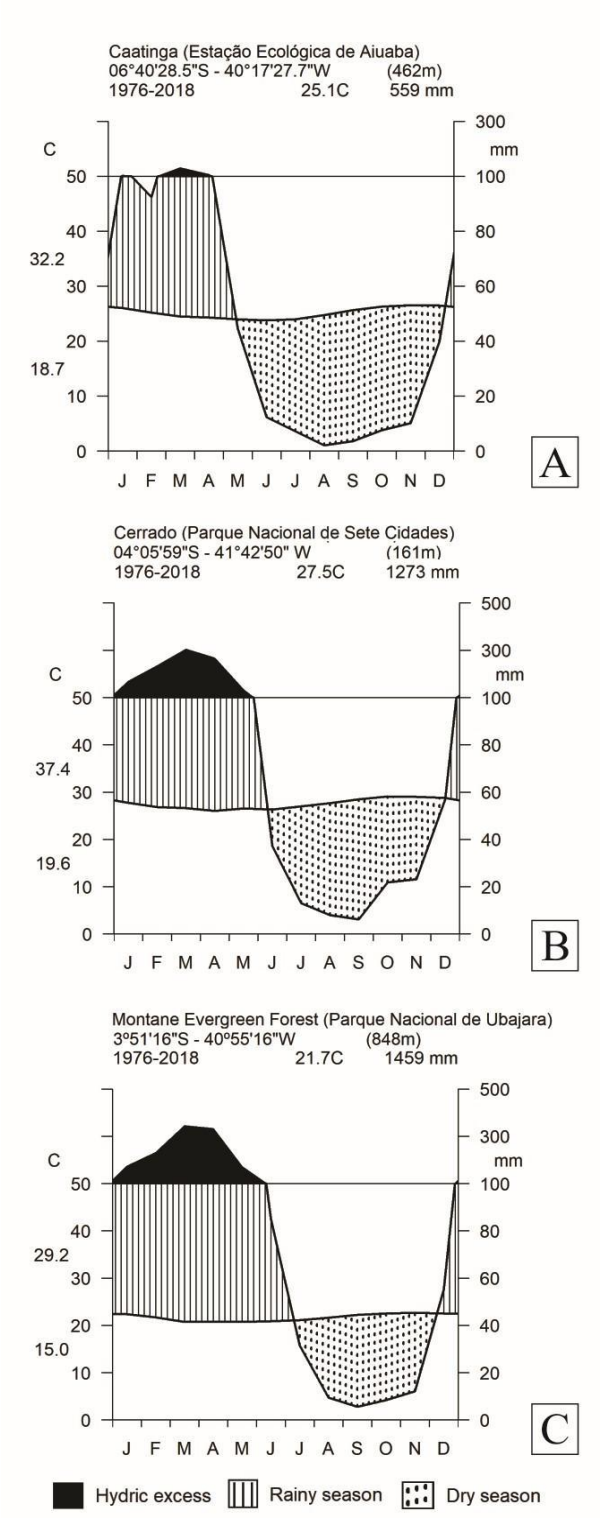

Figure 2. Walter and Lieth climatic diagram, containing historical series (1976-2018) of temperature and precipitation of the Estação ecológica de Aiuaba, of the Parque Nacional de Sete Cidades and Parque Nacional de Ubajara (*x*-axes representing temperature and rainfall and y-axis with the months of year).

Collection of botanical material

The collections were carried out from April 2018 to November 2019, within the preserved core area of the parks, covering all the phytophysiognomies present. A total of 27 species were collected, including nine species in each study site. Only tree/treelet species were collected as root systems vary greatly between herbs and trees/treelets so they may experience water stress differently. The complete list of study species is provided in table 1. Determination of the flowering period of the species was based on field expeditions, available literature, and the INCT - Herbário Virtual da Flora e dos Fungos database (Specieslink, 2020). Voucher material was deposited at the Herbário Prisco Bezerra (EAC), acronyms according to Thiers (2019).

For each species, at least three fertile branches with flowers were collected and fixed in buffered neutral formalin fixative solution (Johansen, 1940). Samples were kept in the fixative and stored at 4° C until analysis. The location of the secretory glands within the flowers was scored based on species descriptions available in the literature, especially identification keys, and analysis under a stereomicroscope (Leica EZ4 D).

Characterization of the chemical nature of the secretion

To identify of the main groups of chemical compounds present in secretions produced by the floral glands, fixed flowers at pre-anthesis and anthesis were cross and longitudinally sectioned without embedding. Embedding was avoided to ensure the integrity of floral exudates as organic solvents used during the embedding process may wash away floral exudates, especially lipophilic material. Sections ~10-12 µm thick were made on a table microtome (LPC, Rolemberg e Bhering, Belo Horizonte, Brazil) with common disposable razor blades, either freehand with leaf petiole pith from *Cecropia* Loefl. as a support material (Silva et al., 2013).

Histochemical tests were carried out on the sections to elucidate the chemical composition of floral secretions. Pectins were detected with Ruthenium Red (Johansen, 1940); total proteins with Xilidine Ponceau (O'Brien and McCully, 1981); total polysaccharides with Schiff's Periodic Acid (O'Brien and McCully, 1981); and lipid compounds with Sudan black B (Pearse, 1980). Slides were mounted as indicated for each test and control assays were performed according to the instructions of each test. Slides were analyzed using an Olympus BX 41TF light microscope (Tokyo, Japan).

Data analysis

The flowering time of each species was determined from the literature and categorized based on the climatic diagram at each site (Figure 1). Two categories were used: (i) rainy – flowering occurring during the period of water surplus; (ii) dry – flowering only during the dry period.

Following flowering time categorization, a frequency table was made for each class of compound (pectins, total proteins, total polysaccharides, and lipid compounds). We then to perform the chi-square test in which the null hypothesis was no difference in the frequency of species with a certain compound among seasons (Gotelli and Ellison, 2013).

Results

Flowering period

Two species (*Byrsonima correifolia* and *Byrsonima pachyphylla*) flowered throughout the year and were found at the Cerrado site (Table 1). Twelve species were characterized as flowering during the peak in rainfall: seven species (Table 1) at the Caatinga site (*Bauhinia cheilantha*,, *Croton blanchetianus*, *Fridericia parviflora*, *Mimosa tenuiflora*, Indeterminate 1, *Jatropha mollissima*, *Poincianella bracteosa*); three species (Table 1) in the Cerrado site (*Bauhinia dubia*, *Combretum melifluum*, *Eugenia* sp2); and only two species (Table 1) in the Montane Evergreen Forest (*Lantana camara*, *Ocotea duartei*). Eight species were found to flower during the dry season: none at the Caatinga site; three at the Cerrado site (*Anacardium occidentale*, *Hymenaea courbaril* and *Parkia platycephala*); and five at the Montane Evergreen Forest site (i.e. *Casearia silvestrys*, *Eugenia* sp1, Indeterminate 2, *Spondias mombin* and *Wedelia villosa*) (Table 1).

Table 1. Histochemical tests performed on species collected at the three study sites. Positive test is indicated by "+" and negative test by "-".

	Species	Total Polysaccharides	Pectins	Total Proteins	Lipids	Flowering period
Caatinga	*Bauhinia cheilantha* (Bong.) Steud.	+	+	+	-	Rainy
	Cordia leucocephala (Moric.) J.SMill.	+	+	+	+	Rainy
	Croton blanchetianus Baill.	+	+	+	+	Rainy
	Fridericia parviflora (Mart. ex DC.) L.G. Lohmann	+	+	+	-	Rainy
	Jatropha mollissima (Pohl) Baill.	+	+	-	-	Rainy
	Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	+	+	+	-	Dry
	Mimosa tenuiflora (Willd.) Poir.	+	-	+	-	Rainy
	Poincianella bracteosa (Tul.) L.P.Queiroz	+	+	+	+	Rainy
	Indeterminate 1	+	+	+	-	Rainy
Cerrado	*Anacardium occidentale* L.	+	+	+	-	Dry
	Bauhinia dubia G. Don.	+	+	+	-	Rainy
	Byrsonima correifolia A. Juss	+	+	+	+	Rainy
	Byrsonima pachyphylla A. Juss	+	+	+	+	Rainy
	Combretum melifluum Eichler	+	+	+	-	Rainy
	Eugenia sp2	+	+	+	-	Rainy
	Hymenaea courbaril L.	+	+	+	-	Dry
	Parkia platycephala Benth.	+	+	+	-	Dry
	Salvertia convallariaeodora A.St.-Hil.	+	+	+	-	Rainy
Montane Evergreen Forest	*Anadenanthera colubrina* (Griseb.) Altschul.	+	+	+	-	Dry
	Byrsonima gardneriana A. Juss.	+	+	+	-	Rainy
	Casearia silvestrys Sw.	+	-	+	-	Dry
	Eugenia sp1	+	+	+	-	Dry
	Lantana camara L.	+	-	+	-	Rainy
	Ocotea duartei	+	+	+	-	Rainy
	Solanum asperum Rich.	+	+	+	-	Dry
	Indeterminate 2	+	-	+	+	Dry
	Wedelia villosa Gardner.	+	+	+	-	Dry

Three species started flowering in the rainy season and kept flowering in the dry season: *Cordia leuchocephala* at the Caatinga site; *Salvertia convallariaeodora* at the Cerrado site; and *Byrsonima gardneriana* at the Montane Evergreen Forest site (Table 1). Only two species were found to start flowering in the dry season and kept flowering in the rainy season: *Libidibia ferrea* at the Caatinga site and *Anadenanthera colubrina* at the Montane Evergreen Forest site (Table 1).

Characterization of the chemical nature of the secretion

All 27 species studied presented total polysaccharides in their floral exudates, including plants that flowered in the rainy season and in the dry season (Table 1). Pectins were also widespread in floral exudates and were present in all but four species (Table 1). These were: *M. tenuiflora* (Caatinga site), which flowers in the rainy season; *S. mombin* and *C. silvestrys* (Montane Evergreen Forest site), which flower in the dry season; and *L. camara* (Montane Evergreen Forest site), which flowers in the rainy season.

Total proteins were found in all floral exudates except for *J. mollissima* (Caatinga site; Table 1). Only six species secreted lipidic compounds: *S. mombin* (Montane Evergreen Forest site); *B. correifolia* and *B. pachyphylla* (Cerrado site); and *P. bracteosa*, *C. blanchetianus* and *C. leucocephala* (Caatinga site, Table 1).

Analyzing the results of the histochemical tests, we observed that the species that secreted lipids at the Cerrado site (*B. correifolia* and *B. pachyphylla*) flowered throughout the year from months with the greatest water availability to months with low availability. In contrast, at the Caatinga site, species that produced lipids (*P. bracteosa, C. blanchetianus* and *C. leucocephala*) flowered in the months with the highest average rainfall. At the Montane Evergreen Forest site, only one of the species collected secreted lipids, *S. mombin* (Table 1).

Data analysis

When relating the flowering period to the secreted chemical compound, we may observe that only the species present in the Caatinga (Table 2) showed a difference in the secretion of pectins which was related to the rainy season ($\chi^2 = 4.5$, d.f. = 1; p = 0.03389). The results of the statistical test carried out are given in Table 2, where the compound was present in all species, the test was not carried out and the table is shown as a "homogeneous result". Comparisons of the three sites using the frequency of the presence of chemical groups found in the floral exudates are given in Table 3. There was no significance when correlating the sites to the presence of chemical groups.

Table 2. Frequency and chi-square test relating the flowering season to the chemical compounds found in the floral exudates of species from Caatinga, Cerrado and Montane Evergreen Forest sites.

Caatinga (Estação Ecológica de Aiuaba)			
Chemical group	Rainy	Dry	Test χ^2
Total polysaccharides			Homogeneous Result
Pectins	7	1	$X^2 = 4.5$; d.f. = 1; p = 0.03389
Total proteins	6	2	$X^2 = 2$; d.f. = 1; p = 0.1573
Lipids	3	0	$X^2 = 3$; d.f. = 1; p = 0.08326
Cerrado (Parque Nacional de Sete Cidades)			
Chemical group	Rainy	Dry	Test χ^2
Total polysaccharides			Homogeneous Result
Pectins			Homogeneous Result
Total proteins			Homogeneous Result
Lipids			Homogeneous Result
Montane Evergreen Forest (Parque Nacional de Ubajara)			
Chemical group	Rainy	Dry	Test χ^2
Total polysaccharides			Homogeneous Result
Pectins	2	4	$X^2 = 0.6666$; d.f. = 1; p = 0.4142
Total proteins			Homogeneous Result
Lipids	0	1	$X^2 = 1$; d.f. = 1; p = 0.3173

Table 3. Frequency and chi-square test relating the three study sites to the chemical compounds found in the floral exudates.

	Number of species at the sites			
Chemical group	Caatinga	Cerrado	Montane Evergreen Forest	Test x^2
Total polysaccharides	9	9	9	Homogeneous Result
Pectins	8	9	6	X^2= 0.6087; d.f. = 2; p = 0.7376
Total proteins	8	9	9	X^2 = 0.0769; d.f. = 2; p = 0.9623
Lipids	3	2	1	X^2 = 1; d.f.= 2; p = 0.6065

Discussion

Regardless the study site (Caatinga, Cerrado or Montane Evergreen Forest) where the plant species was collected, a mixture in the composition of the floral exudates is observed as some species secrete only hydrophilic substances (pectins, polysaccharides and proteins) while others a mixture of hydrophilic and lipophilic substances (pectins, polysaccharides, proteins total lipids).

Of the study sites, the Caatinga site has the lowest water availability (559 mm of rainfall/year) which, in addition to its high average annual temperature (25.1 ° C), results in a high evaporation rate. We found more pectins than expected in exudates at the Caatinga site. This is likely due to the hydrophilic/hygroscopic nature of pectins (mucilage). Pectins may hydrate up to 51 times more than their dry weight (Nobel et al., 1992). A high pectin content would guarantee the hydration of the floral exudates, thus avoiding their crystallization. This high content of pectins in floral nectars for Caatinga species may help us understand how the floral exudates produced in a plant community could change in relation to abiotic factors such as the water availability. Therefore, in future scenarios where climate warming could influence on expansion of hot and dry areas, a more jelly-like the nectar menu would be expected from plant communities (Gärtner et al., 2014; Costa-Coutinho et al., 2022).

Contrarily to our expectations, three of the species studied in the Caatinga (*P. bracteosa*, *C. blanchetianus*, and *C. leucocephala*) produced exudates with lipid compounds. The production of oils is highly costly to the production of carbohydrates (Sangwan et al., 2001; Buchanan et al., 2015; Paul and Eastmond, 2020; Pyke and Ren, 2023; Balbuena et al., 2024;). Therefore, in an environment where there is little water available, one may expect that plants will invest in more sugar-rich floral exudates. However, flowering and availability of resources are strongly linked to seasonal variations in rainfall (van Schaik et al., 1993; Aleixo et al., 2017). In our study, ~78% of the collected species in the Caatinga area flowered only in the rainy season. Since the rainy season is especially short at the Caatinga site, there is great overlap between the flowering period of the species. This may result in elevated competition for pollinators.

The production of floral exudates with different compositions (i.e. those with only hydrophilic compounds or with a mixture of lipophilic and hydrophilic compounds) could influence the preferences of pollinators. Caatinga vegetation has and few generalist plant species and a great diversity of pollinators, and pollinator diversity is likely to be underestimated (Machado and Lopes, 2004). Being attractive to pollinators and producing a satisfactory resource for visits is necessary (Machado and Lopes, 2004; Pyke and Ren, 2023) and may help explain the presence of lipids in Caatinga secretions. Furthermore, the presence of oils in the floral exudates can also help to maintain secretion as liquid, since they do not

dehydrate, thus preventing the exudate from crystallizing.

In contrast to the Caatinga site, one third of the species from the Montane Evergreen Forest site (*L. camara*, *S. mombrim* and *C. silvestrys*) did not present positive results for pectin. This result supports the hypothesis that pectins are required in drier environments to promote floral exudate hydration. Water availability at the Montane Evergreen Forest site is much greater so there is less need for hygroscopic substances in the floral exudate such as pectins.

We expected a significant correlation between the highest quality of floral exudates (i.e. exudates with more oils) and water availability in the Montane Evergreen Forest, as it is a more humid environment and with greater precipitation throughout the year so plants could invest in a more energy-rich resource to pollinators. However, when correlating the results of the histochemical tests and the water availability, no such correlation was observed. On the contrary, out of all the Montane Evergreen Forest species, only *S. Mombin* had oil in its floral exudates and this species flowered in periods with less water availability, from September to October.

The species in the Cerrado did not show any correlation regarding the presence of compounds with water availability. The results of the histochemical tests for species from the Cerrado were more like those species in the Montane Evergreen Forest. Although the Cerrado does not have humidity and pluviometry as a humid forest, its species have morphological adaptations, such as long pivoting roots, which help in capturing groundwater retained in the soil pockets (Hoffmann and Franco, 2003).

Conclusion

The hypothesis that water availability alters the composition of floral exudates so that the quality is lower in more severe environments has not been supported. However, we observed a specific correlation between the composition of floral exudates and water availability only in species collected in the Caatinga, where the presence of pectins was associated with local water availability. A surprising finding was the presence of lipid compounds in the floral exudates of Caatinga species, which indicates a more costly production for the plant, but with greater reward for pollinators. We suggest that lipid production may be a strategy to influence pollinator preference. Although our study was limited to 27 species in three locations, it offers a promising basis for future investigations in the semiarid context of Northeastern Brazil.

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