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SHORT COMMUNICATION - Conservation of Nature

Reproductive Seasonality and Related Above-Ground and Below-Ground Traits in *Andira Humilis*, a Brazilian Underground Tree

Iuri Santos Bulhões[1]
Marco Daniel Medeiros Lima[1]
Kauane Lais Souza Rodrigues[1]
Gabriel Soares Fernandes[1]
Andreza Nascimento Melo[1]
Beatriz dos Reis Queiroz[1]
Wasny Oliveira da Silva[1]
Letícia da Conceição Mota[1]
Jessie Kaila Araújo Silva Miranda[1]
Paulo Sérgio Neves dos Santos[1]
Vitor Alberto Matos Pereira[1]
Maria Thereza Dantas Gomes[1]
Sâmia Paula Santos Neves[1]
Lia D'Afonsêca Pedreira de Miranda[1]
Ligia Silveira Funch[1]

[1]Universidade Estadual de Feira de Santana (UEFS), Departamento de Ciências Biológicas, Laboratório Flora e Vegetação, Feira de Santana, BA, Brasil.

Abstract

We present the first study on the reproductive phenology and above-ground and below-ground trait relationships of *Andira humilis*, an endemic underground tree from Brazil. We studied an *A. humilis* population in caatinga remnants. The phenology seasonality was assessed using circular statistics (monthly frequency) based on herbarium vouchers. We used PCA on functional traits and climate to examine their relationships, and linear regression to assess the effects of mean rainfall and temperature on phenophases. *A. humilis* exhibits seasonality, flowering in the dry season and fruiting in the rainy season. Functional traits (low-wood density and high-water storage) enable flowering during water stress. Temperature drives fruiting, while flowering is independent of rainfall or temperature. Fruiting is less seasonal than flowering, likely due to extended maturation periods. This study highlights the role of *A. humilis* functional traits in adapting to extreme water stress in dry forests.

Keywords: Caatinga, geoxylic suffrutex growth form, leaf traits, saturated water content, wood density.

Plant phenology is increasingly associated with synergistic interactions of biotic and abiotic factors and functional traits (Bezerra et al., 2021; Neves et al., 2022). In tropical seasonal ecosystems, phenological seasonality depends mainly on temperature, rainfall, and traits related to tolerance of seasonal water stress, such as leaf thickness and wood density (WD) (Pereira et al., 2024). For example, while evergreen High-WD species retain leaves year-round due to drought-resistant xylem and thick leaves, showing minimal phenological shifts, deciduous low-WD species synchronize leaf shedding with soil water depletion, relying on stem water storage and rapid regrowth post-rain (Souza et al., 2020; Wright et al., 2021; Rufino et al., 2024).

In these ecosystems, there is a clonal growth form identified as geoxylic suffrutex, recognized for over a century (Lund, 1835). It's characterized by plants with a low above-ground height and a disproportionately large below-ground woody biomass (Pennington 2003). An example is *Andira humilis* Mart. ex Benth. (Fabaceae), an underground tree native of the Cerrado, Caatinga, and Brazilian Amazon (Ramos et al., 2024).

We investigated the seasonality of *A. humilis* using herbarium data, recognizing that herbarium collections are increasingly valuable tools for studying paterns in reproductive phenology (Orellana et al., 2021). Additionally, we studied individuals in Caatinga remnants, investigating below and above-ground traits (wood density, water retention capacity, and leaf traits), and abiotic factors (temperature and rainfall), to evaluate their role in the reproductive phenology. We hypothesized that *A. humilis* exhibits seasonal reproductive phenophases, with significant aggregated phenological activities, associated with water reserve in the aboveground traits and underground systems, without a strong relation with rainfall distribution.

For the functional trait collection (Table S1), we selected an *A. humilis* population in caatinga remnants at the State University at Feira de Santana – UEFS, Brazil, situated in a dry to sub-humid region with a mean annual temperature of 25.1°C and mean annual rainfall of 680 mm (Figure 1A) (INMET, 2024, UEFS weather station). In this area, *A. humilis* individuals stand out with nearly circular crowns and small aerial branches growing from woody underground systems (Figure 1B). The population exhibits horizontally spreading (sympodial) underground systems composed mainly of soboles – a shoot running along underground, forming new plants at short distance (Figure 1C). Aerial branches are less than 60 cm tall. We selected three genets as distant as possible to avoid sampling the same individual. We followed Perez-Harguindeguy et al. (2013) and Trugilho et al. (1990) for the leaf and wood traits collection. For more details see Table S1. The climatic data was obtained from UEFS weather station. We conducted a comprehensive survey of herbarium specimens using the speciesLink platform (CRIA, 2024) for phenological analyses. We reviewed 120 vouchers collected in Bahia and deposited at the herbarium ALCB, CEN, ESA, HST, HUEFS, MBM, MO, NY, SPF, UB, US, VIC, VIES (codes according to Thiers, continuously updated). After verifying the exsiccates identity, we selected 57 vouchers collected around UEFS, Feira de Santana, Bahia, Brazil with the presence of reproductive phenophases. We examined seasonality for herbarium phenological data using circular statistics in Oriana 4.02 software (Kovach Computing Services, 2024). The frequency of each phenophase was calculated based on the total number of vouchers showing the phases per month. The mean angles and *r* vector lengths were calculated (Zar, 2010). The phenological events with significant mean angles ($p < 0.05$) were transformed into mean dates. Phenophases whose vector lengths (r) were > 0.5 were considered seasonal (Morellato et al., 2010). We summarized functional traits and climate by scores of the axes of principal component analysis (PCA) to verify the possible relation between them. We used linear regression to assess the effects of mean rainfall and temperature on phenophases. All analysis were performed using R software, version 4.0.3 (R Core Team, 2020).

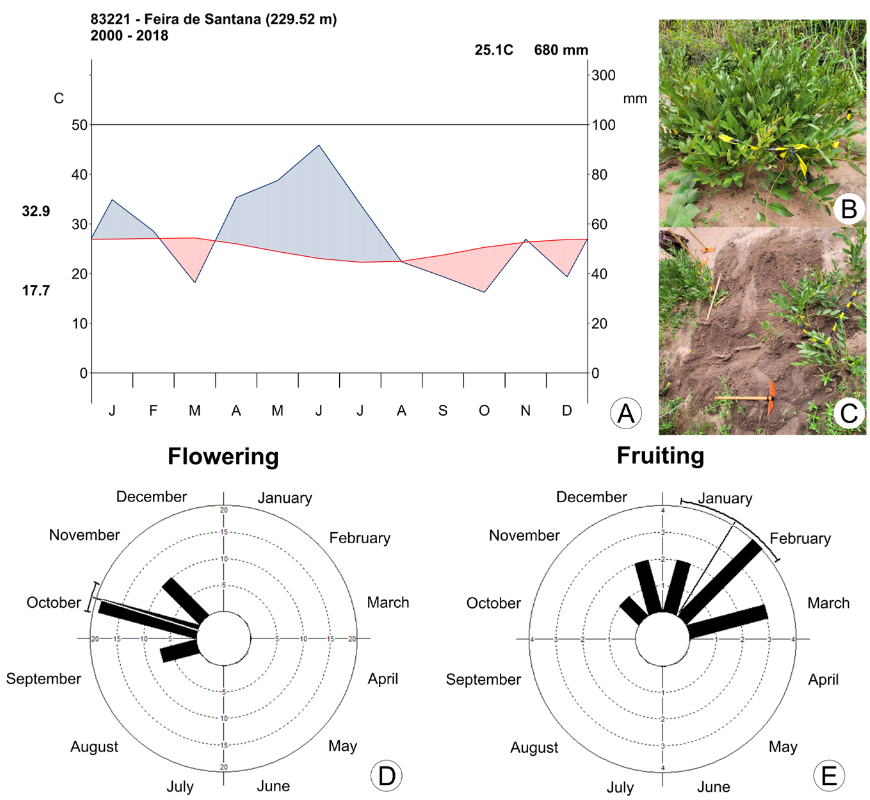

Figure 1. Clime, *Andira humilis* Mart. ex Benth. habit, and phenology. A) Climatic diagram for the municipality of Feira de Santana, Bahia State (INMET, UEFS Station). B) *A. humilis* individuals' circular crowns with small aerial branches. C) Ramets horizontally spreading underground systems. D-E) Circular histograms of the individual frequencies of flowering (D), and fruiting (E), based on herbarium data.

Andira humilis demonstrated seasonality in their reproductive phenophases, the greatest flowering and fruiting activities occurred in October (dry season; *r* 0,94) and February (rain season; *r* 0,80) (Figure 1D, E; Table S2). The below-ground and above-ground traits (Figure 2) are favorable to *A. humilis* flowering during the dry season, such as the low wood density (WD) in the branches (0.45 g/cm³) and below-ground system (0.47 g/cm³) and corresponding wood saturated water content (SWC) of 152% ± 0.22 (in the branches) and 130% ± 0.16 (below-ground system), leaf density (LDE) (0.0919±0.0086 mg.mm^{-3}), succulence (SUC) (0.0126±0.0011 g.cm²), and leaf thickness (LTH) (0.1603±0.0214 mm). The first two PCA axes explained 48,36 % of the data variation (Figure 2) (for the data used in PCA see Table S3 and S4). The first axis explained 27.28% of the variation and showed negative correlation with saturated water in both above (AGSWC = -0.73) and below-ground wood saturated water content (BGSWC = -0.63), LDE (-0.36), Above-Ground Dry Mass (AGDM = -0.21), SUC (1.85^{E-32}), mean rainfall (-5.3^{E-15}) and positive correlation with the remaining functional traits and mean temperature (mT = 5.3^{E-15}). The second axis was responsible for 21.08% of the variance and presented a negative correlation with AGWD (-0.26), BGWD (-0.52), AGDM (-0.28), BGDM (-0.48), SUC (-2.9^{E-32}), LDE (-0.14), and mT (-1.04^{E-14}) and a positive correlation with the remaining functional traits and mR (1.04^{E-14}) (Table S4). No clear grouping was indicated by the PCA (Figure 2).

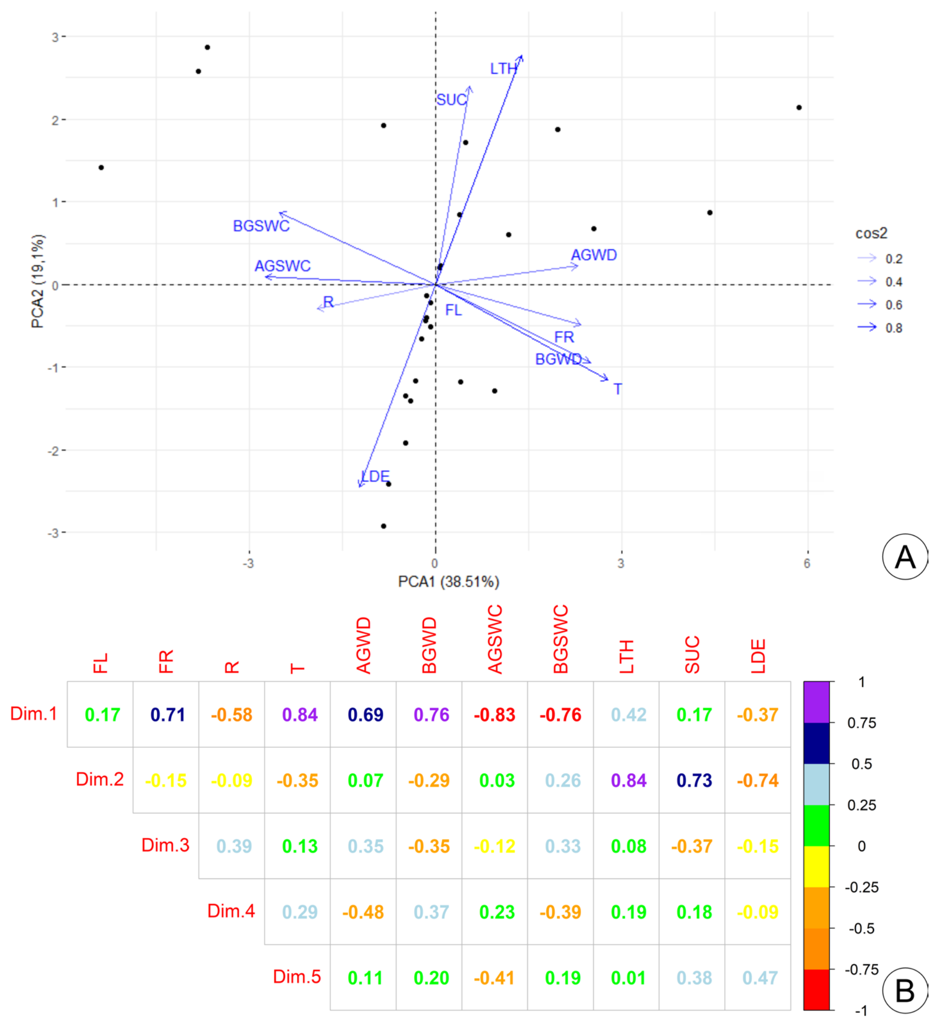

Figure 2. Principal Component Analysis (PCA) for climate variables (mR, mean rainfall, and mT, mean temperature) and functional traits (A) and variables correlations with PCA axes (B). LTH: leaf thickness. SUC: leaf succulence. AGSWC: above-ground saturated water content. BGSWC: below-ground saturated water content. LDE: leaf density. BGWD: below-ground wood density. AGWD: above-ground wood density. AGDM: above-ground dry mass. BGDM: below-ground dry mass. SLM: saturated leaf mass. DLM: dry leaf mass. LMA: leaf mass per area. The black points indicate individuals sampled.

The flowering displayed no correlation with the mR (p = 0,07) and mT (p = 0.91). Fruiting correlated only to temperature (p = 0.003) (Table S5 and S6). The observed strong seasonality of the flowering and fruiting might be sustained by the high-water storage capacity on below-ground systems and aerial branches, which also favored *A. humilis* flower through the dry season (Pereira et al., 2024). Our results highlighted the major role of temperature in modulating fruit production, while flowering was unaffected by rainfall or temperature. The herbarium data indicated that fruiting is less seasonal than flowering, which could be explained by the period required for fruit maturation (Orellana et al., 2021). Here we present the first comprehensive study addressing the reproductive phenology of an underground tree in caatinga remnants, revealing the important role of functional traits in modulating flowering during the dry season, in extreme water stress conditions, and fruiting during the rainy season (Neves et al., 2022).

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CORRESPONDENCE TO

Iuri Santos Bulhões

Conjunto Feira VI, Caminho 41, 8, Bairro Campo Limpo, CEP: 444034-212, Feira de Santana, BA, Brasil
e-mail: pryngos@gmail.com

AUTHORS' CONTRIBUTIONS

Iuri Santos Bulhões: conceptualization (equal), data curation (equal), formal analysis (equal), investigation (equal), methodology (equal), writing – original draft (equal).

Marco Daniel Medeiros Lima: data curation (equal), formal analysis (equal), investigation (equal), methodology (equal), visualization (equal), writing – original draft (equal).

Kauane Lais Souza Rodrigues: conceptualization (supporting), formal analysis (supporting), investigation (supporting), methodology (supporting), visualization (supporting).

Gabriel Soares Fernandes: conceptualization (supporting), data curation (supporting), formal analysis (supporting), methodology (supporting), writing – original draft (supporting).

Andreza Nascimento Melo: conceptualization (supporting), data curation (supporting), investigation (supporting), methodology (supporting), writing – original draft (supporting).

Beatriz dos Reis Queiroz: conceptualization (supporting), data curation (supporting), methodology (supporting), writing – original draft (supporting).

Wasny Oliveira da Silva: data curation (supporting), investigation (supporting), methodology (supporting), visualization (supporting), writing – original draft (supporting).

Letícia da Conceição Mota: conceptualization (supporting), data curation (supporting), investigation (supporting), methodology (supporting), writing – original draft (supporting).

Jessie Kaila Araújo Silva Miranda: conceptualization (supporting), data curation (supporting), investigation (supporting), methodology (supporting), writing – original draft (supporting).

Paulo Sérgio Neves dos Santos: data curation (supporting), formal analysis (supporting), methodology (supporting), software (lead), writing – original draft (supporting), writing – review & editing (supporting).

Vitor Alberto Matos Pereira: formal analysis (equal), methodology (supporting), software (supporting), visualization (supporting), writing – original draft (supporting).

Maria Thereza Dantas Gomes: formal analysis (supporting), investigation (equal), methodology (supporting), project administration (supporting), supervision (equal), writing – original draft (supporting), writing – review & editing (equal).

Sâmia Paula Santos Neves: conceptualization (supporting), investigation (supporting), software (supporting), supervision (supporting), validation (supporting), writing – review & editing (supporting).

Lia D'Afonsêca Pedreira de Miranda: conceptualization (supporting), data curation (supporting), investigation (supporting), project administration (supporting), resources (lead), supervision (lead), validation (supporting), visualization (supporting), writing – original draft (supporting).

Ligia Silveira Funch: conceptualization (lead), formal analysis (lead), funding acquisition (lead), project administration (lead), resources (lead), validation (lead), visualization (lead), writing – original draft (lead).

DATA AVAILABILITY

The entire dataset supporting the results of this study was published in the article and in the "Supplementary Materials" section.

SUPPLEMENTARY MATERIAL

The following online material is available for this article:

Table S1. Above and belowground traits (leaf and wood traits) in *Andira humilis* Mart. ex Benth. (Fabaceae), Northeastern Brazil, indicating abbreviation and the specific units of measurement for each trait, number of sampled individuals, and formulas used for the calculations.

Table S2. Circular analysis of the reproductive phenophases of *Andira humilis* Mart. ex Benth. (Fabaceae) in a caatinga remnant, Northeastern Brazil. ($r > 0.5$ indicates seasonality).

Table S3. Functional traits values of the *Andira humilis* specimens sampled and mean precipitation and temperature in the caatinga remnants.

Table S4. Contributions of the variables to the dimensions of the Principal Component Analysis.

Table S5. Climate and phenological data of *Andira humilis* in the caatinga remnants.

Table S6. The relationship between monthly rainfall and temperature with flowering and fruiting phenophases in the caatinga remnants. 95% confidence intervals. Significant correlations are indicated in bold.

REFERENCES

Bezerra-Silva A, Fagundes ACA, Gomes MTD, Menezes IS, Couto-Santos APL, Cerqueira CO, Miranda LAP, Funch LS. Inflorescence Position Influences Phenological Rhythms in Leguminosae Species. Floresta e Ambiente 2021; 28(4): e20210073.

CRIA – Centro de Referência em Informação Ambiental 2024 'speciesLink: simple search.' Available from: https://specieslink.net/.

INMET – Instituto Nacional de Meteorologia, 2024. [viewed July 2024]. Dados Históricos Anuais [online]. Available from: https://portal.inmet.gov.br/dadoshistoricos.

Kovach Computing Services [viewed July 2024]. Oriana 4.02. Available from: https://www.kovcomp.co.uk/oriana.

Lund PW. Bemaerkinger over vegetationen paa de indre Hojsletter af Brasilien, isaer i plantehistorisk Henseende. Kgl Danske Videnskab Selsk Skrifter 1835; 6: 145.

Morellato LPC, Alberti LF, Hudson IL. Applications of circular statistics in plant phenology: a case studies approach. In: Hudson IL, Keatley M, editors, Phenological research: methods for environmental and climate change analysis. Springer; 2010: 339–359.

Neves SPS, Santos MGM, Vitória AP, Rossatto DR, Miranda LAP, Funch LS. The roles of functional traits in canopy maintenance along a savanna/seasonally dry tropical forest gradient in northeastern Brazil. Flora 2022; 292: 152090.

Orellana JT, Nascimento JOV, Grilo J, Neves SPS, Miranda LAP, Funch LS. Seasonality and the Relationships Between Reproductive and Leaf Phenophases In Myrtaceae Using Field and Herbarium Data. Floresta e Ambiente 2021; 28(1): e20200035.

Pennington RT. Monograph of Andira (Leguminosae, Papilionoideae). Systematic Botany Monographs 2003; 64:1-143.

Pereira VAM, Santos VO, Neves SPS, Villa PM, Rossatto DR, Miranda LAP, Funch LS. The role of functional traits on evergreen canopies maintenance of *Hancornia speciosa* (Apocynaceae) in Capitinga sandy areas. Brazilian Journal of Biology 2024, 84, 1–6, e286125.

Pérez-Harguindeguy N, Diaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, et al. New handbook for standardise measurement of plant functional traits worldwide. Australian Journal of Botany 2013; 61(3), 167–234.

R Core Team. R: A language and environment for statistical computing, version 4.0.3. R Found. Stat. Comput., Vienna, 2020.

Ramos G, Cardoso DBOS, Pennington RT. *Andira* in Flora e Funga do Brasil**.** Jardim Botânico do Rio de Janeiro. https://floradobrasil.jbrj.gov.br/FB29443 acesso 08 jul. 2024.

Rufino M KG, Silva FKG, Salviano VM, Patrício MC, Melo JIM, Trovão DMBM. The LHS scheme and wood density define functional groups of woody species in the Brazilian semiarid? Capturing functional syndromes in the Caatinga. Brazilian Journal of Biology 2024; 84, e280040.

Souza BC, Carvalho ECD, Oliveira RS, Araujo FS, Lima ALA, Rodal MJN. Drought response strategies of deciduous and evergreen woody species in a seasonally dry neotropical forest. Oecologia 2020; 194, 221-236.

Trugilho PF, Silva DA, Frazão FJL, Matos JLM. Comparação de métodos de determinação da densidade básica em Madeira. Acta Amazonica 1990; 20: 307–319.

Thiers B (continuously updated) 'Index Herbariorum: A global directory of public herbaria and associated staff.' (New York Botanical Garden's Virtual Herbarium) Available at http://sweetgum.nybg.org/science/ih/ [Verified 20 August 2024].

Wright CL, Lima AL, Souza ES, West JB, Wilcox BP. Plant functional types broadly describe water use strategies in the Caatinga, a seasonally dry tropical forest in northeast Brazil. Ecology and Evolution 2021; 11(17), 11808-11825.

Zar JH. Biostatistical analysis. New Jersey: Prentice-Hall; 2010.