








Notes and Comments

## The role of functional traits on evergreen canopies maintenance of *Hancornia speciosa* (Apocynaceae) in Capitinga sandy areas

### O papel dos traços funcionais na manutenção de copas perenes de *Hancornia speciosa* (Apocynaceae) em áreas arenosas de Capitinga

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Plant phenological responses occur based on interactions between environmental factors (rainfall, temperature, photoperiod, daily insolation, and soil properties) and functional traits (Ragusa-Netto and Silva, 2007; Pereira et al., 2024; Barros et al., 2023), with wood and leaf traits being the major determinants of plant growth cycles, especially leaf fall and budding, in seasonal ecosystems under well-defined drought periods (dry season) (Neves et al. 2022). *Hancornia speciosa* Gomes (Apocynaceae), known traditionally as *mangabeira*, is a typical species of the coastal environments, savannas, and plateaus, distributed across Brazil (Flora and Funga do Brasil, 2024).

In Chapada Diamantina, *H. speciosa* (Figure 1B) is one of the few tree species that occurs on the Capitingas (Figure 1A), a highland field related phytophysiognomy that occupies small, scattered quartzarenic neosol patches, surrounded by evergreen forest on latosol. The poor sandy soil with high drainage increases the water deficit on Capitinga, during the dry season (June to October), while the clay contents on the surrounding soils favor the maintenance of evergreen forest vegetation.

Given the characteristic sandy soil, this species may be subjected to low nutrient availability and low water retention during drought periods. The understanding of phenological patterns in this species depends on above and below-ground traits that can explain how this species can survive in a sandy environment. We selected *H. speciosa* individuals growing at this sandy ecosystem in Chapada Diamantina (Figure 1A, B) to investigate below-ground (wood density and water retention capacity in the below-ground system) and above-ground traits (leaf traits, wood density, and water retention capacity in the branches) associated with the tolerance of seasonal water stress (Perez-Harguindeguy et al., 2013) and abiotic factors (temperature, photoperiod, rainfall and soil chemical traits) to evaluate its role in *H. speciosa* leaf phenology responses

in Capitinga phytophysiognomy in Chapada Diamantina, Brazil. We hypothesize that functional traits will determine the trade-off to maintain the positive water status and consequently, the evergreen canopy maintenance.

The present study was conducted in Capitinga vegetation, on the eastern edge of Chapada Diamantina (12°27' – 12°38'S and 41°21' –41°22'W, 500 m altitude) (Funch et al., 2021). The region experiences a mesothermic climate, type Aw according to the Köppen system (Alvares et al., 2013), with a rainy season between November and April and a dry season usually between June and October (Figure 1C). Rainfall, relative humidity, temperature, and solar radiation data were obtained from the National Institute of Meteorology (INMET, 2024). Day length was calculated using the Solar Photoperiod Calculator (<http://www.solartopo.com/daylength.htm>). The physicochemical properties of the soils were obtained in each Capitinga site at depths between 0 and 40 cm; each pooled sample was formed by three 330-g subsamples, collected every 50 m in each area (Pereira, 2022). Monthly observations of 54 tagged individuals on three sites in Capitinga phytophysiognomy were carried out from 2019 to 2021. Phenophases intensities were estimated using a semiquantitative scale with five categories (0 to 4, in 25% intervals) (Neves et al., 2022). For the measurement of functional traits, tissue samples were taken from three individuals (Pérez-Harguindeguy et al., 2013), during the dry season.

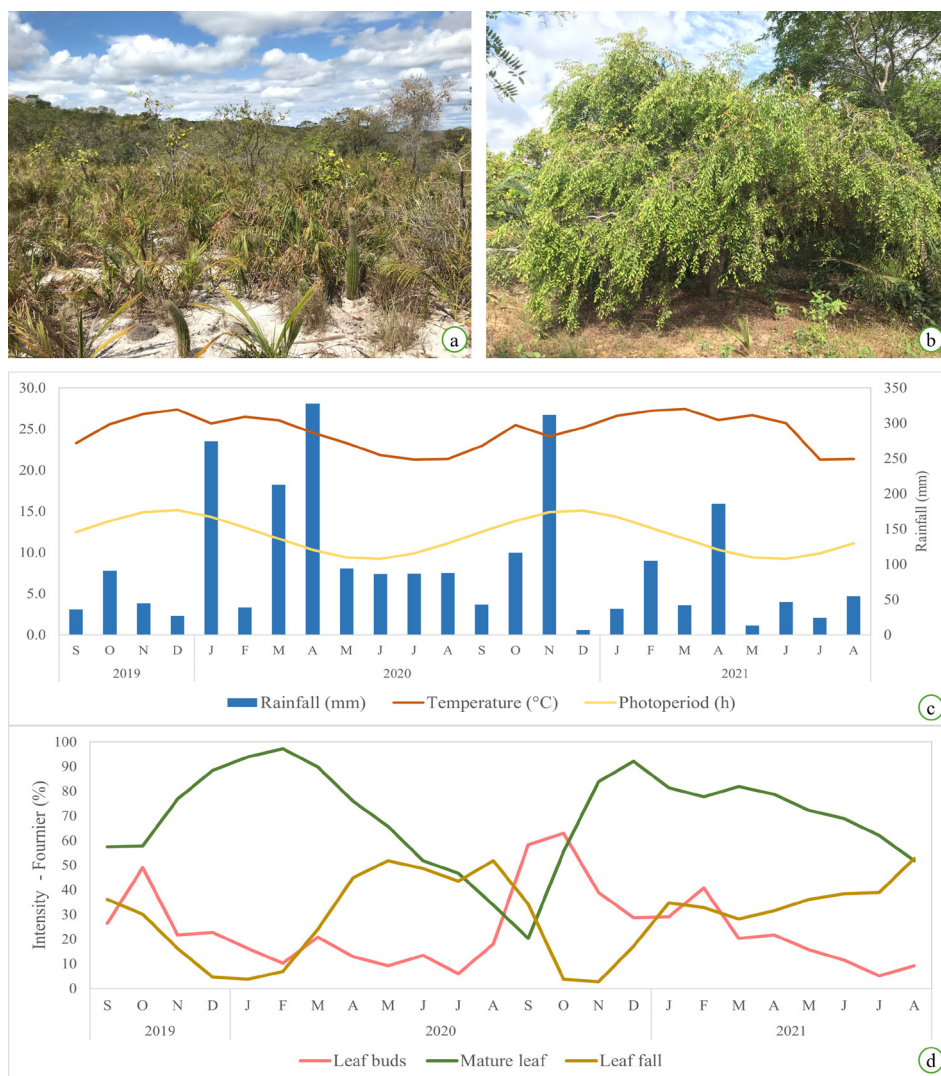
Leaf traits, such as leaf mass per unit area (LMA) ( $\text{g}\cdot\text{m}^{-2}$ ), leaf density (LD) ( $\text{mg}\cdot\text{mm}^{-3}$ ), dry weight (W) (g), succulence (Suc) ( $\text{g}\cdot\text{m}^{-2}$ ), and leaf thickness (LT) (mm), from 10 mature and completely healthy and expanded leaves per individual. Branch and the below-ground system wood density sampling were carried out in three samples approximately 10 cm long and 5 cm in diameter for each individual, which were treated according to Trugilho et al. (1990). The resulting values were used to calculate the

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**Figure 1.** Vegetative phenology pattern of *Hancornia speciosa* Gomes. a) Capitinga vegetation. b) Adult individual. c) Environmental drivers. d) Vegetative phenophase intensity. Data were collected in Chapada Diamantina, Bahia, Brazil, between September 2019 and August 2021.

wood density ( $DM = D_m/V$ ) and saturated water content in wood ( $CAS = 100(M_{sat} - D_m)/D_m$ ) (Trugilho et al., 1990). We summarized functional traits, climate, and soil variables by scores of the axes of principal component analysis (PCA). To avoid the substantial presence of correlated variables, we tested two PCA types per variable category (soil and climate variables). Thus, the soil-functional traits PCA and climate variability-functional traits PCA were tested separately (Schmitz et al., 2020).

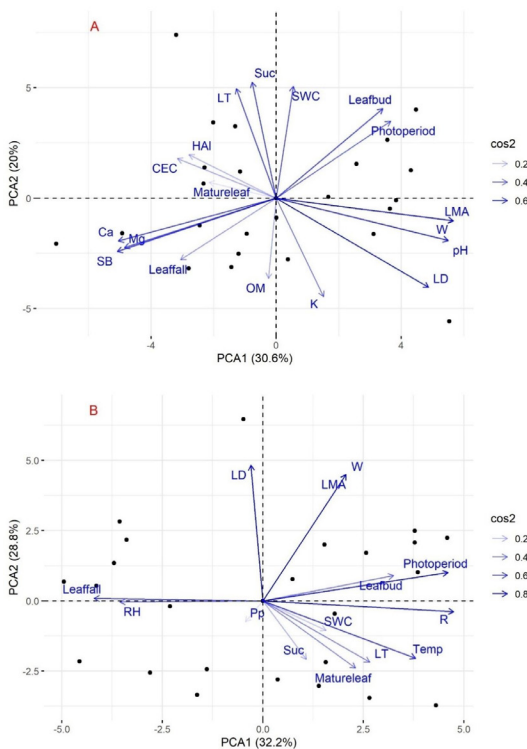
We used linear models to test the main effects of abiotic (climatic and soil variables) and biotic (functional traits) predictors on three phenophases. Predictors were selected based on their data variability contribution of PCAs (Fig. S1 and S2 from Supplementary Material) and collinearity between selected predictor variables using Spearman correlation analysis by variable categories (Fig. S3, S4 and S5 from Supplementary Material). Thus, the following predictors were selected: photoperiod,

temperature, and total exchangeable bases; meanwhile, the biotic predictors based on functional traits were LMA and SWC. The Gaussian error distribution was tested to select the most suitable distribution, i.e., normality was confirmed by the Q-Q graph (Fig S6 from SM). All analysis were performed using R software, version 4.0.3 (R Core Team, 2020).

*Hancornia speciosa* exhibited continuous leaf loss and budding, generally with low intensity, with moderate peaks of budding (62%) and leaf fall (51%), during the dry season (Figure 1D). The below-ground and above-ground traits contribute to the prompt recomposition of the *H. speciosa* canopy (Figure 2), such as the low density in the branches ( $0.37 \text{ g/cm}^3 \pm 0.01$ ) and below-ground system ( $0.36 \text{ g/cm}^3 \pm 0.01$ ) and corresponding saturated water content in the wood of  $63.85\% \pm 0.68$  (in the branches) and  $63.7\% \pm 0.88$  (below-ground system) (Borchert, 1994), suggesting a high capacity of water storage on trunks and

branches, which could maintain leaf budding through desfavorable times.

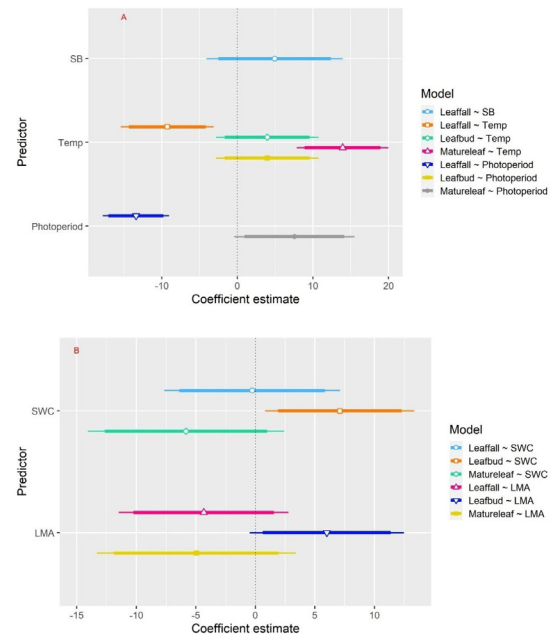
The first two axes explained ~50% of the data variation in both PCAs (Figure 2). The first axis using data soil explained 30.6% of the variation and was negatively correlated with the nutrients (Ca = -0.70, Mg = -0.67) and fertility indices (SB = -0.71, CEC = -0.50) associated with leaf fall phenophase, and positively correlated with functional traits (W = 0.79, LD = 0.68, LMA = 0.79) associated with leaf bud phenophase (Figure 2A). Using the climate-related variables the first PCA explained 32.2% and was positively correlated with irradiation (R = 0.86, p < 0.05), temperature (R = 0.76, p < 0.05), and LT (R = 0.61, p < 0.05) which were associated with mature leaves phenophase. Meanwhile, leaf functional traits presented a significant positive correlation with PCA2, such as LMA (R = 0.83, p < 0.05), leaf density (R = 0.87, p < 0.05), and dry weight (R = 0.83, p < 0.05) which are associated with lower rainfall



**Figure 2.** Principal Component Analysis (PCA) for the soil variables, phenophases and functional traits (A), and climate variables, phenophases (mature leaf, leaf fall, leaf bud) and functional traits (B). For analysis, rainfall (Pp) relative humidity (RH), radiation (R), temperature (Temp), soil organic carbon (C), total potassium (K<sup>+</sup>), calcium (Ca<sup>2+</sup>), magnesium (Mg<sup>2+</sup>), exchangeable acidity (H<sup>+</sup>Al), pH, organic matter (OM), total exchangeable bases (CEC) and total exchangeable bases (SB). For climate variables, precipitation (Pp), relative humidity (RH), radiation (R), photoperiod and temperature (Temp) were included. Furthermore functional traits, such as leaf mass per unit area (LMA), leaf density (LD), succulence (Suc), and leaf thickness (LT), root saturated water content (SWC) and dry weight (W) were included. Cos2 means the relative contribution of the variables represented by the vectors.

values (Figure 2B). The tested models show that both abiotic predictors, temperature (Estimate = -4.34, t = -3.13, p < 0.001) and photoperiod (Estimate = -6.32, t = -6.40, p < 0.001) explained a negative relationship in leaf fall (Figure 3A) meanwhile, the temperature positively and significantly affected mature leaves (Estimate = 6.52, t = 4.75, p < 0.001). According to biotic predictors models, SWC had the strongest positive effect on leaf buds (Figure 3B). The absence of rainfall among the strongest predictors indicates that it may not be relevant to the species foliar dynamics.

The results show that above-ground and below-ground functional traits are linked with leaf phenology of *H. speciosa*, which in turn are important in the tolerance under limited resource availability (water and nutrients) in Capitinga. The results show that despite the increase in temperature, photoperiod, and solar radiation, and the decrease in rainfall and relative humidity, *H. speciosa* exhibits a tolerance response to water deficit through functional traits such as succulence, leaf thickness, and saturated water content in roots. Probably, these traits favor the high proportion of mature leaves allowing growth and function maintenance over time. Thus, the canopy did not suffer a marked reduction in mature leaves, except briefly in September 2020 (canopy cover about 20%), in



**Figure 3.** Standardized regression coefficients of different linear models to test the main effects of abiotic and biotic predictors on phenophases (mature leaf, leaf fall, leaf bud). The following abiotic predictors are included according to the main models: photoperiod, temperature (Temp), and total exchangeable bases (SB); meanwhile, the biotic predictors based on functional traits were leaf mass per unit area (LMA) and saturated water content in the root (SWC). The averaged parameter estimates (standardized regression coefficients) of model predictors, the associated 95% confidence intervals, and the relative importance of each factor expressed as the percentage of explained variance, are indicated.

response to greater leaf fall activity, followed by prompt recombination due to increased leaf budding (Figure 1), maintaining its evergreen canopy trait.

Plant species in resource-poor environments tend to have a resource conservation strategy (Rossatto and Franco, 2017). Our results show that the LMA, leaf thickness, leaf density, and succulence were associated with greater water storage capacity, conservative use resource strategy, and tolerance to water deficit mainly in drylands (Neves et al., 2022; de Freitas et al., 2024).

The nutrient poor environments, high irradiances, and seasonal drought typical of savanna environments are likely to have contributed to the evolution of low specific leaf area of savanna species, concurring to longer leaf life-span and increasing nutrient-use efficiency (Hoffmann et al., (2005). Furthermore, the low leaf area mass shows the low cost of leaf construction under water and nutrient deficit conditions (Kikuzawa and Lechowicz, 2011). In addition, Rossatto and Franco (2017) and Hoffmann et al. (2005) demonstrate how leaf traits allow savanna species to show greater water use efficiency than forest species. This information from the literature anticipates our study that demonstrates that the period of water scarcity did not directly affect the water status of *H. speciosa*.

This ecological pattern has been well reported for trunks, stems and even roots of woody species which have higher storage water capacity as a functional strategy for regulating water potential and avoiding low water availability during drought (Borchert, 1994; Freitas et al., 2024). This strategy allows the maintenance of activities such as leaf production during drought and involves the presence of wood tissues with low densities that will have the capacity to store a higher amount of water and nutrients (Neves et al., 2022). Such strategies are reported mainly for trees, especially for Neotropical tree species (Scholz et al., 2007), but we show here that such mechanisms also involve underground systems.

The relationships of environmental factors and functional traits of *H. speciosa* allow us to infer that it presents a wide spectrum of acquisitive and conservative resource use strategies distributed between different phenophases, which allows its tolerance to resource limitation and maintenance of growth through rapid leaf renewal.

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## Supplementary Material

Supplementary material accompanies this paper.

Figure S1. Significance levels are based on the Spearman correlation coefficient between soil chemical properties, phenophases (mature leaf, leaf fall, leaf bud), functional attributes and the axis of PCA. For analysis, soil organic carbon (C), total potassium (K<sup>+</sup>), calcium (Ca<sup>2+</sup>), magnesium (Mg<sup>2+</sup>), exchangeable acidity (H<sup>+</sup>Al), pH, organic matter (OM), total exchangeable bases (CEC) and total exchangeable bases (SB). Furthermore, functional attributes, such as leaf mass per unit area (LMA), leaf density (LD), succulence (Suc), and leaf thickness (LT), saturated water content in the root (SWC) and dry weight (W) were included.

Figure S2. Significance levels are based on the Spearman correlation coefficient between climate variables, phenophases (mature leaf, leaf fall, leaf bud), functional attributes and the axis of PCA. For analysis, climate variables such as precipitation (Pp), relative humidity (RH), radiation (R), photoperiod, and temperature (Temp) were included. Furthermore, functional attributes, such as leaf mass per unit area (LMA), leaf density (LD), succulence (Suc), and leaf thickness (LT), saturated water content in the root (SWC) and dry weight (W) were included.

Figure S3. Spearman correlation among all individual soil variables measured.

Figure S4. Spearman correlation among all individual climate variables measured.

Figure S5. Spearman correlation among all individual functional attributes variables measured.

Figure S6. Examples to test the most suitable distribution and link function using Q-Q plot for response variables (phenophases).

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