Original Article

The LHS scheme and wood density define functional groups of woody species in the Brazilian semiarid? Capturing functional syndromes in the Caatinga

O esquema LHS e a densidade da madeira definem grupos funcionais de espécies lenhosas no semiárido brasileiro? Capturando síndromes funcionais na Caatinga

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Abstract

For the Caatinga vegetation, it has not yet been definitively established which adaptive strategies best define the functional groups of woody plants and which syndromes emerge from the relationships between functional traits to achieve success in a semi-arid tropical region. To fill some of these gaps, we analyzed a specific set of characteristics that make up the LHS scheme of the plant ecological strategy (leaf-heigh-seed). The LHS scheme captures the functional niche of plants regarding the functional traits specific leaf area (SLA), plant height (HE), and seed mass (SM). We associate wood density (WD) to this scheme because this trait is a key feature for the identification of functional strategies in seasonally dry vegetation such as the *Caatinga*. We measured these characteristics in eight woody species and classified them according to their leaf phenology into deciduous and evergreen. The experiment was carried out between December 2017 and November 2018 in *Caatinga* areas located in the municipality of Barra de Santana, PB, a semiarid region of Brazil. Using cluster analysis, principal component analysis (PCA) and Pearson correlation analyses, we found significant relations between SLA and SM, and HE and WD. The SLA was the main predictor of plant strategy in the *Caatinga*. According to this characteristic, we identified two functional groups: species with a low SLA and species with a high SLA. We also recognized differences between deciduous and evergreen species based on the same trait. The traits measured, which represent the axes of the plant ecological strategy scheme LHS and wood density, are efficient in the discrimination of functional groups in the Brazilian semiarid. These groups relate to leaf phenology of woody species in this vegetation.

Keywords: ecological strategy, functional traits, phenology, seasonally dry vegetation.

Resumo

Para a vegetação de Caatinga ainda não foi estabelecido de forma contundente quais são as estratégias adaptativas que melhor definem os grupos funcionais das lenhosas e também quais são as síndromes que emergem das relações entre os traços funcionais para alcançar o sucesso em uma região semiárida tropical. Com o objetivo de preencher algumas dessas lacunas, analisamos um conjunto específico de características que compõem o esquema LHS da estratégia ecológica vegetal (altura-folha-semente). Com o objetivo de preencher lacunas sobre grupos funcionais na vegetação da Caatinga, analisamos um conjunto específico de características que compõem o esquema LHS da estratégia ecológica vegetal (altura-folha-semente). O esquema LHS captura o nicho funcional das plantas em relação às características funcionais área foliar específica (SLA), altura da planta (HE) e massa da semente (SM). Associamos a densidade da madeira (WD) a este esquema porque esta característica é chave para a identificação de estratégias funcionais em vegetações sazonalmente seca como a Caatinga. Medimos essas características em oito espécies lenhosas classificadas de acordo com sua fenologia foliar em decíduas e perenes. O experimento foi realizado entre dezembro de 2017 e novembro de 2018 em áreas de Caatinga localizadas no município de Barra de Santana, PB, região semiárida do Brasil. Utilizando análises de cluster, componentes principais (PCA) e correlação de Pearson, encontramos relações significativas entre SLA e SM, e HE e WD. O SLA foi o principal preditor da estratégia da planta na Caatinga. De acordo com esta característica, identificamos dois grupos funcionais: espécies com baixa SLA e espécies com alta SLA. Também reconhecemos diferenças entre espécies decíduas e perenes com base na mesma característica. As características medidas, que representam os eixos do esquema de estratégia ecológica vegetal LHS e densidade da madeira, são eficientes na discriminação de grupos funcionais no semiárido brasileiro. Esses grupos estão relacionados à fenologia foliar de espécies lenhosas desta vegetação.

Palavras-chave: estratégias ecológicas, traços funcionais, fenologia, vegetação sazonalmente seca.

1. Introduction

Knowing patterns of structuring and functioning of a plant community is essential to predict responses, resistance, and resilience to increasing anthropogenic interventions (Chazdon, 2014). The diversity-focused approach to functional traits evidences such patterns (Westoby et al., 2002; Wright and Westoby, 2002; Bucci et al., 2004; Fine et al., 2006; Kooyman et al., 2010; Souza et al., 2015). Functional traits are significant characteristics for the establishment, survival, and reproduction of species in their natural environment. The correlation between such traits results in syndromes that determine different strategies of plant species independently of their phylogenetic proximity, thus forming a functional group (Reich et al., 2003; Borges and Prado, 2014).

The choice of traits for the discrimination of functional groups should take into account major environmental stresses to which the plants are subjected (Weiher et al., 1999; Diaz and Cabido, 2001; Kraft and Ackerly, 2010; Rosado et al., 2013), as the variation in traits is a response to the availability and use of resources or to environmental stressors (Violle et al., 2007). In seasonally dry environments, for example, water availability can be considered the main factor affecting growth and reproduction of plants (Kramer and Boyer, 1995). In these environments, the temporal and spatial variation in water availability regulates physiological and phenological responses. However, according to Lima and Rodal (2010) such responses are still little known.

Studies carried out in the *Caatinga* (Silva et al., 2004, 2014; Trovão et al., 2007; Lima and Rodal, 2010; Lima et al., 2012; Souza et al., 2015), a seasonally dry vegetation that covers most of the Brazilian semiarid region, have shown that leaf phenology is associated with a marked water stress, and that the co-occurrence of woody species with distinct leaf phenology strongly indicates different water use strategies (Markesteijn and Poorter, 2009).

Silva et al. (2014) considered that deciduous leaves are an important response to drought. The authors considered leaf traits and wood density to associate them with leaf habits in the *Caatinga*. Other authors also tried to understand the functional groups of the Caatinga based on their hydric relations (Pinho et al., 2019; Wright et al., 2021; Fagundes et al., 2022). However, it has not been established which relations between wood and leaf traits form syndromes (Reich et al., 2003), and therefore discriminate woody functional groups in the *Caatinga*. It is also unclear what are the adaptive strategies defining these functional groups, i.e., what are the competencies that emerge from the relation between traits that reach success in a tropical semiarid region. It has not yet been defined whether the functional groups of trees in the *Caatinga* coincide with leaf phenology, and what is the meaning of the relation between the permanence of leaves and traces of wood and leaf in the perspective of a discriminatory model (Souza et al., 2015).

In order to fill such gaps, we begin by using an approach different from that used in other studies developed on this vegetation. We analyze a specific set of traits that comprise a model for the identification of adaptive strategies known as the Ecological Strategy Scheme LHS (leaf-height-seed). This approach was proposed by Westoby (1998) and tested with efficiency in different types of vegetation (Diaz et al., 2004; Wright et al., 2007; Abe et al., 2018). This scheme proposes a description of the functional niche of plants using three fundamental and independent axes: 1) specific leaf area, 2) plant height at maturity, and 3) seed mass. These three characteristics have a strong foresight ability to predict community responses to environmental changes, or they strongly affect community processes (Westoby, 1998; Cornelissen et al., 2003).

We associate wood density with the LHS scheme. Wood density has been considered a key feature in the identification of plant strategies in seasonally dry vegetation (Lima and Rodal, 2010; Silva et al., 2014). In general, this trait is negatively related to water potential in woody plants subjected to water stress (Ackerly, 2004; Bucci et al., 2004).

The acquisition of air space and resources, mainly water, and its use and stock are operations requiring a set of competencies that define strategies of survival in seasonally dry vegetation. Thus, the dependence relations between plant height and structure, leaf physiology, seed mass and wood density can be syndromes or main dimensions of ecological strategies (Westoby et al., 2002; Wright et al., 2007) of woody plants in the *Caatinga* vegetation, providing an explanation to the delimitation of functional groups in these environments.

In these terms, we elaborate two questions: 1) Are functional traits that make up the axes of the LHS scheme together with wood density characteristics efficient to identify syndromes, capable of consistently pointing out functional groups in the Caatinga? 2) Are the functional groups of woody plants identified from the tested relationship also related to the leaf phenology of these plants? Our hypothesis is that the traits that make up the axes of the LHS scheme in association with wood density can correlate in different ways, forming compromises, syndromes, within the functional spectrum of the Caatinga, composing an effective model for identifying different sets of plant strategies in the woody vegetation of the Brazilian semi-arid region. These strategies are also related to the foliar characteristics in this vegetation.

2 Materials and Methods

2.1. Climate, relief and soil of the study area

The experiments were developed between December 2017 and November 2018. Data collection was carried out at Vereda Grande Farm (7°31.613' S, 36°2.991' W) and Pocinho Farm (07°29.929' S, 35°58.237' W) (Figure 1), at an altitude of 514 and 391 m, respectively, in the municipality of Barra de Santana, state of Paraíba (PB), Brazil. The areas are located in the *Cariri* microregion inside the *Borborema* mesoregion, Brazilian Northeastern (AESA, 2017).

According to the climatic classification of Köppen-Geiger, updated by Peel et al. (2007), the region has a BSwh' climate, hot semiarid, with a dry season lasting nine-10 months and an average annual rainfall of 450 mm.
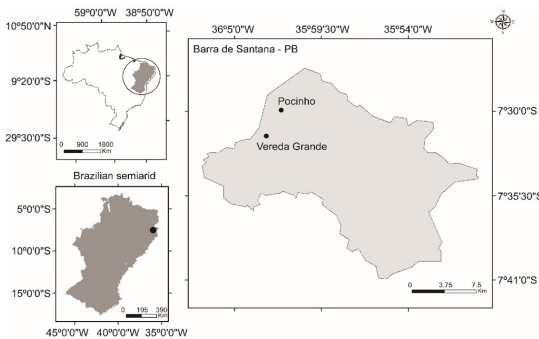
Figure 1. Schematic map of the study area highlighting data collection points in the Brazilian semiarid, Vereda Grande Farm and Pocinho Farm, Barra de Santana, Paraíba, Brazil. Data obtained from the Brazilian Institute of Geography and Statistics (IBGE, 2023). Prepared by F. K. G. Silva.

The minimum and maximum monthly temperature variations are, respectively, 18-22 °C in July and August, and 28-30 °C in November and December. The average monthly relative air humidity is between 60-75%, with the maximum value occurring in June and the minimum in December (Bioclim, 2017). Both collection areas are located on the southwest escarpment of the *Borborema* Plateau, which has an undulating relief and an altitude varying from 400 to 650 m. In the study areas, the soils are solodide solonetz and litolic (Santos et al., 2013).

2.2. Species and number of individuals

We selected eight woody species and 10 individuals per species. These species were chosen according to availability and abundance at the collection sites (Table 1) considering previous studies. All individuals were adults with a diameter at soil level of ≥ 3 cm, and a height ≥ 1 m, according to the methodology proposed by Rodal et al. (2013). We classified each species according to leaf phenology into deciduous (leaf duration of six to nine months) and evergreen (leaf duration of 12-14 months) (Marín and Medina, 1981; Barbosa et al., 2003).

2.3. Determination of LHS scheme traits and wood density (WD)

We measured the leaf functional traits plant height and seed mass following the protocol of Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013). For the measurement of leaf traits, we collected ten expanded and unmarked leaves of any type of senescence or injury from each of the ten individuals of each species.

We determined leaf thickness (LT), leaf area (LA), leaf dry matter (LDM), and specific leaf area (SLA). Leaf thickness (mm) was measured using a digital caliper (Lotus Plus). The leaves were scanned on a digital scanner (Epson L355), and the LA (mm²) was measured using the ImageJ 1.x software. In order to obtain LDM, the samples were placed in an oven at 70 °C for 72 hours, and then weighed using a semi analytic scale (KN300/3). The SLA was calculated by the ratio LA (mm²)/LDM (mg), expressed in mm².mg^{-1}. To calculate LDM and SLA values, leaf petioles were not included.

Plant height (HE) was defined as the distance between the upper limit of the plant's photosynthetic tissues and the soil level. The height of ten individuals per species randomly sampled were measured using a graduated rod. We determined the seed mass (SM) using 150 units from three individuals of each species. The seeds were weighed after drying in an oven at 70 °C for 72 hr. After drying, the seeds of three individuals were mixed, and ten seeds per species were randomly taken for weighing and statistical analyses.

To determine wood density (WD), we selected five individuals per species. A terminal section of the branch of each individual was extracted; approximately 2 cm in diameter and 10 cm in length, the bark with cambium, phelloderm, and phellogen were removed. (Silva et al., 2014). The volume of the sample (cm³) was measured by displacing the water in a graduated vessel following the method of Chave et al. (2006). To obtain the dry matter of the samples, we dried them in an oven (FANEM/320) at 103 °C until obtaining a constant weight, according to Trugilho et al. (1990). The wood density was obtained by the average of five sections of each species: WD = dry mass/volume (Borchert, 1994; Wright et al., 2010; Lima et al., 2012).

2.4. Statistical analyses

The data were transformed (square root) to meet the assumptions of normality and homoscedasticity, and to reduce the effects of outliers. Then, we performed a cluster analysis using the Euclidean distance with the Ward method to verify how the species were grouped. After the groups were formed, we performed a PCA analysis with Euclidean distance to detect which variables were the most important for the distinction between them (Hammer et al., 2001; Gotelli and Ellison, 2010), and a Pearson correlation analysis (Zar, 2010) to verify the relationships among the functional traits of the *Caatinga* woody species and how significant these relationships were. For a better visualization of the groups, the data were analyzed by non-metric multidimensional scaling (nMDS). All analyses were performed using the software PAST 3.2 (Hammer et al., 2001).

3. Results

We found two significant correlations by conducting trait analyses: SLA, HE, SM and WD. SM had a strong positive relationship with SLA (0.859). WD and HE also were positively correlated (0.709) (Table 2).

Cluster analysis with Euclidian distance by the Ward method (Figure 2) evidenced the formation of two groups: (1) low SLA species with high WD and evergreen leaf phenology, and (2) species with high SLA with a deciduous leaf phenology. Within the second group, subsets were identified. This differentiation can be attributed to variations in HE and WD. Different strategies were evidenced by principal component analysis (PCA) (Figure 3). In the first axis of the PCA, the corresponding eigenvector of SLA explains 90.3% of data variation. In the axis two of the PCA, 7.7% of the variation of data can be

Table 1. List of species sampled in the study areas including leaf phenology and mean values of all functional traits.

Species	Phen.	LA (cm²)	SLA (mm².mg⁻¹)	LT (mm²)	HE (m)	WD (g.cm⁻³)	SM (g)
Aspidosperma pyrifolium Mart. & Zucc	DE	38.3	24.3	0.3	5.4	0.6	0.12
Commiphora leptophloeos (Mart.) J.B.Gillett	DE	41.2	16.8	0.2	4.7	0.3	0.10
Cynophalla flexuosa (L.) J.Presl	EV	29.2	6.8	0.6	6.1	0.6	0.15
Jatropha mollissima (Pohl) Baill.	DE	244.8	20.9	0.3	3.2	0.3	0.22
Monteverdia rigida (Mart.) Biral	EV	7.1	4.7	0.5	7.1	0.8	0.03
Cenostigma pyramidale (Tul.) Gagnon & GPLewis	DE	100.9	17.9	0.2	4.8	0.7	0.13
Pseudobombax marginatum (A.St.-Hil.) A. Robyns	DE	435.9	13.5	0.4	5.4	0.5	0.04
Sarcomphalus joazeiro (Mart.) Hauenschild	DE	40.6	27.8	0.1	6.1	0.7	0.45

Phen. = leaf phenology; DE = deciduous; EV = evergreen; LA = leaf area; SLA = specific leaf area; LT = leaf thickness; HE = maximum plant height; WD = wood density; SM = seed mass.

Table 2. Correlations between the functional traits of the LHS scheme (SLA = specific leaf area, HE = maximum plant height, SM = seed mass) and WD (wood density) of the woody species sampled in the study areas.

	SLA	HE	SM	WD
SLA				
HE	0.20589			
SM	0.85883*	0.07953		
WD	0.45686	0.70925*	0.28873	

SLA = specific leaf area; HE = maximum plant height; SM = seed mass; WD = wood density. *Pearson's correlation significant at the significance level of 5%.
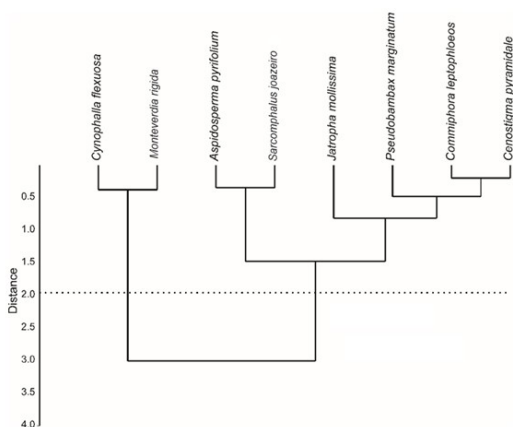
Figure 2. Cluster analysis (in dendrogram) with Euclidean distance and Ward grouping. The cut-off point according to the dotted line was 2.0.

estimator (Clarke 1993). The Sheppard Graph (Figure 4) shows the relationship between the estimated position of the points and the measured position.

4. Discussion

The results highlight two positive correlations between the functional traits analyzed. One between HE and WD and one between SM and SLA.

We recorded higher HE values in plants that also had higher WD values (Table 1), showing the need to increase WD to achieve larger sizes. Poorter et al. (2008) reported that taller plants should invest in strong, high-density stems for their support, which would also help in withstanding environmental stresses, since these plants grow more slowly. Wood density depends on age, resistance to cavitation, and plant height or size (Chave et al., 2009). Species with denser wood are generally resistant to pathogens and mechanical damage (Turner, 2001) and have a smaller stem diameter (Enquist et al., 1999). Thus, they store less water in the wood (Stratton et al., 2000) and can resist xylem cavitation (Hacke et al., 2005). Cavitation resistance is an important trait for plants in water-stressed environments, since the strong negative pressure to remove
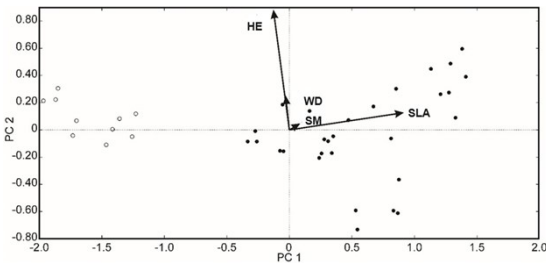
explained by the eigenvector HE. We note this same result in ordering by nMDS (Figure 4). The same sets were separated in multidimensional axes. The stress value in 2D was equal to 0.049, which is considered a good point

Figure 3. Distribution of the *Caatinga* woody species sampled in this study according to the characteristics specific leaf area (SLA), wood density (WD), maximum plant height (HE), and seed mass (SM) based on principal components analysis (PCA). 91% of the variation was explained by the first axis (PC1) and approximately 7.2% was explained by the second axis (PC2). Black circles represent deciduous species and white circles represent evergreen species. The black and white circles also indicate both ecological strategies identified.
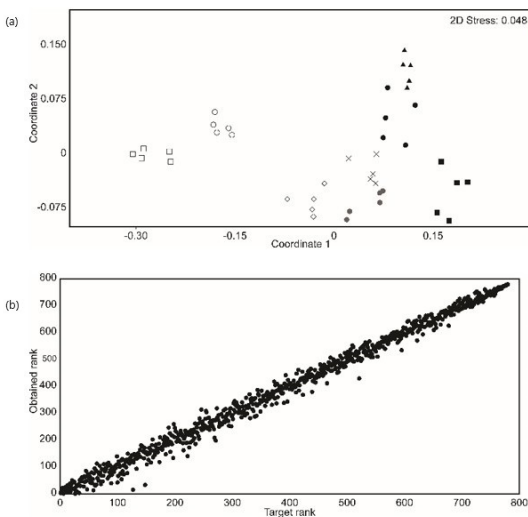

Figure 4. Non-metric multidimensional scaling (nMDS) of the *Caatinga* woody species sampled in this study from the similarity coefficient of Bray-Curtis. (a) Separate sets in the multidimensional axes with the stress value in 2D equal to 0.048, which is considered a good point estimator since it is lower than 0.2. Values higher than 0.2 indicate a large interference from random factors in the graph. The point arrangement is then arbitrary (Clarke, 1993). ● = *Aspidosperma pyrifolium*, ● = *Commiphora leptophloeos*, ○ = *Cynophalla flexuosa*, ■ = *Jatropha mollissima*, □ = *Monteverdia rigida*, x = *Cenostigma pyramidale*, ◇ = *Pseudobombax marginatum*, ▲ = *Sarcomphalus joazeiro*; (b) Shepard graph with expected positional axes *versus* obtained positional axes.

water from the soil may rupture the vessels and cause embolism (Chave et al., 2009). However, plants with less dense wood accumulate more water in the stem and can use this reserve to produce new leaves, flowers, and fruits even in the dry season (Barbosa et al., 2003).

Woody plants do not reach great heights in the *Caatinga*. Phytosociological studies revealed that the average height

of plants in this vegetation type ranges from 5 to 15 meters (Araújo et al., 1995; Ferraz et al., 1998; Amorim et al., 2005; Sampaio, 2010; Pereira Júnior et al., 2013). In environments subject to long periods of drought, woody plants develop without larger height increases, which could lead to water stresses. This is especially observed in species with low WD, more subject to cavitation (Swenson and Enquist, 2007; Chave et al., 2009). Olson et al. (2018) concluded that taller species have larger diameter vessels, which means higher tension in the xylem to raise the water column and, therefore, higher water vulnerability.

Although analyses have shown a positive correlation between SM and SLA, we do not see this association as important to explain different functional strategies of woody *Caatinga* species. All seeds collected are small and have low SM, which is quite common in this vegetation type (Barbosa, 2003). This trait is probably related to the marked water deficit typical of this environment. Small seeds obtain water for germination more easily than large seeds due to greater surface/volume ratio and are more easily dispersed in the wind (Harper et al., 1970; Barbosa, 2003). In addition, after dispersal, they are easily covered by the soil, managing to last long periods until there are favorable conditions for germination (Bakker et al., 1996; Thompson et al., 1993).

SLA represents one of the functional traits that describe the leaf spectrum on which plants are positioned (Wright et al., 2004). The importance of this trait in ecological studies has been highlighted for a long time (Grubb, 2002), since it is related to several other characteristics of leaves and the plant (Wright et al., 2002).

In *Caatinga*, SLA was the trait that best defined the strategies of woody plants, classifying them into two groups: high and low SLA. In a similar study carried out in *Cerrado* (Brazilian savanna), SLA was also the determining factor for recognizing different strategies of woody plants (Abe et al., 2018). However, contrary to these authors, we observed differences in the SLA of deciduous and evergreen species. Moreover, studies carried out in semiarid regions (Ackerly, 2004; Franco et al., 2005; Fu et al., 2012; Souza et al., 2015) have shown consistent SLA differences between deciduous and evergreen species. This identifies two ecological strategies directly associated with the use of water (Souza et al., 2015). Evergreen drought-tolerant species are more conservative in their use of water and have a greater stomatal sensitivity to the effects of drought than deciduous species (Mediavilla and Escudero, 2003).

Plants with low SLA tend to conserve resources in the leaves and generally have long-lived leaves with more scleromorphic traits (Marin and Medina, 1981; Wright et al., 2001, 2002; Ishida et al., 2008). Leaf longevity is a functional trait that indicates differences in carbon gain and growth rate between groups of deciduous and evergreen species (Kikuzawa, 1991; Williams-Linera, 2000; Ishida et al., 2010). In general, this trait is positively associated with leaf mass and negatively associated with photosynthetic capacity and foliar nitrogen and phosphorus content (Reich et al., 1992; Williams-Linera, 2000; Cordell et al., 2001; Wright et al., 2004).

Thus, deciduous plants with high SLA and, possibly, less longevity, have lower specific leaf mass and higher

photosynthetic rate per unit mass compared to evergreen species. These latter species, with low SLA and probably greater longevity, have a high leaf mass ratio, since they invest a large part of the assimilated carbon in leaf development (Wilson et al., 1999). This high investment in leaf structure should reduce photosynthetic capacity, as evergreen species increase the resistance to CO_2 diffusion (Ishida et al., 2008).

5. Conclusions

This study provides important information on the adaptations of woody *Caatinga* plants to the various environmental stresses to which they are subjected. The correlation between HE and WD highlights strategies related to efficiency in water storage and distribution to avoid water stress. SLA is an important predictor of plant strategies in this vegetation type. This trait is related to several other characteristics within the leaf spectrum, comprising syndromes that indicate different competencies to achieve success in the environment. Differences in the SLA of deciduous and evergreen species reinforce the classification of functional groups of woody *Caatinga* species according to their leaf phenology.

Acknowledgements

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