

# COGNIZING BOTANICAL ARCHITECTURAL MODELS IN THE CAATINGA VEGETATION OF NORTHEASTERN BRAZIL

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**Abstract.** Architectural models reflect the genetic designs of tree growth and development from their juvenile to adult phases and the balance between endogenous growth processes and exogenous environmental restrictions. We analyzed six species growing in xeric *Caatinga* vegetation in northeastern Brazil (*Jatropha mollissima* var. *mollissima*, *Mimosa paraibana*, *Sarcophagus joazeiro*, *Aspidosperma pyriformis*, *Croton blanchetianus*, and *Pityrocarpa moniliformis*) in terms of their architectural models and axis categories (growth modes, types of branching, branch geometry, and the presence or absence of reproductive structures). All of the species studied exhibited orthotropic orientation axes and rhythmic growth. As for the other axis categories, there were differences. Two architectural models were identified for the species: the Leeuwenberg model for *J. mollissima* and *A. pyriformis*, and Rauh's model for *C. blanchetianus*, *M. paraibana*, *S. joazeiro*, and *P. moniliformis*. We identify the architectural models associated with the species analyzed, demonstrate their axis patterns, and provide a basis for future studies involving canopy architecture, especially with regard to the Brazilian semiarid region.

**Keywords:** axis categories, canopy architecture, semiarid

Architectural models represent inherent growth strategies that describe how plants develop their shapes and architectures throughout their life cycles, thus illustrating the balance between endogenous growth processes and exogenous restrictions exerted by the environment (Barthélemy and Caraglio, 2007; Taugourdeau et al., 2012). Architectural analysis represents a detailed, multi-level, comprehensive, and dynamic approach to evaluating plant development, bringing together concepts and analytical methods that provide powerful tools for studying the shapes and ontogenies of the various morphological expressions of plants, considering them as a whole, from germination to death (Barthélemy and Caraglio, 2007).

Plants show broad interspecific variability in terms of their shapes that reflect their genetic origins, ontogenetic variability (which encompasses differences between individuals, or juvenile and adult individuals), and phenotypic plasticity, through their variable responses to different environmental conditions (Aguiar, 2014). While there can be variations, each tree follows a specific development program after germination that is controlled by its genes (Hallé, 2010). The final shape of an adult tree, however, can be modified by ecological factors, even though developmental rules are persistent; analyzing these rules is the goal of plant architectural studies. The genetic program for the growth and development of a young tree is referred to as its architectural model (Hallé, 2010; Prado et al., 2020).

Twenty-three architectural models have been described, but the number of variants can be as large as the number of species (Vester, 2002). There are known cases of plants that follow 2–3 architectural models before reaching their

adult phase (Aguiar, 2014), with those variations resulting from factors such as reiteration. Reiteration mechanisms were first described by the Dutch botanist, Roelof Oldeman, and generally refer to the development of a model within another model (Hallé, 2010), a process by which the architecture of a tree adjusts not only to damage suffered in its environment (such as the loss of branches, or stress), but also to environmental pressures, causing it to assume architectural characteristics different from its original model (Hallé et al., 1978; Tourn et al., 1999).

The identification of plant architectural models is possible through the observation and analysis of their architectural units; architectural units, in turn, can be defined as the basic functional and morphological units of a species (Edelin, 1984; Barthélemy et al., 1997), the set of different categories of axes that a species produces until the emergence of its reproductive structures (Barthélemy et al., 1997; Tourn et al., 1999; Barthélemy and Caraglio, 2007). The axis categories can be described by a series of morphological characteristics that include, first, the growth mode, which can be determinate (when meristematic activity is automatically interrupted after a genetically determined structure is completed) or indeterminate (when the apical meristem remains indefinitely operational). Continuous growth is observed when, in general, there are no interruptions during the entire developmental phase (Barthélemy and Caraglio, 2007), although detailed observations have shown that irregular interruptions can occur that are not always correlated with environmental variables (Hallé et al., 1978). Rhythmic growth occurs when vegetative growth is suspended or interrupted during a developmental season (Barthélemy and Caraglio, 2007).

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The second morphological characteristic is the type of branching, which can vary from monopodial (when the branches present an indefinite growth series) to sympodial (when the branches present a defined growth series). In other words, indeterminate growth is observed in plants with monopodial elongation, while determinate growth is observed in plants showing sympodial elongation (Aguiar, 2014). Third, the geometry of branching can be orthotropic (when they grow vertically) or plagiotropic (when they grow horizontally), and, fourth, the presence or absence of reproductive structures, and their positions, which can be terminal or axillary (Barthélemy and Caraglio, 2007; Costa and Longhi, 2018; Prado and Trovão, 2023).

Twenty-three architectural models were recognized among seed plants by Hallé and Oldeman (1970) (Tourn

et al., 1999), whether herbaceous or woody. The greatest variability of these structural models is found in the tropics. Architectural models are genetically determined, and have descriptive utility in perceiving plant forms, although their ecological and evolutionary significance is unclear (Tomlinson, 1983). Each model is defined by a combination of the above-mentioned morphological characteristics, and they are named for the botanists who contributed to that knowledge or who carried out morphological research on plants exhibiting a particular model (Hallé et al., 1978). In light of the structural complexity of the Brazilian semiarid vegetation and the general lack of data and studies related to this topic, we sought to investigate the axis categories of Caatinga species and described the architectural models found in the Caatinga domain.

#### MATERIALS AND METHODS

##### *Study area and the species studied*

The present study was undertaken between November 2022 and October 2023, during which time we examined individual plants growing in the Vereda Grande Farm (07°31'31.5"S, 036°03'05.7"W) and the Trovão de Mello Farm (07°30'10.7"S, 035°57'40.8"W), both located in the municipality of Barra de Santana, Paraíba State, Brazil (Fig. 1). The species were chosen because of their common occurrence in the region (Silva et al., 2014): *Jatropha mollissima* (Pohl) Baill. var. *mollissima* (Euphorbiaceae), *Croton blanchetianus* Baill. (Euphorbiaceae), *Mimosa paraibana* Barneby (Fabaceae), *Aspidosperma pyrifolium* Mart. & Zucc. (Apocynaceae), *Pityrocarpa moniliformis* (Benth.) Luckow & R.W. Jobson (Fabaceae), and *Sarcomphalus joazeiro* (Mart.) Hauenschild (Rhamnaceae). A total of 30 individuals (five specimens per species) were selected that fulfilled the basic inclusion criteria described by Rodal et al. (2013), where, to be considered an adult, a woody Caatinga individual must have a diameter at ground level of  $\geq 3$  cm and a height of  $\geq 1$  m.

##### *Observations of axis categories and the identification of variables*

Individuals of each species were observed and photographed in the field; photographic records were also made focusing on their crowns. Schematic drawings were

made of each individual to facilitate comparisons with the 23 models currently available in the specialized literature (Hallé et al., 1978; Costa and Longhi, 2018). After initial observations of the species and the 23 models, those that appeared to be most similar were selected for detailed studies and comparisons. The analyses consisted of the examination of sets of three basic characteristics (keys) that could be used to determine the architectural models (Hallé, 2010). The first key evaluated the orientation of the principal axes, which could be orthotropic or plagiotropic; the second key evaluated the arrangement of the species' axes, which could be continuous or rhythmical; the third key evaluated the position of the reproductive structures (terminal or axillary). The definition of the latter variable could be used to confirm other axis categories, such as whether the growth mode is determinate or indeterminate, and whether the species has monopodial or sympodial axes. The union of these series of characteristics, and their combinations, allowed the search for compatible architectural models.

##### *Data analysis*

The data resulting from these observations and the identification of the architectural model corresponding to each plant were gathered in a descriptive table (Table 1) designed to identify possible patterns and similarities.

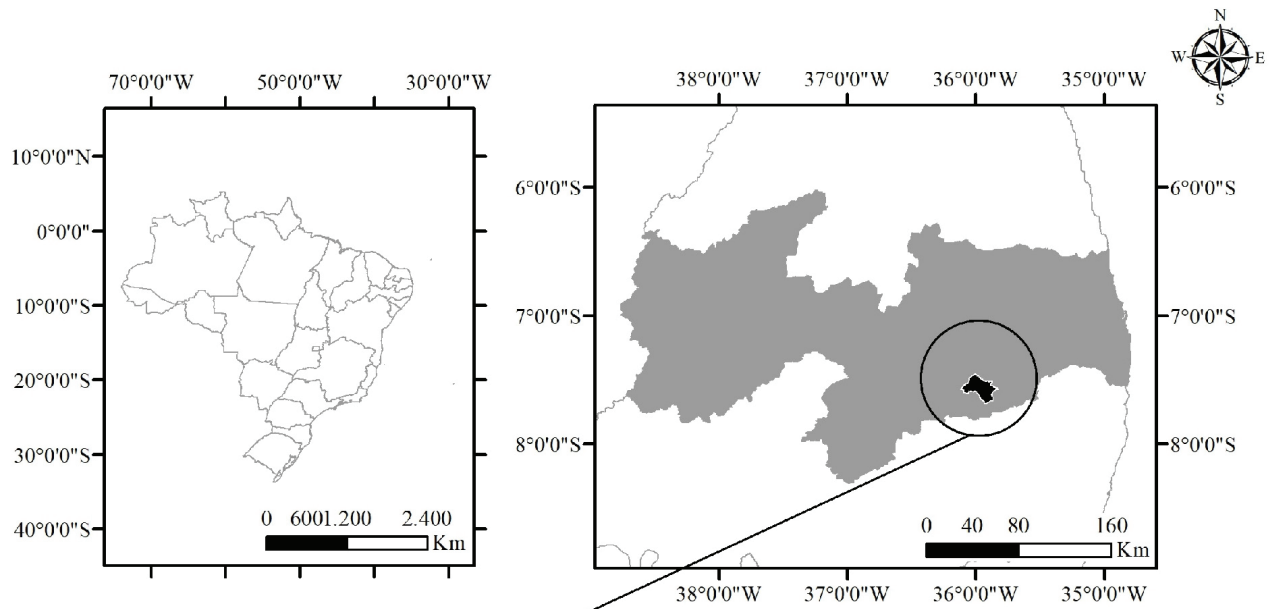
#### RESULTS AND DISCUSSION

Table 1 brings together the axis categories (according to Hallé, 2010) identified in the study species.

All of the species analyzed in this study showed rhythmic growth, which is characteristic of plants having intermittent growth. Another characteristic in common among all of the study species was the presence of orthotropic orientation axes, with vertical (or close to vertical) growth. Regarding the presence and positioning of the reproductive structures, there were variations among the species having terminal or lateral (or even both) reproductive structures, as was seen in *Croton blanchetianus* and *Sarcomphalus joazeiro*. Plants with axillary inflorescences had sympodial branches, as the apical meristem differentiates into other structures (reproductive structures, in this case)

(Aguiar, 2014). The species that had lateral reproductive structures had monopodial branches, with the meristem remaining functional and elongation continuing through the juxtaposition of monopodial extension units (Aguiar, 2014). As such, the growth of plants with sympodial branching was determinate; the growth of plants with monopodial branching was indeterminate.

Two architectural models were recognized: the Leeuwenberg Model and the Rauh Model. The Leeuwenberg model (Fig. 2A-C) is characterized by a series of orthotropic modules, with three-dimensional sympodial branches that are determinate in their growth due to the production of a terminal inflorescence (Hallé et al., 1978). The species that met the characteristics of this model were *Jatropha*



Source: Google Earth Pro

FIGURE 1. Location of the study areas: Vereda Grande and the Trovão de Melo Farm, municipality of Barra de Santana, Paraíba State, Brazil.

TABLE 1. Axis categories found in Caatinga plant species. **A1**, growth mode; **A2**, type of branching; **A3**, geometry of the branches; and **A4**, reproductive structures and their positions.

SPECIES	A1	A2	A3	A4
<i>Jatropha mollissima</i> (Pohl) Baill. var. <i>mollissima</i>	determinate and rhythmic	sympodial	orthotropic	terminal
<i>Croton blanchetianus</i> Baill.	indeterminate and rhythmic	monopodial	orthotropic	lateral and terminal
<i>Mimosa paraibana</i> Barneby	indeterminate and rhythmic	monopodial	orthotropic	lateral
<i>Sarcomphalus joazeiro</i> (Mart.) Hauenschild	indeterminate and rhythmic	monopodial	orthotropic	lateral and terminal
<i>Aspidosperma pyriformium</i> Mart. & Zucc.	determinate and rhythmic	sympodial	orthotropic	terminal
<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R.W. Jobson	indeterminate and rhythmic	monopodial	orthotropic	lateral

*mollissima* and *Aspidosperma pyriformium*. The Rauh Model (Fig. 2D-F) is defined by a determinate architecture, with a monopodial trunk that grows rhythmically and, thus, develops layers of branches morphogenetically identical to the trunk; the flowers are lateral and do not affect the growth of the branches. The Caatinga species studied here that combine the characteristics of this model were *Croton blanchetianus*, *Mimosa paraibana*, *Sarcomphalus joazeiro*, and *Pityrocarpa moniliformis*. Caatinga vegetation is characterized by intermittent growth due to strong climatic seasonality that influences water availability and, therefore, the growth of perennial plants (Silva et al., 2017; Prado and Trovão, 2023). Fluctuations of water availability select for adaptations that reflect climate and soil conditions in this dynamic and seasonal vegetation (Souza et al., 2017; Silva and Cruz, 2018). The fact that the species growing in the Caatinga domain exhibit rhythmic growth is therefore not surprising, as woody species in areas having marked dry seasons evidence interrupted growth that can ensure their survival through inhospitable periods, with the resumption of growth at the beginning of the rainy season (Bathélémy and Caraglio, 2007; Aguiar, 2014).

Orthotropic orientation was another dominant characteristic in the species analyzed. That pattern was found by Costa and Longhi (2018) to be common in species growing in a subtropical deciduous forest. Woody plants with orthotropic axes have, in addition to a vertical (or close to vertical) orientation, radial symmetry, with spiral leaves and branches that extend in all directions (Bathélémy and Caraglio, 2007), aspects observed in the species studied here, which had branches arranged three-dimensionally. Costa and Longhi (2018) identified the Rauh model (Fig 2F) as one of the most common in temperate and tropical regions, reflecting, according to Hallé et al. (1978), its architectural flexibility and capacity for rapid regeneration (Vester and Saldarriaga, 1993; Vester and Cleef, 1998; Vester, 2002; Costa and Longhi, 2018).

The second model identified was the Leeuwenberg model (Fig 2C), which is characterized by having axis categories similar to those of the Rauh model, but differing primarily in the position of the inflorescences (which are terminal, and consequently influence the determinate growth of the sympodial axes). It is well-established that plant species have genetically determined growth patterns and architectural organization, although environmental factors will influence their development (Bathélémy and Caraglio, 2007; Hallé, 2010; Aguiar, 2014). The Leeuwenberg model is characteristic not only of secondary vegetation species, but also of species growing in areas subject to intense environmental disturbances, such as the Caatinga (Beltrán-Rodríguez et al., 2015; Moreno et al., 2017). Similarly, in a study undertaken in a Tropical Semideciduous Rainforest in Yucatan, Mexico, Vester (2002) identified 108 species distributed among 15 models. Another study undertaken in a Tropical Evergreen Rainforest in the Colombian Amazon reported 306 species distributed among 17 architectural models (Vester and Saldarriaga, 1993; Costa and Longhi, 2018), corroborating the idea that the numbers of models tend to decrease with increasing environmental stress arising from seasonality, as is commonly observed in seasonal forests and in accordance with the expectations of Hallé et al. (1978).

Therefore, both of the models identified in this study have characteristics compatible with the Caatinga domain, and it is not surprising that the Rauh and Leeuwenberg architectural models identified are characteristic of temperate and tropical climates with constant and regular disturbances.

Architectural complexity appears to be quite broad in the Caatinga domain, for in a sample of just six species, both Leeuwenberg and Rauh well-characterized axis architectural models were recognized. This work has both pioneering and exploratory characteristics, and should provide a framework for new studies on plant architecture in the semiarid region in Brazil.

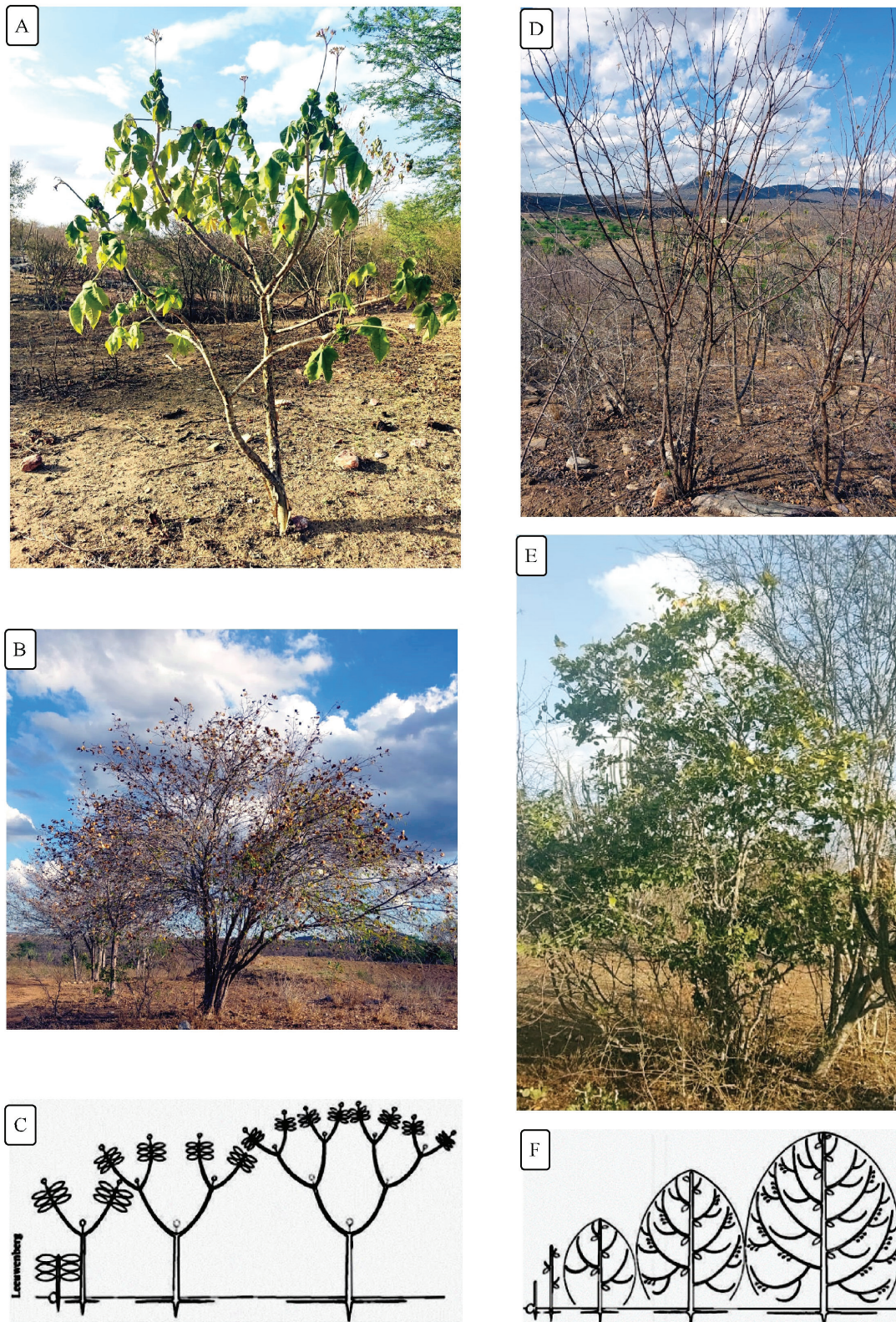


FIGURE 2. Canopy architecture. **A**, canopy of *Jatropha mollissima* var. *mollissima*; **B**, canopy of *Aspidosperma pyriformis*. Photographs by D. A. Souza; **C**, botanical model of Leeuwenberg described by Hallé (2010); **D**, canopy of *Croton blanchetianus*; **E**, canopy of *Sarcomphalus joazeiro*. Photographs by D. A. Souza; **F**, botanical model of Rauh described by Hallé (2010).

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