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Original Article

Architecture of *Mabea fistulifera* Mart. (Euphorbiaceae), a Neotropical semideciduous tree: development and variations in crown allometry between environments

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ABSTRACT

Tree crown growth reflects many aspects of the species' life history. It was postulated that the potential for a pioneer species to invade a deforested area, or maintain a viable population in a forest under intermediate disturbance regime, is related to the tree trunk growth rates, patterns of crown construction, as well as the ability to regenerate broken branches. We investigated if *Mabea fistulifera* Mart. (Euphorbiaceae) crown architecture and tree allometry varies in two contrasted environments in a secondary fragment of Atlantic rainforest: forest edge and interior. First, we described the development of crown architecture by following the growth of the crown in 15 young individuals, with special attention to growth and branching models and to the morphologic differentiation of axes. Secondly, allometric differences in crown construction patterns between environments were studied by quantifying 10 traits in 20 individuals from each environment. Nozeran architectural model was found, a process of parenchymatization of the terminal meristem and a tier of branches form distally followed by an orthotropic shoot forming the next relay axis. This results in modular sympodial branching and polyaxial morphology of branches, allowing this tree species to occupy different environments by quick expansion wherever light availability is higher, towards the upper canopy (forest interior) or towards one side (forest edge). Crown asymmetry occurred towards border sunlit spaces or in response to inner canopy openings caused by hilly topography. Crown structure and growth patterns here found are suitable for a pioneer species adapted to intermediate disturbance regime.

1. Introduction

Plant architecture and its implication for tree ecology and evolution are concepts originally coined by Hallé and Oldeman (1970). Presently, 23 architectural models have been described representing the great diversity of tree growth and crown patterns. Plant architecture is the result of a hierarchical arrangement of growth units or modules (White, 1979; Porter, 1983; Bell et al., 1999; Barthélémy and Caraglio, 2007). In woody plants, the development of the crown involves the reiteration of these units (e.g. Barthélémy and Caraglio, 2007) as part of a genetic program (Hallé et al., 1978; Sussex and Kerk, 2001). However, the interaction between genetic determinism and environmental conditions leads to the outcome of variable crown shapes, a plasticity which is considered highly adaptive (Wu and Hinckley, 2001; Osada et al., 2004; Osada, 2006).

Crown architecture and leaf arrangement, i.e. distribution and density, affect overall light capture of tree species in a forest canopy (Kitajima et al., 2005; Niinemets, 2010; Ford, 2014). Plants growing in full sunny conditions can increase their overall productivity by producing many layers of leaves, i.e. a multilayer crown. On the other hand, trees occurring in shadow environments frequently develop shade-adapted leaves (Horn, 1971), arranged in an upper monolayer to minimize further self-shading. If true, monolayer crown architectures are predicted to be more frequent among late successional species, adapted to grow in the shade, while the multilayer crown architecture would be more frequent amongst early successional ones (Horn, 1971). However, such basic patterns can be plastically modulated to face individual conditions.

Tree crown growth within a forest canopy results in context-dependent interactions in the neighbourhood which are mediated by changes in the distribution of growth units following allometric constraints (Alves and Santos, 2002; Osada, 2011; Yamada et al., 2000).

Abbreviations: PERD, State Park of Rio Doce; CBH, circumference at breast height; G.U., growth units

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Although the actual architecture of a tree crown is an obvious outcome of abiotic and biotic pressures on plant growth, most studies are purely descriptive and do not tackle adaptations to the ecological communities where the trees evolved and more specifically variations in the microhabitat conditions and evaluations of the plasticity of this plant attribute.

Euphorbiaceae is one of the most important and taxonomically complex families of the Brazilian and Neotropical floras. It is among the most diversified families and also floristically common in Neotropical dry seasonal semideciduous forest (França and Stehmann, 2013; Higuchi et al., 2006). This family shows a broad range of life forms and morphologies and is the richest one in plant architectural models, particularly in warm environments (Hallé, 1971). In the genus *Euphorbia*, for example, 11 architectural models have been found (Cremers, 1977). Nevertheless, genera are unequally known and the description of architectural models for the genus *Mabea* is very scarce. For instance, *Mabea piriri*, *M. speciosa* and *M. taquari* are considered to fit Nozerańs model (Ollivier et al., 2007 – Mariwenn Guiana Species Database) but no detailed studies seem to be available to support that statement. Proper morphological descriptions based on architectural principles are needed to fill this gap.

In this paper we describe the crown architecture of the pioneer tree *Mabea fistulifera* Mart. (Euphorbiaceae), focusing on the variation of the architectural model as environmental conditions change. First, we describe the crown structure to ascertain the architectural model for this species. Second, we studied two different environments and very conspicuous environments for this species, forest edge and interior, to understand context-responses of the crown architecture. We predict that interspecific competition for light and space drives the growth of the crown in a way that maximizes the occupation of space, at the expense of symmetry in some cases. We also expect that a modular, easy to regenerate growth patterns may favour a plastic adjustment of the crown to space gaps and light conditions.

2. Materials and methods

2.1. Study species and site

Mabea fistulifera, also known as “canudo-de-pito” or “mamoninha”, is a pioneer species in secondary forests. It is a latescent deciduous tree, able to reach up to 20 m in height. It is recommended in programs for ecological restoration, as it is well suited to nutrient-poor soils and open areas (Lorenzi, 2000). We worked at the State Park of Rio Doce (hereafter PERD) in the mid-basin of Doce river, which is the last continuous large remain of Atlantic rainforest in Minas Gerais State, Brazil. This park has an area of 36,000 ha, with semidecidual forest patches in different successional stages (Silva, 2001).

2.2. Development of crown architecture

To describe *M. fistulifera* development of crown architecture we followed one individual from June 2009 to February 2011 in a common garden, growing in optimal conditions, with no direct competition from other trees. We measured annually plant height, circumference at breast height (CBH), height of the first fork and number of growth units (G.U.). G.U. are defined here as the portion of an axis which develops during an uninterrupted period of extension (sensu Normand et al., 2008; Fig. 1a). To guarantee that the growth of this isolated tree was not atypical, we also followed, from November 2009 to February 2011, 14 randomly chosen individuals with CBH lower than 25 cm under field conditions, at the PERD (19° 46′ 48.36” S, 42° 36′ 02.93” W). These individuals were planted in 1994 in order to restore a perturbed remnant of the forest close to a park road.

To assign a tree to some of the available crown architectural models, four morphological features need to be considered: 1) Growth pattern; 2) Branching pattern; 3) Morphologic differentiation of axes; 4) Position of reproductive organs (Prévost, 1978; Richards, 1996; Bell et al., 1999; Sussex and Kerk, 2001; but see detailed descriptions in Barthélémy and Caraglio, 2007). In this study, we recorded the first three morphological features by focusing mainly on the first-order axis growth and on describing organogenetic processes and lateral expansion.

Growth pattern was described on the basis of two main characteristics. First, we assessed whether *M. fistulifera* had a determinate or an indeterminate growth, according to Bell (1991). In determinate growth, the apex may either abscise or abort after a period of activity or it may transform into a specialized structure lacking further extension capacity. In indeterminate growth, the apical meristem of an axis maintains its growth potential indefinitely. Secondly, we assessed whether growth was continuous or rhythmic. In continuous growth, shoots have no marked endogenous cessation of extension. In rhythmic growth shoots have a marked endogenous periodicity of extension (Barthélémy and Caraglio, 2007). In rhythmic growth the “growth unit” (sensu Hallé and Martin, 1968) is very clear as the axis segment which develops during an uninterrupted period of extension.

Branching pattern can be monopodial or sympodial. In sympodial branching, one or more branches may develop after the death, abscission, abortion or transformation of the apex (Barthélémy and Caraglio, 2007) and an axis produced by one apex consisting of one or more G.U. is called ‘sympodial unit’ or module (Bell, 1991) (Fig. 1a and b). By contrast, monopodial branching is formed by the uninterrupted growth of an indeterminate apical meristem (Hallé et al., 1978).

Morphological differentiation of axes may involve their orientation in space; axes can be orthotropic or plagiotropic. Orthotropy refers to axes whose general orientation pattern is vertical and whose symmetry is radial, with leaves in a spiral, opposite or verticillate arrangement, and associated lateral branches arranged in all spatial directions (Barthélémy and Caraglio, 2007). Plagiotropic axes have a general horizontal to slanted orientation and a bilateral symmetry resulting in leaves and branches being generally arranged in one plane (Barthélémy and Caraglio, 2007).

2.3. Crown architecture and allometric relationships in different environments

We measured crown architecture and its allometric relationships in two natural populations of *M. fistulifera*. The first one, known as the Salão Dourado (19° 39′ 03” S, 42° 35′ 08” W), was in an edge of the forest with a firebreak road (Ribeiro et al., 2008), and consequently profoundly affected by human activities, mainly road management (Silva, 2001). The other area, known as Porto Capim (19° 46′ 16.41” S, 42° 37′ 36.64” W), is 13 km apart from the first population, within an old secondary forest and very similar climates within the park, found in a slope nearby the lake Dom Helvécio. According to Goulart et al. (2005), these two populations show no significant genetic differences.

Twenty individuals were selected in the forest edge in Salão Dourado among those located in the close vicinity of the forest border, i.e., with their crowns expanded towards the road. This road has a 90° curve, heading both to Northeast and Northwest, thus we divided the samples equally between this two directions. Twenty individuals within-forest in Porto Capim were selected, at least 25 m from the forest edge. The hill is positioned towards Northeast, which causes more sun in the morning and more crown-space competition from the North. We randomly selected undamaged and healthy individuals for sampling and all selected individuals had a CBH greater than 25 cm. Ten plant functional traits were chosen to describe crown architecture and allometric relationships. Four traits characterized the whole plant: plant height; height of the first fork; crown depth – plant height minus height of the first fork (Kohyama et al., 1990) – and CBH. Five traits were related to crown architecture: number of sympodial units (equivalent to units of construction in Bell et al., 1999; Fig. 1b); number of twigs per sympodial unit; number of leaves and number of branches. Number of

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