Architectural analysis of *Buxus vahlii* Baill. (Buxaceae) in two different environments in Puerto Rico

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ABSTRACT
The analysis of the architecture of *Buxus vahlii* Baill. (Buxaceae) in western Puerto Rico is presented. Two populations growing in different environmental conditions were studied: one is a coastal forest in the municipality of Rincón and the other is a mountain forest with karstic formations in the municipality of Isabela. The growth pattern in *Buxus vahlii* follows Champagnat's model. Four stages of development were identified: seedling, juvenile tree, mature tree and senescent tree. The stem and branches of the tree are sympodially built by the superposition of mixed orthotropic axes. Two different crown shapes have been recorded in *B. vahlii* in Puerto Rico: in the Rincón forest, the shape is laminar, while in Isabela, it is in-between a funnel and cup shape.

KEY WORDS
Buxaceae,
Buxus vahlii,
stages of development,
tree architecture,
Champagnat's model,
Puerto Rico.

RÉSUMÉ
Analyse de l'architecture de Buxus vahlii *Baill. (Buxaceae) dans deux environnements différents à Porto Rico.*
L'analyse de l'architecture de *Buxus vahlii* Baill. (Buxaceae) à l'ouest de Porto Rico est présentée. Deux populations qui diffèrent dans leurs caractéristiques environnementales ont été étudiées : le premier environnement est la forêt côtière dans la commune de Rincón, le deuxième est une forêt de montagne sur des sols calcaires dans la commune d'Isabela. *Buxus vahlii* croît selon le modèle de Champagnat. Quatre stades de développement des arbres ont été identifiés : germination, arbre juvénile, arbre mature et arbre sénescent. Le tronc et les branches de l'arbre sont de type sympodial, par la superposition d'axes orthotropiques mixtes. Deux formes de cimes différentes ont été observées pour *B. vahlii* à Porto Rico : dans la forêt de Rincón, *B. vahlii* pousse selon un modèle laminaire, tandis que dans la forêt d'Isabela, il peut croître selon un modèle en forme de cône ou de coupe.

MOTS CLÉS
Buxaceae,
Buxus vahlii,
stades de développement,
architecture ligneuse,
modèle de Champagnat,
Porto Rico.

INTRODUCTION

Formal studies of the architectural organization in tropical trees began with Hallé and Oldeman in the 1960's. These authors defined criteria for growth patterns, ramification patterns, morphological differentiation and position of sexual organs in architectural models. Hallé & Oldeman (1970) and Hallé *et al.* (1978) identified 23 architectural models in nature and designated each model using names of important botanists (for example: the Chamberlain model was named in honor to C. J. Chamberlain who studied Cycadaceae which frequently exhibit this model). The architecture of a tree and its growth pattern is defined by the meristematic activity, mostly by the activity of the primary meristems. The apical meristem constructs the main axis and participates in the regulation of the lateral organs, specifically in the regulation of the axillary meristems. Each new axis can bear leaves and its axillary meristems can produce new axes or reproductive organs (Vester 1997).

The axes from which a plant grows can be separated into two states (orthotropic and plagiotropic axes), according to the organization of their organs and the growing direction during their development. Some meristems can change their organization and growth direction between the orthotropic and plagiotropic states. This type of axis is called "mixed axis". Only three architectural models present this type of development: the models of Troll, Mangenot and Champagnat. According to Hallé *et al.* (1978), Troll's model is one of the most common; between 20 and 30% of the trees present an architecture corresponding to this model.

The family Buxaceae is cosmopolitan and includes 5 genera: *Buxus*, *Notobuxus*, *Pachysandra*, *Sarcococca* and *Styloceras*, of which *Buxus* L. is the largest, including 90 species (Balthazar *et al.* 2000); most of the species of *Buxus* are distributed in the Neotropical region. Two species have been reported from Puerto Rico: *B. portoricensis* Alain and *B. vahlii* Baill. (Liogier & Martorell 2000). *Buxus vahlii* is endemic to Puerto Rico and St. Croix (Britton & Wilson 1924). In western Puerto Rico, it grows at middle and low altitudes in forested areas with sedimentary calcareous soils (Liogier & Martorell 2000; Carrero 2001). *Buxus vahlii* was declared as an endangered plant species according to the "Endangered Species Act of 1973" in the Federal Register 50: 32572 (Fish and Wildlife Service USA 1985). This species was studied between 1991 and 1993 under U.S. Department Interior cooperative agreements with the Fish and Wildlife Service and the Department of Biology of the University of Puerto Rico, Mayagüez (Kolterman & Breckon 1992, 1993). *Buxus vahlii*

TABLE 1. — Specimens of *Buxus vahlii* Baill. observed in each forest.

Area	Seedlings	Juvenile trees	Mature tree	Senescent trees
Rincón	10	9	9	7
Isabela	10	9	9	7

FIG. 1. — Rincón forest, municipality of Rincón, Puerto Rico.

FIG. 2. — Isabela forest, municipality of Isabela, Puerto Rico.

has been cultivated in the Fairchild Botanical Garden in Florida, with the purpose of preserving it *ex situ* and eventually reintroducing it in protected areas and historical localities where the species previously grew (Carrero 2001).

There have been relatively few investigations on the architecture of trees in the Caribbean area; the main investigations on this topic have been carried out by Echeverry & Vester (2001), Vester (2002) and León-Enriquez & Vester (2008) in the Yucatán peninsula in México. Studies of tree architecture in the Buxaceae are scarce. Hallé *et al.* (1978) cite only the architectural model for *Sarcococca confusa* in China, a species that grows according to Mangenot's model. As of yet no other studies exist either in *Buxus* or any other genus of Buxaceae.

This paper presents a description of the architectural development of *Buxus vahlii* and compares its stages of development in two different environmental conditions: a coastal forest and a mountain forest from Puerto Rico, a tropical Caribbean island. Differences in crown shape of *B. vahlii* under the different environments are also discussed.

MATERIAL AND METHODS

Field work was carried out between May and December of 2007 in two different areas of northwestern Puerto Rico: a coastal forest at 10 m above sea-level in the municipality of Rincón and a mountain forest with karstic formations at more than 300 m above sea-level in the municipality of Isabela. Rincón (Fig. 1) is located approximately 150 m northwest of the old nuclear plant, heading to the end of the highway. Isabela (Fig. 2) is located approximately 31 m south of Juan Pérez road (Carrero 2001). The towns are located in the Cuadrángulo Rincón (United States Geological Survey 1966) and the Cuadrángulo Quebradillas (United States Geological Survey 1972) of the USGS topographical maps series, at about 7.5 minutes (1:20.000). We studied between 7 and 10 individuals of *Buxus vahlii* in each one of four developmental stages (seedling, juvenile tree, mature tree, senescent tree) and in each area of study (Table 1). The ages of the plants were not considered because they cannot be determined accurately and because the differences imposed by the environment in each area (coastal forest vs. forest in karstic soil) can influence the ontogenetic development rate (Barthélémy 1991; Barthélémy & Caraglio 2007).

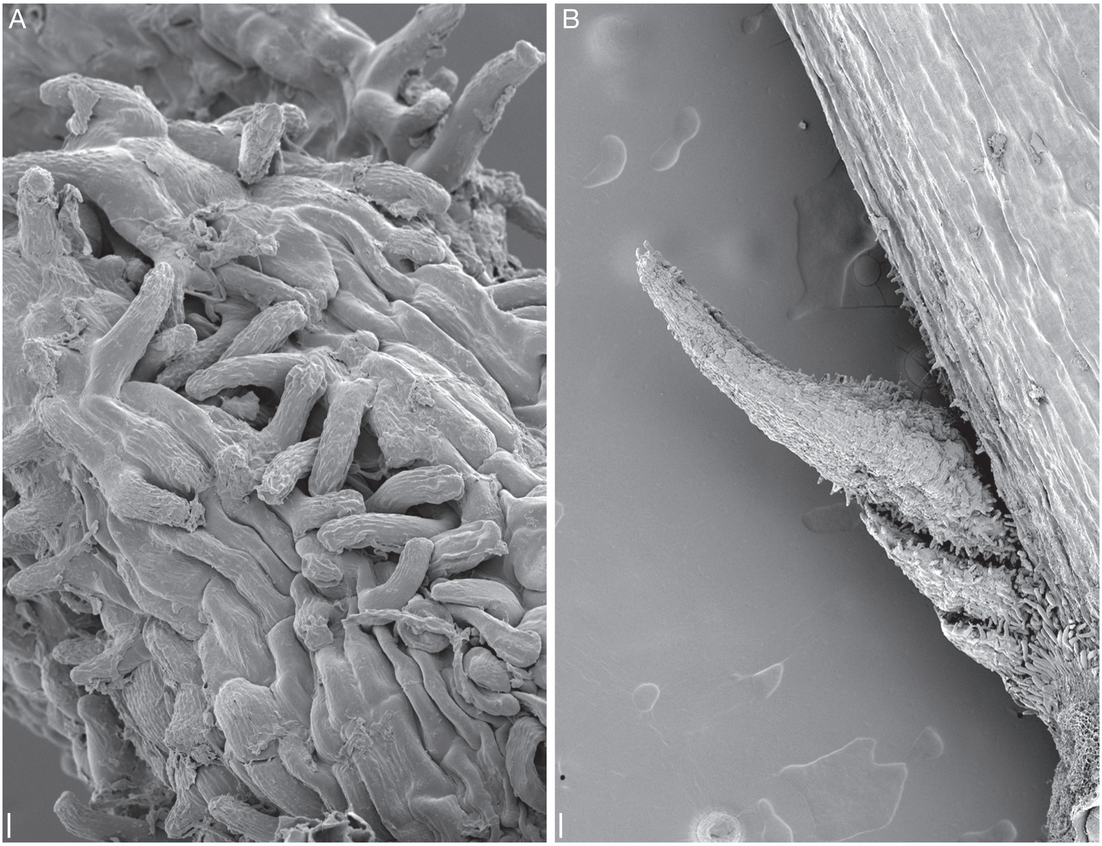

Fig. 3. — *Buxus vahlii* Baill.: **A**, intertwined trichomes around the bud in *Buxus vahlii*; **B**, set of lateral buds. Scale bars: A, 400 µm; B, 100 µm.

Table 2. — Architectural characterization of the A1, A2 and A3 axes of *Buxus vahlii* Baill.

Characteristic	**A1**	**A2**	**A3**
Structure	Sympodial	Sympodial	Monopodial
Growth	Rhythmic	Rhythmic	Rhythmic
Orientation	Orthotropic mixed	Orthotropic mixed	Orthotropic
Symmetry	Radial, with 2 decurrent leaves	Radial, with 2 decurrent leaves	Radial, with 2 decurrent leaves
Number of pairs of leaves per axis	4 or less than 4 (usually on distal portion)	More than 6 or 8	4 to 8
Flowers	No	Yes, axillary	Yes, axillary
Phyllotaxis	Decussate	Decussate	Decussate

Samples of lateral and terminal buds were collected for observation and analysis using electron and compound microscopes. The following measures and observations were made in each type of axis for each tree: destination (determined or undetermined), temporality (continuous or rhythmic), growth direction (orthotropic, plagiotropic, mixed), symmetry (radial or bilateral), presence and position of flowers, phyllotaxis, and number of leaves in each axis. All the observed specimens were schematically drawn to scale and then digitized.

RESULTS

Buxus vahlii shows an architectural development (Table 2) that follows the model of Champagnat. It is a tree that can reach more than 10 m in height; it grows not only in coastal forests but also in the mountainous area of western karstic soils in Puerto Rico. We distinguished three types of axes referred to as A1, A2 and A3. The A1, the first axis to be formed, is orthotropic-mixed, with rhythmic growth, and without reproductive structures. These axes present young leaves on the most juvenile part located at the top, while older leaves die at the base of the growth unit; some axes grow rapidly developing long internodes and thus have many leaves along the axis, while others have very short internodes which present the leaves very close to each other.

The axes A2 are generated from the axillary buds on the A1 axis. Each bud is formed by two structures protecting the meristem, the bud scales, which are covered by intertwined trichomes around the bud (Fig. 3A). In fact, in the axil there is a group of three to five buds (Fig. 3B), of which the largest one is located in the upper portion of the axil. These axes are mixed-orthotropic, with rhythmic growth, bear leaves and may present reproductive structures. The axillary buds on A2 axes produce axes A3 by prolepsis (Fig. 4), have a limited growth and bear leaves and reproductive structures. In both axes A2 and A3, reproductive structures are formed from axillary buds (Fig. 5).

The reiterated axes (A1') can be the result of traumas or adaptations. Traumatic reiteration repairs a damaged axis; this reiteration is total and shows the complete architectural model. Sequential reiteration increases the crown width indicating that a tree has gone form being a juvenile one to a mature one. We distinguish four development phases in *Buxus vahlii*: 1) seedling; 2) juvenile tree; 3) mature tree; and 4) senescent tree.

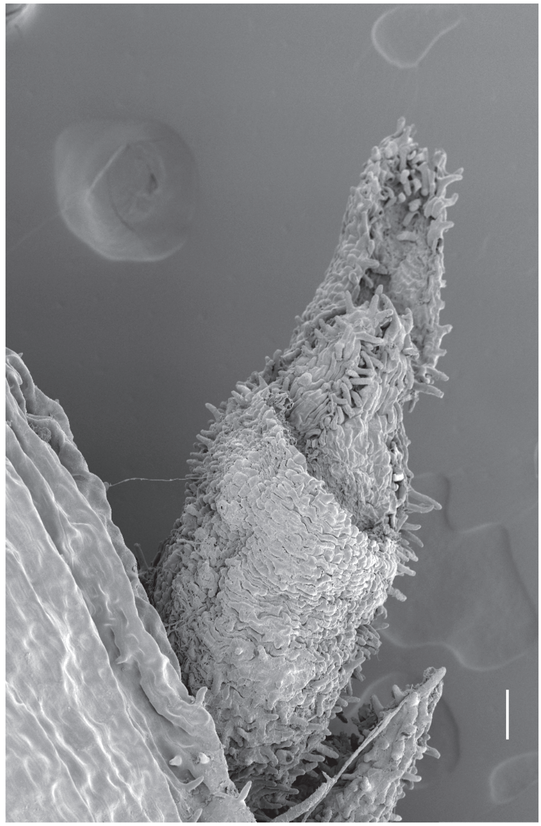

FIG. 4. — Axillar bud on A2 axis of *Buxus vahlii* Baill. Scale bar: 100 µm.

SEEDLING

The early phase of seedling corresponds to the plants that have just germinated. It is characterized by the exhibition of an epicotyledonary axis A1, which is a vertical and orthotropic monopodium, with rhythmic and indeterminate growth, initially without ramifications (Fig. 6). The A1 axes produce simple, complete and much longer than wide leaves, coming along with decussate phyllotaxy. During this phase, the plants can reach 0.2 m in the population of Rincón and 0.25 m in the population of Isabela.

The late seedling phase corresponds to the plants with vigorous growth of the axis A1, which is curved in its distal portion and forms a mixed-orthotropic axis, with rhythmic and indeterminate growth. On axis A1, ramifications of A3 axes of short duration

Fig. 5. — Reproductive structures of *Buxus vahlii* Baill. *G. Carrero 161* (MAPR).

(cladoptosis) can occur. The first axis replacement on the A1 axis is formed in the curved part of the axis; this is the first module corresponding to a single growth unit. In this phase, they do not present flowers or fruits. During this late phase, the plant can reach 0.45 m in the population of Rincón and 0.6 m in the population of Isabela.

Juvenile tree

The axes A1 have formed the trunk of the juvenile tree by a lineal sympodial sequence of replacement mixed axes. The juvenile tree of *Buxus vahlii* grows by modular construction. On the A1 axis, ramifications of A2 axes with different lengths are present (Fig. 7A); these axes form the "branches of the tree". The A2 axes are borne laterally on the distal part of the module and have more leaves than axes A1 or A3. The axes A3 are short and monopodic and grow from the axillar buds on the A2 branches. All axes have rhythmic growth and decussate phyllotaxy. In this phase, all the construction axes are orthotropic. With increasing height, the distal parts which functioned as branches, die leaving a bare trunk.

This phase is characterized by the presence of flowers and fruits. The reproductive structures are borne on the distal parts of A2 and A3 axes. The inflorescence is cymose, axillary. The flowers are small and unisexual. There are many flowers per axis but only one or two mature fruits are found in each node (the fruit is a capsule with three horns and of approximately 6 mm in length). Only the highest plants present reproductive structures in the population of Isabela, but in Rincón the reproductive structures are not limited to the highest plants. All the axes that form the crown present wider leaves in comparison with the leaves found in the first three developmental phases. The crowns of the trees in the population of Rincón are wider and enlarged with respect to the crowns of the population of Isabela, where they exhibit a more oval-circular form. The juvenile tree can reach heights of 1.8 m in the population of Rincón and up to 2.5 m in the population of Isabela.

Mature tree

The whole tree is sympodially built by the superposition of mixed orthotropic axes. The trunk exhibits multiple modules organized in a linear way, which gives it an erect appearance. In this phase the tree reaches its maximum size and has several main branches, which give it a polyarchic organization. According to Carrero (2001), the maximum basal diameters reach 4.3 cm in Rincón and 8.1 cm in Isabela. In Isabela, where plants reach the highest diameters, the bark of the trees is thicker than in the population of Rincón. Flowers and fruits are abundant and frequent in this developmental stage. The crown of the tree has the capacity to reiterate, which promotes the spread of the crown. On the axes A1 or A2 grow reiterated axes (A1'), the main reiterated axes is functioning as a trunk and axes A2' are functioning as branches. The trees in the forest of Rincón can reach heights between 4 and 5 m (rarely 6 m) and from 6 to 8 m (rarely 10 m) in the forest of Isabela (Fig. 7B).

The aspect of the crown shows differences between the two studied populations. In the population of Rincón, we observed that the crown has branches with horizontal orientation and their shape is lami-

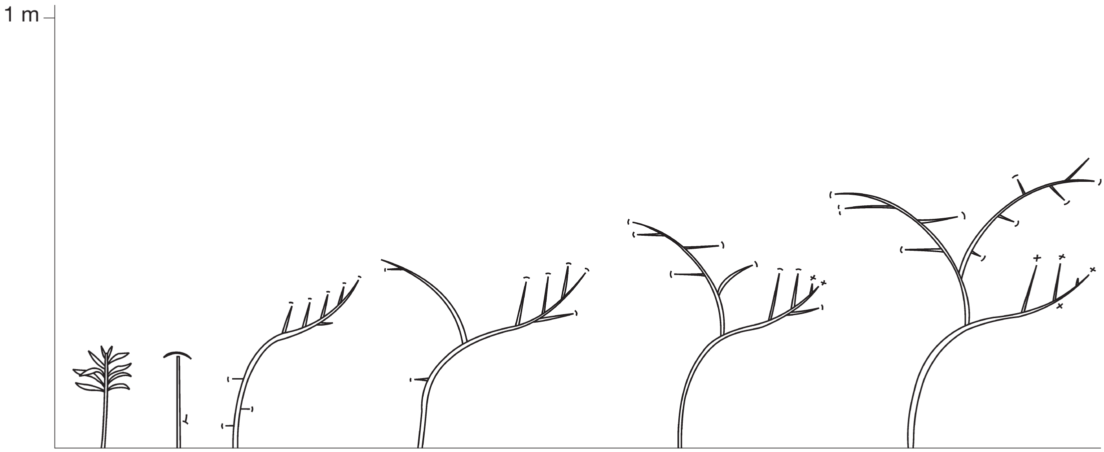

FIG. 6. — Development of seedling of *Buxus vahlii* Baill.

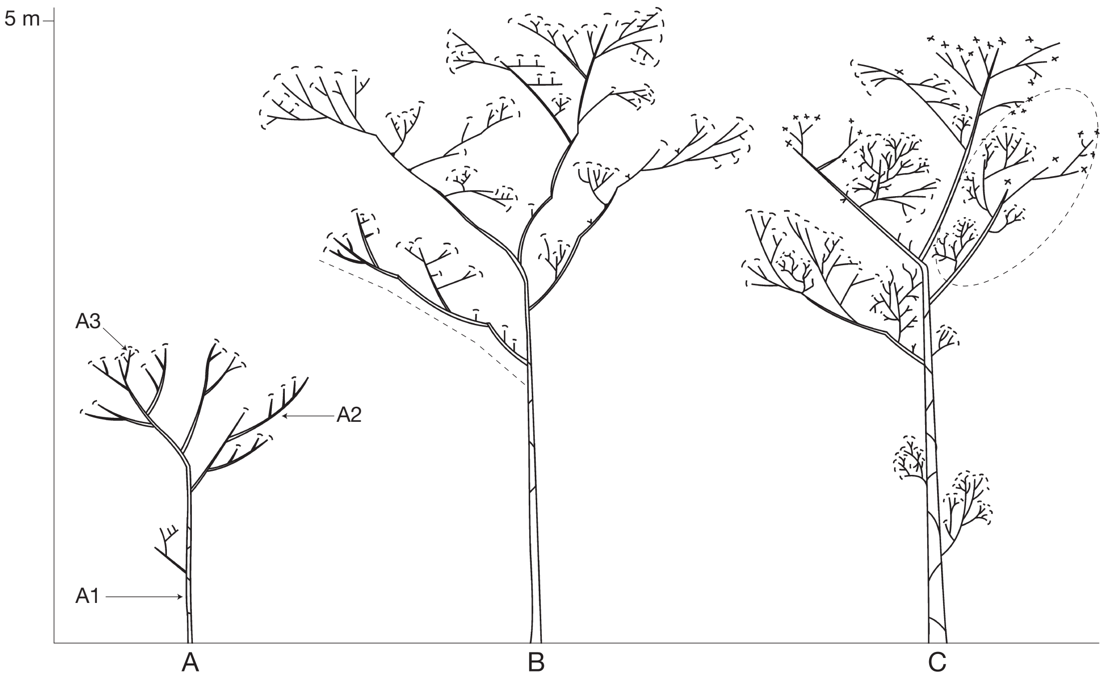

FIG. 7. — Phases of development of *Buxus vahlii* Baill.: **A**, juvenile tree with axes A1, A2 and A3; **B**, mature tree; dashed lines indicate sequence of replacement axes in sequential reiteration; **C**, senescent tree. Circles indicate reiterated axes, crosses indicate dead axes.

nar (*sensu* Hallé *et al.* 1978), occupying the largest quantity of space; on the other hand in the population of Isabela we observe that the crown has more branches with vertical orientation showing a funnel or cup shape (*sensu* Hallé *et al.* 1978), therefore occupying less space.

Senescent tree

The senescent tree loses height in comparison with a mature tree, due to the dead axes in the crown. This phase has a structure similar to the one described for the mature tree stage but multiple reiterates are generated on the axes A1 and A2, forming reiterated complexes. Reiteration appears throughout the main trunk. Dying of the tree begins in the crown and continues downward until reaching the base of the trunk. Reiterates on the trunk were only present in individuals of the Rincón population. Tree crowns maintain the laminated shape in the population of Rincón (Hallé *et al.* 1978), and a funnel shape in the population of Isabela (Fig. 7C).

DISCUSSION

The architectural plan of *Buxus vahlii* develops according to Champagnat's model, independent of the environmental conditions in the forests of Puerto Rico (coastal forest in the municipality of Rincón or mountain forest with karstic soil in the municipality of Isabela). Although we found differences in the height ranges during the different developmental phases, this does not affect the model of the plant. This behavior is a consequence of the variations which are imposed by the environment (Hallé *et al.* 1978). On the other hand, it is generally accepted that it is not possible to recognize a close relationship between the architecture and the dimensions of the tree (Hallé *et al.* 1978; Vester 1997). Also, we observed differences in the architecture of *B. vahlii* in the two forests because the same model leads to different forms; this is a phenomenon of plant plasticity and it is related to the general shape of the crown and the reiteration pattern. Kroon *et al.* (2005) suggest that, in nature, phenotypic plasticity in plants is expressed at a modular level within the individual, i.e. that individual meristems, leaves, branches and roots respond to changes and differences in local environmental conditions.

Formation of the crown in the different sites

Although the architectural elements, which form the crown are the same for the individuals that grow in the forest of Rincón as for those in Isabela, the distribution of the crowns in space is different in each population, which probably is related to the differences in the environment conditions on Rincón and Isabela. Environmental influences have been demonstrated to be able to alter the expression of shape of the crown (like shown here in *B. vahlii*). This capacity corresponds to the "plasticity" of a species (Bradshaw 1965; Kroon *et al.* 2005), just like shaded branches of a tree are likely to develop leaves with morphological and physiological properties that enhance light capture and photosynthetic efficiency under low light conditions (Kroon *et al.* 2005). According to Hallé *et al*. (1978), the crown models vary within limits of possibilities represented by the relationship surface/volume and the photosynthetic efficiency of the organism. The population of Rincón exposes its leaves in the form of a "laminated surface" and the population of Isabela exposes them intermediate between the "cup" and "funnel" shapes (Fig. 8).

The population of Rincón is located at sea level, very close to the coast; there is less density of individuals per square meter than in Isabela forest. In this area, *B. vahlii* lives on low hills (see topographical map, Cuadrángulo Rincón: United States Geological Survey 1966) where the solar radiation is constant most of the day; a laminar model crown indicates that the organism uses more space and has a better possibility to intercept solar radiation (Hallé *et al.* 1978). Studies by Thompson (1993) have shown that information about the spectral composition of light can be perceived at a modular level and that local light cues trigger local plastic responses.

The population of Isabela is located in a mountain area (see topographical map, Cuadrángulo Quebradillas: United States Geological Survey 1972) in which the largest amount of solar radiation is received during the first or the second half of the day, depending on the season. In Isabela, we observed a larger diversity of species (see also Carrero 2001), less available space to access the light resource and a stronger competition among the species of the understory. A funnel-shaped crown indicates that the organism is limited in its disposition in space and in the capture of light (Hallé *et al.* 1978).

With respect to the analysis of crowns, Stoll & Schmid (1998) studied the growth and architecture of branches on mature *Pinus sylvestris* trees at the edge and in the centre of a forest. These authors found that branches exposed to the sunlight at the forest edge showed larger growth increments, more lateral branches, higher survival and reproduction than shaded branches.

Conservation and density of the population in each forest

There is no information on the conservation state or age of the forest of Rincón. For the forest of Isabela, it is known that it was given to the Department of Natural Resources for the creation of the State Forest of Guajataca in 1943; therefore, it is considered that this forest is better conserved than the forest of Rincón. Besides this, Isabela forest is located between mountains, and their topographical conditions probably offer better protection against the environmental events that have occurred in Puerto Rico, like hurricanes.

Differences in the total height of the trees in each population are related to the height of the canopy of the forest. The coastal forest of Rincón exhibits a homogeneous canopy that forms a continuous cover; there is little species diversity and less individuals per square meter (Carrero 2001). The height of the canopy in the forest of Rincón varies approximately from 2.5 m to 6 m (Fig. 1). The trees of the karstic soil in the forest of Isabela vary notably in their total height and the crowns that compose the canopy form a heterogeneous cover; there is more species diversity and a larger number of individuals per square meter, and the height of the canopy reaches more than 6 m (Fig. 2). Also, the amount of available space in the understory is different in both populations, which indicates that differences in environment on which the trees act in different way are already present for seedlings.

Effect of wind

Environmental phenomena such as the wind do not modify the architectural model, but they can have an impact on the growth direction and on the reiteration pattern. In other words, if the wind exerts pressure on the crown of a tree, it makes its axes bend in favor of the wind direction. One of the effects of this type of environmental pressure is the appearance of adaptive reiterations, which are ecological answers to the conditions of the environment that allow the tree to maintain its stability and continue with the development of the architectural program.

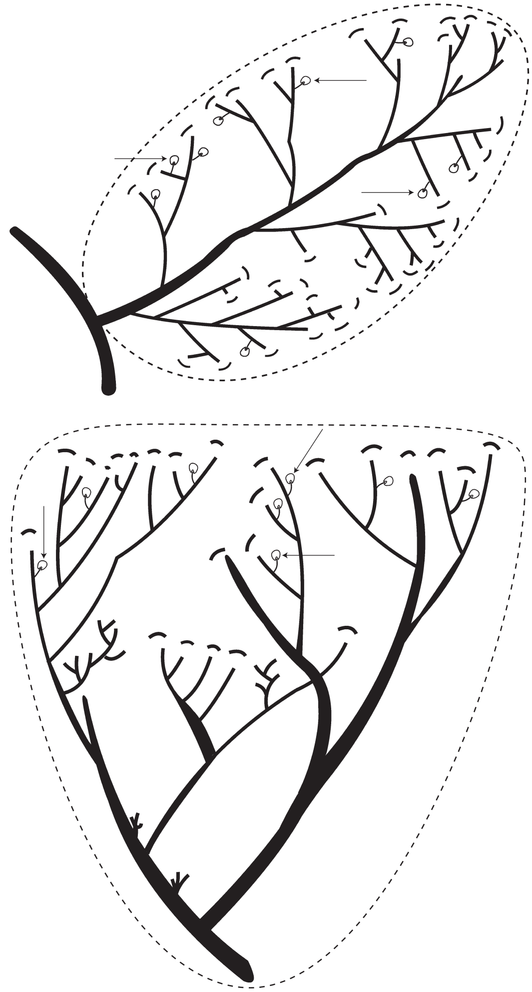

Fig. 8. — Crown shape in *Buxus vahlii* Baill.: **A**, in Rincón forest; **B**, in Isabela forest. Arrows indicate flowers.

Drying caused by the wind is another factor that can affect the development of the axes (Barthélémy & Hallé 1991). The death of the axes provokes a quick answer of the plant, forming new axes in reiteration processes. This type of reiterations is adaptive and can play a decisive role in the formation of the tree crown (Barthélémy & Hallé 1991; Vester 1997).

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