A Monthly e Magazine
ISSN:2583-2212
Popular Article
November 2024 Vol.4(11), 5001-5011

Growth and tree architecture: with particular reference to tropical broad-leaved species

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https://doi.org/10.5281/zenodo.14050286

Introduction

The tropics are home to an extraordinarily diverse range of plant species, stretching from the equator north and south along the latitudinal gradient. Among these species, tropical broad-leaved trees exhibit remarkable variability in growth rates. This diversity is influenced by numerous factors, including access to essential resources such as light, soil moisture, and nutrients, as well as the unique characteristics of individual trees, such as size, vigor, and heredity. The combined effect of these variables reflects the overall growth strategies of tropical trees, making their development a dynamic and multifaceted process. Throughout their life cycle, tropical trees undergo various stages of development, from seedling to maturity, with each phase presenting new environmental challenges and opportunities. As they grow, trees adapt to these changes through successive morphological development of their structural elements, including the stem, branching pattern, crown, and leaves. These changes are either rhythmic or continuous, allowing the tree to respond effectively to environmental conditions and optimize its chances of survival. The overall development of tree architecture, particularly the canopy structure, is a result of the growth of individual shoots and their subsequent proliferation.

The apical meristems, leaves, metamere (shoot units), and crown are the primary above-ground elements that contribute to the overall size and structure of a tree. In tropical environments, where diverse climatic conditions prevail and ecological stability persists over extended periods, tree architectural diversity is pronounced. As a result, studying the growth dynamics of tropical trees offers valuable insights into their development, especially as this growth varies from species to species, and even within the same species under different environmental conditions. The form a tree takes—its shape and structure—depends on how it responds to its particular environment. Several structural factors influence tree shape and architecture, including rhythmic or continuous growth, the orientation of branches, the positioning of lateral meristems, and the differentiation between trunk and branches. Additionally, the position of flowering and the ultimate height of the tree are important elements of its architectural form.

Primary orientation of branches

One of the fundamental architectural characteristics of tropical trees is the orientation of their branches. The apical meristems play a central role in determining the branching patterns of trees, and these meristems may exhibit either continuous or rhythmic growth. Continuous growth is typically found in species that exist in stable environments, such as *Grevillea robusta, Gmelina arborea*, ***Ficus spp., Eucalyptus spp.,*** *Azadirachta indica, Artocarpus heterophyllus, Rhizophora mangle*, etc. In contrast, rhythmic growth is associated with species like *Bauhinia variegata*, *Tectona grandis*, *Shorea robusta*), *Madhuca longifolia*, *Dipterocarpus spp.*, *Dalbergia latifolia*, etc. that experience distinct seasons of growth and dormancy.

Apical meristems produce either orthotropic or plagiotropic shoots. Orthotropic axes are erect, exhibit radial symmetry, and often have a spiral leaf arrangement. They are typically produced by the leading shoot, indicating vigorous young growth. Over time, as trees age or face stress, orthotropic growth tends to decrease. On the other hand, plagiotropic axes are horizontal, exhibit dorsoventral symmetry, and have distichous leaf arrangements. These are more commonly produced by lateral shoots and are associated with slower, weaker growth, particularly in older or stressed trees.

Genetic control and tree form

Tree architecture, including the overall form and structure of tropical broad-leaved species, is strongly influenced by genetic factors. In environments where competition for light is fierce, trees often exhibit forms that are shaped by their genetic predispositions. The ability of a tree to control the growth of its lateral branches through terminal dominance is known as epinastic control. In species with strong epinastic control, the terminal bud governs the length and orientation of lateral branches, resulting in an excurrent growth form, where the tree has a single dominant leader shoot.

In contrast, species with weak epinastic control tend to exhibit a decurrent growth form, where the lateral branches grow more freely, leading to a more rounded or spreading canopy. As trees age, their apical control tends to weaken, resulting in a more decurrent growth pattern. This transition in tree form is an adaptive response to changing environmental pressures, such as reduced light availability in the understory.

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Canopy shyness

An intriguing phenomenon observed in tropical broad-leaved species is "crown shyness," where the uppermost branches of adjacent trees avoid touching each other, creating visible gaps in the forest canopy. Crown shyness is thought to result from the abrasion of lateral branches during windstorms, which causes the trees to maintain a respectful distance from one another. This natural spacing minimizes damage to the trees and allows more light to filter through to the understory, supporting the growth of smaller plants.

Key drivers of tree growth and architecture changes

Several factors influence the growth patterns and structural development of trees, including:

- Light availability
- Branching density
- Browsing history,
- Fire history,
- Plant vigour
- Age-related changing
- Canopy position
- Stock spacing & canopy closer
- Disease and water stress

These factors collectively shape the adaptability and architectural evolution of trees in various environmental contexts.

Tree mechanics and growth strategies

The growth strategy of a tree varies not only between species but also among individual trees of the same species, depending on the environmental conditions they face. To survive and thrive in different environments, trees undergo a range of physical and morphological adaptations aimed at optimizing their chances of success. These adaptations include:

1. *Maximizing light capture* through vertical and temporal adjustments in canopy structure.
2. *Efficient resource allocation* between above-ground (branches, leaves) and below-ground (roots) systems to enhance growth.
3. *Enhancing mechanical strength* to withstand external forces such as gravity, wind, and snow.
4. *Minimizing water stress* during periods of drought by altering water-use strategies.
5. *Optimizing reproductive efficiency* by adjusting strategies for pollination and seed dispersal.

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6. *Navigating evolutionary constraints* that influence growth patterns and developmental pathways.
7. *Overcoming environmental history* by compensating for factors like past shading or damage from wind or other forces.

A critical component of tree mechanics is its ability to withstand wind forces, which plays a significant role in shaping its architecture. The tree's structural integrity, especially its capacity to resist breaking strain from strong winds, largely determines its utility in forests, open landscapes, or agroforestry systems. As a tree grows taller, its susceptibility to wind damage increases, and if wind speeds exceed critical thresholds, the likelihood of breakage escalates (Malhi et al., 2018). Thus, wind becomes a crucial factor influencing tree height growth.

Selective local pressures also contribute to the shaping of tree crown dimensions. For instance, trees growing in open areas have access to more lateral light, leading to deeper crowns. In regions with higher precipitation, crowns tend to be shallower, while in more productive ecosystems, crown depth increases (Shenkin et al., 2020). These factors collectively determine how trees adapt their growth and structure in response to environmental pressures.

Hormonal influence on tree architecture

Tree architecture is significantly influenced by the production of plant growth hormones, as well as cultural management practices like pruning. Pruning stimulates upright growth by increasing concentrations of auxin and altering the auxin-to-cytokinin ratio. In pruned trees, this hormonal shift leads to more vigorous shoot and branch growth, particularly in the upper canopy, compared to unpruned trees. Unpruned or "spreader" trees generally exhibit more horizontal growth and a less pronounced hormonal response.

The impact of pruning also promotes the development of ***sylleptic branches***, which grow directly from buds without a period of dormancy. These branches are particularly important in shaping tree structure, growth dynamics, and adaptability. Sylleptic growth, which is more common in pruned trees, contrasts with ***proleptic growth***, where branches develop after a period of dormancy. The absence of a cytokinin-induced effect in sylleptic growth suggests that auxin primarily drives the architecture of pruned trees, promoting upright growth patterns (Tworkoski et al., 2006). This response to pruning and hormonal regulation demonstrates how external management techniques, coupled with natural hormone production, shape tree architecture and influence overall growth strategies.

Light drives tree growth

Light significantly influences tree growth, with more than 90% of species exhibiting faster growth in response to increased light availability (Rüger et al., 2011). As a critical resource, light serves as a limiting factor for woody species throughout their developmental

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stages in natural forests. This environment presents a vertical gradient of light availability, transitioning from the overstory to the understory. In this context, trees adapt their growth strategies based on their light requirements. Shade-tolerant species thrive in lower light conditions, while light-demanding species grow towards available light, leading to dynamic modifications in canopy structure over time. Consequently, forests typically exhibit a stratified canopy structure, divided into three to four distinct layers: the emergent layer, canopy, understory, and forest floor. This vertical partitioning optimizes light interception, facilitating the coexistence of diverse tree species and enhancing overall forest productivity.

Fire and browsing: architectural influences on trees

Archibald and Bond (2003) noted that trees in savannah ecosystems often exhibit elongated growth forms characterized by small canopies and leaf areas, along with tall, slender, unbranched trunks. In contrast, trees found in arid regions typically develop wider canopies and increased lateral branching. This difference is largely influenced by environmental pressures: savannah trees face significant pressure to achieve rapid vertical growth to escape frequent fires, while trees in arid areas tend to adopt a more defensive, lateral growth strategy. Notably, savannah trees and those from the arid Karoo region display more pronounced vertical and lateral architectural adaptations compared to forest trees. In areas with a history of severe fire, tree species often have sparsely branched, pole-like architectures. Conversely, densely branched, cage-like forms are indicative of regions that have experienced heavy browsing rather than frequent fires.

Influence of successional change on tree architecture

The influence of successional change in forests is evident in both vertical and temporal dimensions, reflecting variations in light gradients from the canopy to the understory and from pioneer to climax species. Yang et al. (2015) examined how patterns of light availability impact plant elements and their parameters, particularly the Crown Exposure Index (CEI), during succession. Within a forest ecosystem, light intensity diminishes from the canopy down to the understory as incoming radiation is intercepted by the canopy layers. The study found significant correlations between CEI and key tree characteristics, such as height, crown area and depth, stem basal diameter, and leaf coverage, which followed the order of canopy trees > sub-canopy trees > understory plants across three successional stages.

Additionally, the distribution of leaves and branch orientation varied significantly among successional stages. Climax species exhibited greater proportions of dispersed leaves and leaned branches compared to mid-successional and pioneer species. Conversely, pioneer species displayed more clumped leaves and vertical branches than their mid-successional and climax counterparts. Notably, climax canopy trees tend to grow taller than pioneer canopy trees, necessitating a change in crown architecture in response to vertical growth throughout forest succession. These temporal changes in tree architecture provide strong evidence of how light conditions evolve during forest succession and relate to the developmental life history of trees, which is crucial for optimizing light interception and ensuring efficient hydraulic transport. This perspective is supported by the findings of various researchers (Niklas and Spatz, 2004; England and Attiwill, 2006; Yang et al., 2014).

Influence of neighbors on tree architecture

The architecture of trees is significantly influenced by the presence of neighboring trees, primarily driven by the need for light interception and mechanical stability against wind pressure (McFarlane and Kane, 2017). When trees are crowded by neighbors, they tend to optimize their growth traits for light competition, often sacrificing wind resistance. Conversely, trees that grow in isolation typically develop traits that enhance their ability to withstand wind. There is compelling evidence of a neighborhood-induced convergence of architectural traits across different species and environmental conditions, including urban settings, not just natural forests.

Under open-grown conditions, where light competition is minimal, trees develop relatively large crowns and broad branches, adopting a squat growth form that enhances their ability to resist strong winds. In contrast, trees growing in the understory, where shading from neighboring trees is prevalent, often exhibit increasingly spindly main stems. These trees typically have slender branches sparsely distributed across a disproportionately large crown volume, a strategy that maximizes light capture. While these under-canopy trees are generally less stable against wind compared to their open-grown counterparts, they have adapted to increase light acquisition by reducing their exposure to wind. This adaptation decreases the risk of stem breakage or uprooting during high wind events, illustrating the intricate balance between competition for light and structural stability in tree architecture.

Tree architectural models

Tree architecture encompasses the overall shape and size of woody plants, as well as the spatial arrangement of their components, including crowns, stems, branches, and leaves (Poorter et al. 2003). This architectural design is influenced by the nature and relative arrangement of each part, ultimately shaping the plant's structure and dynamics. Tree architecture plays a crucial role in determining plant performance, especially in response to environmental stresses. It can significantly impact key whole-plant functions such as photosynthesis, transpiration, and energy balance (Olson et al., 2009; Iida et al., 2011; Sarlikioti et al., 2011).

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To enhance the understanding of tree architecture, Hallé and Oldeman (2012) developed a set of 24 architectural models specifically for tropical trees (Figure 1). These models emphasize major functional characteristics, including the lifespan of the apical meristem and the differentiation of vegetative apical meristems. The apical meristem is central to tree growth, as it is responsible for elongation and serves as the origin of secondary or lateral meristems. Notably, while most trees possess secondary meristems, palms and certain tree ferns do not, which highlights the diversity in tree architecture and growth strategies. By examining these architectural models, researchers can better understand how various tree species adapt to their environments and optimize their growth and resource acquisition.

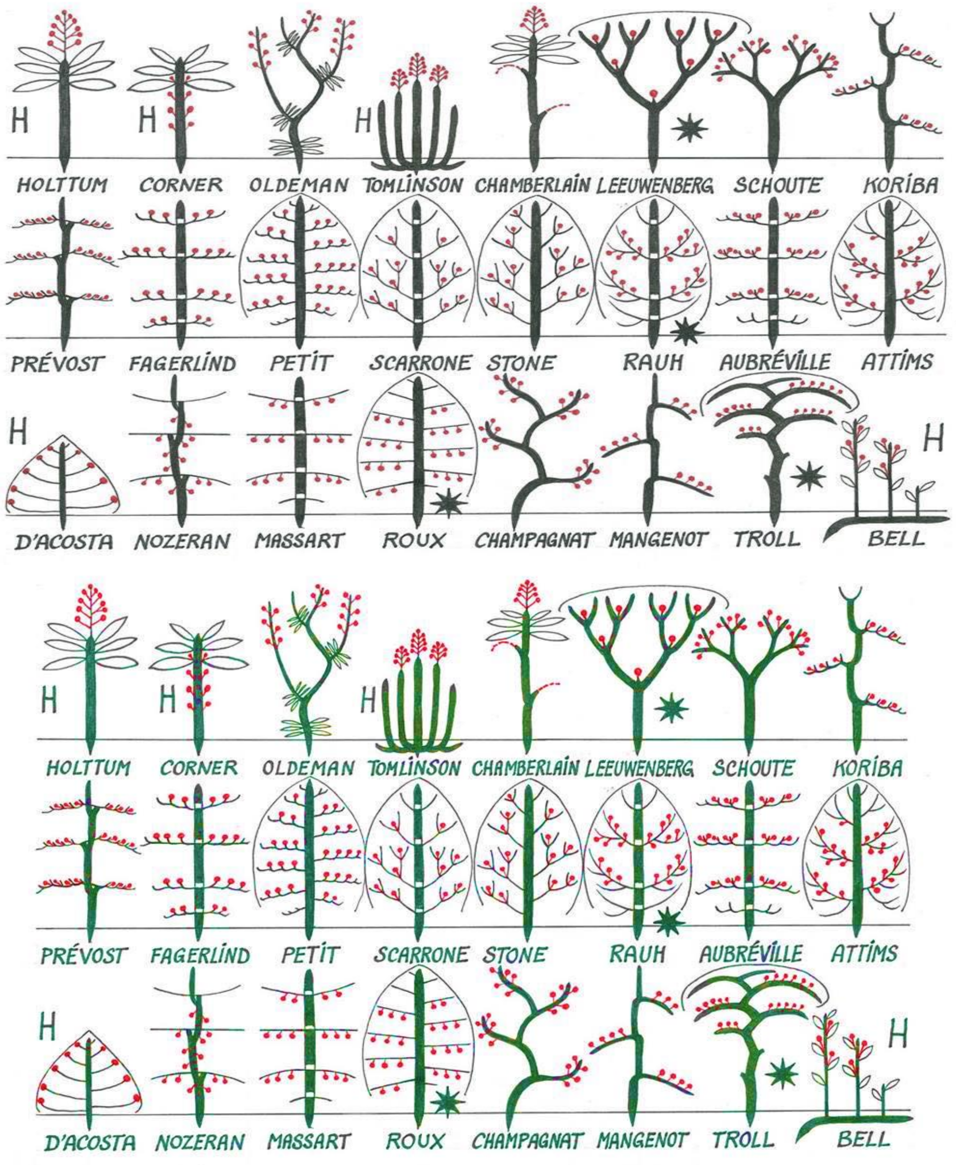

Figure 1. Hallé's tree architectural models (Source: adopted from Terrassa, 2018)

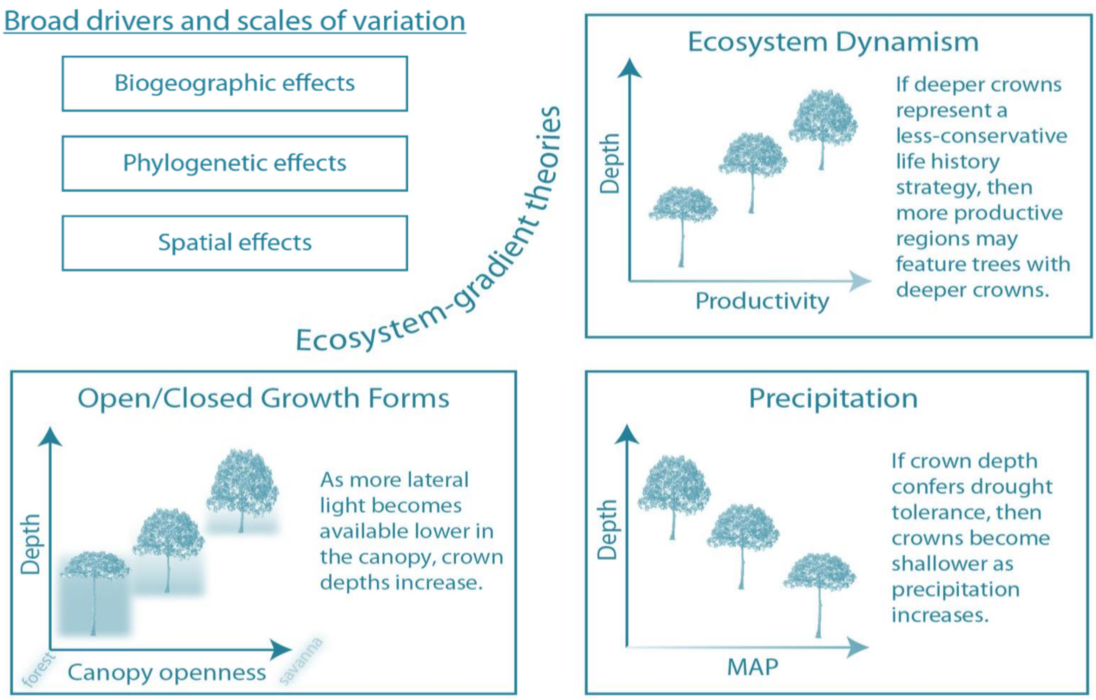

Figure 2. Canopy variation(openness/closeness) in different ecosystem gradients over precipitation, productivity and light availability. (Source: adopted from Shenkin et al., 2020)

The complexity of tree structures can be understood through a combination of vertical and horizontal measurements, along with the internal branching patterns, such as the degrees of branching. Larger trees tend to exhibit greater structural complexity compared to smaller trees, not merely due to their size but because of their more intricate architecture. It is reasonable to assert that the architectural designs of tall trees differ significantly from those of small herbs and shrubs.

Both biotic and abiotic stresses, including wind, light, soil moisture, nutrients, and slope, significantly influence the architectural development of trees (Fig. 2). Among these factors, light availability is often the most limiting, leading to various crown shapes ranging from spherical to flattened canopies. These adaptations are responses to climatic conditions and the surrounding environment, allowing trees to optimize light interception for photosynthesis.

Supportive modelling theories

Trees exhibit various shapes, growth rates, and interactions with their surroundings as they develop, balancing above-ground biomass. Several classical theories help explain these dynamics, including Metzger's theory, the Pipe Model theory, the Self-Thinning Rule, the Logarithmic Spiral Technique, and Leonardo da Vinci's concept of tree form, all of which have significant applications in forestry (Ramanan et al., 2020).

Metzger's Theory is one of the most widely accepted, describing how trees adapt their form based on their environment. Trees growing in open spaces tend to be shorter with rapidly tapering boles, while those in close-canopy conditions develop long, nearly cylindrical boles. In complete isolation, trees develop larger crowns, which place significant mechanical pressure on the base. As a result, these trees prioritize allocating growth materials to the base, often at the expense of height to ensure structural stability (Tworkoski et al., 2006).

The Pipe Model Theory suggests a synchronous development between the crown, trunk, and root systems, maintaining a constant proportional relationship throughout the tree's life. This model reflects how resources are distributed to balance growth and stability. In contrast, ***Leonardo da Vinci's Rule*** states that all branches of a tree, when combined at any given height, equal the thickness of the trunk. Essentially, if the branches were folded upward and compressed, the tree would resemble a single trunk of uniform thickness from top to bottom. This idea follows the principle that "all structures, whether natural or engineered, must obey the laws of physics."

Trees continuously adapt to their mechanical environment, with external forces shaping their growth patterns. This emphasizes the importance of understanding mechanical influences when studying tree development. These classical theories provide insights into the adaptive strategies trees employ throughout their life cycles, especially in response to the specific environmental conditions they inhabit.

Another significant phenomenon in tree growth is ***thigmomorphogenesis,*** where mechanical stress, such as wind or touch, leads to permanent changes in tree form. For instance, trees in valleys often develop dome-shaped crowns, while those in exposed conditions exhibit flat, widespread crowns that tilt toward the leeward side due to constant wind exposure. These adaptive growth responses highlight how environmental forces shape tree architecture over time.

Crown architecture throughout succession

Shukla and Ramakrishnan (1986) reported that the rhythmic extension growth of the leader axis, identifying variations in leaf morphology and branch organization within different architectural models. Early-successional species exhibit rapid extension and radial growth rates compared to their late-successional counterparts. This increased growth over a more extended period results in a sparse arrangement of branches in early-successional species, enhancing leaf exposure to light. Conversely, late-successional species demonstrate slower growth rates within a shorter time frame, leading to denser canopies with mutual leaf shading. Additionally, early-successional species tend to have a greater number of first-order branches, which exhibit plasticity in their orientation to maximize light interception.

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Durand (1997) highlighted that two distinct vertical strata establish similar structures to reach the canopy and capture light throughout the plant's growth stages, from seedling to maturity. For example, *Vateria indica* displays rhythmic, orthotropic, and lateral flowering, while *Knema attenuata* showcases rhythmic, plagiotropic, and short flowering branchlets, both ultimately conforming to Massart's architectural model by mid-age. In a related study, Chandrashekara (1996) examined the growth and architecture of tree species in agroforestry systems, particularly within agrisilvicultural contexts. In these systems, shade-demanding agricultural components intercropped in block plantations influence branch orientation and leaf arrangement, shaping the overall geometry of the tree crown. This adaptive strategy enables the tree crown to optimize light interception effectively.

Concluding remark

The growth and architecture of trees are significantly influenced by their surrounding environment, intrinsic traits, competition for light, and the availability of nutrients. As trees develop, their structures continuously adapt to changing conditions, showcasing a remarkable capacity for modification in response to external pressures. Tropical trees, in particular, exhibit greater architectural diversity compared to those in temperate regions, reflecting their unique environmental challenges and opportunities. The crown architecture can be represented by various models that illustrate the inherent growth strategies of different species, highlighting how they attain their distinct forms over time.

Furthermore, the rhythmic extension growth of tree leader axes, branch organization, and leaf morphology all play vital roles in shaping tree architecture through different successional stages. Understanding these architectural dynamics offers valuable insights into the life history of forest stands and their evolving structures over time. By examining tree architecture, we can better appreciate the intricate relationships between trees and their ecosystems, paving the way for informed conservation and management practices.

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