Tree Crown Architecture: Approach to Tree Form, Structure and Performance: A Review

Echereme Chidi B., Mbaekwe Ebenezer I. and Ekwealor Kenneth U

Department of Botany, Nnamdi Azikiwe University, P.M.B. 5025, Awka, Nigeria

Abstract- Crown architecture of trees is the manner in which the foliage parts of trees are positioned in various microenvironments. Trees tend to attain a characteristic shape when grown alone in the open due to inherited developmental programme. This developmental programme usually implies the reiterative addition of a series of structurally equivalent subunits (branches, axes, shoots, leaves), which confer trees a modular nature. The developmental programme is the result of plant evolution under some general biomechanical constraints. The functional implications of the modular nature and the biomechanical constraints of shape, which in addition to the environment where the tree grows determine the tree crown architecture. Plant performance has a crucial link between its phenotype and its ecological success, and the crown architecture becomes ecologically and evolutionary relevant when it affects performance. Crown architecture is crucial for light capture and for the distribution of light to each particular photosynthetic unit of the crown. Tree crown architecture can be represented with 'models' which delineate the basic growth strategies that determine the successive architectural phases. More growth 'models' have been identified for the tropical trees than in the temperate trees. The forms and morphogenesis of trees are far more variable in the tropics than in the temperate regions.

Index Terms- Trees, Crown architecture, developmental programme and performance

I. Introduction

The crowns of trees possess a striking forms and structures, which are difficult to interpret. This phenomenon is termed crown architecture. The study of plant architecture emerged as a new scientific discipline some 30 years ago, and derived, in several ways, from earlier works on plant morphology (Oldeman, 1974; Hallé *et al.*, 1978). Plant architecture involves the manner in which the foliage is positioned in different microenvironments and determines the flexibility of a shoot system to take advantage of unfilled gaps in the canopy, to allocate and utilize assimilates, and to recover from herbivoury or mechanical damage (Kuppers, 1989).

Tree architectural studies were first initiated in tropical regions and were, at first, concerned with the analysis of the aerial vegetative structure of tropical trees (Hallé and Oldeman, 1970). Since their definition, architectural concepts have provided powerful tools for studying plant form or even tropical forest structure and the understanding of its dynamics (Vester, 1997). Investigations based on these concepts quickly spread to temperate species(Stecconi *et al.*, 2000), herbs (Perreta *et al.*, 2000), lianas (Caballé, 1998) and root systems (Atger and Edelin, 1994*a*).

Several factors influence the forms and structures of tree crowns. Commenting on the contributing factors to crown architecture, Randolph and Donna (2007) asserted that individual tree crown conditions is the result of a combination of many factors including genetic traits, growing site characteristics and past and present external stresses (e.g., drought, insect outbreak, fire, e.t.c.). The results of these factors include different branching patterns, different shapes of boles, orientation of the leaves, branch angle, e.t.c. The architecture of a plant depends on the nature and on the relative arrangement of each of its parts; it is, at any given time, the expression of equilibrium between endogenous growth processes and exogenous constraints exerted by the environment.

Tree crowns are highly variable. The general shape varies from relatively dense conoids for young and healthy trees of excurrent habits to wide open hemispheric shapes for older trees of deliquescent habits (Cris, 1999). Shapes and branching habits of tree trunks and crowns are far more variable in the tropics than in temperate regions. A recent classification of form and morphogenesis in young tropical trees has identified as many as about 21 types or 'models' even though only about 25 per cent of the African species were taken into account (Hallé and Oldeman, 1970).

The Plant Design

The shape of a given plant is determined by the shape of the space that it fills, but most plants attain a characteristic shape when grown alone in the open due to an inherited developmental program (Horn, 1971). This developmental program usually implies the reiterative addition of a series of structurally equivalent subunits (branches, axes, shoots, leaves), which confers plants a modular nature. This developmental program is the result of plant evolution under some general biomechanical constraints. For instance, the shape of the crown of a tree is constrained by the fact that the cost of horizontal branches is greater than that of vertical branches (Mattheck, 1991).

Modular Nature of Plants

In the crown of most vascular plants, it is easy to recognize a hierarchical series of subunits. The largest subunit is the branch, which is made up of modules (Porter, 1983). Module is a general term that refers to a shoot with its leaves and buds, and the term can be applied to either determinate (structures whose apical meristem dies or produces a terminal inflorescence) or indeterminate shoot axes (Waller, 1986). Modules are, in turn, made up of smaller subunits consisting of a leaf, its axillary buds, and the associated internode. These small subunits have been

called metamers (White, 1984). Since plants have many redundant modules or organs that have similar or identical functions (e.g., leaves or shoots transforming absorbed light into biomass), plants have been seen as metapopulations (White, 1979). Such redundant modules are not fully dependent on one another, and, in fact, individual modules continue to function when neighbour organs are removed (Novoplansky *et al*., 1989).

The Concept of Reiteration

Although some plants conform to their architectural unit during their whole life, most plants repeat their architectural unit during their development, late in ontogeny, or under particular conditions. Oldeman (1974) named this process 'reiteration' and defined it as a morphogenetic process through which the organism duplicates its own elementary architecture, i.e. its architectural unit. The result of this process is called a 'reiterated complex' (Barthélémy *et al*., 1991) or a 'reiterate' (Millet et al., 1998a). Reiteration encompasses several aspects (sprouts, root-suckers, etc.) that have been known incidentally by botanists for a long time. The fundamental interest of this concept resides on its regrouping all these phenomena into a coherent whole, to bring out a common morphogenetic event. Matheck (1991) called this developmental programme. This developmental programme is the result of plant evolution under some general biomechanical constraints (Matheck, 1991).

Reiteration at first was considered as an opportunistic (non-automatic) process (Hallé *et al*., 1978). 'Opportunistic reiteration' may today be considered as any kind of reiteration linked to the individual history of each tree and may have two main origins: (1) 'adaptive reiteration' is a response to an increase in resource levels whereas (2) 'traumatic reiteration' is a response of a plant after it has been damaged and lost a major part of its structure.

Branching: The Framework of a Crown Architecture

Although the architecture of some trees consists only of a single vegetative axis during their whole life span, most display a more complex architecture consisting of several axes, one derived from another by a repetitive process known as branching.

Plants exhibit an extraordinary variety of branching patterns. The branching and consequent growth of trees and shrubs can be characterized by vertical or longitudinal, and horizontal or lateral symmetries. Vertical symmetry is characterized by growth of branches at the top (acrotony) or at the base (basitony), whereas lateral symmetry is characterized by branch growth at the upper or lower side of the lateral branch (epitony and hypotony, respectively). Logically, shrubs exhibit a basitonic branching, whereas trees are characterized by acrotonic branching. Analogously, while typical trees exhibit a hypotonic branching, most shrubs and small trees exhibit epitonic branching. However, there are many exceptions to these rules. For instance, the pyramidal shape of the crown of many conifers is due to the combination of basitonic branching (typically a shrub pattern) with a monopodial growth of the bole.

Apical Control and Apical Dominance Shaping Trees

Shoot branching patterns can be greatly affected by apical control and apical dominance (Wilson and Keathy, 1994). Apical control is the inhibition of a lateral branch growth by shoots above it (distal shoots). It refers to the physiological condition governing the excurrent (single stem, pyramidal) or decurrent (branchy) pattern of growth. Apical dominance is the tendency for current year's lateral buds to remain dormant as the shoot expands. Species with strong apical dominance have weak apical control and this results in branchy trees whereas species with weak apical dominance have strong apical control and this results in columnar tree.

Plant Biomechanics: Coping with Gravity and Wind

While plant architecture is an outcome of many selective pressures, the shapes of plant parts, their elasticity, and resistance to strain, are constrained by well-known mechanical principles (Niklas, 1992). Because aerial plant parts face the obvious forces of gravity and wind, a fraction of the biomass must be devoted to support. As mechanical structures of similar shape become increasingly inefficient with increasing size, the fraction required to support plants increases rapidly with increasing plant size. For instance, the strength of a column (e.g., a branch or a stem) scales with the square of its diameter, whereas its mass increases with diameter squared times length (Gere and Timoshenko, 1997). For any given plant, the mechanical costs associated with its crown geometry must be balanced with the photosynthetic benefits associated with its light-capture efficiency.

Although gravity leads to static loading of a plant based on the weight of individual parts, the dynamic loading caused by wind is often transitory (Speck *et al*., 1990). However, the wind exerts permanent modifications of the overall shape of plants and affects the anatomy and density of the wood, inducing biomechanical changes at architectural and anatomical levels (Ennos, 1997). The greatest effects of strong winds on trees are seen near the tree line, where most species exhibit the so-called krummholz form (Ennos, 1997). Krummholz refers to environmentally dwarfed trees, in which the crown is a prostrate cushion that extends leeward from the short trunk (Arno and Hammerly, 1984).

Crown architecture is crucial for light capture and for the distribution of light to each particular photosynthetic unit of the crown, but must also serve several other functions. The architectural design of a given plant must provide safety margins to cope with gravity and wind; therefore, biomechanical constraints must be taken into account when assessing the influence of morphology and architecture on plant performance.

Structural Determinants of Light Capture

Canopy photosynthesis rate depends on the biochemical capacities of the foliage as well as on the distribution of light within the canopy (Sinoquet *et al*., 2001). A major outcome of variation in crown architecture is modification of the overall light harvesting and the efficiency of light harvesting. The total leaf area supported by given crowns is the most basic structural property that affects the fraction of absorbed radiation. However, the distribution and arrangement of leaves within a crown can strongly modify the light harvesting efficiency of unit foliage area (Cescatti and Niinemets, 2004). As the three-dimensional arrangement of leaves in a crown is difficult to measure, light interception and canopy photosynthesis is often simulated assuming that foliage is randomly dispersed throughout the canopy volume (Beyschlag and Ryel, 1999).

Crown Architecture in Extreme Light Environments

Light can be a limiting resource in understoreys of dense stands or for plants subject to strong neighbourhood competition, whereas light can be excessive and even harmful in open environments where plant metabolism is impaired by environmental stresses. Plant shape and size have been shown to change as a function of the light environment, and plants are capable of orienting their light-capturing surfaces in different ways to increase or decrease the leaf surface area projected in the direction of ambient light (Cescatti and Niinemets, 2004). Plants exhibit a remarkable within-species and within-individual variability in their structural features. For instance, branching pattern of trees is not stationary, and it has been shown that the variation of branching pattern can be the result of developmental–phenotypic interaction (Steingraeber, 1982). While in some cases it can be due to a malfunction of the genetic program, in most cases this variability is a plastic response to local conditions, and light is possibly the most spatially and temporally heterogeneous environmental factor affecting plant survival and growth. Structural plasticity of plants enables a fine-tuning with environmental changes so that the efficiency of the limiting processes at each stage is maximized. A common environmental change experienced by plants is the decreasing availability of light with the advance of succession. It has been shown for the succulent thalophyte *Salicornia europaea* that morphological changes in the branching patterns during succession maximized light interception (Ellison and Niklas, 1988). However, even phylogenetically close species differ in their capacity for a plastic response to the light environment (Valladares *et al*., 2000). Interestingly, certain species that exhibit architecture suited to high irradiance conditions do not change significantly when grown in the shade. That was the case for mangroves in Malaysia: architecture and allometry of shaded mangroves were consistently more similar to those of exposed mangroves than to shaded, broad-leaved, evergreen, rainforest trees (Turner *et al*., 1995).

When Light is Scarce

When plants grow in dense stands or in the understory, the resource of radiant energy becomes scarce, unpredictable, and patchy. In these environments, evolution has led to two principal approaches for survival: shade avoidance and shade tolerance. Angiosperms, in particular, have evolved an impressive capacity to avoid shade. The so-called shade avoidance syndrome involves accelerated extension growth, strengthened apical dominance, and retarded leaf and chloroplast development, among other processes (Smith and Whitelam, 1997). Here the focus is on the functional aspects of the crown of plants that tolerate shade and on the structural features that are relevant for such tolerance.

The Concept of Architectural Model

For a tree species the growth pattern which determines the successive architectural phases is called its architectural model, or shorter, its model (Hallé and Oldeman, 1970). The architectural model is an inherent growth strategy that defines both the manner in which the plant elaborates its form and the resulting architecture. It expresses the nature and the sequence of to the fundamental growth programme on which the entire architecture is established. The identification of the architectural model of any given plant is based on the observation of the features belonging to the four major groups of simple morphological features: (1) the growth pattern, i.e. determinate vs. indeterminate growth and rhythmic vs. continuous growth; (2) the branching pattern, i.e. terminal vs. lateral branching, no branching, monopodial vs. sympodial branching, rhythmic vs. continuous branching, immediate vs. delayed branching; (3) the morphological differentiation of axes, i.e. orthotropic vs. plagiotropic vs. axes with mixed morphological and/or geometrical features (with plagiotropic and orthotropic portions); and (4) lateral vs. terminal flowering.

Each architectural model is defined by a particular combination of these simple morphological features and named after a well-known botanist. Although the number of these combinations is theoretically very high, there are apparently only 23 architectural models found in nature. Each of these models applies equally to arborescent or herbaceous plants, from tropical or temperate regions, and which can belong to closely related or distant taxa. Architectural models are a convenient starting point for interpreting plant form, but there is a series of variations and exceptions to each program of development that complicates classification and suggests the search of additional descriptions of crown shapes. For instance, *Arbutus sp*. exhibit two different architectural patterns depending on the light environment, and *Acer pseudoplatanus*, as with many other woody plants, undergo significant changes of branching patterns during the ontogeny, switching from one model to another (Bell, 1993).

Tree Growth Types or 'Models' in the Tropics

Many palms, tree-ferns and a few dicotyledons have a single stem which is normally unbranched throughout life (Fig. A). These are all 'palm-like' trees, but in addition the juvenile stages of a number of others, for example some Meliaceae and Dipterocarpaceae, are unbranched for a number of years.

The great majority of trees branch sooner or later and can be divided into three types: firstly those where the branches are all of equal status (see Figs. B, C), secondly where there are clearly different orders of branches (see Figs. E-H), and the third type where the main stem consists of a succession of sympodially growing axes whose terminal parts curve over and form branches (Fig. D).

The crown shape of mature tree depends partly on which of these categories it belongs to, but also on its adult characteristics and the environments in which it has grown.

The majority of tropical trees possess a smooth, light-coloured bole of a cylindrical shape. Some, however, show features such as fluting, spiral twisting, large spines as in *Fagara macrophylla* or *Erythrina mildbraedii* (utilized as 'rubber stamps'), adventitious roots such as in *Afrosersalisia nobilis*.
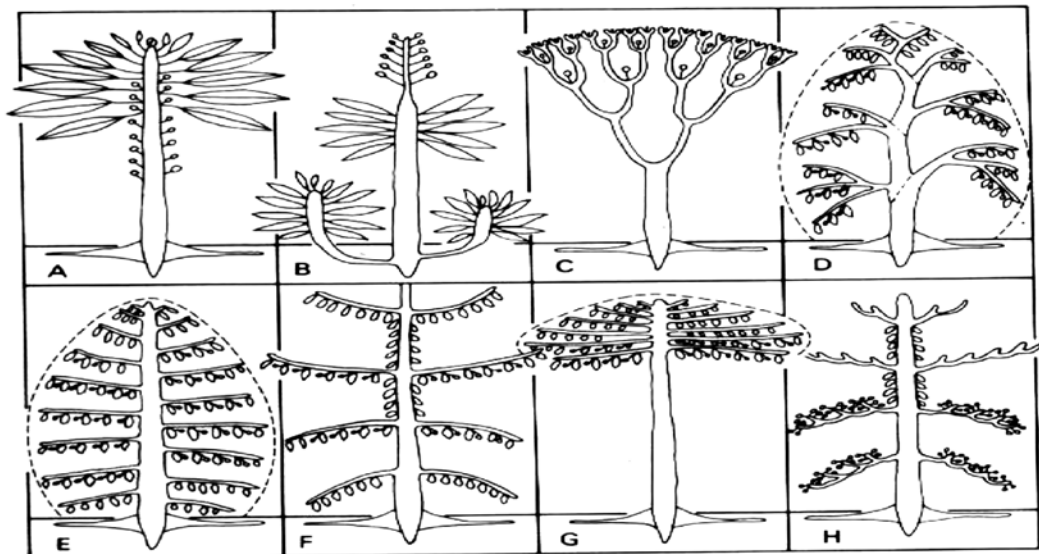
Diagrammatic interpretations of some branching and repro-ductive patterns in tropical trees, according to the classification of 'models' by Hallé and Oldeman (1970):

Unbranched trees:
 A — Model of Corner; e.g. *Elaeis guineensis, Mauritia flexuosa, Cocos nucifera, Pycnocoma angustifolia, Phyllobotryum soyauxianum, Ficus theophrastoides.*

Branched trees:
 branches all of equal status:
 B — Model of Tomlinson; e.g. *Raphia gigantea, Euterpe oleracea.*
 C — Model of Leeuwenberg; e.g. *Manihot esculenta, Plumeria acutifolia, Rauvolfia vomitoria, Anthocleista nobilis, Alstonia sericea.*

sympodially-formed trunks and branches:

num, Cassia javanica, Parinari excelsa, Pterocarpus officinalis. (Also the European tree, *Tilia platyphyllos.*)
branches of different status:
 E — Model of Rauh; e.g. *Hevea brasiliensis, Pentadesma butyracea, Entandrophragma utile, Triplochiton scleroxylon, Cecropia peltata, Artocarpus incisa, Musanga cecropioides, Khaya ivorensis.* (Also many common European trees; e.g. *Quercus, Fraxinus.*)
 F — Model of Massart; e.g. *Ceiba pentandra* (see Plate 18), *Diospyros matherana, Pycnanthus angolensis, Anisophyllea* spp.
 G — Model of Cook; e.g. *Phyllanthus mimosoides, Panda oleosa, Canthium glabriflorum, Glochidion laevigatum.*
 H — Model of Aubréville, otherwise known as 'pagoda-trees'; e.g. *Terminalia catappa, T. ivorensis,* (see Plate 23A), *Sterculia tragacantha, Omphalocarpum elatum, Manilkara bidentata.*

Tree Growth Patterns in the Temperate Regions

The following shoot growth processes are predominant in most temperate tree species:

Preformed (Fixed Growth)

Here, a pattern of bud development, dormancy and activation found in many trees that survive periods of environmental extremes by going dormant is common. In the case of rhythmic growth, all the metamers and organs of the future elongated shoot may be present at an embryonic stage in a bud before the elongation of the shoot deriving from it; in this case the shoot is referred to as 'preformed' and its constitutive organs as 'preformed organs' or 'preformation', 'early leaves', or 'fixed growth' (Hallé *et al.*, 1978). At bud break, the preformed primordial elongate, with expansion limited by the number of primordial cells formed the previous year. The duration of preformed organs at an embryonic stage in a bud may vary from several days or weeks (Sabatier *et al.*, 1995) to several years (Meloche and Diggle, 2001). Examples of trees with preformed growth pattern include Oaks (*Quercus spp.*), Douglas-fir (*Pseudotsuga menzeisii*) (PlateII), Hickories (*Caya spp.*), Spruces (white) (*Picea glauca*), Ashes (*Fraxinus spp.*) and some pines (white) (*Pinus strobes*). Trees with preformed growth generally form distinctive annual rings (ring porous) because of difference between early and late wood.

Neoformed (Sustained Growth)

Not all primordial develop prior to active shoot elongation. In other cases, more organs than those included at an embryonic stage in the bud are elongated. These supplementary, non-preformed elements are referred to as 'neoformed organs' (i.e. 'neoformation' or 'late leaves', 'sustained growth' (Plate I).As a consequence stems or shoots may comprise only preformed metamers) or, more rarely, may be entirely neoformed (El-Morsy, 1991). In many cases, a preformed part can be followed by a neoformed part and thus give rise to a mixed shoot (Souza *et al.*, 2000). Species having neoformed growth include Sweet gum (*Liquidamber styracifua*), Hemlock (*Tsuga canadensis*), Red alder (*Almus rubra*), Yellow polplar (*Liriodendron tulpifera*), and Red maple (*Acer rubrum*). Trees with neoformed growth produce less definitive growth rings (diffuse porous) because there is little difference between wood formed early in the season and wood formed later in the growing season.

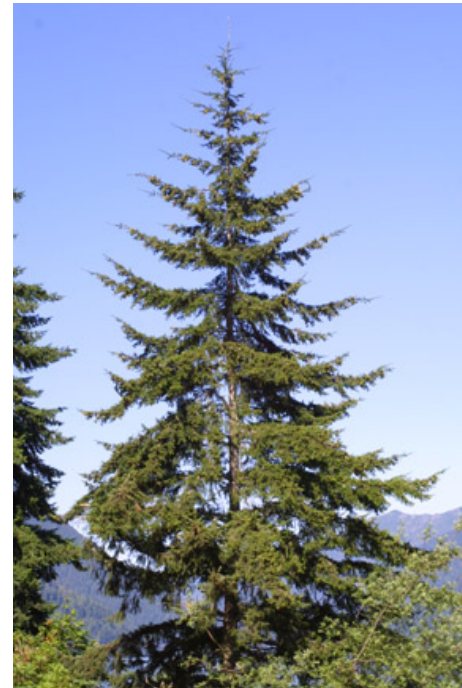**Plate I***: Tsuga Canadensis*

Neoformed Growth

Plate II: *Pseudotsuga menzeisii*

Preformed Growth

II. CONCLUSION

Crown architectures of most trees are intricately variable. The functional implications of the two general aspects, the developmental programme and the biomechanical constraint of shapes, which in addition to the environment where the trees grow, determine the tree architecture.

The architectural design of a given plant must provide safety margins to cope with gravity and wind; therefore, biomechanical constraints must be taken into account when assessing the influence of morphology and architecture on plant performance. Crown architecture is crucial for light capture and for the distribution of light to each photosynthetic unit of the crown since canopy photosynthesis rate depends on the biochemical capacities of the foliage as well as on the distribution of light within the canopy.

Crown architecture of trees can be delineated with 'models', which is an inherent growth strategy that defines both the manner in which the plant elaborates its form and the resulting architecture. It expresses the nature and the sequence of to the

fundamental growth programmes on which the entire architecture is established.

The crown architecture of trees is far more variable in the tropics than in the temperate regions.

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AUTHORS

First Author – Echereme Chidi B, Department of Botany, Nnamdi Azikiwe University, P.M.B. 5025, Awka, Nigeria, chidiechereme@yahoo.com; +2347038285601
Second Author – Mbaekwe Ebenezer I, Department of Botany, Nnamdi Azikiwe University, P.M.B. 5025, Awka, Nigeria
Third Author – Ekwealor Kenneth U, Department of Botany, Nnamdi Azikiwe University, P.M.B. 5025, Awka, Nigeria