UVED Resource

Plant Growth Architecture and Production Dynamics

Preliminary Course: Architectural Botany

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Contents and Objectives

Botany: Plant architecture

This section presents an overview of plant architectural analysis, a botanical approach to study plant structures.

Using the identification of several morphological criteria and considering the plant as a whole, from germination to death, architectural analysis is essentially a detailed, multilevel, comprehensive and dynamic approach to plant development.
Completed by precise morphological observations and appropriate quantitative methods of analysis, recent research in this field has greatly increased our understanding of plant structure and development and has led to the establishment of a real conceptual and methodological framework for plant form and structure analysis and representation.

At whole plant level, the architecture of a plant can be seen as a hierarchical branched system in which the axes can be grouped into categories which define the *architectural unit* of a species, a central concept in architectural methodology. At older growth stages, this architectural unit may be duplicated in the plant crown, through reiteration processes.

The architectural approach is a tool for describing plant organization, for knowledge of a plant's life history, and for plant structure sampling and measurements.
This methodology can be applied to describe the structure and dynamics of plants, based on the static information provided by different individual plants.

Despite their recent origin, architectural concepts and analysis methods provide a powerful tool for studying plant form and ontogeny.

Course Objectives

The aim of this course is to enable students to:

- Discover plant architecture and its interests
- Understand the organization of plant structure
- Learn about the main architectural analysis concepts
- Acquire the ability to define the framework of the architectural unit of a given plant

Botany. Architectural Analysis

Plant architectural analysis is introduced step by step from the lowest morphological levels up to the architectural unit concept, illustrated on a specific example.
Preliminary architectural concepts are introduced first.

The different levels of plant structure organization are then presented (phytomer, growth unit, branched system, architectural unit, and whole plant).

Axis typology is introduced from morphological and geometrical traits, whose combinations define architectural models.

Instancing axis typology traits to a specific plant species defines the Architectural Unit.

Lastly, definition of the Architectural Unit is illustrated on a specific plant (wild cherry tree).

Course content map

Preliminary Architectural Concepts

About Plant Architecture

The architecture of a plant depends on the nature and relative arrangement of each of its parts; it is, at any given time, the expression of a balance between endogenous growth processes and exogenous constraints exerted by the environment.

The aim of architectural analysis is, by means of observation and sometimes experimentation, to identify and understand these endogenous processes.

Using the identification of several morphological criteria and considering the plant as a whole, from germination to death, architectural analysis is essentially a detailed, multilevel, comprehensive and dynamic approach to plant development (Barthélémy and Caraglio, 2007).

This architectural approach was developed in the 70s for tropical trees (e.g. Hallé and Oldeman 1970; Hallé et al. 1978) to understand and apply a comprehensive analysis of the structure and dynamics of plants.

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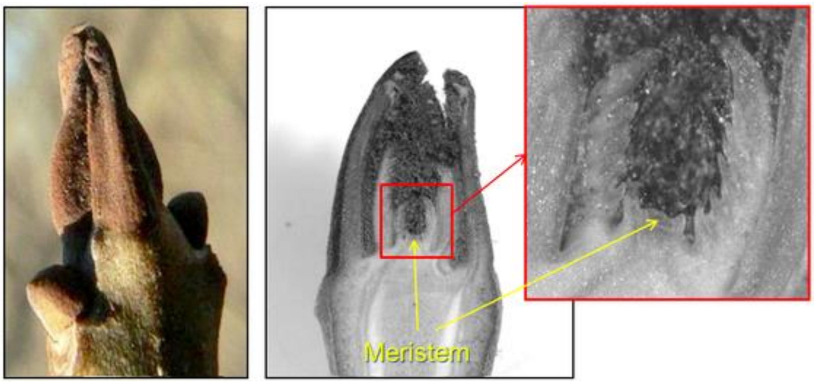
Preliminary Architectural Concepts

Plant growth and development result from the activity of meristems.
Structure establishment results from **primary growth**, while growth thickness results from **secondary growth**.

The shoot apical meristem

A (shoot apical) meristem is a set of embryonic cells situated at the apical part of each axis. These particular cells are always able to divide and thus to generate new cells, which can then differentiate into specialized cells constituting tissue (pith, epidermal tissue, vascular bundles, etc.) or leaf organs.
The division activity of meristematic cells also generates small sets of embryonic cells: the axillary meristems from which lateral shoots grow.



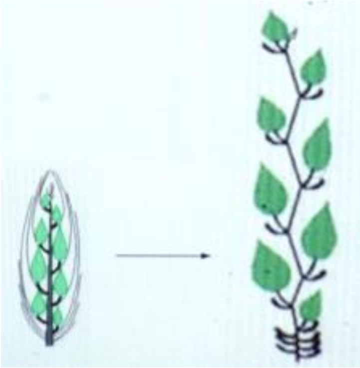
The bud. Fraxinus excelsior (Photos: Y. Caraglio, CIRAD)
Left: An apical bud. Middle: microscopic view of the apex.
Right: zoom centred on the meristem.

Two elementary processes lead to tree development: growth and branching.

Growth

The **growth** process originates in the apical bud where the apical meristem tissue is located.
At this place, cell division and elongation take place to generate new elements of the leafy axis (node, internode, leaf, axillary bud), which expand when buds break.

Growth thus involves two different consecutive processes: organ formation, called **organogenesis**, and **organ expansion** (extension phase).



Organ formation and organ expansion on the beech tree.
Leafy axis formation starts in the bud in late autumn, while expansion (left) occurs the following spring.
(Fagus sylvatica, drawing E. Nicolini, CIRAD)

Organ expansion. (Acer pseudoplatanus, photo Y. Caraglio, CIRAD)
Left: the closed terminal bud
Right: four steps of a leafy expansion (with its leaves).

Branching

The **branching** process builds **branches** at leaf axils; it relies on the delimitation of a zone of embryonic cells just next to the initiated leaf, i.e. the axillary meristem.

The branching process allows a plant to explore many directions, from one axis through new lateral axes. It includes the initiation and development of lateral buds.

Axillary meristem and branching (Photos: Y. Caraglio, CIRAD)
Left: microscopic view with axillary meristems (Pisum sp)
Right: a branch resulting from a branching process (Eryobotria japonica)

Plant organization

When observing a plant we can very easily recognize some of its constitutive elements.
The lowest fundamental structural unit of the plant body is the **phytomer**.
Successive phytomers derived from a given meristem build an axis carrying leaves: the **leafy axis**.
Sets of leafy axes develop, with the branching process, into a branched system.
When the tree reaches maturity, the branched system is replicated by a **reiteration** process, building the whole tree.

Phytomers and the leafy axis levels

The fundamental structural unit of the plant body is called a **phytomer or metamer**.

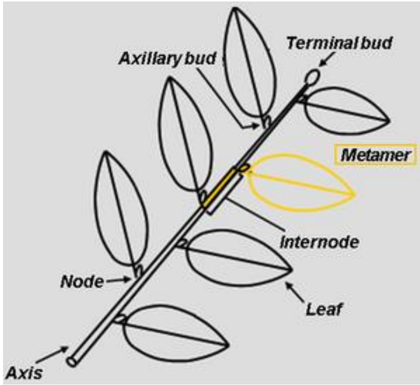
A phytomer is formed by a node with its leaf (or leaves), its axillary bud(s) and the subtending node.
Successive phytomers derived from a terminal bud thus build a leafy axis.

By way of its elementary growth process, a plant is made up of a succession of phytomers.

Each node carries one or more leaves.
Two successive nodes derived from a given meristem are separated by an internode.
An axillary bud can be found in the axil of each leaf.

The set of successive phytomers derived from a given meristem expresses a physical direction, an axis carrying leaves: the **leafy axis**.

The tip of the axis carries the apical meristem (apical bud, also called terminal bud), while axillary buds, in leaf axils, allow branching.



The leafy axis (drawing D. Barthélémy, CIRAD)
The leafy axis results from successive phytomers (or metamers) arising from apical bud growth and development.
In yellow: a metamer with its internode, its node, leaf and axillary bud.

In many species the edification of an axis is due to a rhythmic process of growth. The terminal or apical bud periodically breaks (in northern temperate countries in springtime) and new organs of

the leafy stem are expanded.
This new stem portion thus elaborated during a continuous expansion phase is called a growth unit.

Growth units and annual shoot levels

As defined by Hallé and Martin (1968), a **growth unit** is the portion of stem expanded during an uninterrupted phase of expansion.

The **growth unit**, in a plant structure, is a key notion for plant structure modelling and simulation.

Branch of Cassava (photo M. Jaeger, CIRAD)
Two successive growth units on a cassava branch. (Manihot esculenta)

In some temperate species, shoot expansion may occur in one, two or more successive events giving rise to an **annual shoot** made up of one or a succession of several growth units or growth cycles occurring in a growing season.

More generally, rhythmic growth can be expressed several times during a growing season: this is called **polycyclism**, while the appearance of a single growth unit is called **monocyclism** (Bugnon and Bugnon, 1951 or Lanner 1976)

An annual shoot on a young pine (Pinus halepensis) (Photo Y. Caraglio, CIRAD)
This annual shoot (delimited in yellow) is a case of polycyclism, built from two growth units (in red).

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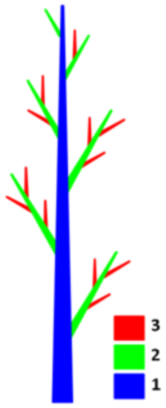
Branched systems

The branching process builds branches in leaf axils.
The branching process allows a plant to explore many directions, from one axis through new lateral axes building a **branched system**.

The description of a branched system implies the use of a precise topological terminology.

Branching develops a natural hierarchy in the plant structure.
On a given axis position, this hierarchy is classically defined from its order, a numeral ranking for the number of branching processes involved up to reaching the axis position, starting from the seed.

In plant architecture analysis, it is usual to use ordinal numbers and to consider the main stem arising from the seed as the order 1 axis, whereas the axes it gives rise to are referred to as order 2 axes and so on.

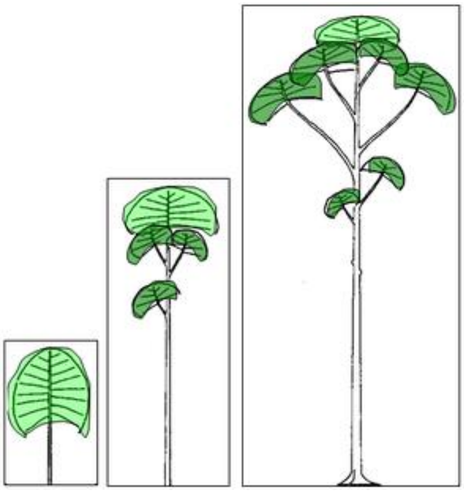


Branching orders, identified by their rank number and colour (drawing M. Jaeger, CIRAD)
The branching order 1 axis, is the main stem, arising from the seed.
Branching order 2 axes, in green, stand for branches borne by the order 1 axis
Branching order 3 axes, in red, stand for branches borne by the order 2 axes

In a sympodial system, a rigorous use of this terminology will lead to the reference of the successive sympodial units as axis orders 1, 2, 3, etc. In the architectural botany approach, each rectilinear succession of modules, even though not strictly emitted by a single meristem, will be considered as an axis and will represent an "apparent branching order".

Reiteration

During its development, a plant becomes bigger.
This increase in size of the plant body is often possible by a duplication of the existing architecture.
This phenomenon, first described on big tropical forest trees, was called **reiteration** by Oldeman (1974).



Tree development by the reiteration process.
Two steps of the development of reiteration on mature trees (C. Edelin, CNRS)

*Reiteration allows trees to optimize space occupancy according to available energy, so called **immediate reiteration** (see further)*

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Oldeman R.A.A. *1974. L'architecture de la forêt guyanaise. Mémoire no.73. Paris: O.R.S.T.O.M.*

Organization levels

Several levels of organization in the plant structure can be observed, revealed and used for plant edification understanding, modelling and simulation (Barthélémy, 1991, Godin and Caraglio, 1998).

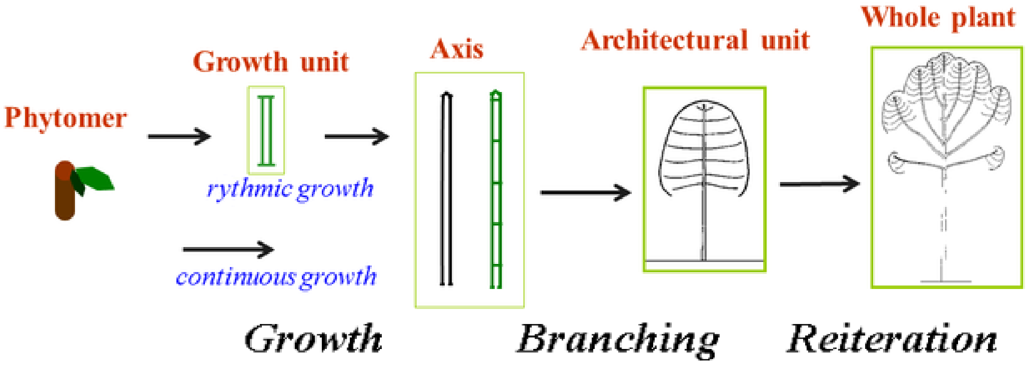
From the most elementary, the three repetition phenomena, growth, branching and reiteration, build the plant and give rise to several levels of organization, as follows:
The lowest description level is the phytomer, to be considered as the basic element of plant structure establishment.

Then successive phytomers build a stem or an axis from a growth process. When growth is rhythmic, growth units appear consecutively.

A succession of phytomers (continuous growth) or growth units (rhythmic growth) then give rise to an Axis.

In the axil of leaves, branches appear, building a branched structure. We will see further that when this branched system develops, various categories of axis appear, some may specialize (bearing the sexuality for instance). This third hierarchical level builds the **architectural unit**.

When the plant matures, the reiteration process, allowing the development of a crown, is involved in defining the whole plant organization level.



Organization levels of a plant (Drawings D. Barthélémy, CIRAD)
The phytomer defines the first level.
The axis defines the second one, resulting from the growth process.
(Axes are composed of growth units if growth is rhythmic.)
The architectural unit defines the third level, resulting from both growth and branching.
The whole plant level results from the occurrence of the reiteration processes.

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Axis typology.

Plant typology basics

Architectural analysis is based on morphological stem characterizations for studying plant form and understanding its dynamics.

These traits are usually modelled as pictograms on plant scheme drawings and relatively to:
The flowering position and its impact on the growth strategy
The growth pattern, qualified according to its dynamics
The branching pattern, qualified according to its dynamics in position and time
The geometrical pattern

We will see that a combination of these traits leads to the definition of the architectural models.

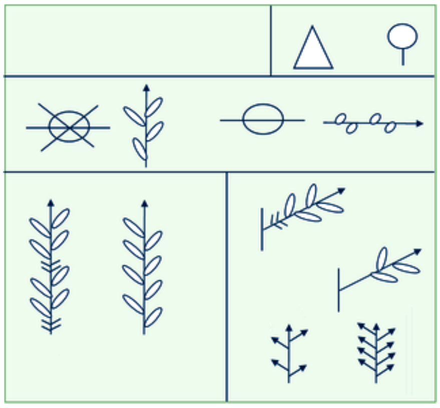
Axis typology pictograms

On the plant axis, growth expressions are reflected by morphological markers, such as bud scales, short internodes, reduced leaves, etc.
The knowledge of such morphological markers is very helpful for biologists and foresters for a posteriori stem growth analysis.

These markers characterize phytomers and axes according to four major groups of simple morphological features, which are:

The flowering position
The growth pattern,
The branching pattern,
The axis geometrical pattern

The morphological features are associated with specific pictograms, as shown below, characterizing various states related to each of them.



Axis morphological traits (Pictograms Y. Caraglio, CIRAD)
Top: vegetative or flowering
Middle: phyllotaxis and plagiotropy
Bottom left: growth (rhythmic vs continuous)
Bottom right: branching (immediate vs delayed, rhythmic vs continuous)

Sexuality and development

Determinate and indeterminate growth
When a terminal meristem can produce all the life span of the plant, its bearing axis has **indeterminate growth** (a theoretical viewpoint).
Whereas, when meristem production is limited in time, ending with a flower differentiation or a tendril or a spine or by death of apical meristem, its bearing axis shows **determinate growth**.

The sexuality position therefore impacts on plant development.
Lateral flowering does not change the axis development strategy.
Apical flowering stops axis development.
In this case, axis development is only possible from axillary buds.

Sexuality position and axis development (Photos D. Barthélémy, CIRAD)
Left: lateral sexuality and indeterminate growth (Cocos nucifera)
Right: terminal sexuality and determinate growth (Isertia sp)

Monopodial and sympodial development

Plants with **monopodial** development grow upward from a single meristem. They add leaves to the apex each year and the stem grows longer accordingly.

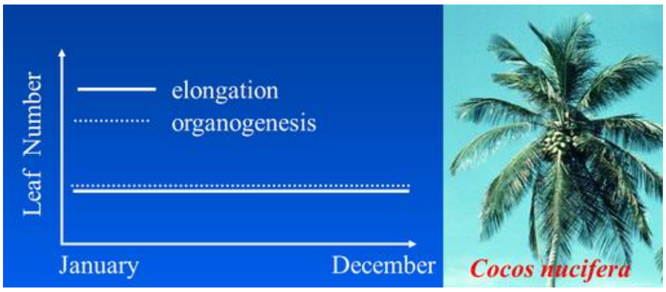
Plants with **sympodial** development have a specialized lateral growth pattern in which the apical meristem is terminated.
The apical meristem can either be consumed to make an inflorescence or other determinate structure, or it can be aborted.
Growth is continued by a lateral meristem, which repeats the process. The result is that the stem, which may appear to be continuous, is in fact derived from multiple meristems, rather than a monopodial plant whose stems derive from one meristem only.

Monopodial and sympodial development (Photos D. Barthélémy, CIRAD)
Left: Monopodial and indeterminate growth (Albies alba)
Centre: Sympodial development, with terminal sexuality and determinate growth (Plumeria sp)
Right: Sympodial development, with terminal sexuality and determinate growth building a single stem (Ailanthus altissima)

Continuous and Rhythmic Growth

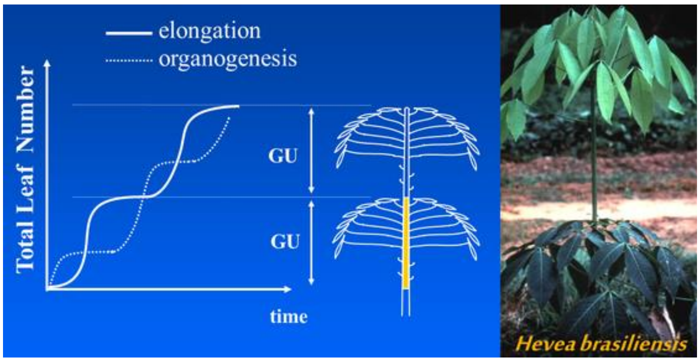
Continuous growth

In continuous growth, both organogenesis and elongation are continuous, stable and regular. Axis length increases and leaf appearances are regular.



Continuous growth
Elongation follows organogenesis and both processes are stable and regular as shown by the coconut palm (Drawings and Photo D. Barthélémy, CIRAD)

Rhythmic growth
In rhythmic growth, organogenesis is not continuous, showing pauses between organ creation phases. Elongation is also periodic. Rhythmic growth builds growth units, corresponding to organogenesis cycles.



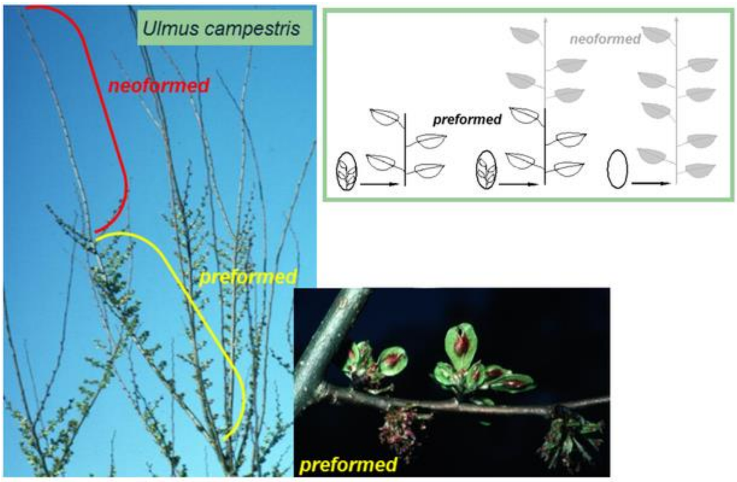
Rhythmic growth (Drawings and Photo D. Barthélémy, CIRAD)
Organogenesis is not continuous, and, on the rubber stem elongation occurs with a constant delay

Rhythmic growth: pre-formation and neo-formation processes

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 **pre-formed** and its constitutive organs as **pre-formed organs** or the pre-formation process.

In other cases of rhythmic growth, more organs than those included at an embryonic stage in the bud can be elongated: these supplementary, non-preformed elements are referred to as **neo-formed organs** or the neo-formation process.

This terminology was introduced by Hallé and al. in 1978, but first referred to by Critchfield, in 1960, defining early leaves and late leaves, for pre-formed leaves and neo-formed leaves, respectively.



Pre-formed and neo-formed shoots (Photo and drawings D. Barthélémy and Y. Caraglio, CIRAD)
Top, right: pre-formed, pre-formed and neo-formed, neo-formed leaves and their elongated shoots.
Left: pre-formed and neo-formed shoot portions on a young tree, showing different characteristics on the pre-formed shoot portion.
Bottom, right: Close up of a Field Elm pre-formed shoot.

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Critchfield W.B. 1960. Leaf dimorphism in Populus trichocarpa. American Journal of Botany, 47, pp. 699-711.

Branching patterns

Branching patterns are defined from several properties:
- the way branching appears in positions along the bearing axis
- the way branching appears over time (immediate or delayed)
- and, for rhythmic growth, the way it is distributed in growth units.

Continuous, diffuse, rhythmic branching

The branching pattern takes into account the topological distribution of sibling axes on a parent axis.
Depending on whether all the axillary meristems of a stem develop into lateral axes, or whether lateral axes are grouped as distinct tiers with an obvious regular alternation of a succession of unbranched and branched nodes on the parent stem, branching is respectively referred to as **continuous** or **rhythmic**.

In some cases, neither all nodes of a parent axis are associated with a lateral axis, nor is there any obvious regular distribution of branches in tiers, and the branching pattern is then called **diffuse**.
In this case, axis development is only possible through branching in the axil of existing leaves.

Branching patterns (Photos and drawings D. Barthélémy, CIRAD)
Left: Continuous branching (Mitragyna inermis)
Centre: Diffuse branching (Simmondsia chinensis)
Right: Rhythmic branching (Cecropia obtusa)

Branching delays.

The branching event occurrence date is important to consider in the establishment of the ramification structure.

Immediate and delayed branching

Morphological traits help in understanding whether the branching process was immediate or delayed in time.

Immediate branching
In the case of immediate branching, called **sylleptic**, the new branched shoot shows a long first internode, i.e. a long **hypopodium**.
The first leaves of the branched shoot also show a similar type and size, then the next leaves, or the bearer leaves.
Lastly, the diameter of the new shoot is often similar to the bared one.

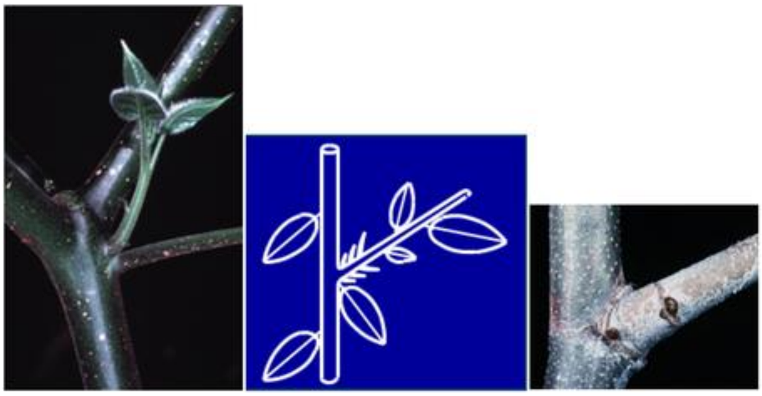
Immediate (or sylleptic) branches result from the development of a newly initiated lateral axis without the apical meristem of that axis having had an intervening rest period.

Immediate branching (Photos and drawing D. Barthélémy, CIRAD)
Left: Persea americana, right: Acacia dealbata
Both first leaves and internodes of the branched shoot are similar to the other ones, and the first internode is long

Delayed branching

In the case of a **delayed branching**, also called **proleptic**, the new branched shoot usually shows successive short internodes at its base.
The first leaves of the branched shoot are also reduced when compared to the following leaves, or the bearer leaves.
On the shorter internodes, spines or **cataphylls** may be found instead of reduced leaves.
And the diameter of the new shoot is usually smaller compared to the bared one.

Proleptic or delayed branches are the result of the discontinuous development of a new lateral axis, with its apical meristem having experienced an intervening period of rest.



Delayed branching (Photos and drawing D. Barthélémy, CIRAD)
On the new shoot, the first internodes are short and bear reduced leaves
Left: On the newly elongated shoot, the diameter is significantly reduced when compared to the bearer (Cyphomandra hartwegii)
Right: Scars on this past branch show a short hypopodium (Platanus sp)

Note
It may be difficult to define the branching occurrence mode on old past branches.
The observer may come up against the disappearance of morphological marks due to organ pruning and secondary growth.
In such cases, similar younger branching patterns should be considered; and if none are available, destructive wood transverse section analysis may help to retrieve information.

Branching position

In rhythmic growth, the distribution shape of the branching process within the growth units is a characteristic feature.

Acrotony or basitony are frequently considered as two fundamental phenomena underlying, respectively, the *arborescent* or *bushy* growth habit (Troll, 1937; Rauh, 1939; Champagnat, 1947; Barnola and Crabbe, 1991).
Nevertheless these authors refer mainly to the acrotonic branching of growth units or annual shoots in the arborescent case, whereas they consider the proximal branching at the base of the whole individual when considering bushy plants.

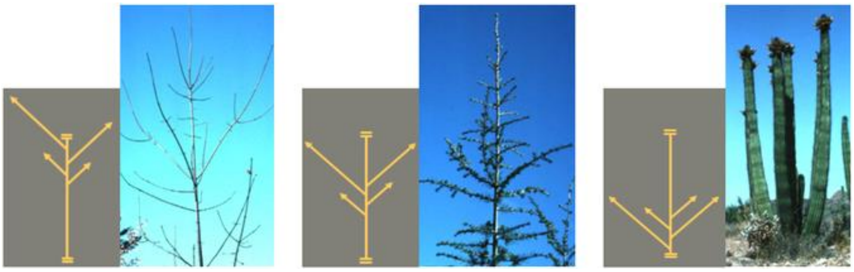
In architectural botany, acrotony and basitony terms are used at the growth unit or annual shoot levels.
The branching patterns within those growth units may be different on various axis orders, within the same species. It is however understood that, along a stem, a similar branching pattern appears in consecutive growth units.

More precisely:

Acrotony is the prevalent development of lateral axes in the upper (distal) part of the parent growth unit or annual shoot.

Mesotony is the term used to name privileged development of ramifications from the median part of a growth unit or annual shoot.

Basitony is the privileged development of lateral axes in the lower (proximal) part of the parent growth unit or annual shoot.



Branching position (Photos and drawings D. Barthélémy, CIRAD)
Left: Acrotony (Fraxinus excelsior)
Middle: Mesotony (Cedrus atlantica)
Right: Basitony (Stenocereus thurberi)

Note:
Acrotony, mesotony, and basitony can be seen as various states of a single branching gradient within the shoot.
They can be symbolized by a simple geometrical drawing:
∇ for acrotony, ◊ for mesotony, and Δ for basitony.

Privileged branching arrangements

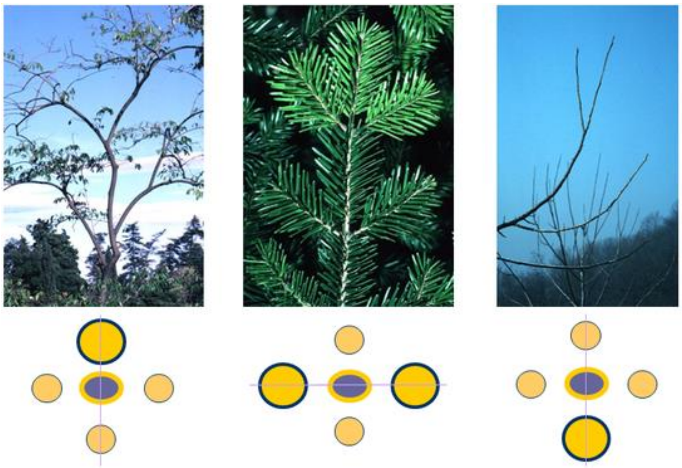
The botanist Troll introduced in 1937 three modalities to describe the privileged arrangement of lateral axes.

They refer to the parent axis position, considering a cross-section close to the ramification.

Epitony stands for privileged arrangements of lateral axes on the upper position of the parent axis. This is a common case on many fruit trees.

Amphitony stands for the privileged development of ramifications in the nearly horizontal.

Hypotony stands for the privileged development of lateral axes in the curvature zone of the parent axis.



Privileged branching arrangements (Photos and drawings D. Barthélémy, CIRAD)
The lower diagrams illustrate the branch arrangements around the parent axis (in grey). Privileged axes are circled in black.
Left: Epitony (Diospyros lotus)
Middle: Amphitony (Abies alba)
Right: Hypotony (Juglans nigra)

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Axis orientation and phyllotaxis

Growth direction

On most plants and more evidently in trees, two major types of axes may be distinguished according to their vertical or horizontal growth direction.

Orthotropy refers to axes whose general orientation 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.

Plagiotropic axes have a general horizontal to slanted orientation and a bilateral symmetry owing to leaves and branches being generally arranged in one plane.

Some stems can be orthotropic then plagiotropic, or vice versa; they are called **mixed axes**.

Lastly, some stems have no particular orientation and are called **ageotropic**.

Growth orientation (Photos D. Barthélémy)
Left: Orthotropic stem (Cecropia sciadophylla)
Right: Plagiotropic branches (Xylopia nitida)

In the aboveground vegetative part of most woody plants, orthotropy is generally associated with plant skeleton construction and the colonization or exploration of the vertical space, whereas plagiotropy is generally more concerned with exploration and exploitation of the horizontal space and reproductive functions (photosynthesis, flowering).

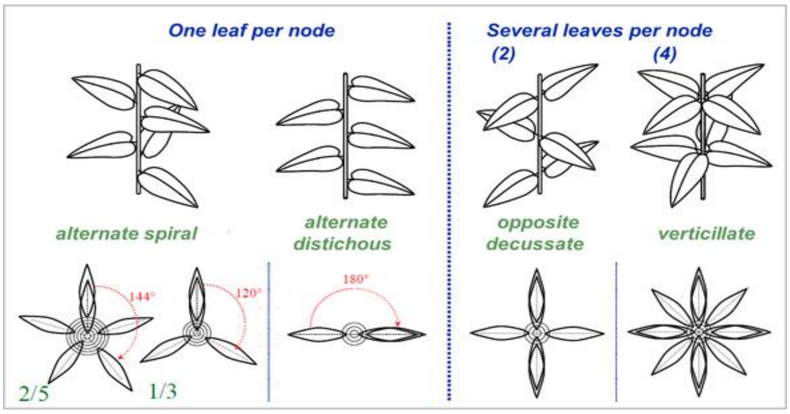
These terms can also be used to describe root axes.

Phyllotaxis

Phyllotaxis represents the leaf arrangement along an axis.

The main common arrangements are the **alternate spiral for an orthotropic axis**, and **alternate distichous** (bilateral symmetry, all leaves lie in the same plane).

The term **verticil** or **whorl** concerns the arrangement when more than one leaf is inserted at the same node.
Opposite decussate defines the specific case of two leaves per node.



Phyllotaxis
Classic phyllotaxis on an orthotropic axis (Drawing P. Heuret, INRA)

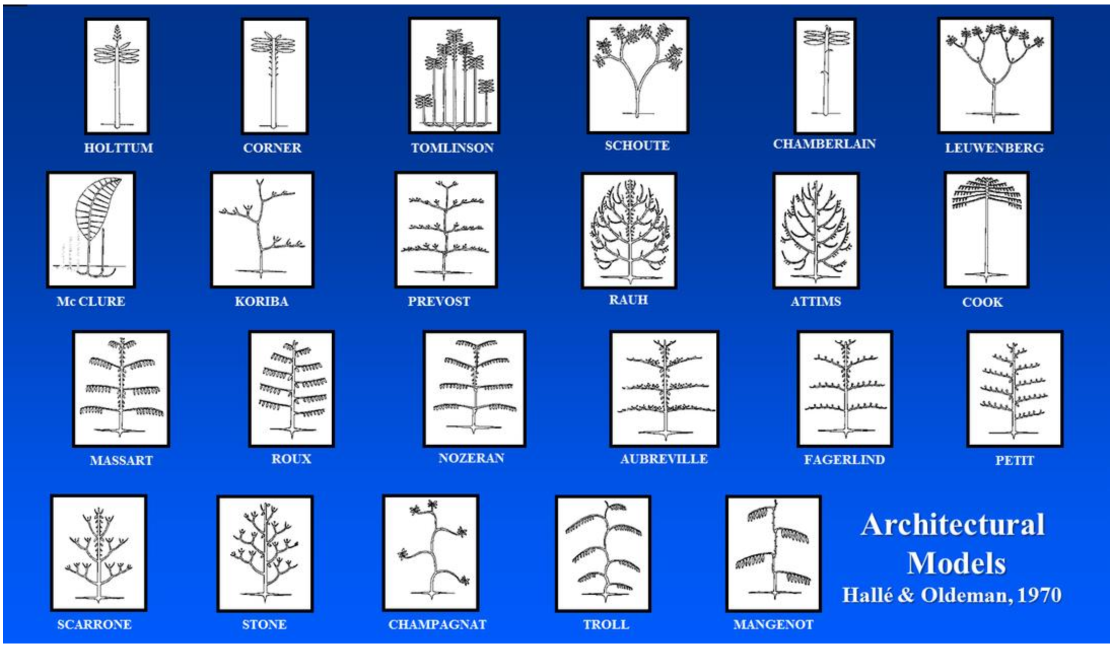
The Architectural Model.

Architectural models

The four major groups of simple morphological features presented until now (i.e. the growth pattern, the branching pattern, the morphological differentiation of axes and the sexuality position) can be combined to describe various growth strategies.

Each **architectural model** is defined by a particular combination of these simple morphological features on the main stem and main branches, 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.

Detailed information on each architectural model can be found in Hallé & Oldeman (1970) or Hallé et al. (1978).

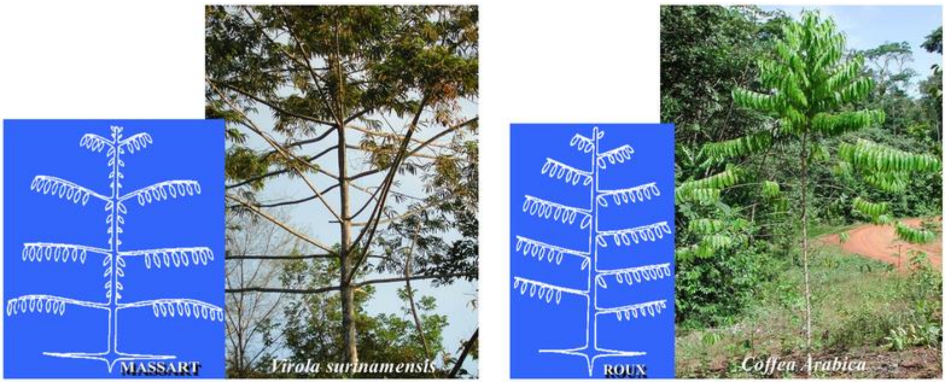


The 23 Architectural Models as defined by Hallé.

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 activity of the endogenous morphogenetic processes of the organism, and corresponds to the fundamental growth programme on which the entire architecture is established.

Architectural model examples

The following figure shows two models differing according to their growth and branching pattern, rhythmic in one case, continuous in the second one. They share mutually an orthotropic trunk and plagiotropic branches. Sexuality positions are also lateral in both cases, growth is thus indeterminate.



Massart and Roux Models (Photos D. Barthélémy)
The Massart Model shows indeterminate rhythmic growth and rhythmic branching
The Roux Model shows indeterminate continuous growth and continuous branching
Both the Massart and Roux models show an orthotropic stem and plagiotropic branches

Bibliography

Hallé, F., Oldemann, R.A.A. 1970. Essai sur l'architecture et la dynamique de croissance des arbres tropicaux. Paris: Masson.

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Architectural Unit

Architectural Unit Section

The typology introduced to characterize shoots led us to introduce the Architectural Model.

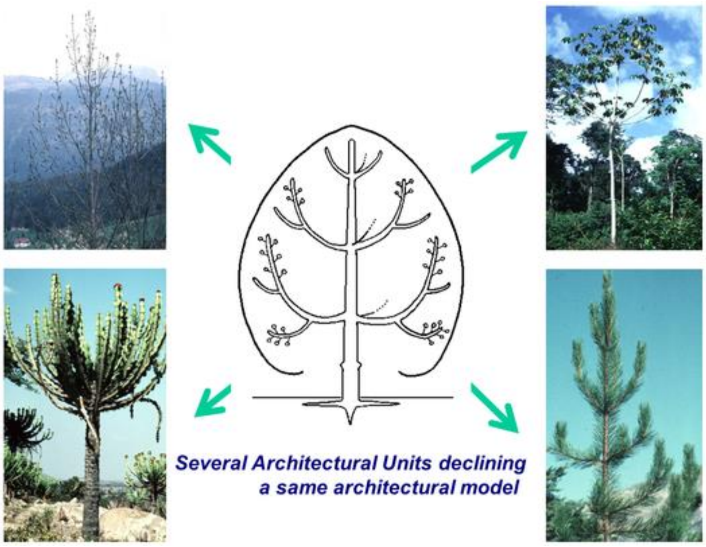
The architectural model defines a structure establishment strategy but is not discriminative in specific species studies. The following section will cover:
Some Architectural Model limitations
Describing a specific species: the architectural unit
Reiterations and the sequence of development
The notion of morphogenetic gradients
The notion of physiological age

At the end of this section, the set of tools detailed so far allows architectural analysis for a wide range of plant species.

The architectural model concept is too large and synthetic to be pragmatically useful in the field to approach species specificity.

Architectural Model limitations

Focusing architectural analyses on particular traits on each type of axis elaborated during plant development usually leads to the stem (trunk) being distinguished from other axes, such that each set of axes exhibits specific features (on young trees).



Expressions of Rauh's model (Drawing and Photos D. Barthélémy, CIRAD)
Top left to right: Fraxinus sp, Cecropia sciadophylla
Bottom left to right: Euphorbia sp, Pinus sp.

Why is the Architectural Model ambiguous?

Architectural Model definition simplifies the axis typology. Considering the 23 models, the underlying combination is quite reduced and can be defined as follows:

Trunk (main stem) growth: rhythmic or continuous, determinate or not
Main stem branching: none, diffuse, continuous or rhythmic
Branch growth: determinate or not, orthotropic or plagiotropic
Flowering position: terminal or lateral

For example, the fine growth patterns in the rhythmic case (polycyclism for instance), as well as the branching pattern distribution (acrotony), or arrangement (epitony), or phyllotaxis are not considered.

Moreover, the sets of branches are considered without distinction. The Architectural Model is thus not exhaustive as regards the various axis categories.

Instantiating the Architecture Model on a given species thus means:
1. Defining the set of morphological patterns for each category of identifiable axes, with the same precision
2. Completing the information by qualitative and quantitative morphological data (number of phytomers per growth unit, phyllotaxis value, etc.)

The Architectural Unit

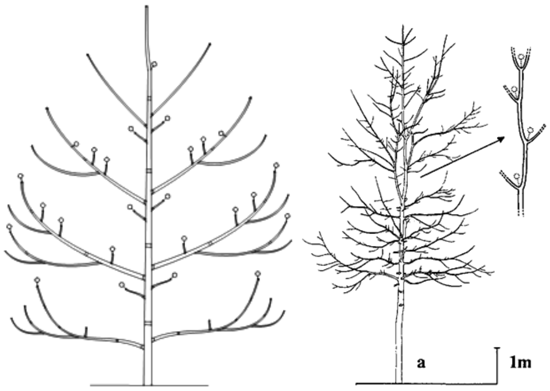
Focusing architectural analyses on particular traits on each type of axis elaborated during plant development usually leads to the stem (trunk) being distinguished from other axes, such that each set of axes exhibits specific features (on young trees).

A schematic representation of the plant body can be made, **a diagrammatic representation**, completed by a table describing all the distinctive traits of the categories identified within the tree architecture.

This set of information (diagram and table) constitutes the **architectural unit** (Edelin, 1977, Barthélémy et al., 1991).

The Architectural Unit can be seen as the detailed, specific expression of its architectural model.
The Architectural Unit of a given species is defined from a set of constitutive axis categories of this species.
The structure and function of each category is characteristic of its rank, and for each species the number of axis categories is finite.
Identification of the architectural unit is achieved by a complete diagnosis of the functional and morphological features of all its axis categories, including the four typological morphological features (growth, ramification, direction, sexuality), but not limited to these.

The **architectural unit** represents the fundamental architectural and functional elementary unit of any given species.



Juglans nigra (Drawings S. Sabatier, CIRAD).
*The = symbol stands for growth unit limits, while the **o** symbol stands for female inflorescence*
Left: Juglans nigra diagrammatic representation of its Architectural Unit.
Right: a young Juglans nigra (drawing).
Top, right: close-up of the tip of the main stem, showing the sympodial growth.

	Axis 1 (trunk)	**Axis 2 (branches)**	**Axis 3 (twigs)**
Growth direction	orthotropic	oblique, nearly orthotropic	no preferential direction
Phyllotaxis	alternate spiral	alternate spiral	alternate spiral
Branching	rhythmic, acrotonic	rhythmic, hypotonic	rhythmic, amphitonic and epitonic
Growth (rhythmic)	long annual shoots polycyclism	long annual shoots	short annual shoots
Sexuality	terminal for female, lateral for male	terminal for female, lateral for male	terminal for female, lateral for male

Juglans nigra Architectural Unit table composed of three axis categories: trunk, branches and twigs

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Edelin C. 1977. Images de l'architecture des conifères. Thèse de Doctorat (Sciences biologiques option Biologie végétale). Université de Montpellier II, 255 p.

Barthélémy, D., Edelin, C., Hallé, F. 1991. Canopy architecture, in: Raghavendra A.S. (Ed.), Physiology of trees, John Wiley and Sons, Chichester, 1991, pp. 1-20

Reiteration

The **reiteration** process plays a key role in mature tree crown construction.
As first stated by Oldeman, (1974) the reiteration process may involve the expression of the total architectural unit, so called **complete or total reiteration**, or the expression of part of the developmental sequence duplicating only part of the species architectural unit, so called **partial reiteration**.
Moreover, reiterated complexes may originate from dormant meristems. In this case such complexes are called **proleptic or delayed reiterations**.

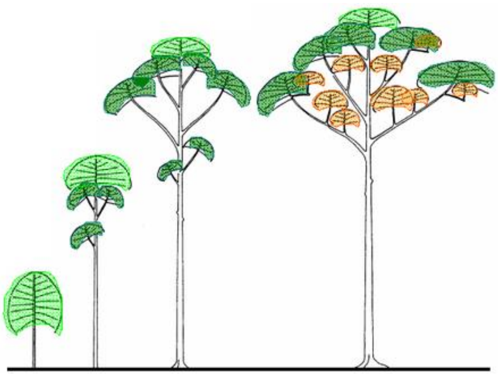
By contrast, reiteration may result from a shift in the functioning of the apical meristem of a growing shoot that will finally produce a low differentiated structure, i.e. a branch apex that after some time of functioning gives rise to a supernumerary trunk.

In this case, the reiteration is described as **sylleptic, or immediate reiteration**.
Either of these delayed or immediate reiterations may be qualified as total or partial.

Reiteration was originally only considered as an opportunistic process, with two main origins.
- **Adaptive reiteration** is a response to an increase in resource levels.
- **Traumatic reiteration** is a response of a plant after it has been damaged and lost a major part of its structure.

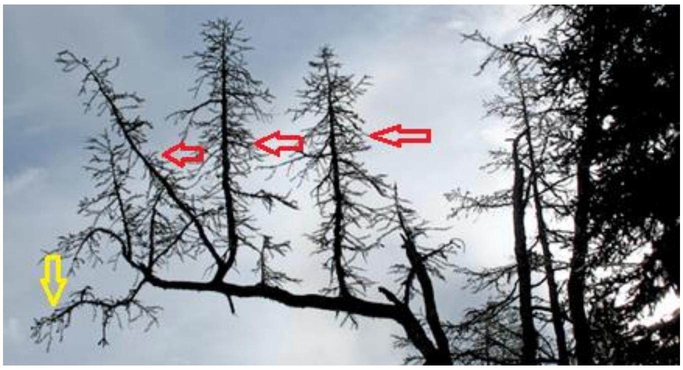
However, it is now demonstrated that, beside these cases of opportunistic reiteration, the same process of repetition may be involved in the inherent growth pattern of a species and occur automatically during plant development after a definite threshold of differentiation.

This latter case is a common feature of tree development and crown construction and is referred to as **automatic or sequential reiteration**. It has also be shown that environmental conditions affect the reiteration process. In many cases, resource pressure limits the process. Immediate reiteration can be considered as a mean allowing trees to optimize space occupancy according to available energy.



Stages of development involving reiteration. The case of Shorea stenoptera (Drawings C. Edelin, CIRAD)
Left. The young tree: the architectural unit.
Middle. Adult trees. Two steps of immediate automatic reiteration in crown establishment.
Right. The mature tree. Delayed reiterations appearing at older stages.

Traumatic reiteration is a delayed process, since it arises from dormant meristems awakened after the traumatism. It can also be total or partial.



Traumatic reiteration on Alpine Larch. (Photo courtesy M. Kauffman, BACKCOUNTRY PRESS)
Red arrows: Complete traumatic reiterations.
Yellow arrow: Partial traumatic reiteration.

The occurrence of reiterated complexes seems to be a move backwards within the plant's developmental sequence.

For instance, the reiterated complexes resulting from the transformation of a branch, or from the development of a dormant meristem, implies that the plant expresses again the juvenile growth pattern of the organism developed from seed.

This is well illustrated in cases of regeneration in which, when a trunk is cut, sprouts resembling young trunks are formed from the stump, whereas reiterated complexes that develop after a branch has been damaged have an architecture similar to that of that branch.

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Oldeman R.A.A. 1974. L'architecture de la forêt guyanaise. Mémoire no.73. Paris: O.R.S.T.O.M.

Edelin C. 1977. Images de l'architecture des conifères. Thèse de Doctorat (Sciences biologiques option Biologie végétale). Université de Montpellier II, 255 p.

Barthélémy, D., Caraglio, Y. 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny. Annals of Botany, 99 (3) : pp. 375-407 19 (access to paper and pdf)

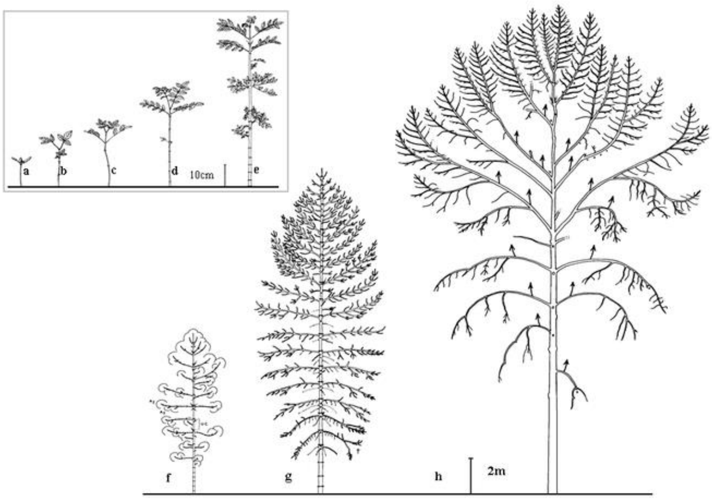
Sequence of development

From germination to death, the development of a plant is like the expression of precise and ordered sequences of morphogenetic events.

The **architectural sequence of development** of the species summarizes the main morphological stages of differentiation of plant ontogeny.

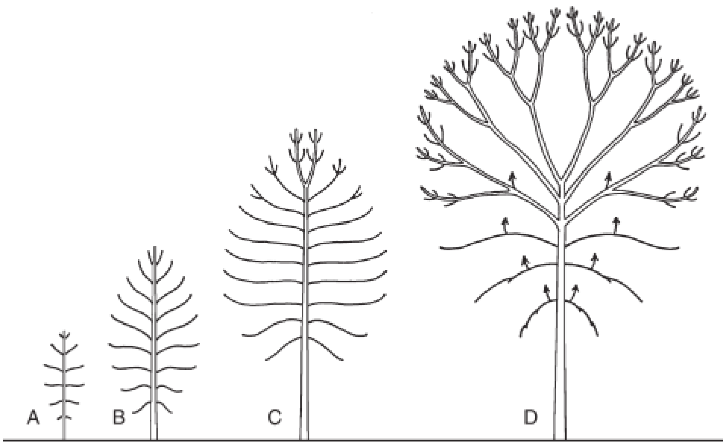
Those stages usually follow this path:
- The young tree expresses its architectural unit
- The adult tree duplicates (reiterates) it at the top of the main stem. This process of reiteration is sequential and gives rise to a more complex crown
- The mature tree has a crown made up of a succession of reiterated complexes
- The senescent tree shows a fragmented crown with dead main branches and delayed reiteration processes

The following example illustrates several main morphological stages.

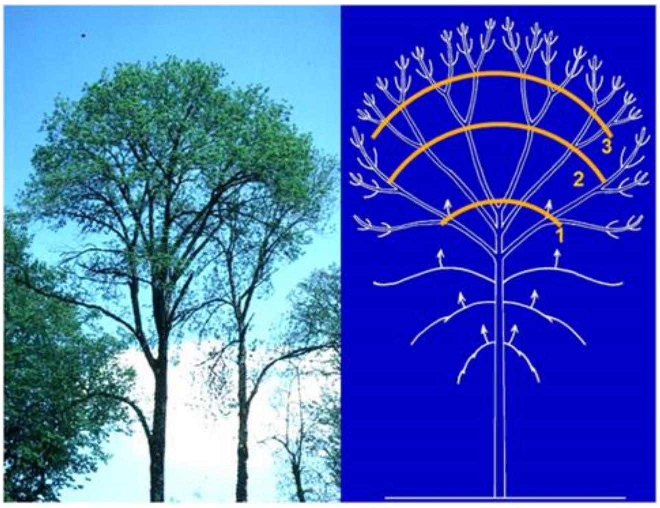


Architectural sequence of development in Fraxinus excelsior: Drawings of some key morphological stages (Drawings D. Barthélémy, CIRAD)
Top Left: The young plant (a, b, c, d, e); from the seedling to the first growth units. Scale: 10 cm.
From the young plant to the mature tree with its reiterations (f,g,h). Scale: 2 m.
Arrows in (h) show delayed reiteration complexes.

The following example shows a classic sequence of development, including automatic reiteration occurrence.



Diagrammatic representation of the architectural sequence of development in Fraxinus excelsior (to compare with the drawing above)
(from Barthélémy et al.,2007); highest category axes are not represented.
The young plant expresses step by step (A and B) its architectural unit (in B)
The plant duplicates the architectural unit automatically during the following stages of development (C and D)
The mature plant builds a complex crown made of a succession of reiterated complexes (D).
At later stages, delayed new reiterated complexes appear (arrows in D).



Succession of reiterated complexes in Fraxinus excelsior (Photo and drawing courtesy D. Barthélémy, CIRAD)

Left: a crown view.

Right: delayed reiterated complexes (arrows) appear in successive waves, gradually colonizing the crown.

Bibliography

Barthélémy, D., Caraglio, Y. 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny. Annals of Botany, 99 (3) : pp. 375-407 19 (access to paper and pdf)

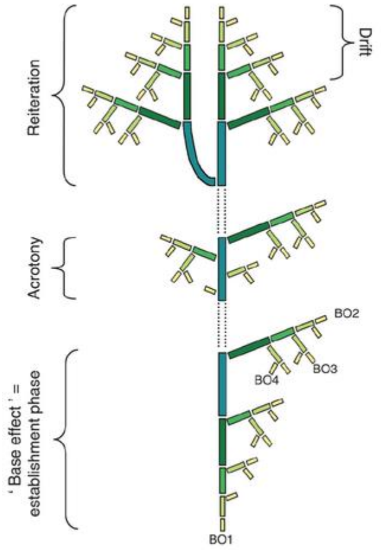
Nicolini, E., Chanson, B., Bonne, F. 2001. Stem growth and epicormic branch formation in understorey beech trees (Fagus sylvatica L.). Annals of Botany, 87 (6) : pp. 737-750 (access to paper and pdf)

Morphogenetic gradients

At whole plant level, the **morphogenetic gradients** notion was defined by (Barthélémy et al.,1997a) in order to take into account the intrinsic organization rules of plant structure and was shown to be a powerful in explaining the observed structure and series of modifications of botanical entities during the ontogeny of any plant species.

These morphogenetic gradients reflect the various processes of differentiation related to morphogenetic repetition phenomena that can be identified in plant construction:
In the **establishment growth phase** of any plant grown from seed, a **base effect** gradient can usually be observed, related to the gradual appearance of more vigorous axes.
Acrotony: within annual shoots and growth units of most rhythmically growing trees, an increasing acropetal gradient of lateral axes vigour can often be observed.
Drift: decreasing vigour can be observed as a general feature linked with axis ageing;
sequential **reiteration** stands for the automatic duplication of the sequence of development and associated gradients of the main axis by another axis.

These gradients can be summarized in the following figure:



Morphogenetic gradients (after Barthélémy et al.,1997a).

Theoretical and diagrammatic representation of the distribution of elementary botanical entities with similar characteristics (i.e. presenting the same physiological properties and represented by the same size and colour rectangle on the diagram) according to some main morphogenetic gradients very commonly observed in seed plants.
For the initial structure and reiterated complexes, four branching orders are illustrated (BO1 to BO4), BO1 representing the main axis;
the base effect is a gradient linked to the establishment growth phase;
acrotony, with an increasing gradient of lateral axis vigour, is common in rhythmically growing trees;
drift is a general feature related to axis ageing;
reiteration, stands for the duplication of the sequence of development.

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Edelin C. 1977. Images de l'architecture des conifères. Thèse de Doctorat (Sciences biologiques option Biologie végétale). Université de Montpellier II, 255 p.

Barthélémy, D., Edelin, C., Hallé, F. 1991. Canopy architecture, in: Raghavendra A.S. (Ed.), Physiology of trees, John Wiley and Sons, Chichester, 1991, pp. 1-20

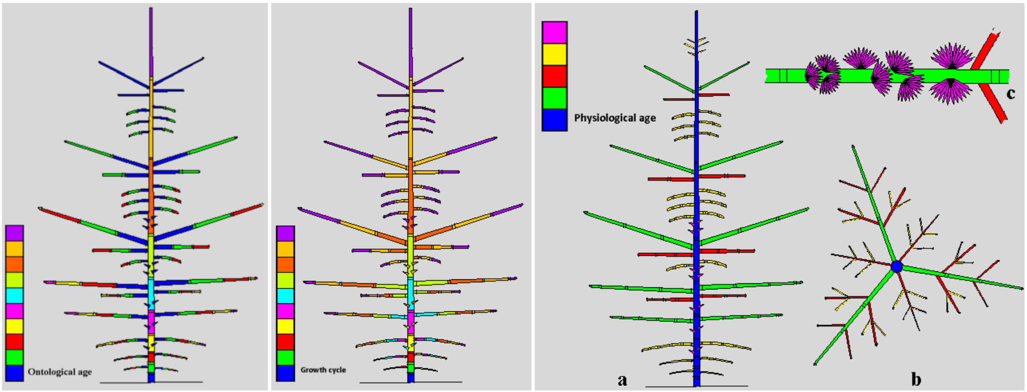
Physiological age

While describing the various elementary botanical entities (phytomer, growth unit, annual shoot) , their differentiations should be examined according to three gradients in time, called chronological, ontogenetic and physiological ages, respectively.

The **chronological age** or calendar age corresponds simply to the period (i.e. year, month, week or day of formation for instance) in which the elementary botanical entity was edified.
The **ontogenetic age** refers to the elapsed time after seed germination (the ontogenetic time unit considered may be a year, a day or a growth cycle according to the specific complexity and growth pattern of the species).
The **physiological age** of a meristem refers to the degree of differentiation of the structures it has produced.

The physiological age may be estimated a posteriori by a non-limitative series of qualitative and quantitative criteria. For example, the short axes of many trees are typical features of *physiologically aged* structures: growth units are short, bear flowers and have a short lifetime. These highly differentiated axes may be considered as *physiologically old* whatever their moment of appearance.
By contrast, main axes consisting of vigorous growth units and/or annual shoots may be considered as *physiologically young* products and generally appear only in the young tree.

On architectural units showing a clear axis typology, the physiological age is set as an index of this typology, starting from 1 to the trunk (if monopodial), up to the brachyblasts, given the highest physiological age.



Age identifications on diagrammatic representations of Cedrus atlantica (Drawings S. Sabatier, CIRAD)
Left: chronological ages, defined from the successive growth sequences.
Middle: ontogenetic ages, defined from the successive growth sequences, relative to the axis appearance date.
Right: physiological ages, defined from the axis typology.
a) tree elevation view, b) view of a tier of branches, c) view of a branch annual shoot bearing a short shoot.

The identification for a botanical entity of these three ages is fundamental for understanding the comprehensive architecture of a plant or even its plasticity, i.e. the effects of the environment on its development and structure.

It permits the precise characterization of all elementary levels of organization within the more integrative individual architecture and allows a precise multi-level description of plant architecture and organization.

Bibliography

Barthélémy, D., Caraglio, Y. 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny. Annals of Botany, 99 (3) : pp. 375-407 19 (access to paper and pdf)

An Example.

Architectural Analysis of the Wild Cherry (*Prunus avium L. Rosaceae*)

Seedling and young stage

Under nursery conditions seedlings present an unbranched stem bearing, above pulpy cotyledons, spiral alternate entire leaves with two stipules at the base of the petiole.
Each year the apical meristem produces an axis portion which, from the base to the top, bears in succession a series of cataphylls, abortive leaves, green leaves with axillary buds and finally some small leaves without visible axillary buds.

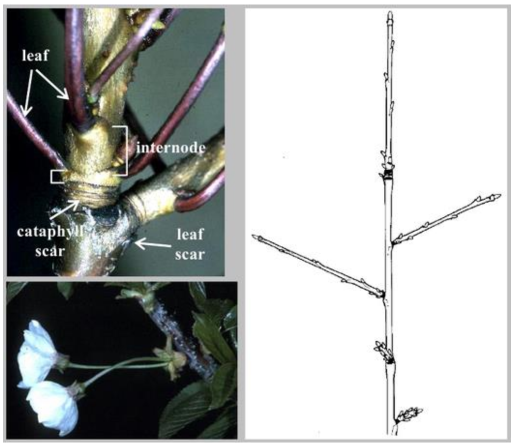
In Wild Cherry, cataphyll scars marking the limit between two successive annual shoots (see fig. 1) may remain visible on the bark of axes for as long as 10 to 20 years.

On a young tree, annual shoots normally appear in one single flush of growth, although under good growth conditions two, or more rarely three, successive flushes of growth (respectively named 'spring shoot', 'shoot of Saint-John' and 'August shoot' according to their time of occurrence) may be observed.
Axillary buds give rise to long shoots in their upper part and to short shoots in their lower part (see fig. 2) the year following the development of an annual shoot.
As for most forest species native to temperate areas, branching is thus delayed by one year (i.e. branching is proleptic).
As the tree grows, the annual shoots of the main stem bear bigger and more ramified branches in a distal position, whereas short lateral axes develop in a proximal position.

Flowering

In the open field, the first flowering occurs on three to four-year-old trees.
Inflorescences are borne on short shoots and the most proximal part of long one-year-old shoots (fig. 3).

Each leaf node of a short shoot may bear a lateral inflorescence while only the first leaves of long shoots do so.



Prunus avium young stage and close ups (Y. Caraglio, CIRAD)
Top Left: Figure 1. Morphological markers resulting from tree growth.
Scars of cataphylls associated with short internodes indicate the winter halt in growth.
Right: Figure 2. Structure of a two-year-old stem portion.
Bottom Left: Figure 3. Lateral inflorescence.

Wild Cherry Tree (adult)

Adult tree

In all mature wild cherry trees four different categories of axes may be recognised.
The main stem is an orthotropic monopodial axis with indefinite and rhythmic growth; its branching pattern is rhythmic.
Branches are horizontal or slanted with long-term definite and rhythmic growth and monopodial and rhythmic branching.
Branchlets present a horizontal growth direction, have medium-term definite and rhythmic growth and bear only brachyblasts.
Brachyblasts are very short axes producing a single cluster of leaves each year; they do not have a precise growth direction, they experience short-term determinate growth (5 to 7 years) and remain unbranched.

Wild Cherry Tree Architectural Unit

This precise organisation concerning the kind and relative position of morphologically discernible categories of axes corresponds to the expression of the specific functional elementary architecture, the architectural unit (table 1 and fig. 4).

	Main stem	Branches	Branchlets	Brachyblasts
Growth	Indeterminate	Long term determinate	Medium term determinate	Short term determinate
Growth direction	Vertical	Horizontal to slanted	Horizontal growth direction	No precise growth direction
Flowering	First leaves of GU bear inflorescence	First leaves of GU bear inflorescence	First leaves of GU bear inflorescence	All leaves of GU bear inflorescence
GU size	8 to 50 leaves	8 to 30 leaves	10 leaves	3 to 7 leaves
Branching	Bears 4 to 6 long shoots	Bear 2 to 4 long shoots	no	no

Table 1. The Architecture Unit table of Prunus avium. GU stands for Growth Unit
The table summarises the morphological traits of all axis categories.

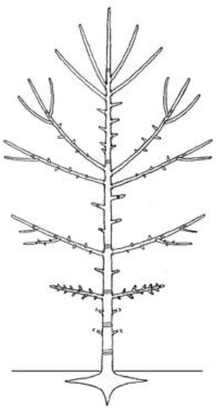


Figure 4. The Architecture Unit diagram of Prunus avium. (Y. Caraglio, CIRAD)

Mature Tree

The tree continues its development according to this pattern for numerous years and may reach a height of 20 to 25 metres under forest conditions, with a small crown similar to that of a young tree, and still conforms to its architectural unit (fig. 5b).

As the tree becomes older, some branches located in the upper part of the tree become larger and similar in structure to the main stem (fig. 5c and fig. 6b).

This morphological transformation results from a duplication of the initial architectural unit and corresponds to a reiteration process that is involved in the mature tree crown construction.

At this stage, the tree reaches its maximal height (fig. 5d).
The process of duplication continues and the crown of an old tree is built up by numerous forks consisting of ultimate axes made of short shoots (fig. 6c).

At this time the sagging of limbs of the crown results in the formation of the tabular-shape crown. After 18 to 20 years these axes die.

New structures then take place from latent buds located on the well-developed branches and appear progressively closer to the point of branch insertion as the tree ages.

Floriferous structures may derive from buds associated to those scars which are limiting the shoots. This ultimate process determines the senescent phase of the tree.

The Wild Cherry Tree sequence of development

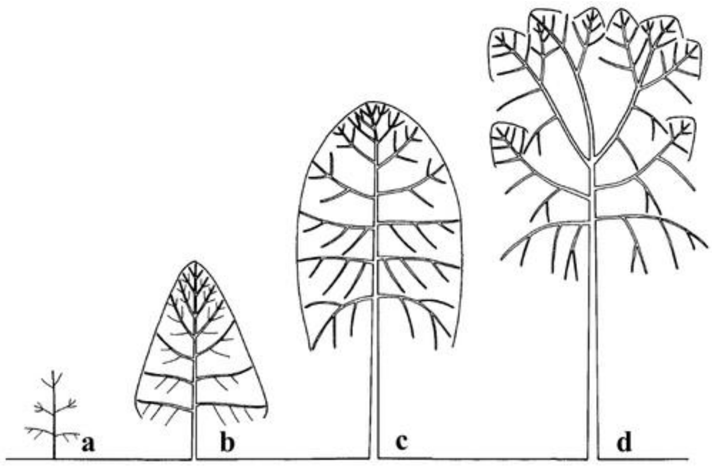


Figure 5. Diagram of the Wild Cherry sequence of development in a forest environment. (Ultimate axes are not drawn)
a : young vegetative tree
b : young tree conforms to its elementary architecture
c: construction of the mature crown which becomes rounder
d : adult tree exhibiting a tabular-shape crown.
(Y. Caraglio, CIRAD)

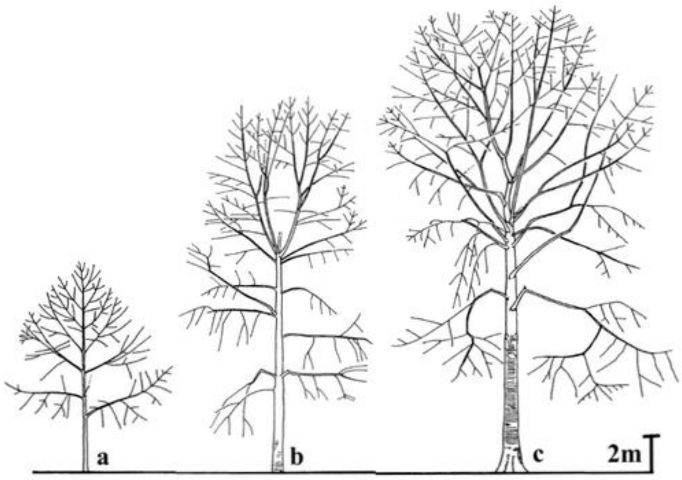


Figure 6. Young (a), adult (b) and old Wild Cherry trees (c) in a forest environment. (Drawings Y. Caraglio, CIRAD)

Architectural Study Case

Morphology and architecture of Cedrus atlantica Manetti

Growth in Cedar is rhythmic and all axes are built up by a succession of annual shoots. The shoot growth rate decreases progressively from the main stem, which grows in a vertical direction, to the branches and the branchlets, which grow in a horizontal direction.

Young tree and architectural unit

At the young development stage, the tree presents a pyramidal form. This architecture shows a very precise organisation as regards the nature and relative position of morphological discernible categories of axes.
In young individuals of *Cedrus atlantica*, five different categories of axes may be identifiable.

- The main stem is a vertical monopodial axis with indefinite and rhythmic growth. Its branching pattern is rhythmic.
- The branches may have differed (proleptic) or immediate (sylleptic) development according to their position on the annual shoots. The branches are arranged in pseudowhorls. They have a horizontal to slanted direction of growth. Branches have long term definite and rhythmic growth and follow a monopodial and rhythmic branching pattern.
- Branchlets are regularly arranged on branches more or less in a single plane. They have long term determinate growth. Their direction of growth is horizontal. Like branches, the branching pattern of branchlets is differed or immediate development.
- Twigs have rhythmic branching with differed development. Twigs have medium-term determinate growth.
- Brachyblasts have short-term determinate growth, and remain unbranched. They bear terminal male or female cones.

Adult tree

After the expression of its architectural unit, the tree will continue to develop its trunk and to remain regularly branched. The oldest branches increase their volume by a process of partial reiteration of the architectural unit. At the top of the branches, a sub-apical bud of the annual shoot develops into a vigorous shoot.
This phenomenon gives rise to a fork formation. Thus, the repeating of this process leads to the development of branches. In subsequent years, this phenomenon of fork formation gradually invades the branches.

Sexuality appears at this development stage of the tree.
The female or male flowers are terminal on brachyblasts, which are formed by 3 or 4 vegetative short shoots.
Female flowering affects brachyblasts borne by the most vigorous axes: the main stem, the branches and reiterated branchlets.
Male flowering is located on brachyblasts corresponding to the highest orders of branching.

Cedrus atlantica. (Photos S. Sabatier, CIRAD)
Top left to right, and bottom: From young tree to mature tree
Bottom right female (top) and male cones (bottom)

As the tree continues its development, new branches located in the upper part of trees develop in accordance with the architectural unit of these species. In the lower part of trees, the branches form more and more shorter annual shoots and finally die.

The architecture of the old tree tends to bend and only some branched systems still grow upwards.

Old tree

As the tree becomes older, the growth of the main stem gradually decreases. The direction of growth becomes oblique to horizontal. The main stem gradually follows the development pattern of a branch. This phenomenon involves the edification of a "tabular form" of crown.

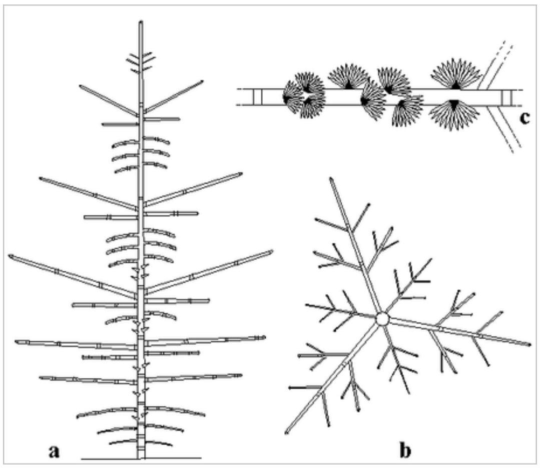


Diagram of a Cedrus atlantica architectural unit (S. Sabatier, CIRAD)
a) tree elevation view
b) view of a tier of branches
c) view of a twig annual shoot bearing several short shoots

Supplementary resources

On-line architecture course (in French and English)
Video courses on Plant Morphology and Plant Architecture.
Url: http://amap.cirad.fr/stic-asia/en/courses.html

Architecture végétale (in French)
Architecture basis, notions, plates and glossary.
Url: http://amap.cirad.fr/architecture/accueil.html

Mediterranean Pines and Cedars. (in English)
A data bank on architecture and morphology.
Url: http://amap.cirad.fr/Pines_cedars/mpc2000.html

Bibliography

Recommended reading:

Barthélémy, D., Caraglio, Y. 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny. Annals of Botany, 99 (3) : pp. 375-407 19 (access to paper and pdf)

Barthélémy, D., Caraglio, Y., Sabatier, S. 2009. Crown architecture of valuable broadleaved species. In Spiecker H.,

Hein S., Makkonen-Spiecker K., Thies M. (Eds). Valuable broadleaved forests in Europe. Leiden: Brill (European Forest Institute Research Reports, vol. 22).

Hallé, F., Oldemann, R.A.A. 1970. Essai sur l'architecture et la dynamique de croissance des arbres tropicaux. Paris: Masson.

Hallé, F., Oldemann, R.A.A., Tomlinson, P.B. 1978. Tropical trees and forests. Berlin: Springer-Verlag.