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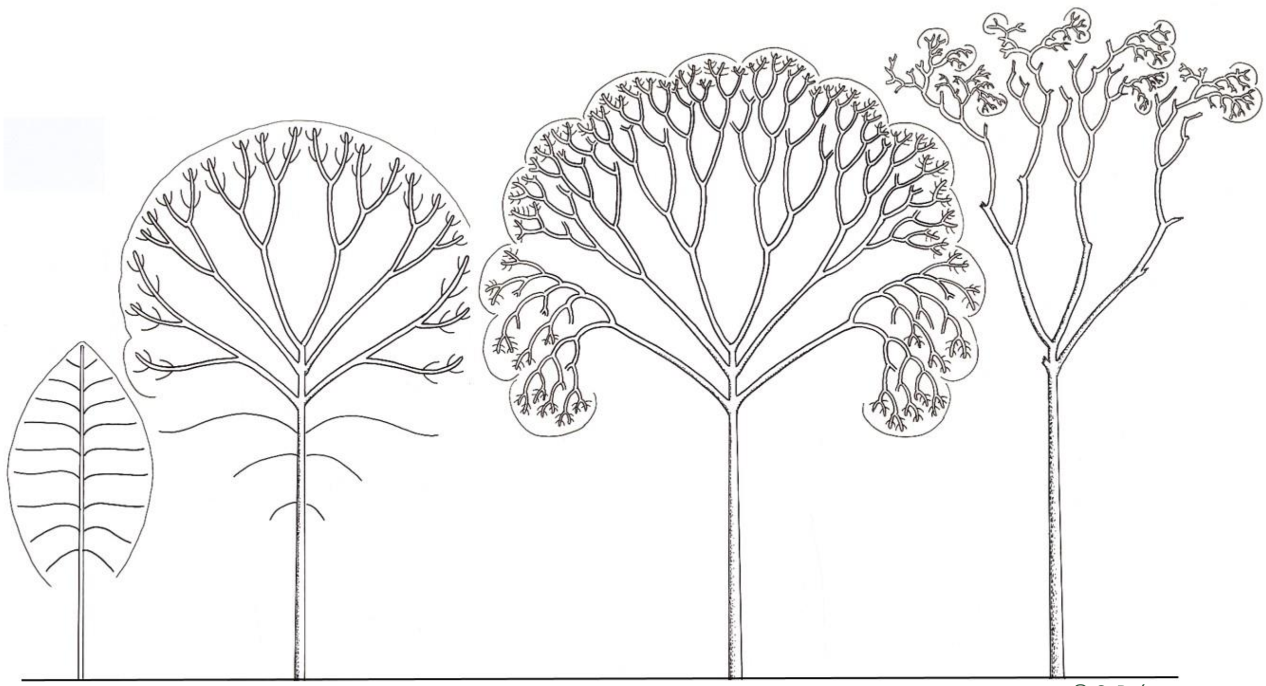
# Introduction to tree architecture





*This fact sheet on tree architecture was developed as a complement to the European Arboricultural Standards. However, it is not part of the European Arboricultural Standards and has not undergone an extensive public consultation process. It is purely informative: an introduction to tree architecture for all interested.*

Co-funded by the Erasmus+ Programme of the European Union

V2 – August 2022

# 1. What is tree architecture?

Tree architecture is a sub-branch of plant architecture: it is the branch of science that explains the dynamics of tree growth and development and tree reaction to the environment, explaining why a tree looks how it looks. In essence it describes the nature and the mutual arrangements of the different parts of the tree. It is important to acknowledge that the architecture of each individual tree, as we see it, is always the expression of an equilibrium between internal growth processes and external environmental factors. We often refer to these external factors to explain tree growth (soil, light, water, wind, etc.), as the main determining factors of tree form. But apart from those external constraints, each tree also holds an internal 'blue print', which is largely species specific, be it with genetic variation between individuals of the same species. This fact sheet focuses on the endogenous growth processes which influence tree development and on the processes steering tree reaction to external factors. It is a brief overview of the advances in contemporary tree architecture research and an introduction to the theme.

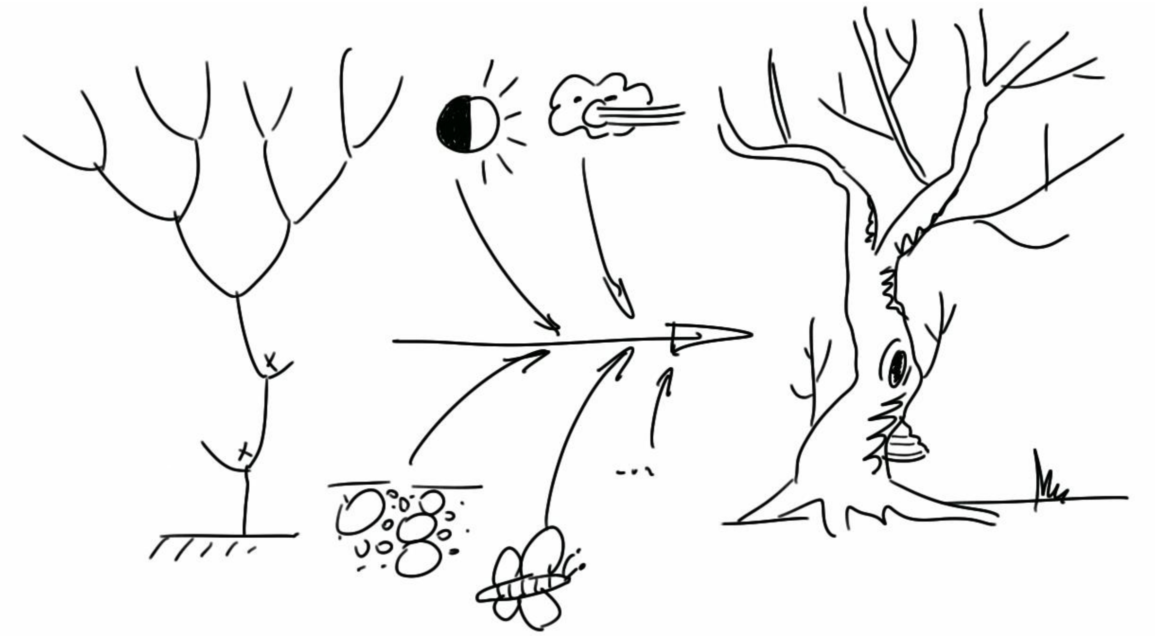


*Figure 1: each individual tree as we see it (right) is the result of a development process, driven by endogenous development processes originating in the tree's genetic blue print (left), but influenced and modelled by environmental factors (middle) and the tree's reaction to them.*

Tree architecture is based on the observation of fixed and repetitive phenomena in plant structures, including the development processes from which they originate. Although tree architecture can be used as a tool to describe the structure of an individual tree and to assess the influencing environmental processes and factors, it must in first instance be regarded as a means to describe and predict the dynamics of tree growth and development in a general way. Thus tree architecture is based on the observation and schematisation of many individuals of the same species, in situ, in different development stages and different environments. It is paramount to base the architectural description of a species on many observations, as the aim is to isolate the endogenous development processes and rule out the variation introduced by genetic variability and environmental factors. The identified architectural characteristics are generally valid for all individuals of the same species or even for multiple species.

# 2. Key concepts

## 2.1 Architectural characteristics

Architectural characteristics are plant traits that distinguish them from other plants, just like other plant characteristics, which are not architectural (e.g. leaf form, flower colour, …). There is a multitude of characteristics to describe the architecture of a plant, but below we will focus on some of the most important ones in order to understand the key concepts of tree architecture.

### 2.1.1 Growth rhythmicity

Growth rhythmicity is a major architectural characteristic: some trees have strong rhythmicity in the functioning of their meristems, while others lack this rhythmicity.

In tree species with strong **rhythmic growth**, the apical meristem switches between an active mode and a latent mode. During the active mode, the meristem develops new tissues. During the latent mode, the meristem is encapsulated in a protective structure: a bud. This can protect the meristem from harsh environmental conditions like frost. Rhythmic growth also induces changes in dimensions of leaves and internodes along the same axis. However, buds are not only formed in winter: some rhythmically growing species also form buds during the growing season, installing a kind of 'resting period' for primary tree growth. The meristem can regain activity later in the growing season and produce another flush of tree growth. This characteristic of having multiple flushes per growth season is called **polycyclism**. The most known example of this is the so called Lammas growth of pedunculate oak (the second flush in late June). Note that pedunculate oak can have more than two such growth flushes. Also other species like Fagus sylvatica and Pinus halapensis can exhibit polycyclism.

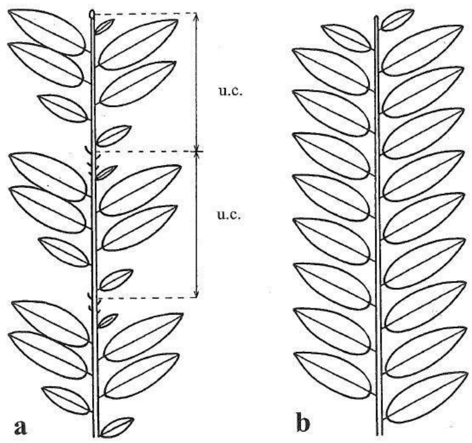



*Fig 2: a: tree species with strong growth rhythmicity and distinct growth units (u.c.); b: tree species lacking growth rhythmicity. © Jeanne Millet*

It must be specified that the meristem is not entirely dormant during the latent mode: within its protective bud, the meristem is actively preforming the next growth unit, completely with all the leaves, internodes, flowers, etc., be it in a miniature state. This can be seen as bud size increases during the dormant period.

In tree species lacking strong growth rhythmicity, the functioning of the apical meristems does not fundamentally change through time, at least in the development of lateral axes. The pace of tissue development by the meristem can increase or decrease (or even halt, although this is disputed), influenced by environmental factors like temperature, but there is no distinct dormant period with bud formation and leaves and internodes are constant in size along the same axis.

Through evolution, the seasons in temperate regions have imposed rhythmic growth on most tree species. The harsh winter season, with low temperatures, is a hard time to keep meristems going. Most tree species have resorted to protect their apical meristems in a winter bud. Note that also many evergreen coniferous species like spruce, fir or pine are rhythmic growers and form buds during winter.

### 2.1.2 Monopodial vs. sympodial growth

**Monopodial growth** refers to the characteristic of continuing growth from the same apical meristem. The main axis generally maintains its dominance, with subordinate lateral axes, which do not challenge the dominance of the main axis.
**Sympodial growth** refers to the characteristic of relaying apical dominance from an axis to one or more lateral axes, originating from subterminal buds. The original axis either changes its growth direction or stops growing, in which case its apical meristem can abort or transform into another type of structure (e.g. flower, tendril, thorn, etc.)
Sympodial growth can lead to a linear sympode, in which the apical dominance is transferred to a single axis, or to a fork, in which the apical dominance is shared between multiple axes.
Note that trees from temperate regions often combine both monopodial and sympodial growth within the same tree as a part of their normal architectural development (e.g. monopodial growth on the main axis, sympodial on the side axes). Environmental factors (e.g. frost damage to terminal buds) can give rise to sympodial tree structures, also in tree species that naturally have a monopodial growth pattern.

*Pictures 1&2: left: monopodial growth of Picea abies; right: predictable spontaneous abortion of the apical meristem of Ailanthus altissima at the end of the growing season. In the next growing season, the extension growth will be realised by an axis growing from one of the meristems in the leaf axils,* leading to sympodial growth.

### 2.1.3 Branching

Branching or ramification refers to the capacity of a plant to form side axes on the main axis. In many cases the side axes are differentiated from the main axis, leading to multiple axis categories.

Some plants (e.g. most palms) only have one apical meristem, which is active throughout their life. They do not form side branches. All trees from temperate regions however, do form side branches, which leads to the installation a large perennial structure of stem(s) and branches.

Side axes (branches) in trees originate from lateral meristems situated in the leaf axils along the main axis. Each leaf axil hosts one or more lateral meristems.
**Continuous branching** refers to the growth pattern in which all lateral meristems produce a side axis which is more or less similar in size.
**Rhythmic branching** refers to the growth pattern in which some lateral meristems produce vigorous side axes, but other lateral meristems are not active or only form small side axes. Depending on the

location of the strongest side axes on the main axis, we distinguish acrotony (strongest side axes situated in the distal part of the growth unit), mesotony (strongest side axes situated in the middle part of the growth unit) or basitony (strongest side axes situated in the basal part of the growth unit. Note that most tree species from temperate regions exhibit a rhythmic branching pattern, in particular acrotony.

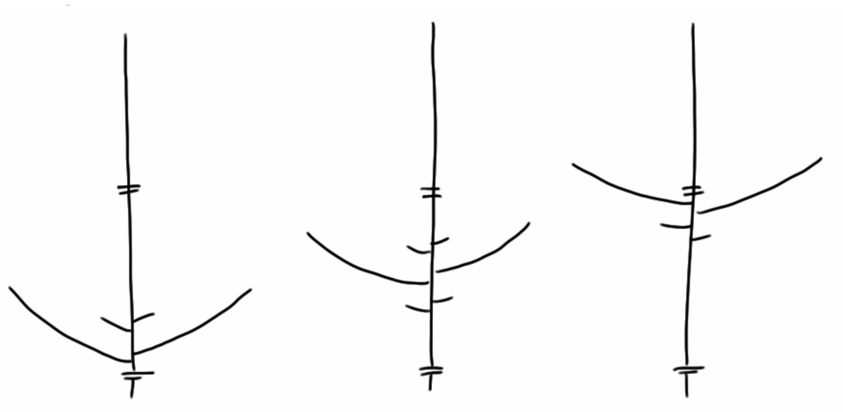


*Figure 3: different forms of rhythmic branching: left basitony, middle mesotony, right acrotony.*

*Picture 3: strong acrotony in Prunus avium*

### 2.1.4 Morphological differentiation between axes

Based on the orientation and the symmetry of an axis, we can distinguish between orthotropic and plagiotropic axes.
**Orthotropic axes** (from the Greek '*orthos*': straight and '*tropos*': direction) grow more or less upright and have a radial symmetry (around the main axis). Their radial symmetry is the result of the radial disposition of the leaves and/or side axes and their similar dimensions in all directions.
**Plagiotropic axes** (from the Greek '*plagios*': oblique and '*tropos*': direction) grow horizontally or oblique and have a bilateral symmetry. Their leaves and/or side axes are arranged in a horizontal plane or their development is favoured on the lateral side of the main axis.
Note that orthotropic and plagiotropic axes can occur together in the structure of an individual tree, with different axis categories having different characteristics. This combination of axis categories gives the tree its typical habit.

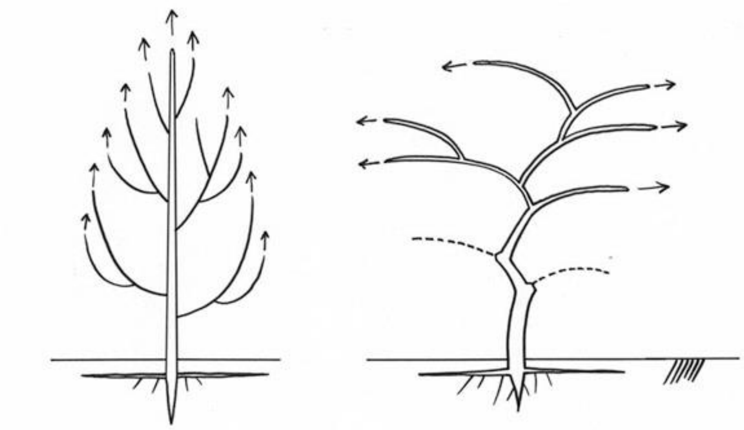


*Figure 4: left: tree with only orthotropic axes; right: tree with only plagiotropic axes © Hallé*

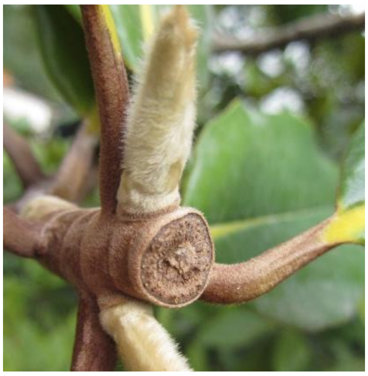
A third category are **ageotropic axes** (from the Greek ‘*a*’: without, ‘*geo*’: earth and ‘*tropos*’, direction), which do not have a preferential orientation or symmetry. These are axes that exhibit the characteristics of senescence: short growth units, stunted growth, lack of branching, etc. These can occur on senescent trees or on declining trees.

Note that the arrangement of leaves (phyllotaxis) has an impact on the arrangement of side axes, as these originate from lateral meristems situated in the leaf axils. For example if leaves are arranged on opposite sides of the axis, this favours a bilateral symmetry. However, side axes can rearrange themselves, so phyllotaxis is not the only determining factor for axis symmetry.

*Picture 4: ageotropic axis of Platanus x hispanica*

#### 2.1.5 Terminal vs. lateral flowering

The last major architectural characteristic we cover is the position and origin of flowering. Trees can either flower terminally (i.e. flowers are formed in a terminal bud) or laterally (i.e. flowers are formed from axillary buds).
Terminal flowering always impact the tree’s architecture, as the prolongation of the flowering axis must be resumed from one or more axillary buds, which leads to sympodial growth.
Lateral flowering does not impact the tree’s architecture: the tree can either grow monopodially or sympodially. But in the latter case, sympodial growth is not imposed by the flowering mode.



*Picture 5: terminal flowering always impacts the tree’s architecture (Magnolia spp.)*

## 2.2 Architectural models

The origin of contemporary tree architecture was the definition of architectural models by Hallé and Oldeman in the 1970’s (Halle & Oldeman, 1970; Hallé et al, 1978). They defined 24 architectural models, including 3 theoretical models, that had not been observed in reality at that time. Each architectural model is defined according to a specific combination of architectural characteristics, which together describe the fundamental dynamics of growth of a particular group of tree species.

Based on the multitude of available architectural characteristics, one would expect a high number of potential combinations and thus architectural models. However, research has shown that only a limited number of combinations of architectural characteristics exist in reality. Since the definition of the original architectural models by Hallé and Oldeman, some revisions have been proposed and recently 2 extra architectural models have been added (Oldeman model and Acosta model) (Hallé & Keller, 2019).

Note that the architectural models as defined by Hallé and Oldeman originally refer to the young tree (older trees of the same species may have differing growth dynamics) and that some tree species exhibit intermediate characteristics between models.

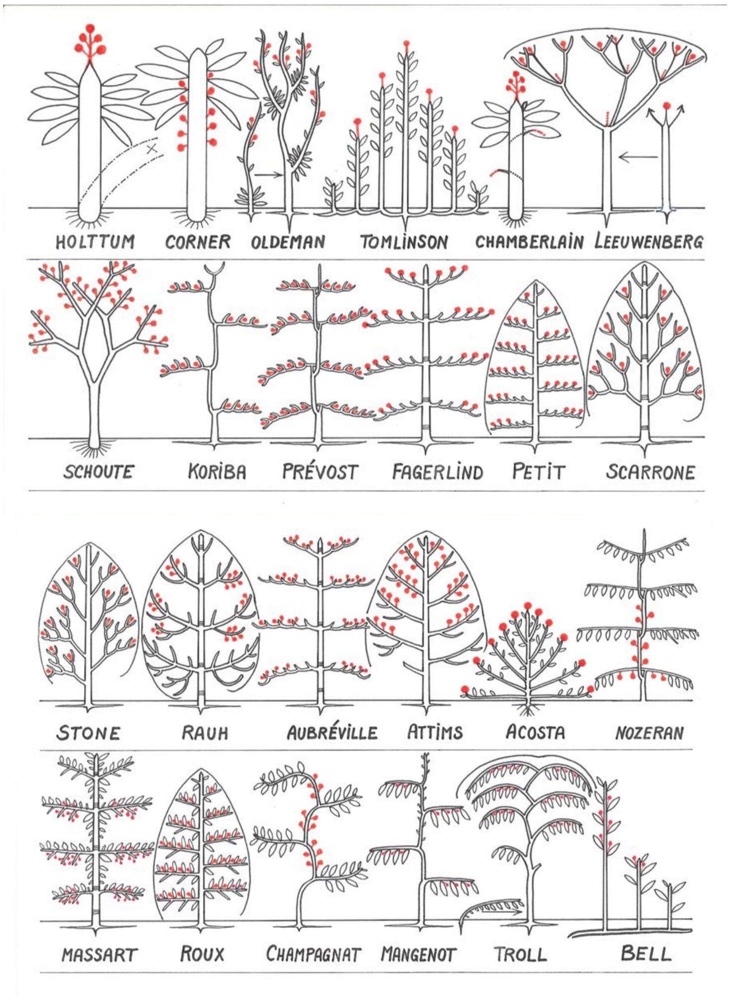



*Figure 5: the 24 architectural models currently used © Hallé, 2017*

The diversity and the complexity of architectural models has changed during tree evolution over hundreds of millions of years. The original simple and highly hierarchic models (e.g. of tree ferns), some of which still exist today, evolved into more complex models, that in some cases have proven to be very successful. Specific combinations of architectural characteristics, different from the ones we know today, were found in fossil plant records (Chomicki et al., 2017). They represent architectural models that currently do not longer exist, probably because they were outcompeted by more successful models during the course of evolution.

## 2.3 Hierarchy vs. polyarchy

Hierarchy refers to a strict organisation and ranking of axes in a tree, generally with 1 main axis. Hierarchy in the (young) tree is what distinguishes trees from shrubs. Polyarchy is the absence of hierarchy, permanently or temporarily, leading to equivalence between axes. Young trees generally exhibit strong hierarchy, but depending on the architectural model of the species, hierarchy can be more or less pronounced.
Tree species with high hierarchy have a rather predictable development, but might be less flexible in responding to environmental factors, e.g. in case of traumatic events impacting on the main axis.
Other tree species (e.g. *Quercus robur*) exhibit a recurrent, but temporary lack of hierarchy, leading to the emergence of recurrent forks, which are resorbed in the hierarchic organisation of the young tree. In these species, dominance can be transferred between axes, which gives a less predictable development, but more flexibility. These tree species can generally restore hierarchy quite well after a traumatic event, as the transfer of dominance between axes is part of their normal development.

*Picture 6: two young Platanus x hispanica trees, the one on the left polyarchic (i.e. installation of the crown), the one on the right hierarchic (i.e.architectural unit).*

*Pictures 7&8: Quercus robur seedling; left picture in May, showing polyarchy after the terminal bud did not sprout; right picture same tree in August of the same year, clearly demonstrating that hierarchy has been restored without any intervention*

The degree of hierarchy in a specific tree is not an appreciation of its intrinsic quality: both trees with hierarchy and polyarchy can be qualitative trees, suitable for planting. However, depending on the tree's location, some degree of hierarchy might be favourable, e.g. during formative pruning of street trees, while a more polyarchic development might be favoured in open grown park trees.

## 2.4 Reiteration and duplication

Reiteration as an architectural concept is the repetition of the basic architectural model (or a part of it) in the structure of a tree, originating from a meristem (instead of a seed). Reiterations can occur in many forms and contexts.

Duplication refers to the formation of a fork in an axis, as part of a tree's predictable development while building its crown. It used to be considered a form of reiteration, still referred to as 'sequential reiteration' in literature. Duplication differs from reiteration in the fact that it is a continuation of the morphogenetic development of the tree, while reiteration is backtracking development: an ontogenetically younger axis develops on an older axis.

Reiteration occurs rather unpredictably, adapting and repairing a tree's structure as a reaction to environmental influences and events (e.g. a traumatic event or physiological stress, or opportunistic). Layering, root suckering, phoenix regeneration, etc. are all forms or reiteration. A *total reiteration* is the repetition of the architectural model of a whole tree (including the stem). A *partial reiteration* is the repetition of the architectural model of part of the tree (e.g. a branch).

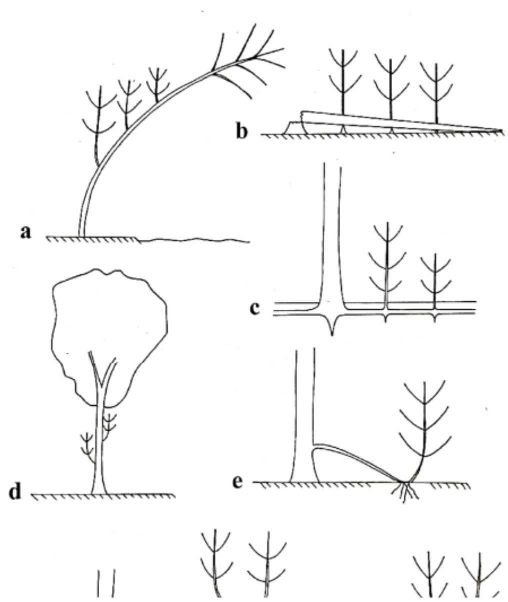



*Figure 6: different types of reiteration; a: epicormic shoots on a leaning tree; b: epicormic shoots on a fallen tree; c:root suckers; d: epicormic shoots on the stem; e: layered branch; f: basal shoots; g: regrowth on a stump; h: regrowth from (root) cutting; i: main fork through duplication © Millet*

*Picture 9: reiteration in Abies spp.*

## 2.5 Tree development strategies

### 2.5.1 Young tree: hierarchy

Most young trees exhibit some form of hierarchy, which allows them to build a dominant stem. Depending on the tree species, this hierarchic period can be long or short, the degree of hierarchy can be strong or moderate, and the growth dynamics by which they establish their trunk can vary. Note that a good physiological health is a precondition for establishment of hierarchy in the young tree. Young trees that are stressed, may lose hierarchy, either temporarily, or permanently. For example a lack of resources (light or others) may force the tree to go into a kind of waiting state, forming 'waiting forks'.

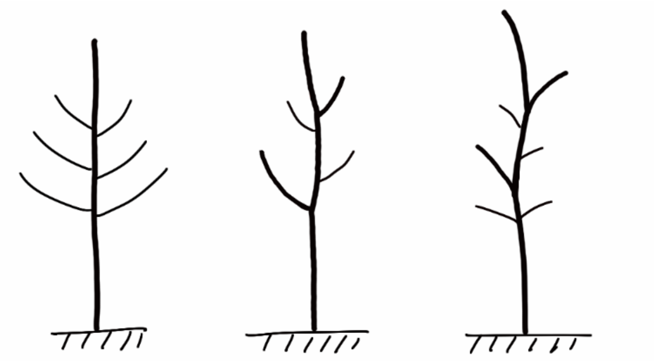


*Figure 7: the growth dynamics vary, but young trees generally exhibit strong hierarchy (not all architectural tree models are represented)*

Plant species that do not have at least a (short) period of strong hierarchy are generally not considered trees, as they lack a dominant stem.

### 2.5.2 Gigantism

There is a group of trees that retain strong hierarchy throughout their lives: they just continue to grow bigger, but stick to the growth dynamics associated to their architectural model, which in this case is generally very hierarchic. The mature tree structure then resembles the young tree structure, only bigger. This strategy, called gigantism, is quite general among conifer species (spruce, fir, Douglas fir, …).

But also tree species exhibiting gigantism as a strategy can reiterate, ending up with a polyarchic structure. The main drivers of this process are catastrophic event (e.g. the top breaking off) and, in their later life stages, hydrological constraints linked to their height.

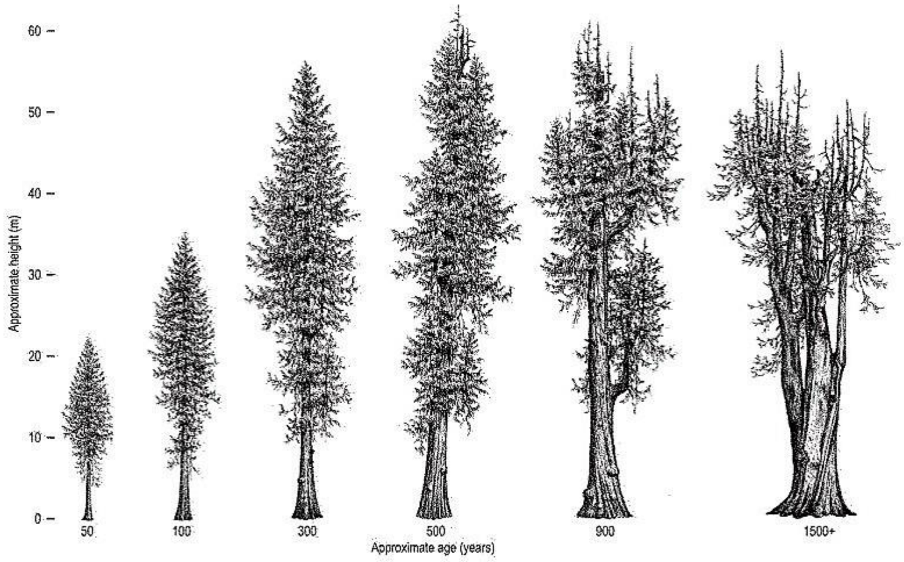



*Figure 8: development of Thuja plicata, exhibiting gigantism for many centuries, but eventually reiterations appear in the ancient tree, as hydrological constraints linked to tree height limit the continuation of gigantism. © Van Pelt*

### 2.5.3 Building a crown by duplication

Other tree species have a different strategy: they first build a stem to rise above their competitors, and then establish a crown. The stem is built by exhibiting strong hierarchy during their young development stage. Later, they switch to an alternation of polyarchic moments and longer hierarchic periods, building a crown by duplication (sequential reiteration). During the polyarchic moments, main forks are installed in the tree crown, sharing dominance. Note that some tree species (e.g. some *Populus* spp.) may install main limbs equivalent to the main axis, while still continuing to extend the main axis, which gives rise to a structure resembling a succession of goose feet rather than a succession of forks.

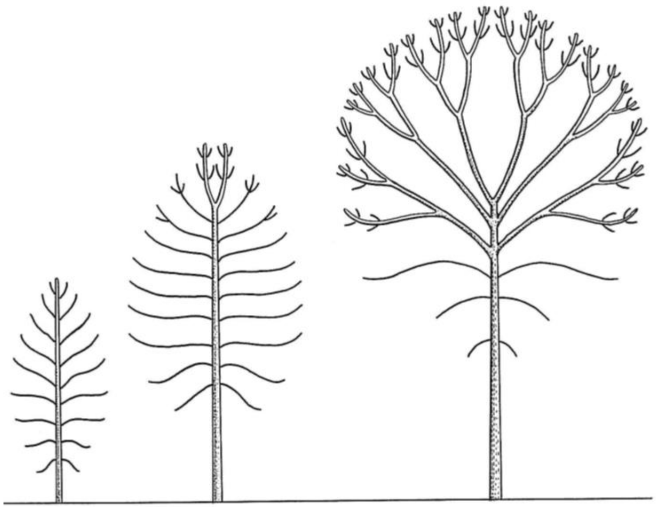


*Figure 9: building a crown through duplication; left: the architectural unit of the young tree, with strong hierarchy; right: a mature tree with a clear distinction between the stem and the crown, consisting of three successive duplications, installing main forks (© Drénou)*

A permanent, main fork in the tree crown is not to be confused with an accidental fork, which is not predisposed in a tree's development, but which is the result of an external trauma. In the case of accidental forks, the fork elements continue their normal development pretty much independent of

each other: they do not share dominance, but compete each other for dominance. (Note however that accidental forks are also reiterations.)
An evaluation of the number of reiteration/duplication waves in the crown of a tree, combined with an analysis of the structure of the terminal architectural units, is generally used to define its development stage.
Throughout its development, the tree exhibits a gradual size reduction and eventually impoverishment of the terminal architectural units. This process culminates in the appearance of the minimal architectural units in senescent trees (see below).

# 3. Development stages

It is important to acknowledge that with trees, unlike with humans, there is no strong relationship between chronological age (i.e. age since germination or planting) and ontogenetic age (i.e. development stage). This means that without actually seeing a tree, it is quite impossible to define its development stage on the basis of its chronological age alone. In fact, ancient trees, with high chronological age, can actually be in a younger development stage than mature trees. It is important to make this distinction because identifying the development stage is more useful to inform management decisions than knowing the chronological age of a tree.
However, 'ancientness' is still a very important concept to acknowledge the value a tree has, both its intrinsic value and its cultural, historical, social, landscape and biodiversity value. Many people unfamiliar with tree architecture struggle to acknowledge that the label 'ancient' (meaning chronologically very old) does not really tell us something about the development stage the tree is in. We have to respect the importance of this 'ancient' label to attribute value to a tree, but what one needs to inform management is an architectural analysis of the development stage the tree is in.

## 3.1 Generic tree development series

We can get a general idea of the development stage of a tree by analysing its main stem and crown structure, combined with an evaluation of the terminal shoots.
As long as the tree consists of a single architectural unit (i.e. no duplications), it is considered a young tree. Of course, the architectural unit looks differently depending on the tree species.

*Picture 10: young Platanus x hispanica, illustrating the architectural unit of the species*

The tree reaches adulthood when the first permanent, main fork is installed in its structure. Note that we are referring here to the main fork that is predisposed in the tree's development, not an accidental fork. Leading up to this moment, the tree will have established its maximal number of axis categories (see below) and side branches will most probably already have started forking.

During the trees adult life, the size and the complexity of the crown increases as periods of hierarchy alternate with moments of polyarchy, installing successive main forks through duplication. Note that during this process, the terminal architectural units (terminal shoots) of the tree decrease in size as their number increases. And as trees mature, they will also lose complexity in their terminal shoots by establishing a decreasing number of axis categories, ending up with the minimal architectural units of a senescent tree.

*Picture 11: terminal shoots of a senescent Acer pseudoplatanus, showing the minimal unit of the species*

As a generic tree development series, valid for many tree species, we could summarise tree development stages as:

- one architectural unit (0 reiterations/main forks): **young tree**; establishing a single trunk;
- 1-4 main forks in the crown: **adult tree**; exploring space, building a crown;
- 5-10 main forks in the crown: **mature tree**; the tree has reached its maximal dimensions;
- > 10 main forks in the crown: **senescent tree**; progressive death of terminal shoots, leading to the natural death of the tree.

Note that one should not solely focus on the number of main forks in the crown, but combine this observation with a thorough evaluation of the architecture of the terminal shoots of the tree. Not only is the above generic tree development series not exact science, environmental factors might influence the establishment of accidental or opportunistic forks, adding 'noise' and complicating the analysis of the crown.

Note that tree species exhibiting the gigantism strategy also go through the development stages defined above. But this process cannot be readily seen in their overall appearance. However, there are changes in terminal shoot structure and orientation and in the position of male and female flowers in the crown during the ageing process.

## 3.2 Tree species specific development series

Through observation and architectural analysis of many individuals of the same tree species, in all development stages, the generic tree development series can be further tailored to suit an specific tree species. The tree species specific development series describes the architectural unit of the young tree, the predisposed development and the associated changes in architecture. This architectural analysis is the subject of the scientific research on tree architecture. One should be careful not to jump to conclusions on the tree species specific architecture based on the observation of a limited number of individuals (let alone based on one tree).

The architectural unit of a tree species is in fact the specific expression of the generic architectural model for a specific tree species. It describes how the general development features that make up the architectural model are 'put to practice' in a specific tree species. It is the internal 'blue print' of the tree species, referred to earlier. The description of the architectural unit of a tree species takes the form of a table describing the maximum number of axis categories and their architectural characteristics. This table is complemented by a description, both in text and in drawings, of the characteristics of the adult, mature and senescent tree.

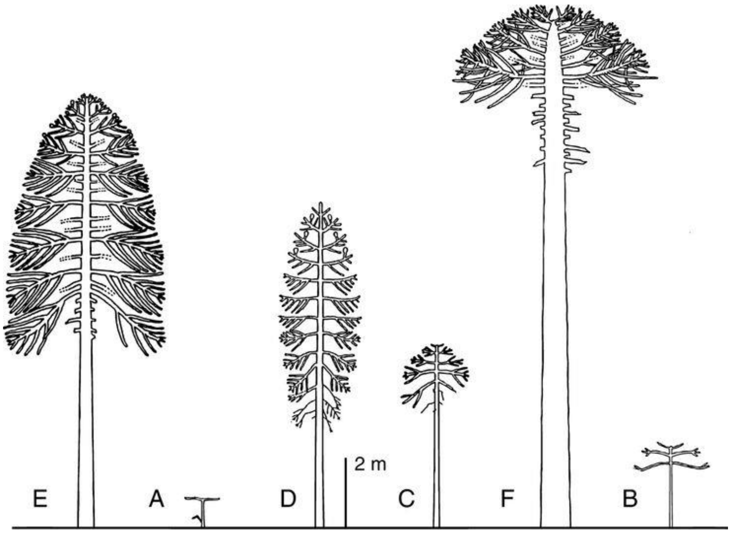



*Figure 10: example of a tree species specific development series (Araucaria araucana, a tree species with 3 axis categories) © Grossfeld*

| A1 | A2 | A3 | A4 | A5 |
|---|---|---|---|---|
| linear sympode | linear sympode | linear sympode | linear sympode | linear sympode |
| rythmic growth | rythmic growth | rythmic growth | rythmic growth | rythmic growth |
| | annual module of +/- 15 nodes | annual module of +/- 10 nodes | annual module of 7 nodes | annual module of 5 nodes |
| Ramification rythmic, delayed, acrotonic | Ramification rythmic, delayed, acrotonic | Ramification rythmic, delayed, acrotonic | Ramification rythmic, delayed, acrotonic | Short shoot, no ramification |
| orthotropic | plagiotropic | plagiotropic | plagiotropic | plagiotropic |
| radial symmetry | bilateral symmetry | bilateral symmetry | bilateral symmetry | bilateral symmetry |
| infinate lifespan | finite lifespan (long term) | finite lifespan (medium term) | dies after 1 – 6 years | dies after 1 – 4 years |
| no flowering | no flowering | no flowering | terminal flowering | terminal flowering |

*Table 1: example of a descriptive table for the architectural unit, the genetic 'blue print' of the species (Platanus x hispanica, a species with 5 axis categories) © Caraglio*

Note that the maximal number of axis categories is species specific and limited: e.g. 3 for *Fraxinus excelsior*, 4 for *Quercus robur*, 5 for *Fagus sylvatica* and *Platanus x hispanica*, 6 for *Thuja plicata*.

## 3.3 Senescence

The last life stage of a tree, senescence, deserves a bit more attention, because it often gets confused with decline, which it is not. They might both be associated to dieback of the terminal shoots, hence the confusion, but the origin of this dieback is different. Senescence is related to ontogenetic age, to development: it is defined as the last phase in an organisms development, before natural death. Decline can be defined as a regression 'somewhere along the way', not linked to a specific development stage and often due to environmental factors like drought, soil degradation, etc.

Decline can be temporary and reversible: if the trigger of the decline disappears, the tree can recover, by either restoring its original crown, developing a secondary crown, falling back on existing branches lower down in the structure or even developing low epicormic shoots, which can gain independence over time.

Senescence is unavoidable: it is the culmination of development, the final stage of a long life as an individual. Once a tree is senescent, there's no way back: the tree has lost the capacity to produce epicormic shoots which would allow it to restructure its crown. Being senescent does not necessarily mean the tree will die any time soon, but any branch that dies or breaks, will not be replaced by epicormic shoots.

However, unlike humans, some trees have the ability to avoid senescence by escaping their individual development and by reinventing themselves as a colony of semi-independent functional units, which can 'regain' youth and start their individual development all over again. Once a tree reaches this 'colony state', it has the potential for eternal life.

See below for more information on the non-linear development of trees and on all the side routes to the 'normal' development of trees described above.

## 3.4 Variability in individual tree architecture

Of course not every individual tree develops along exactly the same pathway, following the above rules. That would mean that every pedunculate oak throughout the world would look exactly the same, if in the same development stage, and would also age exactly in the same way. This is clearly not the case, there is a large degree of variability in tree form and development, even within the same tree species. Two of the main drivers behind that variability in individual tree architecture are genetic variability and environmental factors (e.g. soil, climate, …)

### 3.4.1 Genetic variability

Although all trees of the same species largely share the same genetic code, there is a certain degree of variability impacting on their growth: some trees grow faster, others slower, some more hierarchic, some more bushy. This genetic variability might influence the way trees develop and look. Some features described above can be seen more readily in one tree than in another, so one could say that certain individual trees are more 'true' to their species' blue print than others.

Also, with each cell division, there is a chance of installing a mutation, a 'typo' in the DNA. As all living organisms, trees have developed ways to avoid these mutation and to correct them if they occur. But the occurrence of these small mutations is a driver of genetic variability. It must not be seen as something negative, as it leads to genetic diversity and hence resilience in a tree population. Sometimes, we even try to profit of these mutations, by selecting desirable one (e.g. a special leaf form, leaf colour or growth form) and capture them in a cultivar, a 'cultivated variety'.

*Pictures 12 & 13: two Ginkgo biloba trees in the same avenue, illustrating genetic variability within the same species*

### 3.4.2 Variability induced by the environment

Also the environment, e.g. soil, can induce variability in the way trees look. Planting a genetically identical tree on a rich, humid soil and on a poor, dry soil, will result in two completely different trees: trees adapt their growth and development to their environment. Part of this adaptation can even be passed on to future generations.

*Picture 14: old, but small (< 3m height) Quercus robur on a rocky slope*

# 4. Non-linear development of trees

The above descriptions might trick the reader in believing that tree development is a linear process, starting with a young tree and ending with senescence and natural death, the same way as it is with us, humans. But trees have evolved mechanisms allow them to explore side routes and variations to their 'normal' development described above. Their main tool to do so is the development of epicormic shoots, which they use to restore or reorganise their crown or even completely reinvent themselves.

## 4.1 Epicormic shoots

An epicormic shoot (from the Greek 'epi' – upon and 'kormos' – tree, trunk) can be defined as any shoot that does not originate in the predictable development of a tree's structure: it is a shoot that is formed in an unpredictable way, on an unpredictable spot. What is predictable of course depends on the tree species, but for many temperate trees the predictable development is that a shoot arises from a bud (either terminal or axillary) that has gone through one season of winter dormancy. This means a bud is formed at the end of the growing season and it flushes in the next spring.
All shoots arising from buds (or meristems) that have gone through a longer dormancy period (be it 1 year extra or 100 years extra), are considered to be epicormic shoots, in this case originating from 'latent buds'. Epicormic shoots can also be formed directly from the cambium, as and when needed. In this case the epicormic shoot is considered to have originated from an 'adventitious bud' (even though there was no real bud involved in the process). The capacity to produce epicormic shoots differs between tree species and generally decreases with age. Note that epicormic shoots are generally present even in healthy trees. But they are most important to the tree when it is subject to stress

*Picture 15: epicormic shoots on the stem of Quercus robur*

As in branches, also epicormic shoots can differ morphologically, both in growth direction and in symmetry. We can distinguish orthotropic, plagiotropic and ageotropic epicormic shoots. Depending on which type op epicormic is present and/or predominant, one can predict the future tree development to some degree.

## 4.2 Stress

Any type of stress leading to a decline in physiological functioning can cause a tree to leave its predictable development process. This can be both environmental stress (e.g. drought, soil degradation, …) and so called 'internal' stress (e.g. increased hydrological resistance in its structure). They key message is that stress is the main driver for trees to explore side routes and variations to its 'normal' development, by triggering its epicormic growth to try and overcome it.
Note that some degree of stress is a perfectly normal thing to happen to a tree. We're talking about organisms that can live for centuries or even millennia, so it would be very surprising if not a single form of stress would occur during their lifetime. Depending on tree species, development stage, physiological health and environment, the tree can go into either one of the following processes.

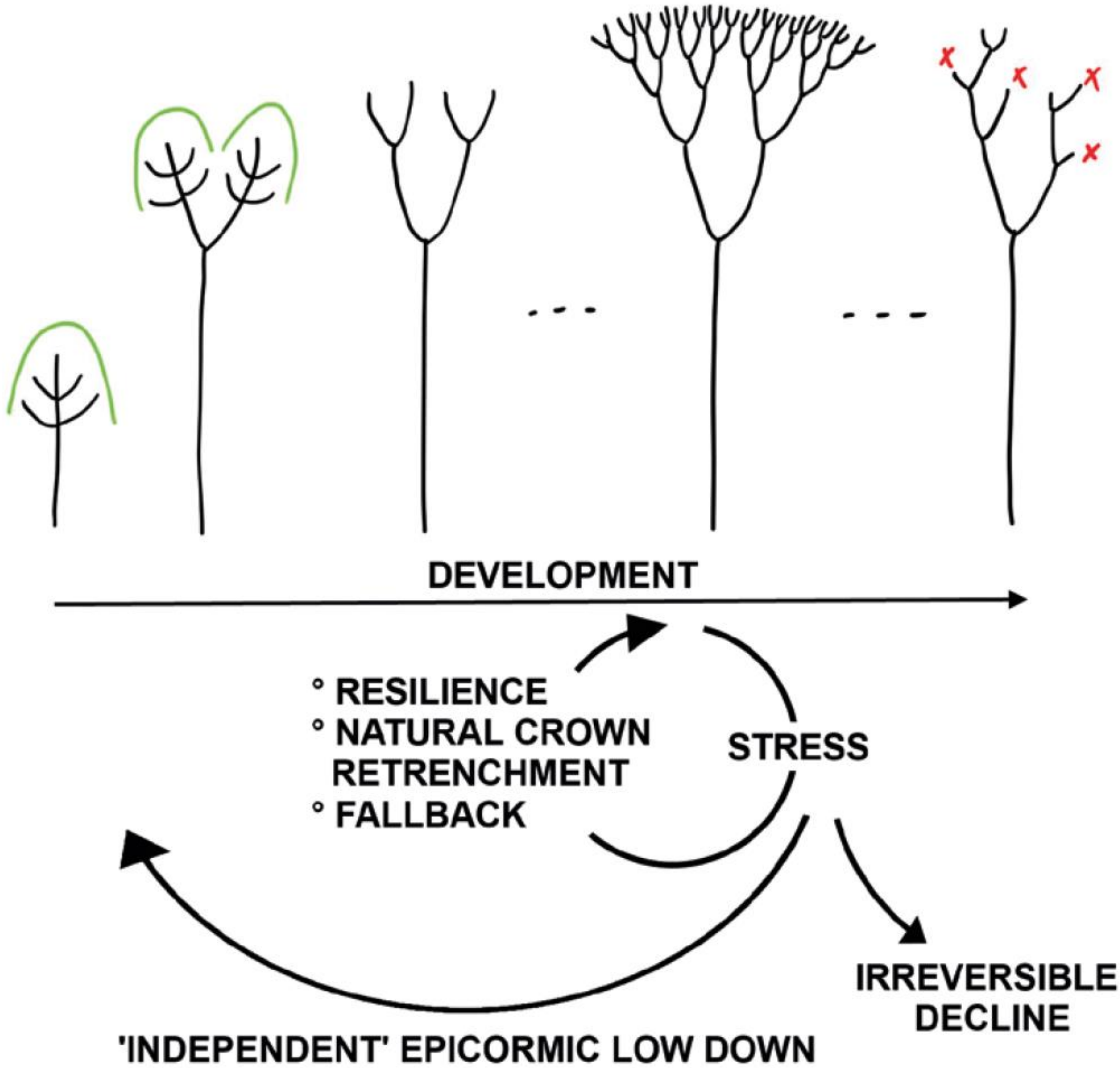



*Figure 11: overview of non-linear pathways of development and reaction of a tree (adapted from Drénou)*

## 4.3 Resilience

Resilience is the process in which a tree restores its primary crown after undergoing physiological stress: the tree goes through a physiological 'dip' and then just resumes its original development and normal architectural dynamics.
In particular orthotropic epicormic shoots in the upper canopy are involved in this process of crown restoration.
Note that the process of restoration of the primary crown can take some time and that even in a resilient tree large parts of the primary crown can be dead or missing.

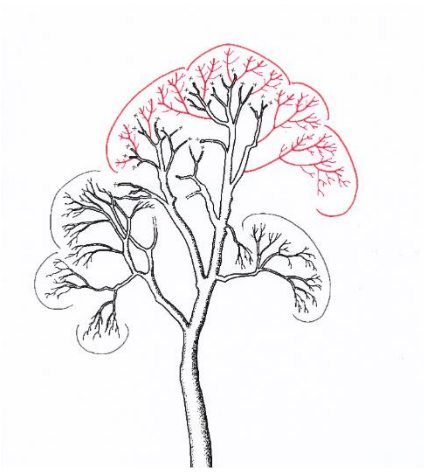


*Figure 12: a resilient tree, forming orthotropic epicormic shoots (in red) to restore the original canopy (in black) © Drénou*

## 4.4 Crown retrenchment

Crown retrenchment is a reorganisation of the tree following stress: the tree does not succeed in restoring its primary crown (and thus being resilient), but it overcomes the physiological stress by developing a secondary crown lower down in its structure. This secondary crown consists mainly of plagiotropic epicormic shoots on the lower limbs and the stem. By developing these more vigorous shoots closer to the root system, the tree is able to overcome physiological stress and continue its development, be it smaller than it was before.

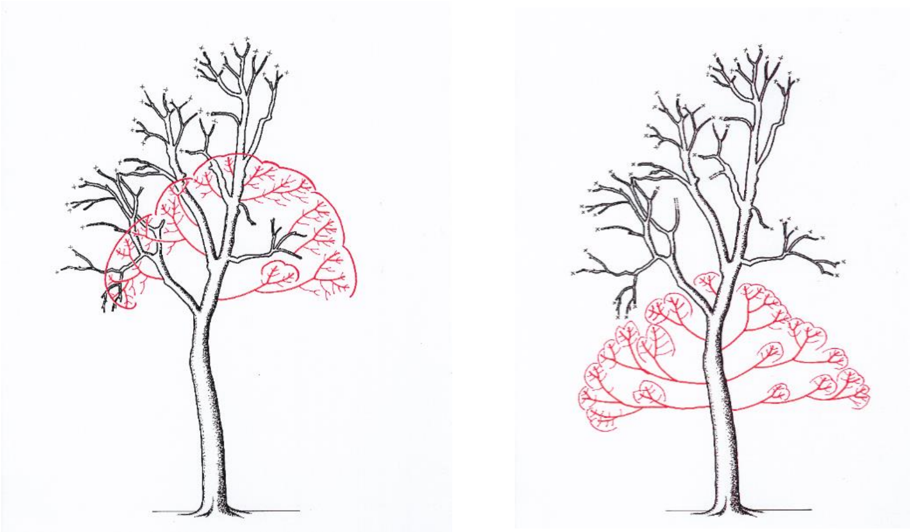


*Figure 13: two examples of crown retrenchment, left the secondary crown is nested in the primary crown, on the lower limbs; right the secondary crown is installed below the primary crown, on the main stem. © Drénou*

Often, crown retrenchment is mistakenly seen as a development stage following the tree's normal development, e.g. in ancient trees. However, crown retrenchment is not a development stage, it is a 'tool' trees have to cope with physiological stress and disorganisation. It can be caused by external stress (e.g. drought) or internal stress (e.g. hydrological constraints in the tree's vascular system). This means that crown retrenchment can occur with trees in any development stage, both young and old trees. The misunderstanding of seeing crown retrenchment as associated with the final life stage of a tree comes from the fact that most ancient tree have gone through the process of natural crown retrenchment, maybe even multiple times. In fact, crown retrenchment is not the final life stage of a tree at all, quite the contrary. Only when a tree is no longer to capable to form epicormic growth and go through the process of crown retrenchment, it really enters its last life stage: senescence.

Note that just the presence of epicormic shoots low down in a tree's structure is not enough to be designated a secondary crown. We can only truly speak of a secondary crown if the epicormic growth is well developed and in some way structured hierarchically. It can take many decades for a tree to develop a secondary crown capable of replacing the original crown.

*Picture 16: well organised secondary crown on Quercus robur © Vikki Bengtsson*

## 4.5 Fallback

Some trees exhibit decline of the primary crown, which ends up in a completely dead upper canopy, but are unable to replacing this by a secondary crown. They don’t have the capacity to form epicormic shoots, so they ‘isolate’ the declining part and continue to function with their unaltered lower branches, originating from their primary structure.
As the tree does not form a secondary crown consisting of epicormic shoots, we cannot designate this a crown retrenchment process.

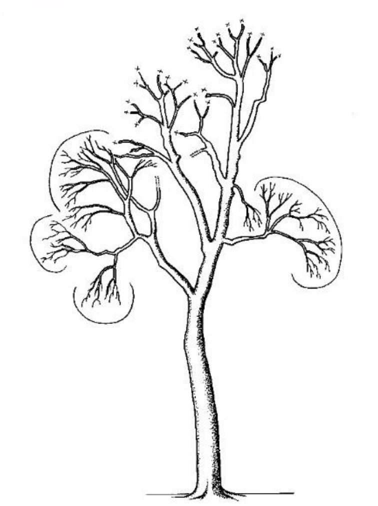


*Figure 14: fallback: no epicormic shoots visible, just upper canopy is dead and the tree continues to function with its lower branches © Drénou*

## 4.6 Irreversible decline

If a tree, following a stress event, does not exhibit any viable restoration process, it is deemed to get caught up in irreversible decline. The tree might exhibit epicormic growth, but this will mainly be of the ageotropic kind: with short growth units, stunted growth, lack of branching, etc. This type of epicormic shoots often does not even succeed in keeping itself alive, let alone restore parts of the crown. Over time, it continues to loose viable parts of the crown, without these being replaced by new ones. Irreversible decline eventually ends up in death, but note that a tree in this process does not necessarily die rapidly, depending on the biotic and abiotic environmental factors.

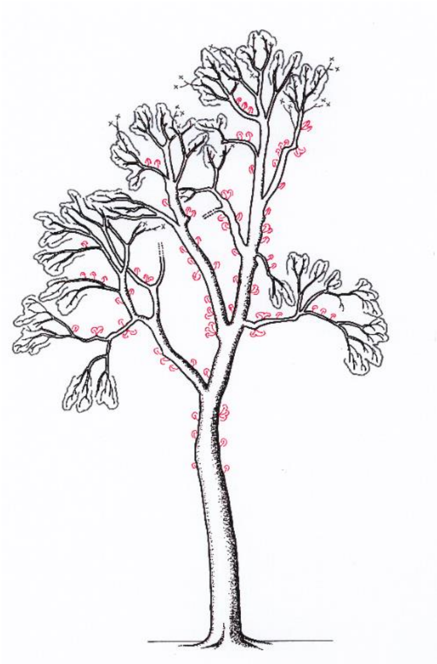


*Figure 15: tree in irreversible decline: impoverished ramification throughout the crown, epicormic shoots (in red) only of the ageotropic © Drénou*

*Picture 17: example of Quercus robur in a state of irreversible decline*

## 4.7 Individual or colony?

When a tree lives for a very long time, interacting with its environment, it can end up in two very distinct pathways: it can either remain an individual or it can become a colony.
Some trees (or tree species) have a tendency to conserve a strong individuality, sticking to their linear development, coping with environmental stresses without being diverted. These trees do not take side routes to normal development, but gradually develop from a young tree into maturity, to end up in senescence. It is important to note that this is a one-way road: there is no way back. As a tree grows older, it gradually loses the capacity to explore the side roads offered by development of epicormic shoots, adventitious roots, suckering, layering, etc. Note that it can take centuries or even millennia for a tree to eventually end up into senescence, but at the end only awaits the natural and unavoidable death of the tree.
In other cases, at some point in their life, trees can develop vigorous epicormic shoots low down in their structure, often connected to adventitious roots in their hollowing stem. Or they develop layered branches, root suckers, etc. All of these structures can regain the characteristics of a young tree and thus kind of reverse back into a younger life stage. They compartmentalise from the rest of the ageing tree and gain (semi-)independence. And that way they start the development process all

over again. At this point, the individual tree has become a colony of (semi-)independent functional units, that each develop at their own pace. This is not a one-off phenomenon, the tree can reinvent itself over and over again and at this point it has reached a state of potential immortality. Note that trees must get into this state of colony before they reach or even approach senescence: as they age, their capacity to react decreases. The triggers that lead to this state-of-colony are generally recurring environmental stresses the tree has to cope with.

*Picture 18: old ash tree has now become a colony © Daggfeldt*

# 5. Tree diagnosis: how to read a tree's architecture

The main challenge at this point is how to include these concepts of tree architecture into our common arboricultural practices. Because tree architecture can be applied in many field of arboriculture: tree pruning, tree surveying, evaluation of physiological health, supporting management decisions and even predicting their chance of success. But one can only really incorporate this by careful and repeated observation, by learning how to look at trees in a different way, preferably under the guidance of someone more experienced in the topic. Often, when someone points out an obvious architectural trait in a tree, one starts to see it everywhere and it becomes almost impossible to 'unsee' it, to the point where one might wonder how on earth it was possible not to notice it. The most important message for people wanting to introduce tree architecture in their arboricultural practice is not to despair. It is normal not to see the forest for the trees when you first start with it. Persistent observation of trees will eventually lead to understanding.

The architecture of many individual tree species has been thoroughly researched by scientist and published in scientific literature (often as part doctorate's theses). Of course, this is the first resource to go to when exploring the architecture of a specific tree. Unfortunately, not much of the scientific literature on the topic is available in English, most of it being published in French and only translated into other Roman languages (Spanish, Italian). On the other hand, not all tree species have even been described architecturally, as this is a lengthy scientific process, based on the observation in the field of many trees of the same species, in differing environmental conditions and of differing development stages. However, from careful observation, a trained eye can rapidly distinguish basic architectural characteristics, even in a single tree, that allow to evaluate its development, reaction and, more importantly, predict its future to some extent.
In a nutshell, an architectural diagnosis of a tree consist of the following steps:

- Assess the original structure of the tree, arising from its development:
    - Identify the development stage the tree is in;
    - Evaluate if the original upper canopy and terminal shoot structure look as can be expected of a tree of that species in that development stage (mortality, ramification, etc.);
- Assess the presence, type and distribution of the epicormic shoots:
    - Where are the epicormic shoots?
    - How do they look?
    - Are they structured in any way?
- Compile the above information in order to identify the physiological state and the development or reaction process the tree is in.

## 5.1 The ARCHI method

There is a standardised methodology to assess a tree's architecture, which is called the 'ARCHI method' and has been developed by Christophe Drénou (CNPF – IDF). This method allows to expand a visual assessment of a tree into a prognosis of its future development.
The methodology distinguishes two superimposed images: the first image allows to understand how the tree develops, the second image how it repairs itself and responds to stress factors.

### 5.1.1 Image n° 1 – original development

The first image consists of the stem, the main branches, the secondary branches and ultimately the terminal shoots, bearing leaves. This image is the result of a genetically programmed development process. When the tree is young, it branches according to very precise rules, which has allowed Hallé and Oldeman to define 24 architectural models. When the tree becomes adult, it can remain true to its initial model (e.g. *Picea* spp., *Sequoia* spp. *Pseudotsuga menziesii*, *Araucaria* spp.) or it can duplicate during its development. This mechanism, automatic and predictable, is the origin of the establishment of main forks. Most broadleaved trees (*Platanus* spp., *Quercus* spp., *Fraxinus* spp., etc.), but also some coniferous trees (*Pinus pinea*, *Pinus halepensis*, *Taxus baccata*, *Ginkgo biloba*, etc.) develop in this way.

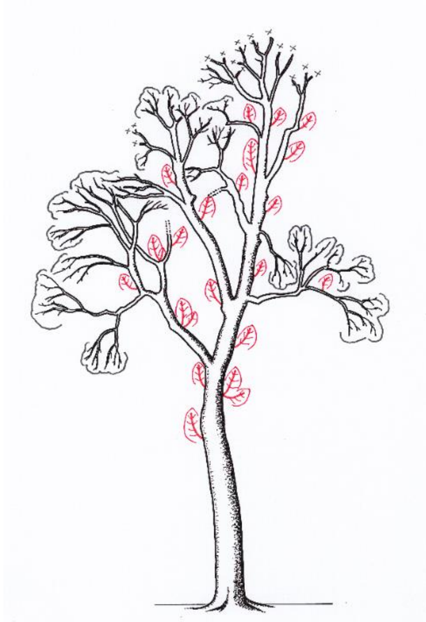


*Figure 16: representation of a tree consisting of two superimposed images: original development in black, epicormic shoots in red © Drénou*

### 5.1.2 Image n° 2 – epicormic shoots

The second image consists of all epicormic shoots. Contrary to popular belief, these epicormic structures do not ‘parasitise’ the tree they grow on. On the contrary, epicormic shoots have a determining role in physiological restoration, mechanical strengthening and architectural resilience. A tree that has epicormic growth is a tree that produces new leaves, often bigger than the ones born by the original twigs, and thus reactivates transpiration, the driver behind its hydrological circulation processes. The appearance of epicormic shoots lower down, set back from the terminal branches, shortens the distance between roots and leaves, which facilitates sap flow, as well as the larger annual rings of the epicormic shoots, compared to the branch they grow on. And last but not least, the new vessels of the epicormic shoots serve to get around hydraulic pathways that are damaged or no longer usable due to cavitation.

### 5.1.3 ARCHI types

In the ARCHI-method, the following types (physiological states), are distinguished (also see above):

- ***Healthy***: a tree without any significant symptom of crown degradation and whose architecture is in accordance with its development stage. A healthy tree is not necessarily ‘perfect’ and can even show ‘normal’ mortality or show signs of historic mortality (e.g. in a previously stressed tree or a tree that has suffered branch damage from felling nearby trees, which does not change its health status).
- ***Stressed***: a tree that undergoes stress, which can be seen by changes in its architecture (impoverishment of ramification, mortality, possibly the appearance of epicormic shoots, …), without it being possible for the observer to instantly decide on its future restoration or further degradation, based on the assessment. Felling stressed trees means lowering the number of potentially resilient trees in a population. It is better to wait a couple of years in order to give the tree time to express itself. The evolution of a state of stress depends on aggravating factors or favourable factors like the climate, competition, biotic factors, soil compaction, wounding, …

- ***Resilient***: a tree whose crown development resumes normal architectural dynamics, after a deviation from the normal. This is mainly thanks to the development of orthotropic epicormic shoots in the upper canopy. Note that a resilient tree can still show signs of mortality. Resilience is not to be confused with resistance, e.g.: the cork oak supports drought very well, but its capacity to produce orthotropic epicormic shoots after an architectural disorganisation is very limited, especially in mature trees. So the cork oak has high resistance, but low resilience.
- ***Crown retrenchment***: a tree in the dynamic formation process of a new, secondary crown below the original canopy, which eventually dies. Trees in crown retrenchment decrease the distance between leaves and roots to adapt to their environment. Not to be confused with dieback in the upper canopy. Crown retrenchment is rare in dense tree stands because the tree needs light to establish an organised secondary crown below the original one.
- ***Fallback***: a tree that does not have a living upper canopy, but continues to function with unaltered lower branches from its original structure. The tree does not form a secondary crown, so it is not in a crown retrenchment process.
- ***Irreversible decline***: a tree with a degraded crown (impoverished ramification, abnormal mortality) without any viable restoration process (epicormic shoots are almost absent or, on the contrary, abundant but (almost) all of the ageotropic type). A tree in irreversible decline does not necessarily die rapidly, depending on the biotic and abiotic environmental factors.

Careful observation of an individual tree (image n°1 and image n°2) allows to assess in which of the above types the tree can be classified. This classification automatically leads to a prognosis of the tree's future development, allowing to support management decisions.

#### 5.1.4 ARCHI keys

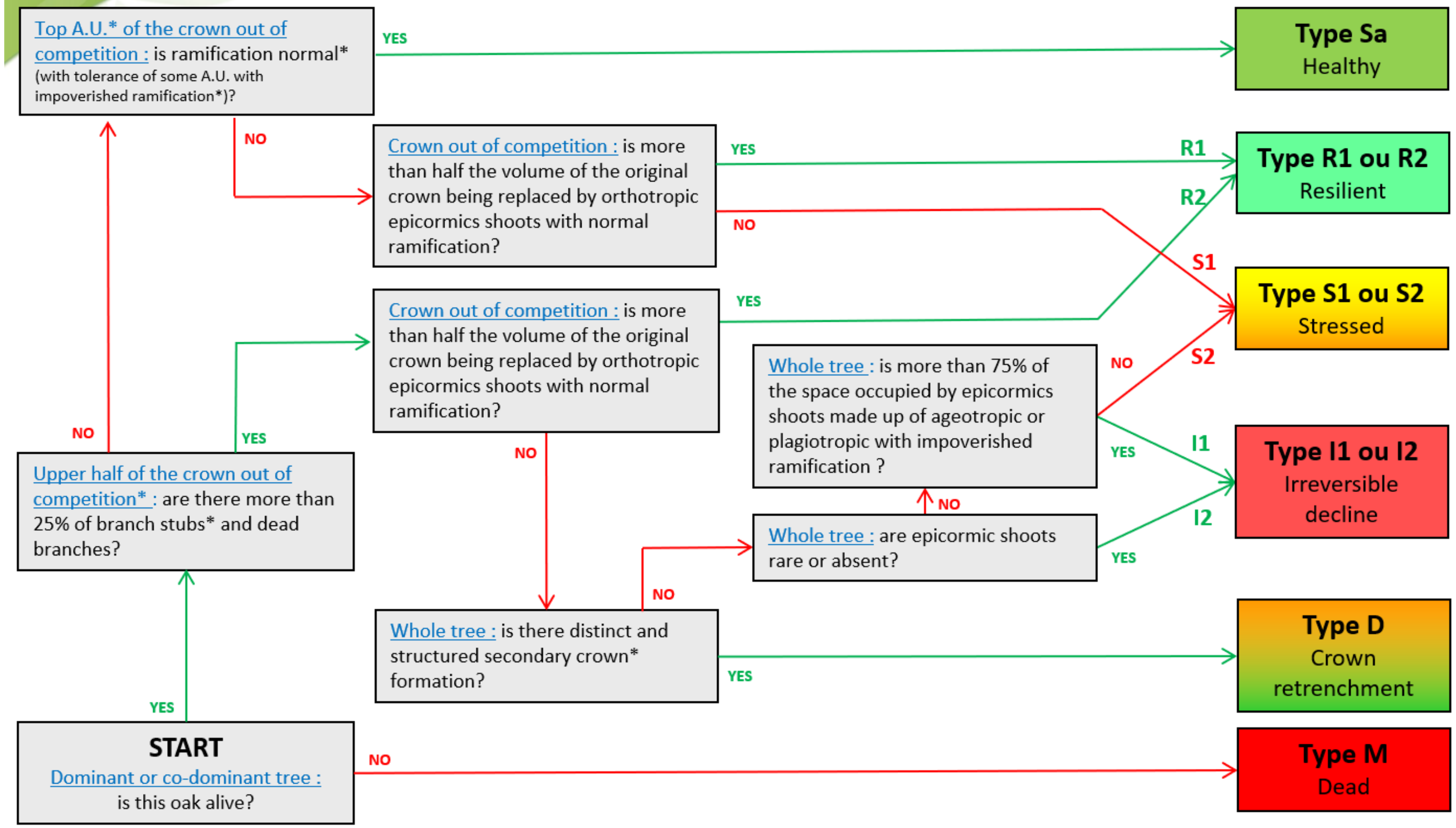
For several tree species, a dichotomous ARCHI key (in French language) has been developed by Christophe Drénou, in order to support, facilitate and objectify the architectural analysis of individual trees. These keys are tree species specific. For some species the key includes an assessment of the development stage of the tree.

Currently (2022) ARCHI keys are available for the following species: *Castanea sativa*, *Quercus* (*robur* + *petraea* + *pubescens*), *Quercus suber*, *Quercus ilex*, *Fagus sylvatica*, *Pseudotsuga menziesii*, *Picea abies*, *Pinus* (*sylvestris* + *nigra* subsp *laricio* var *corsicana* + *nigra* subsp *salzmannii* + *uncinata*) and *Abies alba*.

The ARCHI keys can be downloaded from:
https://www.cnpf.fr/nos-actions-nos-outils/outils-et-techniques/archi

Below is a screenshot of one of the ARCHI keys (for *Quercus* spp.). (©Drénou)

# ARCHI key for oaks (*Quercus robur, Q. petraea, Q. pubescens*)




**Crown out of competition**: part of the crown excluding the lower or lateral areas, subject to competition for light and space.

**Branch stub**: a broken off branch with a diameter over 3cm, of which the wound is not yet overgrown with callus.

**A.U.: Architectural unit**: basic architecture of a tree characterising the young development stage. The first architectural unit builds the stem, the following architectural units originate from each other by duplication and form the crown.

**Normal ramification**: ramification is qualified as being 'normal' when the transition from a major axis to the short shoots is progressive, following a gradient of intermediary axes with decreasing dimensions.

**Impoverished ramification**: the ramification of a main axis is impoverished if; i) it directly carries short shoots without producing intermediate branches, which gives it a columnar form; ii) it carries non-ramified twigs, which gives it a filiform structure; iii) it suddenly loses its apical dominance and elongates by forming axes arranged in densely packed, small forks.

**Secondary crown :** a secondary crown is described as structured when there is strong hierarchy between the epicormic shoots.

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Co-funded by the Erasmus+ Programme of the European Union