Architectural development of some citrus trees from seed planting to first blooming

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Abstract — Introduction. To verify that the properties found in the differentiated organs are transmitted to the citrus clones vegetatively propagated, it is fundamental to determine the differentiation process preceding fruiting. This work presents a study of tree architecture which is essential to the understanding of the plant development. **Definitions and general introduction on tree architecture**. The definition of the terms commonly used in tree architecture is therein completed by the terminology specific to citrus plant architecture. **Materials and methods**. The observations on citrus species were performed under a Sudanese-type climate. The trees were placed under conditions favourable to their development. Qualitative observations – with labelling, photographing and drawing – were made as soon as the seedlings started developing to follow the development of the trees. The morphological characteristics of the species chosen were described. **Tree development from seed germination to fructification**. After characterizing the germination of *Citrus* seeds, development of *Citrus medica* L., *C. hystrix* DC., *C. reticulata* and *Fortunella japonica* (Thunb.) Swing were analysed. The structures A developed by citrus trees consist of a mixed sympodium bearing plagiotropic sympodial branches; the structures B consist of plagiotropic branches developed at the extremity of an orthotropic module; the first flowers appear on the oblique or vertical ramifications of the structures C at the top of the tree. **Discussion**. The reason for the early fruiting of the grafted trees corresponding to a rapid morphogenetic evolution is still unknown. Could it be a consequence of the grafting of lateral meristems of structures C? or, could the mechanical process involved in grafting stimulate the development of fruit-bearing structures while reducing the vigour of the tree? **Conclusion**. The fact that the meristems used for grafting are selected at different stages of development of a citrus tree could explain the heterogeneity of the plants generated by this type of vegetative propagation. © Éditions scientifiques et médicales Elsevier SAS

***Citrus* / biological development / cell differentiation / growth / Côte d'Ivoire**

Développement architectural de quelques agrumes du semis aux premières floraisons.

Résumé — Introduction. Pour vérifier si les propriétés des organes différenciés sont transmises aux clones d'agrumes multipliés par voie végétative, il est indispensable d'identifier les étapes de différenciation précédant la production du fruit. Ces travaux présentent une étude de l'architecture qui est essentielle pour la compréhension du développement de la plante. **Définitions et introduction générale sur l'architecture de l'arbre**. La définition des termes généralement utilisés en architecture de l'arbre a été complétée ici par la terminologie spécifique à l'architecture des agrumes. **Matériel et méthodes**. Les observations d'agrumes ont été effectuées sous climat de type soudanien. Les arbres ont été placés en conditions favorables à leur développement. Des observations qualitatives – avec étiquetage, photographie et dessin des plantes – ont été faites dès le début du développement des plantules issues de semis afin de suivre le développement des arbres. Les caractéristiques morphologiques des espèces choisies ont été décrites. **Développement des arbres de la germination à la fructification**. Après une caractérisation de la germination de la graine des agrumes, le développement des espèces *Citrus medica* L., *C. hystrix* DC., *C. reticulata* et *Fortunella japonica* (Thunb.) Swing a été analysé. Les structures A développées par les agrumes sont formées par un sympode mixte portant des branches sympodiales plagiotropes ; les structures B sont constituées de branches plagiotropes développées à l'extrémité d'un module orthotrope ; les premières fleurs apparaissent sur les ramifications obliques ou verticales de structures C à la cime des arbres. **Discussion**. La raison de la mise à fruit précoce des arbres greffés, qui correspond à une évolution rapide du mouvement morphogénétique est encore inconnue. Serait-elle due au greffage de méristèmes latéraux de structures C ou devrait-elle être attribuée à l'acte mécanique du greffage qui contribuerait à accélérer le développement de structures fructifères, en abaissant la vigueur de l'arbre ? **Conclusion**. Le prélèvement, à différents stades du développement d'un agrume, de méristèmes utilisés pour le greffage pourrait expliquer l'hétérogénéité des plants obtenus par ce type de multiplication végétative. © Éditions scientifiques et médicales Elsevier SAS

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RESUMEN ESPAÑOL, *p. 61*

1. introduction

The varieties grown in the main citrus producing areas are vegetatively propagated. Budding of rootstocks grown from seed is the most commonly used technique.

In tropical Africa however, most citrus plants are grown directly from seed mainly because grafted trees have a short life span. Even though grafted trees bear fruit early, they often suffer fatal damage as a result of grafting: scion/rootstock incompatibility and necrosis at the graft union due to viroses.

Trees grown from seed experience two major problems:

– a general dieback resulting from a gummosis induced by *Phytophthora* spp. which attacks the bark and the radicels of the trees,

– an overextended period of time between seed planting and fruit production. The trees often suffer from gummosis and die soon after fruiting. The trees spared the disease are productive and have a very long life span.

Plant breeders choose citrus plants grown from direct sowing for new varieties. Pathologists take an active interest in this method of propagation to regenerate plants hosting pathogens with nucellar embryos found in the seeds of numerous citrus species. Each plant is vegetatively propagated for evaluation. Budding is the most commonly used method. In that case, the scion comes from a sole meristem from the mother plant.

For a good number of shrubby species, the same properties acquired during the morphogenetic development of the mother plant are found among the plants obtained by the vegetative propagation of one of its differentiated organs. For example, the budding or grafting of plagiotropic axes of coffee trees [1] or *Araucaria heterophylia* [2] generate early fruit-bearing plagiotropic plants. As a consequence, one would naturally wonder if citrus plants have the same ability and if the differentiation level of the organs, from which the meristems originate, could have an impact on the future of the grafted tree.

This hypothesis could be confirmed by observing orange or mandarin trees. These trees, excessively thorny when grown from seed, have none or very few thorns when the cultivars are vegetatively propagated.

To develop methods which would help promote early fruiting in citrus plants grown from seed or to verify that the properties found in the differentiated organs are transmitted to the clones vegetatively propagated, it is fundamental to understand the development of citrus plants and to determine the differentiation process preceding fruiting. The study of tree architecture, the subject of this work, is one essential though not sufficient approach to the understanding of the plant development which will need to be corroborated by other methods.

2. definitions and general introduction on tree architecture

The definition of the terms commonly used in tree architecture and previously published [3–6] is therein completed by the terminology specific to citrus plant architecture as mentioned in Caraglio and Barthélémy's previous works [7].

2.1. monopodial or sympodial growth

A monopodial growth is defined by the indefinite growth of an axis formed by the continued development of its apical meristem. The axes formed are called monopodia.

The growth is sympodial when the apical meristems have a definite function and the plant consists of a series of axes called modules.

When a relay develops in the exact continuation of the main axis, the sympodial stem imitates a monopodium and is referred to as a pseudomonopodium [8].

2.2. acrotony, mesotony, basitony

Acrotony is defined by Troll [8] as "the development of the shoots principally at

the top of the main stem which remains the largest branch".

"Opposite to the definition above, basitony refers to the development of vigorous shoots mainly at the base of a stem".

"Mesotony describes the development of the lateral shoots mainly in the middle of a stem" [7].

2.3. hypotony, amphitony, epitony

This terminology refers to the development of the lateral shoots on a horizontal or oblique stem.

Hypotony is defined by Troll [8] as the "development of the lateral shoots on the under side of the main axis".

"Amphitony refers to the development of the shoots mostly on lateral parts of the main axis".

"Epitony refers to the growth of vigorous shoots mainly on the upper part of a stem" [7].

2.4. syllepsis and prolepsis

These terms take on a different meaning depending on authors and the time when they were used. Following are the definitions by Hallé et al. [9] used in this article.

Syllepsis refers to the immediate growth of a shoot from a lateral meristem. Arboriculturists talk of 'anticipated' branches and Bompar [10] refers to them as branches with an 'immediate growth'.

"Prolepsis refers to the development of a particularly elongated axis from a lateral meristem after a period of dormancy during which it is often found inside a bud. When the bud bursts, it produces a proleptic branch characterized by cataphylls and short internodes located at its base" [7]. Edelin [11] talks of 'delayed' branches and Thiébaut et al. [12] describes them as branches with a 'deferred' development.

Whether proleptic, delayed or postponed, the term used describes phenomena of a different nature. Plants with a rhythmical growth develop acrotonic lateral meristems at the same time as the terminal meristem. Plants with a sympodial growth produce mesotonic or basitonic latent lateral meristems which develop well after the terminal meristem or the relay meristems (*figure 1*). To describe these distinct pro-

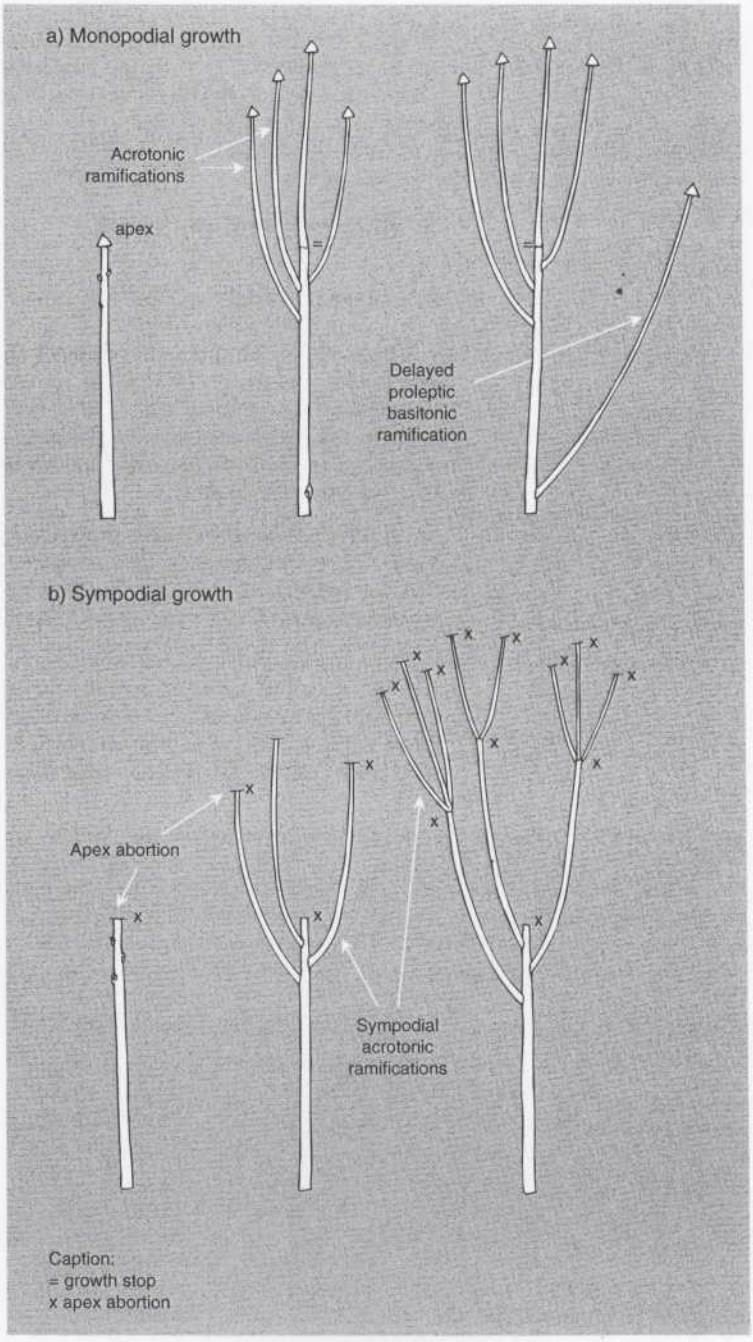


Figure 1.
Development of acrotonic lateral meristems on axes characterized by (a) monopodial or (b) sympodial growth.

cesses, we referred to the terms used by Goguey-Muethon [13]: 'early proleptic axis' or 'relay proleptic axis' in the first case when the apex aborts, and 'delayed proleptic axis' in the second case.

3. materials and methods

3.1. plant material

These studies on the architecture of citrus plants began in 1992. The genera belonging to the Citreae tribe and specifically to the Balsamocitrinae and Citrinae sub-tribes (*table I*) of the rutaceae family were of particular interest.

All the trees observed were grown from seed. For species intended for commercial use, the seeds used came from the fruits of a same cultivar.

If some citrus plants such as orange trees all belong to the same botanical species, others as the mandarin trees belong to different species and can exhibit architectural behaviour entirely different amongst themselves. The use of polyembryonic species makes it possible to accurately reproduce the propagated cultivar thanks to the breeding of plants grown from nucellar embryos.

The species were studied after observing a group of trees with similar behaviours. Some scarce variants probably with a hybrid origin were not taken into account.

Table I.
Citrus trees belonging to the Citreae tribe, observed during a study on tree architecture.

Sub-tribe	Genus and species	Vernacular name
Balsamocitrinae	*Swinglea glutinosa* (Blanco) Merr.	–
Citrinae	*Fortunella japonica* (Thunb.) Swing.	Marumi kumquat
	F. margarita (Lour.) Swing.	Nagami kumquat
	F. obovata Hort. ex Tan.	Fukushu kumquat
	Citrus aurantifolia (Christm.) Swing.	Lime
	C. aurantium L.	Sour orange
	C. hystrix DC.	Mauritius papeda
	C. limon (L.) Burm.	Lemon
	C. limonia Osb. *(C.volkameriana)*	Volkamer lemon
	C. maxima (Burm.) Merr.	Pummelo
	C. medica L.	Citron
	C. meyeri Y. Tan.	Meyer lemon
	C. paradisi Macf.	Grapefruit
	C. reticulata Blanco	Mandarin
	C. sinensis (L.) Osb.	Orange
	C. sinensis (L.) Osb. × *Poncirus trifoliata* (L.) Raf.	Citrange

3.2. conditions of the observations

3.2.1. climate

The observations were performed in the Korhogo area, North of Côte-d'Ivoire, at 9.5° N lat., where the climate is of a Sudanese-type. The rainy season starts somewhere around the third and fourth week of March and ends in October or November. August records the highest level of rain. The total annual pluviometry ranges from 900 to 1 500 mm but generally averages 1 200 mm. A short dry period, which lasts about 3 weeks, usually occurs late June and July.

The Harmattan, a cool, dry, sandy North wind from the desert, blows from December to February. The absolute minimal temperatures oscillate between 13 and 15 °C depending on the years, whereas the evapotranspiration is maximal in January with a pluri-annual average of 255 mm.

The highest temperatures, sometimes reaching as high as 41 °C, are recorded between April and June.

3.2.2. tree agronomic management

Even though directly grown in the field, the trees were placed under conditions favourable to their development: irrigation during the dry season, fertilization, phytosanitary measures, etc. Yet, the systemic treatments, used in sprinkler and basin irrigation and applied to protect trees against specific enemies, were not 100 % effective. These citrus plants grown from seed experienced sanitary problems more severe than those observed on forest plants or rustic fruit trees. For example, the trees affected by tristeza, a viral disease interfering with tree growth and causing anomalies in the metabolism as well as distorted axes,

showed a biology and architectural behaviour entirely different from those of healthy trees. In other cases where the trees selected for the study died from diseases attacking their root system, the observations were directed towards new trees grown from a batch of seeds of the same origin and showing a behaviour similar in many ways to the first trees.

3.2.3. observations

Qualitative observations were made as soon as the seedlings started developing. They consisted in labelling, photographing and drawing the plants to follow the development of the trees during their developmental stages. As the plants grew, certain species were less interesting than others which seemed to be better representative of some unique phenomena. As in the architectural cases described by Hallé and Oldeman [9, 14], these characteristic species correspond to 'milestones'. The other species with less specific behaviours show intermediate functions between these milestones.

Later on, the studies were mostly directed towards species of the *Citrus* and *Fortunella* genera, which seemed to correspond to these milestones. The observations were performed so as to complement the studies achieved by Nicolini [3]. Among all the species, *C. medica* L. (citron tree, Corsican var.), *C. hystrix* DC. (combava), *C. reticulata* Blanco (mandarin tree, var. Frémont), *Fortunella japonica* (Thunb.) Swing. (Kumquat Marumi) were chosen.

3.3. morphological characteristics

Citrus leaves are arranged around the stem in a spiral with a phyllotaxy of 2/5 or 3/8 depending on species. The rotary direction of the spiral varies with each level of ramification [15].

At the axil of each leaf, a scaly bud can be observed. This bud occasionally develops axillary meristems at the axil of the preleaves. A lateral thorn, more or less developed, may either abort or reach 10 cm or so. The position of the thorn in relation to the bud indicates the direction in which the phyllotactic spiral rotates: if the thorn is situated on the left of the bud, the spiral goes from right to left, and vice versa [15, 16].

The stem of the citrus plants has a sympodial growth as the result of the abscission of its apical extremity. A module can however consist of several units of growth. At the extremity of a unit, the internodes are relatively short and generally thornless; in the middle, the internodes are long and may grow relatively long thorns.

When several modules are superposed, they form a pseudomonopodium. The junction between two modules is revealed by a growth ring on the stem. This mark tends to disappear as the branch matures which makes it difficult to detect a posteriori the modules which had formed a sympodium. It may be necessary then to compare the position of the bud in relation to the thorn: a change in phyllotaxy indicates a ramification consequent to an abortion of the apex. But the reverse is not true, because the relay of a module 'n' can be ensured by a module 'n + 2' situated at the axil of the primordia of the meristem 'n + 1'. The phyllotaxy of the module 'n + 2' will then be similar to the phyllotaxy of the module 'n'.

4. tree development from seed germination to fructification

4.1. seed germination

The germination of *Citrus* seeds is characterized by the growth of the radicle and the elongation (about 0.5 cm) of the hypocotyl while, for most species, the cotyledons remain underground. However, the fleshy cotyledons of grapefruit trees (*C. maxima*) rise above the soil surface and the cotyledons of combava (*C. hystrix*) and lime trees (*C. aurantifolia*) grow into two cotyledonal leaves with chlorophyll.

The epicotyl, which later develops, produces at its extremity a pair of opposite incipient leaves. When the axis temporarily stops developing, the ovoïd leaves start unfolding. When growth resumes, the developing leaves appear small and round,

and are slightly out of line along the stem. The upper leaves are slightly larger than the leaves growing underneath. This phenomenon becomes more obvious as other leaves emerge; the internodes get longer; the phyllotaxy is spiral-like, and the leaf surface progressively spreads to its maximal size.

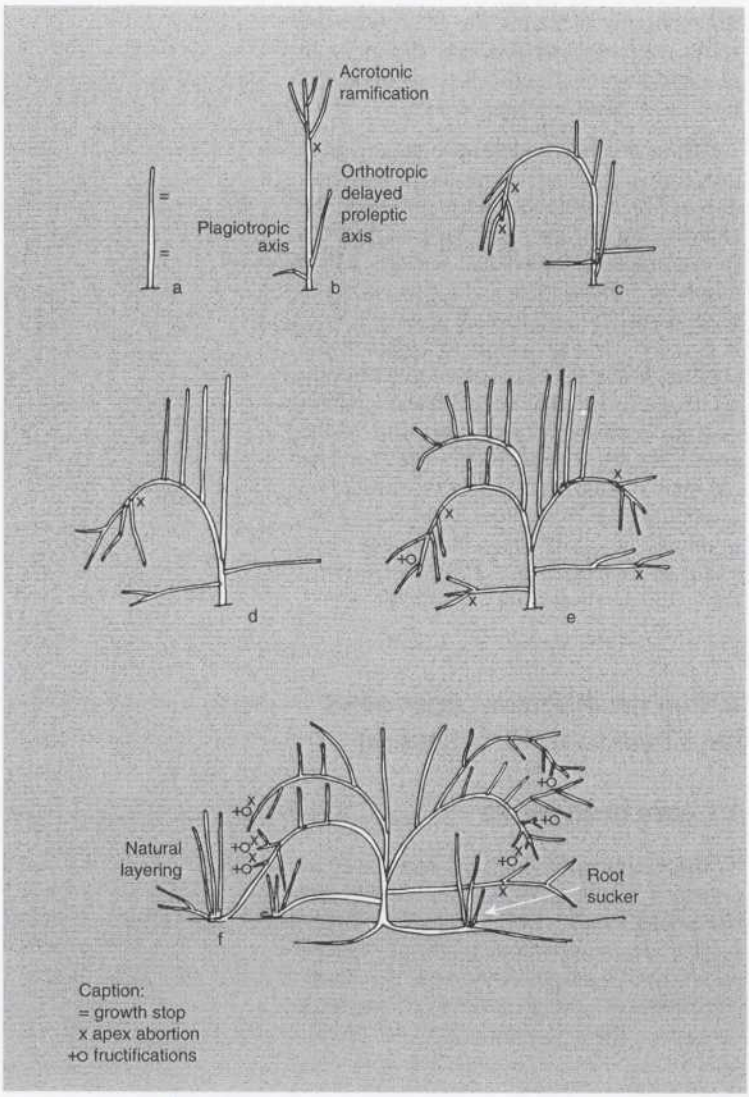


Figure 2.
Growth of a citron tree (*C. medica* L.): a) rhythmical and monopodial growth of the axis 1; b) acrotonic vertical ramifications produced by axis 1 whose apical extremity may or may not have aborted; orthotropic or plagiotropic delayed proleptic axes developed at the base of axis 1; c) curving of axis 1; d) development of orthotropic or plagiotropic delayed proleptic axes either at its base or on the outside of its curve; e) curving of the most vigorous axes; f) layering of the lower branches when in contact with the ground and development of orthotropic axes.

4.2. development of citron trees, *Citrus medica* L.

After germination, a phase common to all species of the genus *Citrus*, the main axis of the citron tree (axis 1) continues its vertical growth. When it reaches about 30 cm, the tree growth stops regardless of the environmental factors. A few days later, the plant resumes its vertical growth. Because these growth spurts occur repeatedly, the citrus tree growth is said to be rhythmical. Axillary vertical axes may develop on these extremities when the plant growth is suspended and proleptic axes develop at the base of axis 1.

If the apex of axis 1 aborts, the subterminal axillary meristems produce relay axes and form a pseudomonopodium (*figures 2a, 2b*).

During the next stage of development, axis 1, whether ramified or not, bends. New epitonic proleptic axes develop on its upper side and accentuate the curving of the tree. Under conditions extremely favourable to plant development during the prior months, the tree bends early, 3 to 4 months after transplanting the plant to the field. The plant tissues are supple and the tree is extremely curved (*figure 2c*). When the growth is slow and the tree bends 1.5 year after its plantation, the trunk loses its flexibility. Soon, the apical part of the tree bends and gets closer to the ground. Its initially vertical ramifications are now horizontal. The proleptic axes, with a late growth which developed on the upper side of axis 1 after bending, are exclusively vertical. The axes which develop at its base are either orthotropic and strong and grow rapidly, or plagiotropic at the very beginning or after drooping (*figure 2c*).

The largest vertical axes originate either from the base of the tree or from the curved part of the tree. Their length decreases as they develop closer to the apex of the central axis (*figure 2d*). These orthotropic axes have a rhythmical growth pattern. Shorter internodes without assimilative leaves indi-

cate temporary growth interruptions. There are no rings.

Like axis 1, the strongest axes located at the base of the trunk bend, which causes the development of delayed proleptic axes on their upper side. The strongest axes originate near where the main axis bends (*figure 2e*). This phenomenon is repeated several times. While axis 1 and its first branches bend when slightly above the ground, the next axes arch at a higher level and the orthotropic part of these mixed axes is longer than for the axes that first drooped. The horizontal or oblique branches developing on the lowest part of the trunk droop while others rest on the ground where they root and grow bunches of orthotropic axes (*figure 2f*). Reiterated orthotropic complexes also arise from roots. The process is called natural layering and suckering.

At this stage of development, a citron tree (*figure 3*) has:

– monopodial or pseudomonopodial main stems, first orthotropic, then mixed after they bend and droop,

– plagiotropic, sympodial ramifications on the apical part of these main stems; other plagiotropic stems at the base of the trunk and the branches; their growth is delayed compared to their main axis,

– orthotropic axes growing either at the base of the trunk or on the upper side of the curved or horizontal parts of all the other types of axes; these axes are less vigorous as they grow closer to the distal extremity of the main axis, and the most vigorous ones tend to bend more or less towards the outside.

During the following stages, other series of vertical axes with a determinate growth develop on all axes and more specifically on the horizontal parts. These proleptic axes are characterized by a moderate growth (50 cm for the first module, relatively shorter for the next series). Usually, terminal and axillary flowers start developing on the second module of these sympodia.

To sum up, the basic structure of citron trees is characterized by a mixed orthotropic pseudomonopodium which becomes plagiotropic when curving and drooping. This stem generates sympodial plagiotropic ramifications on its basal and apical extremities as well as orthotropic delayed proleptic axes. The most vigorous axes are situated at its base or where the stem bends. The less vigorous ones grow in the apical part of the mother-stem. The flower-bearing modules grow on these sympodia (*figure 4*). The axes 1 of these ramified structures originate either from the base of the tree trunk or from the curved part of another mixed axis.

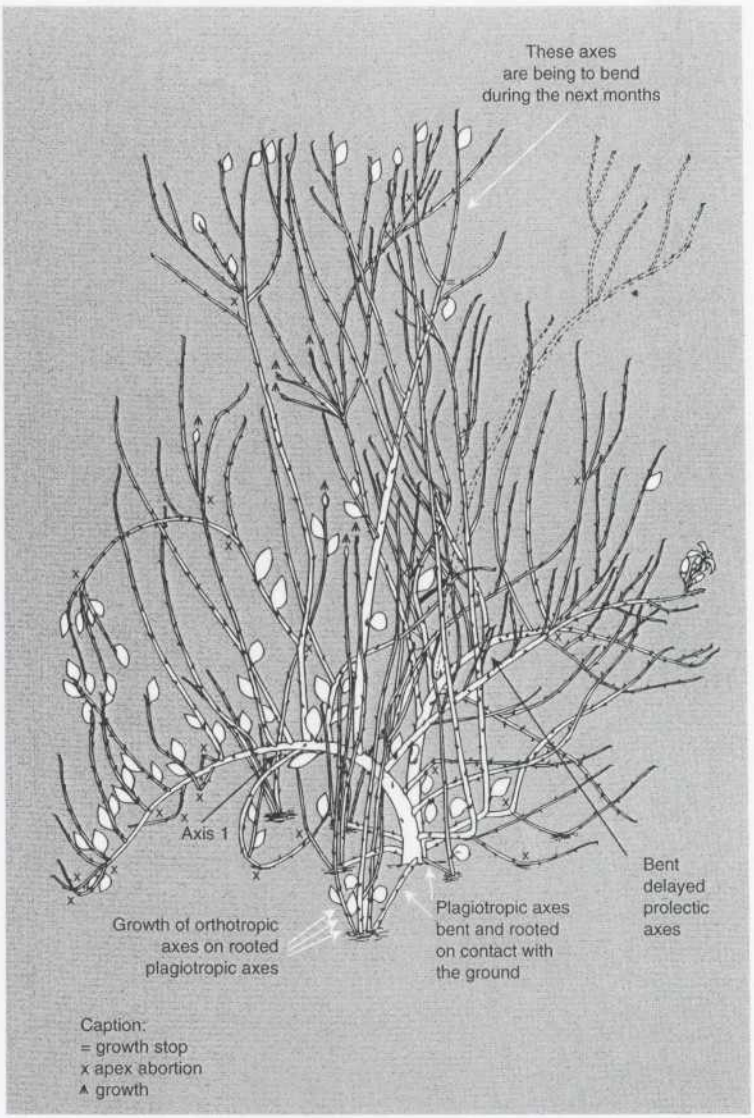


Figure 3.
Adult citron tree.

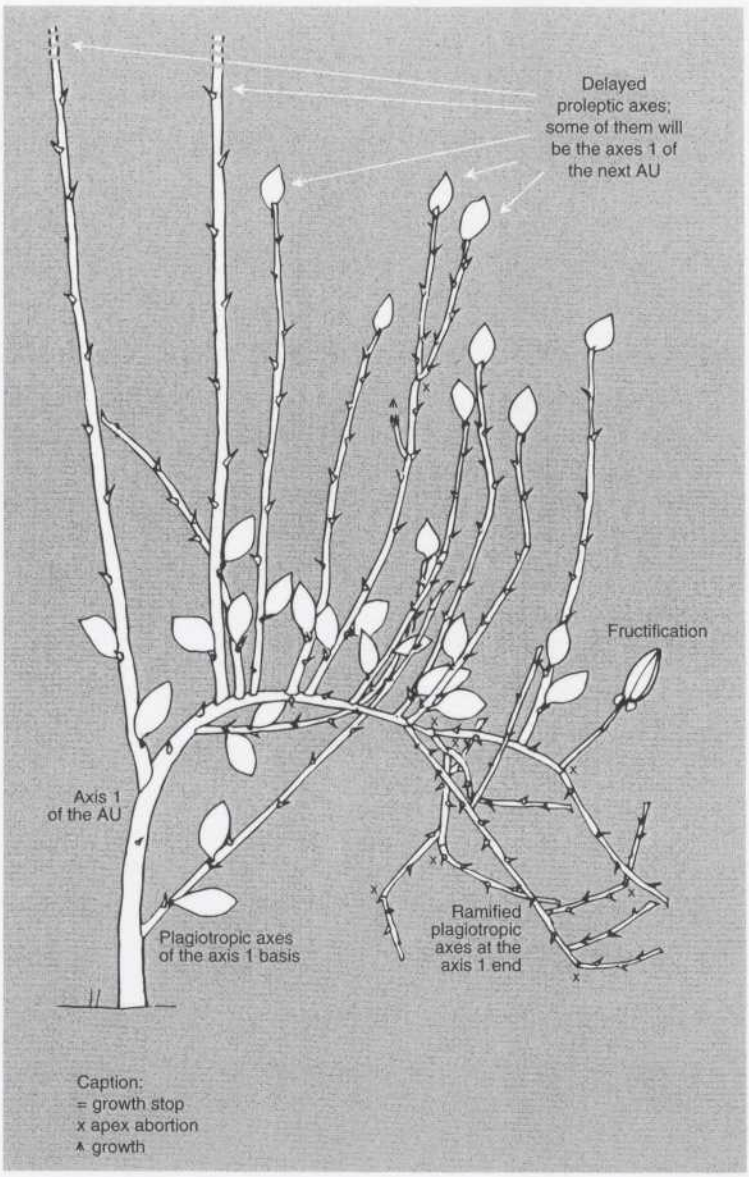


Figure 4.
Architectural unit (AU) of a citron tree.

4.3. development of combavas, *Citrus hystrix* DC.

The main axis (axis 1) produced by a combava seed grows vertically. When it reaches 20 to 30 cm, its terminal meristem aborts and the plant develops from a subterminal meristem by producing an oblique module shorter than the previous one. The third module grows horizontally and the following ones have a positive geotropism. At this stage of development, the main stem consists of a series of modules which form a mixed structure (*figure 5a*). Pseudodichotomy and trichotomy (development of two or more branches at the extremity of an axis) are not unusual.

At the same time, horizontal proleptic axes grow at the extremity of the first segment and on the curved part. These branches are sympodial and ramify at the extremities of the modules. Even when there is only one ramification, the successive modules do not follow a continuous straight line which makes the branches look uneven.

At the end of this stage of development, the structure of a combava consists of a sympodial mixed stem with plagiotropic sympodia (*figure 5b*). We will refer to it as the structure A.

Vigorous vertical axes start developing on the vertical part of the axis grown from seed, on the curved part of the same axis, or on the proximal sections of the horizontal axes. Usually, two to three axes of this particular type grow on each of the young plants observed. They all develop on the trees at the same time and stop growing after a while. When 50 to 60 cm long, their apical meristem aborts (*figure 5c*). After a period of rest, the axillary meristems observed at the extremity of these axes generate horizontal sympodia. These extend longitudinally and branch into subterminal modules which are produced successively (*figure 5d*). These structures, referred to as the structures B, consist of a vertical module with plagiotropic sympodia at its apical extremity.

Vertical axes develop on either the apical extremity of the vertical axis of these structures or on the proximal part of the plagiotropic sympodia. They branch and form a structure identical to the previous one. This process is repeated and the tree is formed by a succession of such structures (*figures 5e, 5f, 6*).

Structures C then develop on the horizontal branches located at the top of the trees. They consist of a vertical axis which produces oblique subterminal modules when its terminal meristem aborts. The

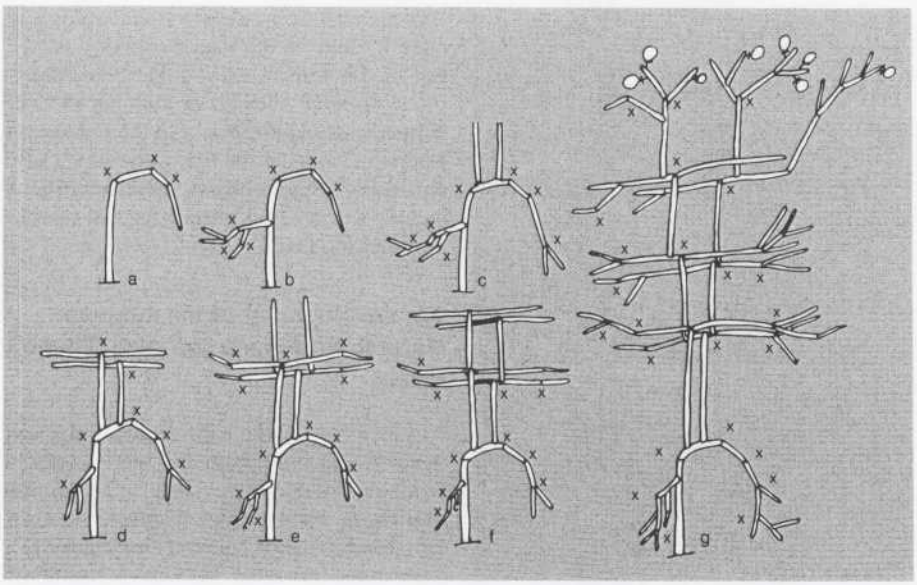


Figure 5.
Growth of a combava (*C. hystrix* DC.):
a) and b) development of the structures A;
c) delayed proleptic vertical axes produced by structures A; the apex of these vertical axes aborts;
d) development of vertical modules at the origin of the structures B;
e) and f) vertical development of the trees with the superposition of structures B;
g) adult combava.

modules in turn produce oblique subterminal modules, etc. Usually, terminal or axillary flowers are observed on this third level (*figure 5g, 5f*).

These structures C, which correspond to Leeuwenberg's models, gradually occupy most of the tree from top to bottom and from the center outwards. As these structures develop, the modules decrease in length and sexuality starts at an early stage.

To sum up, during their first stage of growth, combavas have a mixed structure. Their trunk and branches are sympodia (*figure 5b*). The structures which develop next consist of a vertical trunk constituted with one single module – and even one single growth unit – and of sympodial plagiotropic ramified branches (*figures 5d, 6*). During the third stage, the structures C correspond to some of Leeuwenberg's models (*figures 5g, 7*). Each new structure appears as soon as the structure on which it grows reaches a certain stage of development. It soon expands with ramifications developing in the apical extremity of the plagiotropic modules. The next structure to develop, whether its growth pattern is similar to or different from the structure which is bearing it, indicates the transition from a plagiotropic acrotonic ramification to an orthotropic, basitonic, and epitonic growth.

4.4. development of mandarin trees, *Citrus reticulata*

As a result of polyembryony and despite the fact that the Frémont variety is a hybrid of mandarins and tangelos, all the different trees grown from seed exhibit similar behaviours and are true to the parent type.

In their first stage of development, mandarin trees and combavas are identical. They consist of a mixed sympodial structure with plagiotropic, sympodial, and ramified branches (*figure 8a*). Then vertical axes develop either on the apical extremity of the module grown from seed or on the proximal part of the plagiotropic axes (*figures 8b, 9*). They have a rhythmical growth and can reach several meters before their apical meristem aborts.

Following a growth interruption, meristems, subterminal at the time of the interruption, can generate oblique branches which develop at the same time as their main axis. If the main meristem of the vertical axis aborts, several axes then originate from the subterminal meristems (*figure 8b*). These axes are oblique, almost vertical. After several levels of ramification, the modules become shorter, and terminal or subterminal flowers are observed (*figure 8c*). The weight of the fruit may cause the fruit-

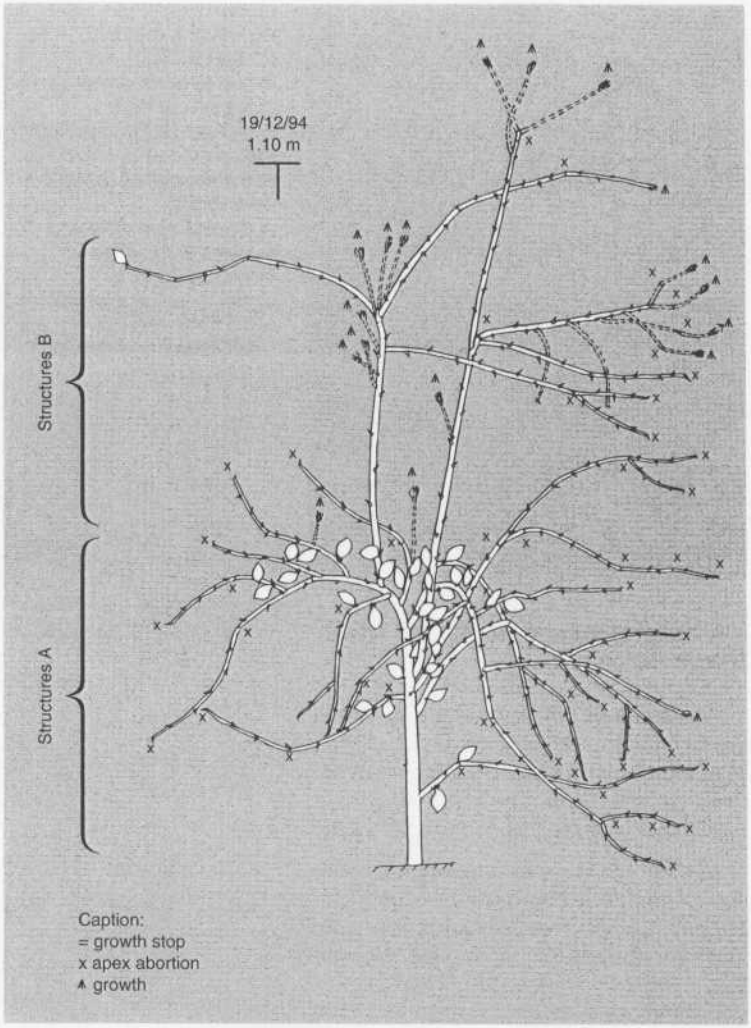


Figure 6.
Second stage of growth of a combava characterized by the development of the structures B.

bearing module to bend (*figures 8d, 10*). In the next stages of development, proleptic structures of the same type start invading the tree from top to bottom.

Orange trees and grapefruit trees have the same type of architecture except that the lower part of the trees consists of a succession of several mixed axes each time growing more vertically. The stage of development into mixed axes for both species lasts longer than for the mandarin trees, and orthotropy is progressively acquired.

These three species – mandarins, oranges and grapefruits – experience a phase during which proleptic structures true to Leeuwenberg's models start invading the axes located in the tree periphery. At the top of the vertical axes, subterminal structures develop; they form another level of subterminal ramification. On the oblique or horizontal axes of the tree periphery, these structures originate from lateral meristems located on any part of the terminal or subterminal modules.

4.5. development of the kumquat Marumi, *Fortunella japonica* (Thunb.) Swing

As for most of the *Citrus* species, the axis developing from a kumquat seed produces a mixed sympodium with a horizontal branching system. One vigorous vertical axis develops from this structure (*figure 11*). Sometimes, but very seldom, a couple of axes may be observed. Oblique axes develop on the apical part of this vertical axis. When their apex aborts, they grow modules on their extremity. These modules bear flowers at the axil of the subterminal leaves.

The vertical axis of the structure which originated from the initial structure is referred to as axis of order 1. This axis produces oblique axes of order 2 which generate fruit-bearing ramifications of order 3. Among the axes of order 2, some are more vigorous than others. They straighten up and ramify at their extremity. These ramifications are sterile, but the modules that they later produce do bear fruit. The axes of order 2 become the axes of order 1 of a new structure.

Kumquats therefore consist of a succession of structures true to Leeuwenberg's models. Their modules of order 3 are fruit-bearing modules (*figure 12*).

Citrus trees of the *Fortunella* genus have an earlier sexuality than trees of the *Citrus* genus.

4.6. results from the observations on the development of citrus trees

The citrus trees observed (of the *Citrus* genus) first developed a mixed ramified structure. For some particular trees such as

the combava, the mandarin tree, the lime tree, the orange tree, and the grapefruit tree, the central structures consisted of sympodia with a first module growing vertically. The next modules seemed to grow more and more horizontally with each series of new modules. For other trees such as the citron tree, the central structures consisted of monopodia – or pseudomonopodia – initially orthotropic, then mixed when bending and drooping. The axis 1 of *C. limonia* bent very slightly.

The vegetative growth of certain species, such as the lime trees or the citron trees, continued with the development of a succession of mixed structures identical to those developed during the first stage of growth. The structures of combavas which developed during this second stage, consisted of a vertical module with horizontal ramified sympodia. They were almost similar to the structures A. Other citrus trees such as the Frémont mandarin trees adopted a different mode of growth. This growth pattern conforming to one of Leeuwenberg's models consisted of orthotropic sympodia with acrotonic vertical or oblique ramifications. In some intermediate cases (orange and grapefruit trees), the plants developed a series of mixed structures before producing any vertical branches. Regardless of the growth pattern adopted by the citrus trees during this particular stage, their growth was exclusively vegetative.

Later on, all the species studied started developing structures C either at the extremity of the vertical axes or on the upper side of the horizontal branches located at the top of the trees. Other axes 1 of structures C then successively developed from the top of the tree to its base, and from the extremity of the branches inwards. These structures C are true to some of Leeuwenberg's models. Their axes produced subterminal ramifications when their apex aborted or when the terminal meristem changed into a floral meristem. The first flowers to appear were either terminal or axillary; they developed on the axes of order 2 or 3 of these structures.

These observations confirm Nicolini's [3] who demonstrated that the upper part of both *Poncirus trifoliata* and *C. volkameriana* consists of structures (structures C) identical to Leeuwenberg's models. These structures bear the very first blooms. The same applies to lime trees which exhibit mixed branches generating terminal or epitonic structures C.

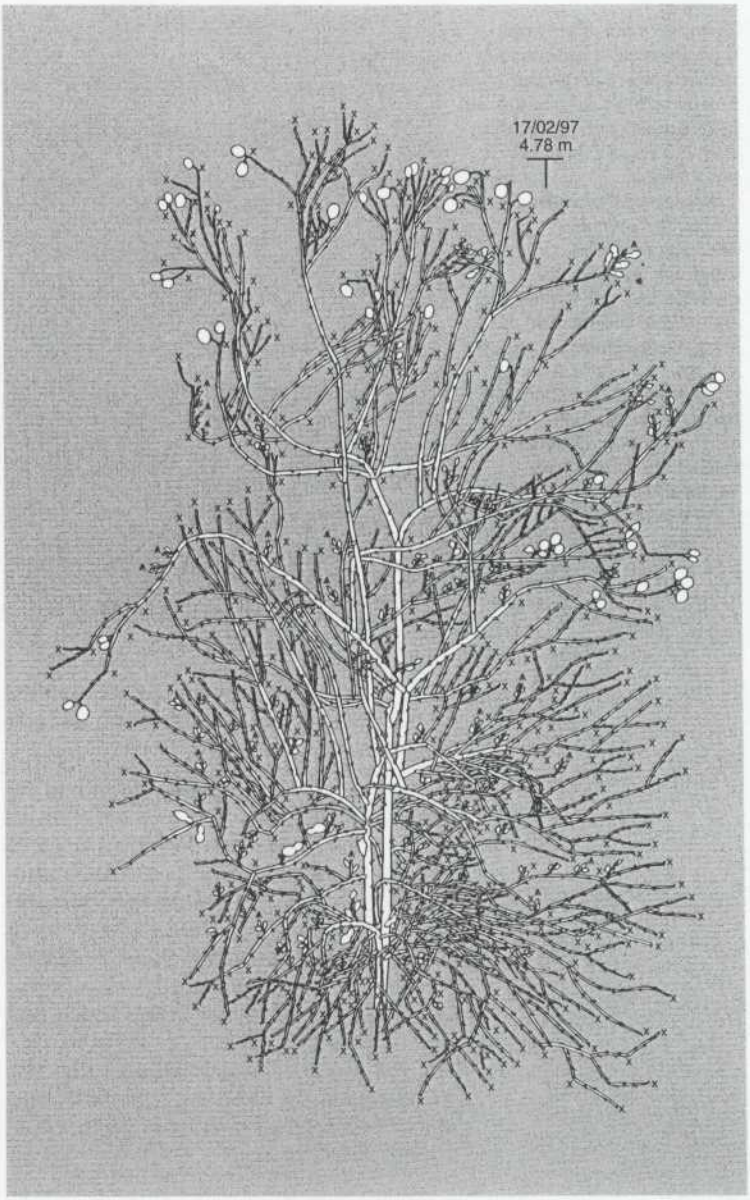


Figure 7.
Third stage of growth of a combava characterized by the development of the flower-bearing structures C.

When the branch of a tree, a mandarin tree for example, bends beneath the weight

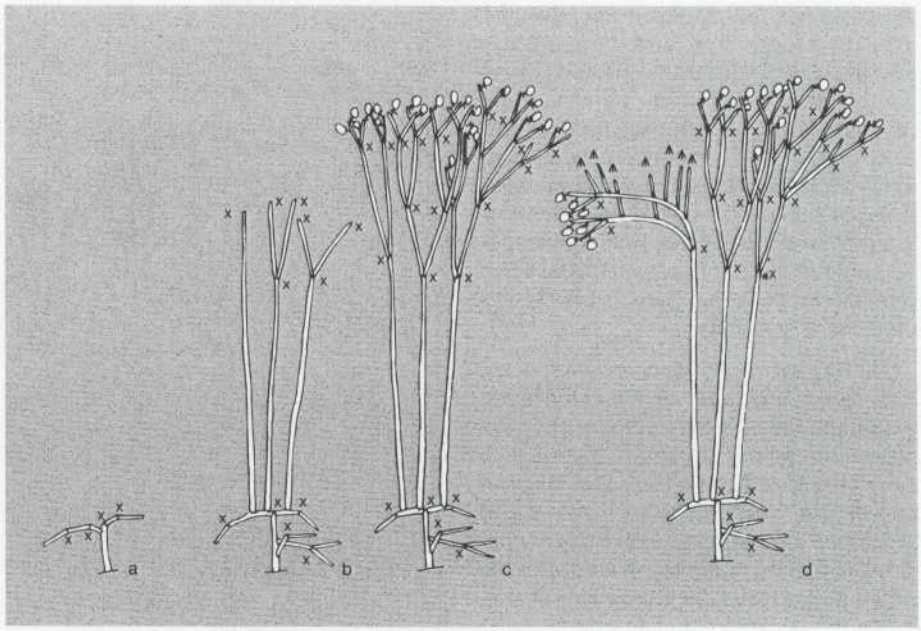


Figure 8.
Growth of a mandarin tree:
a) development of a structure A;
b) development of delayed proleptic upright axes at the distal extremity of the axis 1 or on the upper part of its ramifications;
c) development of vertical or oblique sympodial ramifications on the orthotropic axes whose apex has aborted; terminal or subterminal flowers develop on the last modules of a group of ramifications;
d) the modules bend beneath the weight of the fruit; development of orthotropic epitonic ramifications on the horizontal section of the module.

of the fruit, it produces epitonic structures C at the point where it bends or on its horizontal parts.

After developing vegetatively and on the outside, these trees filled up with flower-bearing structures C in their third stage of growth. These structures grew in the opposite direction, that is from top to bottom and from the periphery inwards. The main branches which so far were barely ramified started developing numerous delayed proleptic ramifications. The trees, which had first built their framework, or skeleton, during the stage of vegetative growth, then started growing the axes 1 of the subsequent flower-bearing structures C in a centripetal direction.

The development of structures C in trees formed by a succession of mixed structures, which developed during the stage of vegetative growth, corresponds to a drastic change in their mode of growth. It is not a progressive phenomenon characterized by the development of a new type of axes after a certain level of growth as in the cases of metamorphosis described by Edelin [11]. For the trees which achieve their stage of vegetative growth according to Leeuwenberg's models, could the structures which formed during this particular phase be of the same nature as structures C?

All the observations come to the following:

– During the juvenile phase of the citrus trees studied, the modes of development varied greatly with the species and the ontogenetic stages. But, regardless of the growth patterns adopted during this stage, all the trees eventually followed Leeuwenberg's models at one time or another and developed flowers on the axes of order 2 or 3 of these structures. These structures C, which were first observed at the top of the tree, in its center, started developing towards the periphery and downwards. They developed on the main branches following a centripetal direction.

– Most of the species observed changed their mode of growth as they developed. They first started with the formation of mixed structures and completed their growth according to a Leeuwenberg's model.

– Regardless of their architecture, the vegetative growth of the different citrus trees studied which followed the development of the structures A proceeded in two steps: first, the trees built their framework

or 'skeleton'; second, they filled up with proleptic centripetal structures C on the supporting branches forming the frame. Sexuality was centrifugal on the elemental structures (structures C) and centripetal on the rest of the tree where the structures C developed.

– The flower-bearing structures C are very similar to the small crowned axes described by Costes [17] in her study on the development of lichees and related genera. The development of these particular structures in adult trees is currently the subject of other studies.

– Despite the great confusion resulting from the fact that different meristems can produce relay axes, it is clear that the trees developed according to a definite process consisting of precise steps. The development of delayed proleptic axes (the main axes of the structures) coincides with some of these steps which are imperative for the trees to reproduce.

The *Fortunella* sp. changed their mode of growth to go from a structure A to structures C with flowers on the axes of order 3. A series of flower-bearing structures C succeeded the development of the initial mixed structure of the trees. This mode of growth reminds one of the development according to Leeuwenberg's models of the citrus trees of the genus *Citrus* during their second stage of growth despite a few differences. For example, trees such as kumquats build their framework with a succession of flower-bearing structures C, whereas the trees of the genus *Citrus* previously mentioned build an exclusively vegetative framework during the second stage of development. This frame then fills up with flower-bearing structures (*figure 12*). The phenomena observed during the second stage of the vegetative growth of the *Citrus* are not noticed in kumquats. If existent, these phenomena are too swift to be noticed; they could consist of a ramified vegetative structure C with a corresponding flower-bearing structure. The kumquats bloom the second year following seed planting whereas the orange and mandarin trees wait 5 to 6 years before they yield fruit.

The growth of lime trees, *C. aurantifolia* (Christm.) Swing., is transitional to the mode of growth of both the kumquats and the other species of the genus *Citrus* observed. During the second stage of growth, lime trees build their framework by superposing mixed pseudomonopodia, and, while completing their framework, they start producing flower-bearing structures C on the second or third mixed structures.

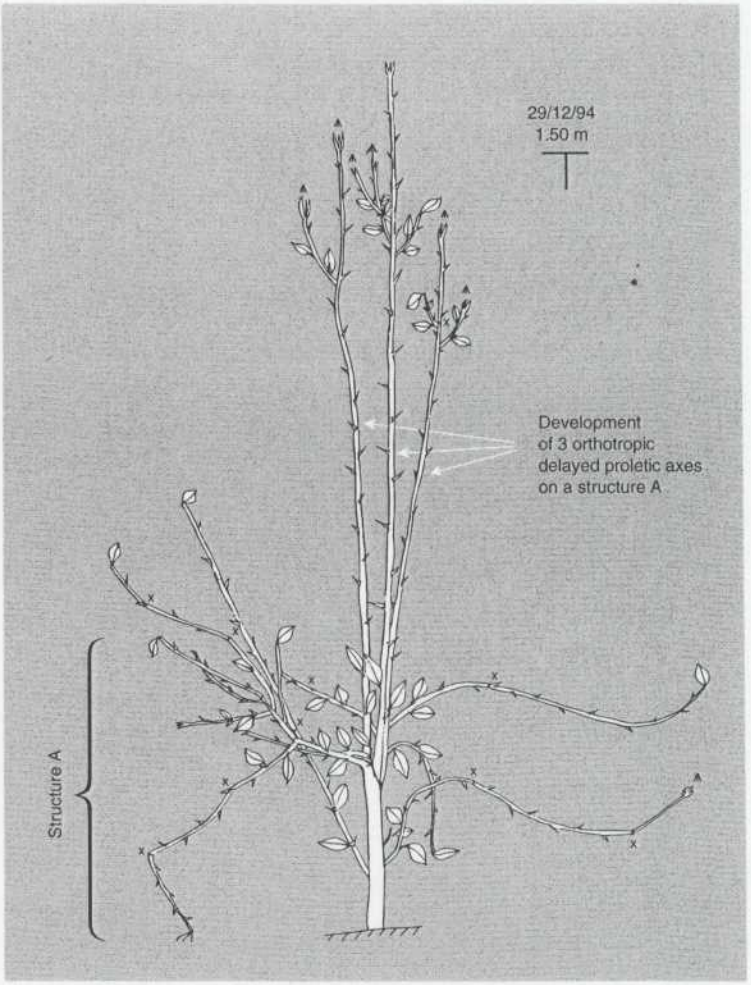


Figure 9.
Frémont mandarin tree at the beginning of phase 2 characterized by the development of vertical axes at the apical extremity of the module grown from seed.

5. discussion

The notion of reiteration has considerably evolved since the time when the bases for plant architecture were first established. It was first defined by Oldeman [18] as the

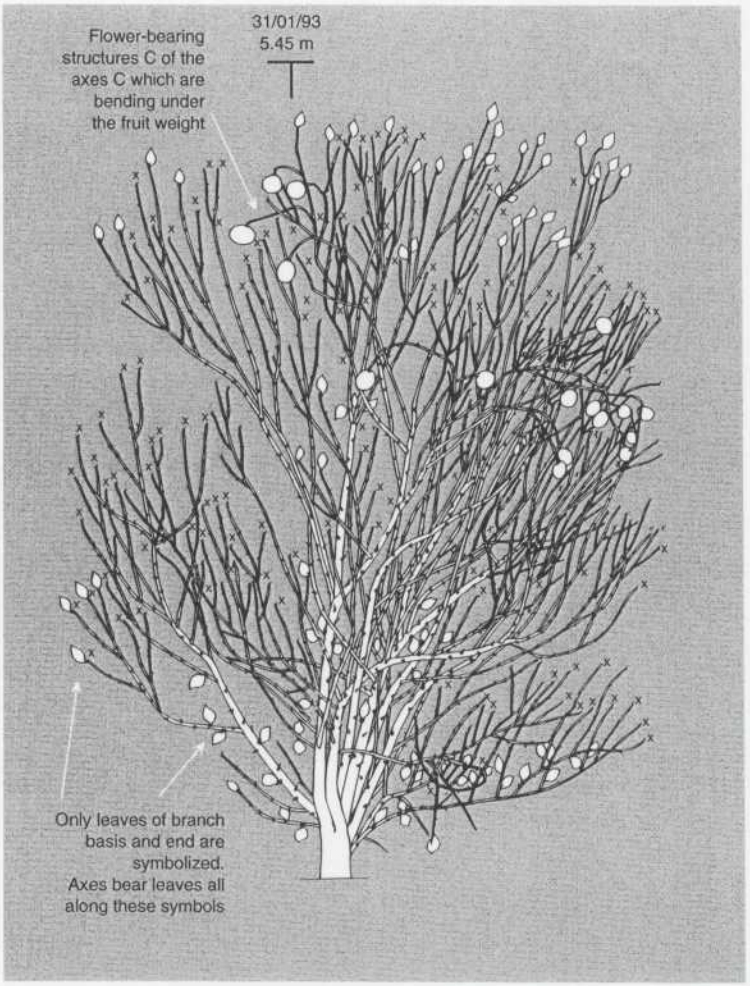


Figure 10.
Frémont mandarin tree at the beginning of phase 3 characterized by the development of the flower-bearing structures C.

"development of lateral axes characterized by sequences of differentiation occurring during the development of the model... These sequences experience a latency period before achieving an architecture partially or totally similar to the model..." This notion referred then to the development of structures of substitution as a result of a trauma or a change in the environment (adaptive reiteration); reiteration occurs for example when the tree is over-exposed to light. This phenomenon was considered as an opportune reaction.

Later on, Edelin [11] defines the sylleptic reiteration with automatic, endogenous properties as a part of the general development of the monopodial tree. It also reveals a progressive loss of the controlling capacity of the terminal meristems. These reiterated complexes are mostly observed at the crown of adult or old trees. In juvenile trees or 'trees with a future', on the other hand, the architecture is identical to the architectural model. Trees such as guava trees consist of the repetition of a structure corresponding to the initial model [4–6, 19]. The reiterated complexes are therefore an integral part of the sequential development of the plant. The term 'architectural unit' suggested by Edelin [20] to describe such a structure is used to avoid the contradictory meanings of the adjectives 'reiterated' and 'sequential' found in the expression 'sequential reiterated complex'.

Citrus trees, especially combavas with their spatiotemporal succession of three distinct types of structures, give a new dimension to plant growth. Considering the fact that these structures develop and come one after the other following a specific order, they form an intermediate level of organization between the architectural unit and the entire plant. This unit of superior level in combavas, for example, consists of the succesion of: 1 structure A + 3 or 4 structures B + n structures C.

The development of plagiotropic axes in monopodial or sympodial trees with differentiated axes indicates a morphogenetic evolution towards sexuality. If the plagiotropic axes which grow at the base of the tree are naturally pruned before bearing flowers, equivalent axes developing higher on the trunk or their ramifications will flower.

Citrus trees of the genus *Citrus* grow plagiotropic branches in the very first stages of the vegetative development: the structures A consist of mixed or plagiotropic axes; the main axes of the architectural units of the citron trees are mixed and develop plagiotropic branches; the structures B of the combavas consist of plagiotropic axes developed at the extremity of an orthotropic module, etc. The oblique ramifications of mandarin, orange, and grapefruit trees become horizontal when drooping or when the distal extremity of their main axis bends. In a group of acrotonic ramifications originating from an orthotropic axis, the mod-

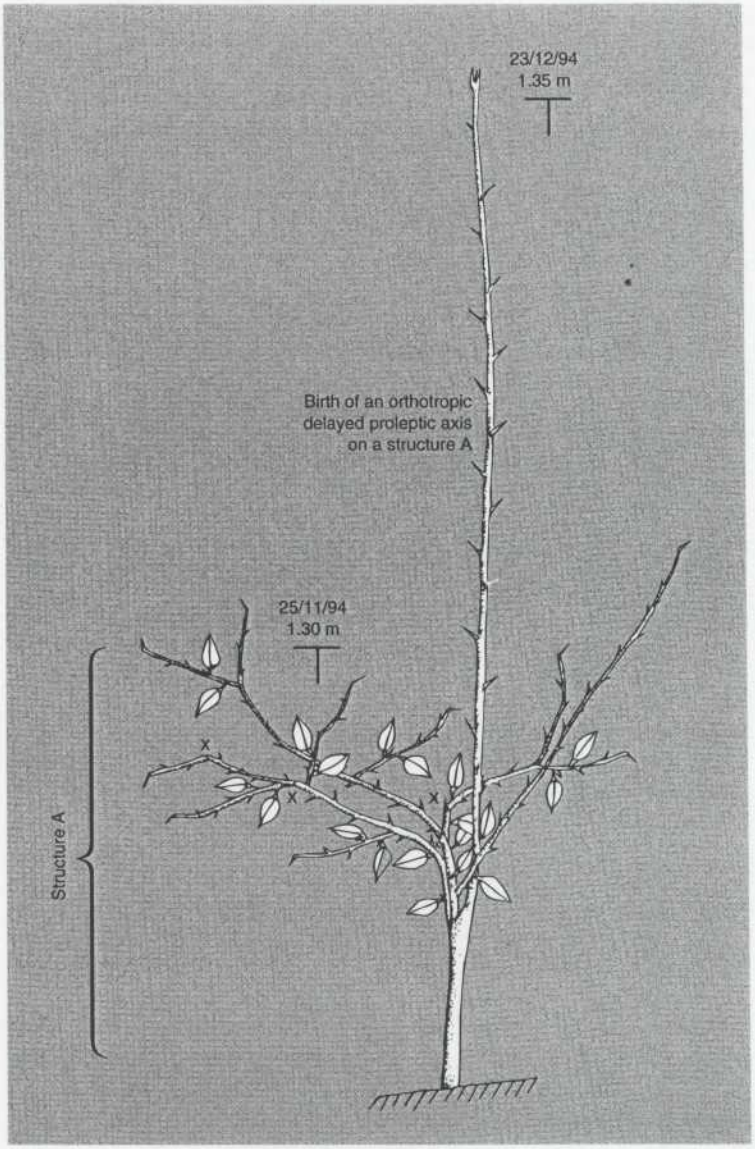
ules closest to the apex of the mother branch are almost upright, whereas the modules developing near the base are almost horizontal. In conclusion, all these trees develop plagiotropic shoots very early. Those which developed during the early stages remain sterile. The first flowers appear on the oblique or vertical ramifications of the structures C at the top of the tree; these organs appear to be less differentiated than the plagiotropic axes which developed during the previous stages and bear fruit only after developing structures C.

The plagiotropic shoots, located in the upper part of the tree, produce sexual structures. This is mostly due to the fact that they support structures C with a deferred development and not because they ramified in a sequential way to reach an order compatible with the development of sexuality.

All the axes of the grafted combavas grown under the same conditions as the trees grown from seed previously described are vertical or oblique and bear fruit early. By grafting meristems of structures C, it would be possible to bypass the phases 1 and 2 and go directly to the stage of development of the structures C. This is also true for other species such as the mandarin, orange and grapefruit trees. But because of the absence of structures B in these species, the phenomenon is less visible.

On the contrary, when the scions originate from axes which are the result of a morphogenetic evolution, the grafted meristem generates a short horizontal axis which produces a vigorous orthotropic axis. This axis is at the origin of a ramified complex which bears fruit relatively early; its vertical growth however corresponds to a dedifferentiation.

The reason for the early fruiting of the grafted trees corresponding to a rapid morphogenetic evolution is still unknown. Could it be a consequence of the grafting of lateral meristems of structures C ? or could the mechanical process involved in grafting stimulate the development of fruit-bearing structures while reducing the vigour of the tree? A morphogenetic gradient on the growth units or on the sympodial modules could also be taken into consideration.



6. conclusions

These observations will direct future studies essential to a better understanding of the mechanisms involved in tree development and fruiting; they also allow one to arrive at some practical conclusions.

The development of flower-bearing structures is preceded by phases during which sterile structures are produced despite the presence of plagiotropic rami-

Figure 11.
Kumquat at the beginning of phase 2: development of a vigorous, vertical axis on the initial structure A.

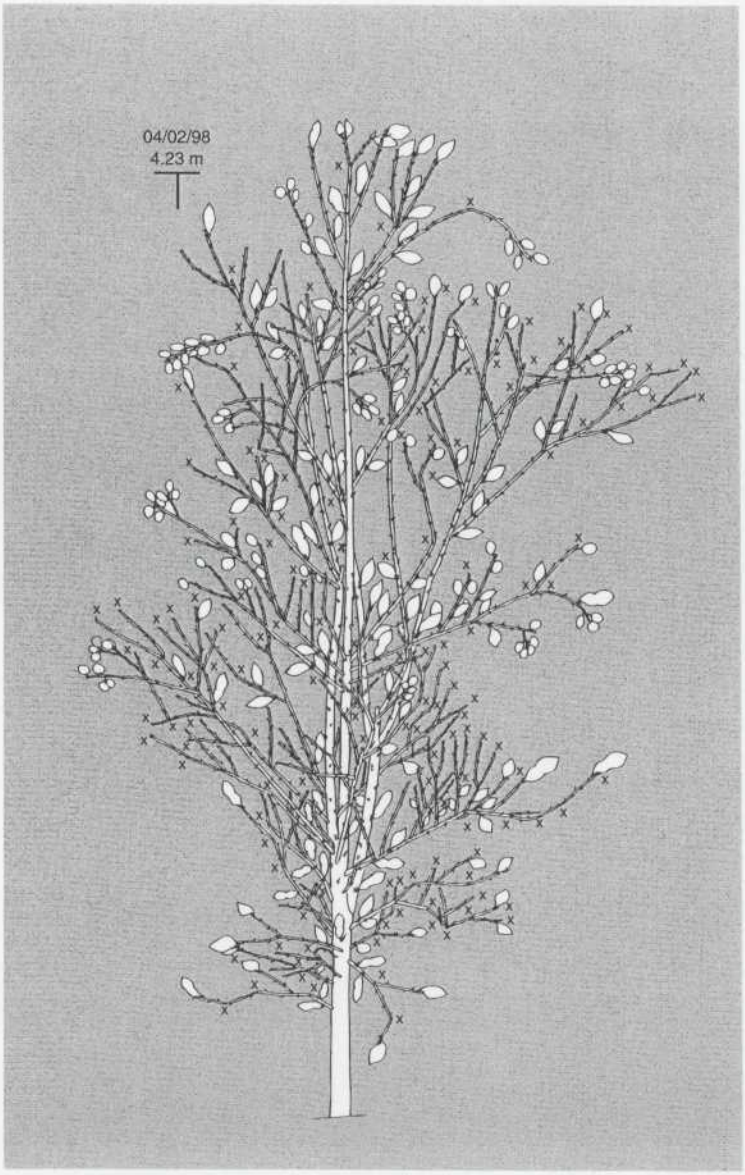


Figure 12.
Adult kumquat formed by fruit-bearing structures C developed on shoots of order 3 or of a higher order.

fied complexes. This phenomenon explains why fruiting in trees grown from seed occurs later than in grafted trees. The presence of plagiotropic sterile shoots is unusual for arboriculturists who are accustomed to the culture of grafted plants. The lack of knowledge about this phenomenon could lead them to serious mistakes such as pruning the tree inappropriately (for example, cutting off the vertical axes to trigger the growth of plagiotropic shoots).

To stimulate the fruiting process in citrus trees grown from seed while avoiding the problems related to rootstock/scion incompatibilities, it would be possible from then on to resort to self-grafting. A priori, scions from flower-bearing structures C would be the best choice for this propagation method. With these particular scions, the tree would not have to go through the entire morphogenetic cycle before fruiting. Only adequate experiments will confirm the effectiveness of such a method.

These observations helped to define stages of development and structures specific to each species. Some differentiated organs apparently have no further evolution. It is essential to research the morphogenetic potential of the lateral meristems selected at different levels of each structure of a citrus tree, to assess the shape, the vigour, and the fruiting potential of the trees generated after grafting these different types of buds.

The fact that the meristems used for grafting are selected at different stages of development of a citrus tree could explain the heterogeneity of the plants generated by this type of vegetative propagation. It could be the source of the differences in behaviour observed between old lines frequently reproduced by grafting and lines rejuvenated by seed planting. The extra-vigour gained by a regenerated line grown from a somatic embryo cannot be totally attributed to the elimination of pathogens, because the plant developed from the embryo shows juvenile characteristics such as substantial vigour and the necessity to go through the entire morphogenetic cycle before fructification. When grafting its meristems on vigorous rootstocks and cultivating the plants obtained in zones favourable to vegetative growth, it will take a long time before they yield their first fruit.

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Desarrollo arquitectónico de algunos cítricos procedentes de semillas en las primeras floraciones.

Resumen — Introducción. Para verificar si las propiedades de los órganos diferenciados se transmiten a los clones multiplicados vegetativamente, es indispensable identificar las etapas de diferenciación que preceden la producción del fruto. Estos trabajos presentan un estudio de la arquitectura que es esencial para la comprensión del desarrollo de la planta. **Definiciones e introducción general sobre la arquitectura del árbol**. La definición de los términos que se suelen emplear en la arquitectura del árbol se completa aquí con la terminología específica de la arquitectura de los cítricos. **Material y métodos**. Las observaciones de cítricos se realizaron en un clima de tipo sudanés. Los árboles se colocaron en las condiciones propicias para su desarrollo. Para seguir el desarrollo de los árboles, se realizaron obser-

vaciones cualitativas – con etiquetado, fotografía y dibujo de las plantas – desde que empezaron a desarrollarse las plántulas procedentes de semillas. Se describen las características morfológicas de las especies elegidas. **Desarrollo de los árboles de la germinación a la fructificación**. Tras una caracterización de la germinación de los granos de cítricos, se analizó el desarrollo de las especies *Citrus medica* L., *C. reticulata* y *Fortunella japonica* (Thunb.) Swing. Las estructuras A desarrolladas por los cítricos están formadas por ejes mixtos o bien plagiótropos; las estructuras B están formadas por ejes plagiótropos desarrollados en la extremidad de un módulo ortótropo; las primeras flores aparecen sobre ramificaciones oblicuas o verticales de estructuras C en las copas de los árboles. **Discusión**. Se desconoce aún el porqué del precoz cuajado del fruto de los árboles injertados que corresponde a una evolución rápida del movimiento morfogenético. ¿Podría deberse al injerto de meristemas laterales de estructuras C o quizá deba atribuirse al acto mecánico del injerto que contribuiría a acelerar el desarrollo de estructuras fructíferas, disminuyendo el vigor del árbol? **Conclusión**. La extracción, en diferentes fases del desarrollo de un cítrico, de meristemas para el injerto podría explicar la heterogeneidad de los plantones obtenidos mediante este tipo de multiplicación vegetativa.
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Citrus **/ desarrollo biológico / diferenciación celular / crecimiento / Côte d'Ivoire**