PLANT MORPHOLOGY AND ARCHITECTURE COURSE

So, today we'll look at the results of a discipline that was born about thirty years ago with the publication of synthesis work from Halle and Oldeman in '70 and Hallé, Oldeman and Tomlinson in 1978 on vegetal or plant architecture. What is it? This is a new approach, very original, that is it takes into account the growth dynamics of plants and the whole of the plant. We will therefore analyse the nature and the relative position of the various parts of a plant during its growth and as a function of the conditions.

At a given time, the vegetal architecture of an individual will be the result of a balance between the endogenous processes that is inside the plant and influence of environmental factors and therefore the purpose of this architecture is to identify the endogenous architectures vis-à-vis the exogenous architecture or which result from technical conditions.

Before moving on to the notion of vegetal architecture itself, or plant architecture, let me remind you of the morphology and criteria which are being used to identify the plant, that is to "read" its architecture. First, a plant is always composed of two parts: an aerial part and an underground part. And what characterises the parts are the organs which are borne and especially in the aerial part the organs that will be used for photosynthesis and which, of course, are the leaves. The root system may have different structures. Usually it is comprised of main roots and secondary roots. The limit between the two zones is what we call the "neck". This is a boundary where the anatomical differences make it possible to identify the difference between one and the other. Therefore, the aerial part which is, of course, visible, except in some plants which are epiphytes which grow on other plants and therefore the root system is also highly visible. So, as I said, this is the aerial part or we also call it the caulinary part from *caulus* in Latin, which means «stem», and a root part often underground, in most cases underground, and composed of roots.

I will not go into details for the root systems, but will pay attention to understanding the aerial part and its functioning. As you see it is composed of fundamental or basic entities which are themselves a part which is a stem, which we call the internode, a portion here where the leaves can be inserted, we call it the node, and, of course, the most, in most cases, a complex green part which we call the leaves with, of course, at the connection here one of several buds, lateral buds.

This is essential because this is what will define the structure of any vegetal and lateral bud here. All this is forming what is called a metamere or also referred to as a phytomere. Why the two names? Well, simply because metamere comes from the animal world such as most of the notions we find in botanics (botany), defined initially in the animal world and then which were subsequently to the vegetal world. The metamere is the basic entity of the body like of a ring worm that repeats itself but there is, of course, no head and no tail or posterior part, although this could be discussed, as you can see, a structure that will be repeated through this basic structure that will be produced during the growth which is one of the main phenomenon of vegetal growth.

How do the organs get formed? Well, they start at the apical part. There are axes for the caulinary part and this is what we call the meristems. This will be a terminal bud for a stem which will make it possible to give birth to the organs you see over there with a central zone which composed of embryonal cells that will divide and give birth to the various structure of the plant. And therefore, we are dealing here with the apical dome which is at the centre of what we'll call the apical meristem bearing in mind that this structure is highly fragile and most often it is protected by the start of the first leaves you can see here which are, when they're not differentiated, they're called *initium* and then *primordium* when we are able to identify their structures.

These are young leaves. The formation process of these structures from the apical dome is what we call organogenesis. We'll come back to this point later on. Organogenesis, that is the formation of the organs, and once the organs have been formed they can expand and grow and we call this the elongation process. And the assembly of the two processes, organogenesis and elongation, giving what we call the growth.

If the growth results from the functioning of the primary meristems, we'll talk about primary growth which results from the caulinary or root meristems. These are mainly organogenesis and elongation processes of stems and roots resulting from the functioning of the primary meristems, as we saw earlier on, of stems or roots in which case we will find them in the most apical zones of the roots as I will show you later on.

There is another situation for growth. It's called the secondary growth found mainly in dicotyledon, that is, trees, shrubs and it is expressed in a very different way. Through the functioning of a secondary meristem, the structure of which is cylindrical, which is called, in vegetals that have it, we call it a cambium. And this cambium will produce wood in the trees, which is important for your future profession. This secondary meristem, or cambium, will produce inside, of course, wood, or xylem when we're in the young stage, and towards the outside phloem, wood produces the raw sap and of course when produced the elaborated sap coming from photosynthesis.

Other key points on vegetal growth: we'll establish a distinction between what we call the proximal and distal parts to make a different, to differentiate between the high part and the low part and we'll see why in such a vegetal, for example, on the other side of the neck we'll see on the stem, which is here (I remind you that the boundary is the neck) there is a proximal part which is the closest to the site of origin, that is the neck, and a distal part which is, of course, the one that is most remote from it. That is for the stem. Of course the same principle would apply for the roots except that it would be reversed, the proximal part being close to the point of insertion and the distal part being close to the end or to the extremity.

Why should we use terms like this instead of "top" and "bottom"? Well, you can see here that in the root the lowest part is the distal part whereas it is the opposite in the stem. It would be the same thing with a little branch or branchlet that would be hanging. The proximal part would be, in fact, highest whereas the distal part would be the lowest. Therefore they are morphogenetic terms that define the structuration (structuring) and the birth and growth of organs and which are different from geometrical terms, which indicate the altitude of a structure with respect to gravity. What else could I say in order to explain the general phenomena?

Let's talk about an important phenomenon: the pre-leaves, of structures which are often neglected in teaching whereas they have quite remarkable structures in vegetals. If we take a look at the lateral buds there will be several type of structures that make it possible to identify their positions and their birth. Namely, the first leaves which are formed by the lateral meristem and which we call the pre-leaves. In dicotyledons there are always two pre-leaves, the alphas and betas, which are opposite and on the other side of the bud. If we were to draw a diagram here with the leaves here, the axial leaves, and here the bearing axis, which we'd call AP on this diagram, we can show the position of the two pre-leaves. This is the bearing axis here, the axial leave being here and the lateral axis or the central part here of the bud before its growth, of course, the pre-leaves will be therefore lateral, alpha and beta. They will always be in that position. That is constant in vegetal and it's rare because very few phenomena are so constant. In dicotyledons two lateral pre-leaves; let's say that I am the bearing axis and the two pre-leaves would be like my two arms. In monocotyledon there will be only one pre-leaf and it will be backed against the bud and I will show it to you now. In monocotyledons one pre-leaf only. What should be noted, what is worthy when we will do studies, is that the most primitive families of dicotyledons such as the piperaceae will have only one pre-leave like monocotyledons so they're neutral and they are essential. In monocotyledons it is rice, orchids and wheat and this pre-leaf, in fact, will embody the twig or the bud and it will have a sort of bi-faired shape with a double fairing…Well, you know what is the fairing or the hull of a boat…You've got two here and it is backed against, that is, it is here, between the bearing axis and the born axis.

Last criteria and we'll look at before moving on to the illustrations, this is a specific criterion, very useful to describe vegetals, and which is called phyllotaxia. Phyllotaxia or phyllotaxy is the mode of arrangement of leaves on their bearing axis. We'll skip this because you will find that in many books. We will make a distinction between the alternate phyllotaxis, that is when there is only one leaf per node, in which case we will see several, well, we'll have several solutions. The alternate spiral phyllotaxis, which is quite frequent in many species, which leads to an arrangement of the leaves in all directions which will give us a radial symmetry, that is there'll be leaves in front, others will be lateral, and so on and so forth. Others will be at the back and there will be leaves that will be distributed on a spiral and if we were able to show their expressions on the meristem. Whereas there will be a so-called distichious alternate phyllotaxis if the leaves are along a same plane, that is on the left and right of a plane which could be shown like this. Therefore leaves which are along a same plane alternate distichious phyllotaxis but in each case there is only one leaf per node. Therefore it is called the alternate phyllotaxis.

We will now find a situation with two leaves per node and it's called the opposite crossed phyllotaxis. Opposite means there are two leaves per node and crossed means that from one pair to the next one or to the previous one there is an angle of 90° between the two sets of leaves. I could show this in this way and as you can see the leaves will form two octagonal planes as we shall see in the illustration and, of course, they could be secondary re-arrangements. I'm referring here to the strata that exists in the meristem.

Last type of arrangements it is the so-called verticillus (whorled) in which case there are several leaves per node. That is, the leaves will be distributed from the same point on the stem as this is the case in some species such as dyera costulata or possibly it is found in some individuals of vegetals which may have an opposite crossed phyllotaxis as is often the case.

To illustrate this course, and particularly the first part on the vegetal morphology, let me give you a reminder of what is a vegetal. Vegetal morphology is not an old discipline. It was created by Goethe in 1789, that is, when we were happily slaughtering one another during the French revolution. Goethe was also a poet and he did this study, observation, of vegetals and he was able to understand that they have a root system and a caulinary system, but mainly he was able to show that the various organs that formed the leaves, be it the primitive leaves such as the dicotyledons or the subsequent leaves which could have different structures such as simple here or here with diverticulae, these leaves were all the expression of a basic organ which is called the *Urblatt* which repeated itself and would metamorphose during the growth. This notion of vegetal metamorphosis does not only apply to the succession of metameres on a stem but also at the level of the global architecture of the vegetal which is in some cases may go into total metamorphosis. The main progress of Goethe's work was to show that all those organs, be they vegetative or the portions of the organs of the *fleur* it's not the *pétale*, and others, they were all the expression of an elementary organ that transformed during the growth which, of course, is evidenced by the works of modern genetics. The structure of plants in a dicotyledon is always similar with the root and caulinary systems, buds which are terminal at the top of the axis or at the node which is most frequent in today's vegetal.

What do they look like, these meristems? They are domes of small embryo cells you can see here in the labiate. And you can see the denser zones which correspond to what we call the initial ring from which the auxiliary buds for the leaves will come out. And you see them here as meristems. The roots also have their primary meristems. They are called the primary root meristems. That could be about here. That is the organ of genetic zones whereas a part of larger cells corresponds to the cap which protects the apical meristem as it penetrated the ground. There are primary meristems and in some vegetal there is also a secondary meristem which has the shape of a cylinder in the stem and in some cases, as you can see here in this maclura, they form several successive rings. And it's not always the case especially in some tropical species. Primary growth, as we saw, is the result of two processes, organogenesis and elongation. Organogenesis is the formation of new organs which takes place around the apical dome, near the initial ring, and we have initiates or primordia which will then turn into leaves and then finally they will be the fully extended leaves. There is always the same structure and we see the repetition of an elementary entity, an internode, the node with the leaves and the nodes with the lateral buds. This phenomenon is key because growth is simply a reiteration process. This terminal meristem is most often protected because it is very fragile within a specific structure. Here it is in a viorne (viburnum). The meristem would be around here and as you can see it is protected by young leaves. However, such leaves are a very small representation of the larger ones. This is what you can see in a persea Americana and you can see the leaves are simply smaller but they have exactly the same structure as the adult leaves. In this case there is no differentiation between the starting leaves and the adult leaves. We talk about "bare" buds. Whereas we will talk about "scaled" buds when during a rest phase the terminal meristem is protected by transformed leaves which are called cataphylls which are scaly leaves which could be green or not and which will rapidly fall during the elongation process. These cataphylls are only transformed leave structures you can see here they are more hard and then they will leave room to assimilating leaves. At the junction of the leaves there will be a bud, but, of course, there will be also several lateral buds. This is the case for this chestnut tree. You can see here the scar of the leave and you can see one, two, three buds each with different potentials.

What is essential here is that will find at each of the bud the two alpha and beta lateral pre-leaves that will make it possible to identify that they are auxiliary buds. In this gleditsia triacanthos the leave would be here with only the scar it's gone. You will see the traces of the pre-leaves on the other side of structures and you can see that at a few millimetres the same lateral buds from the same axil can give birth to different structures. Here there is a short branch, here a long branch and here a thorn. So as you can see differentiation takes place very early in the meristem because when the organs grow they give different structures.

In these two plants you will find each time whenever there is auxiliary buds the two alpha and beta leaves and we are talking about surnumerary, surnumeral buds. This is the same thing for a forsythia, which is an oleaceae from another family. But it's very different in various ulmacae this Zelkova and the diagram which shows the auxiliary complex of an orme (elm) or a *Celtis australis*, which as you know is the lotus tree…near Montpellier it is used to do forks in Sauve. Sauve is a small village near Montpellier where they do wood forks with three teeth (prongs) and of course a long handle and for this they will use this morphological specificity, that is they will cut just above the buds. They will allow the tree buds to grow and then the axis will give the handle and the lateral axis will give the three branches of the fork, which will have to be bent to turn them into a fork. In which case we are not dealing with other numerous buds but there is a main bud with the two pre-leaves, alpha and beta, and each pre-leave in the bud will lead to a lateral bud and you get the alpha and beta pre-leaves. So you can see a very specific structure, for example in the apricot tree. This lateral bud here will give one axis whereas the two lateral buds will give the leaves.

So for structures which are almost microscopic or very, very small at least, there is a very early differentiation and this should be borne in mind.

Last criteria we analyse is the phyllotaxis, that is the mode of arrangement of leaves on the stem. There will be first a so-called alternate phyllotaxis, that is the leaves are inserted isolate (isolated) at each node and this can be, well, in spiral, for example the leaves will be arranged along a spiral and will, of course, go in all directions in space, which is the case for this impatiens and you can see the youngest leave and the level of anteriority and you could almost draw a spiral to group the leaves along the stem. And this is what you may or may not have done as you were a kid in school, kindergarten, you know, you give a potato and you do spirals on a potato. Well, it's the same thing except that the potato is a bulged axis instead of being a stem. The alternate phyllotaxis characterises the trunk of several trees because before branching the trunk will arrange the leaves in all directions for a better capture of light. Spiral alternate phyllotaxis can be characterised by what we call a phyllotaxic index, that is the number of turns over the number of leaves found to come back to the same vertical line which is called an orthostich. If you take the glutinous aulne (alder) and the first leave is here and to find a leave on the same orthostich you will do one turn of the spiral and you will count one, two, three leaves which mean the phyllotaxis index is one over three, that is 360° over three, that is 120° between the various leaves. For vegetals in alternate spiral phyllotaxis the indices are 1/3 or 2/5 that will most often be found. 2/5, that is you will do 5 leaves and two turns of spiral before you have a leave which is just below the first you started from.

Another case of alternate phyllotaxis is the distichous phyllotaxis. In anonaceae here, and you will see that there is only one leave per node but the leaves are arranged along the same plane which is that on board, therefore we talk about an alternate distichous phyllotaxis found in various species of trees but also shrubs such as this phyllanthus which is an euphorbiaceae, the leguminous, for example this Judas tree, you see exactly the same arrangement along the plane or even in other vegetals such as the irises or here an orchid from Venezuela, the Maxillaria valenzuelana, which as you can see has the leaves along the same plane.

So other types of phyllotaxis, the crossed opposite phyllotaxis, because there are two leaves on the same node and they are so-called opposed. From one pair of leaves to the next one you can see that the leaves form a 90° angle so this is why they are so-called crossed opposite phyllotaxis and I think the real opposite phyllotaxis without being crossed does not exist and so far has never been described. Therefore we can assume that would be cause of depletion of the meristem because both the lateral nerve stem and auxiliary leaves would grow on the same side of the meristem.

Another type of crossed opposite phyllotaxis frequent in other families, in the melastomaceae for example, and the verticillé (whorled) phyllotaxis there will be several leaves at each node, here in this Peperomia where there will be between 5 and 6 leaves on the same node and Peperomia belong to the pepper family, the piperaceae. In an Apocynaceae Dyera Costulata and you will see the six leaves which are on the same point of insertion. Often they will be verticillar phyllotaxis in families which otherwise would be with opposite crossed phyllotaxis. As the case here there would be this phenomenon in Rubiaceae with the Duroia, if some of you know it, in which we also have this verticillus phylotaxis.

Phyllotaxis is the mode of arrangement of leaves in the buds. That is the start up of leaves but they could be also secondary re-arrangements in several ways, for example, this is an opposite crossed phyllotaxis but you will see that because of a torsion of the internodes the leaves will progressively be brought back to a same plane which could make us think to an opposite phyllotaxis but it's simply a secondary rearrangement. This phenomenon is found in Cornus, here in Cornus mas and you see that the leaves are along the same plane but if you, in fact, look at the internode it is twisted and it brings the leaves back along the same plane. In other cases it is not the internode that will twist but the foliar limbs that will be brought back along the same plane and this is found in a Maytenus, Maytenus chubutensis, and you will see that leaves are distributed to occupy space as best as possible. We thought that secondary re-arrangement can be very confusing.

So, let's get back to the morphological characteristics and mainly what we call the growth phenomena, mainly primary growth which we will not discuss the functioning of the cambium. Let me remind you that primary growth of the stem results from two phenomena: organogenesis which is the formation of organs and elongation which is the elongation, the lengthening, of the organs once they've been formed.

First, depending on the modes of elongation of the organs, there is a growth that we call a continuous growth. In which case, if we measure the elongation of the stem as a function of time and you will see that this elongation is more or less continuous even though there may be fluctuations in some cases as shown in the main growth. This continuous growth is an absence of stoppage of elongation. We see this in many palm trees and in some tropical species bearing in mind that this is, in fact, very rare. In most cases when there is continuous growth in fact there is a stem onto which the leaves will have the same size, more or less, with internodes of identical length and therefore there will be no markers of growth or stoppage of growth as we shall see afterwards. Most often in continuous growth the organogenesis in fact will take place in a parallel way and there will be here organs which take form as the elongation takes place.

Let me remind you in this continuous growth there are several palm trees, Rhizophora, or even vegetals which are potentially with a continuous growth but which are modulated by the environmental factors. This is the case for cypress trees if they are cultivated in a stable continuous condition they can have almost a continuous elongation whereas if there is a cold winter or very dry summer this elongation may be modulated or even sometimes stopped in the most severe cases. There can be fluctuations but there is no stoppage as such.

So, in the case of continuous growth is it necessary to have a certain constance (constancy) in the length or could there be fluctuations? And could there be rhythmic growth, for example? Well, in the case I will show you this is for the rhizophora, the mangrove, this was demonstrated several years ago, so if I show this in weekly growth there will be elongations which would have this shape. They fluctuate depending on the seasons. It would be roughly to a small dry season whereas the rest of the time this would be a rainy season or organogenesis sometimes, in fact, will be offset and there will be accumulations of parts which will add up with the elongation. This is the rhizophora mangle, which is the large mangrove of the Caribbean and the Americas, this has been demonstrated by Tomlinson and Gilles for individuals growing in Florida in conditions which are not equatorial which are sort of tropical to subtropical.

Now we move on to another type of growth which is very different and this is what we call the rhythmic growth. And let me remind you that we consider that we are here dealing with the elongation and we're not looking at the organogenesis. So, rhythmic growth... Here you should remember this is the major growth mode of vegetals and it is not associated with climate where there is a very strong seasonality. Many plants or vegetale even in equatorial conditions will have a rhythmic growth called an endogenic growth despite stable and favourable conditions. The elongation will stop over a certain period of time. This is the case in the Hevea Brasiliensis, for example, the rubber tree, and if we measure the elongation length or height of the trunk of several individuals, as shown by Hallé and Martin, hevea brasiliensis, it is a euphorbiaceae, so this is the rubber tree…As I said the study was carried out by Hallé and Martin, carried out on this species…And if we measure the elongation we can see that it takes place in sort of waves. It stops, it goes, and stops and resumes and so on and so forth. In fact, this rhythmicity corresponds to a clearly defined duration in equatorial zones. This elongation phase and rest that is the beginning of the elongation of the stem until it resumes again lasts about 45 days in equatorial conditions. It can be slightly modified in tropical or subtropical conditions. What is interesting to note here is that the stem will be formed by means of a series of portions which were built up during the period of continuous elongation and these portions will be called the growth units. The hevea leaves are trifolia and very often, well, you will see at the basis the cataphylls which therefore indicate a structural rhythm which superimposes itself to temporal rhythmicity. This portion of stem here between the two references which indicate stoppages of the growth corresponds to what Hallé and Martin called a unit of growth. I will often call it the UC.

You can see already that with respect to continuous growth this is a new phenomenon that is the repetition of a biological entity which is embodying more than the metamere. That is we will repeat the metameres but also the level of growth units when we have this rhythmic growth which again, let me tell you, is the main mode of growth of vegetals even of they are equatorial vegetals. All this will lead to the presence of markers of the rhythmic growth and the markers later on will be illustrated but they can be morphological or macro-anatomic. Very often there are cataphylls at the basis of the growth unit. Why cataphylls? Because they are structures that protect the bud during the unfavourable period, that is winter in temperate zones or summer in dry tropical zones. And the cataphylls will remain at the basis of the growth unit and will indicate the successive entities.

Well, why is it important? Because when they fall, well, they leave scars on the stem that can be identified, sometimes tens and tens of years afterwards, and therefore when you look at a tree you can reconstitute its history and see how it was formed. For other markers could be the structure of the pith, for example, or narrowing and we see this on slides later on.

Still in the rhythmic growth, we can see several cases for the rubber tree, for example, there will be a repetition every 45 days of a new growth unit more or less identical to the previous one which means that the stem has an articulated structure and will appear as a succession of unit growths that cannot be differentiated. In other species, for example, you will see different structures. On oak trees, there will be, for example, a first growth period that will take place in May, another one in May or April, it will depend on the species, and then there will be another one taking place in June and possibly for other species, right now if you go to the country you will see that green oaks have new leaves therefore in October there will be a new growth period or growth wave. As you can see therefore that there is a lack of homogeneousness throughout the year and depending on individuals there could be one in May, one in June or possibly only the May or June waves which means that there can be several growth units within a same year and we call this the monocyclic or polycyclic principle.

So we talk about a monocyclic species when it does only one growth unit per year and we'll talk about polycyclic axis or species when several growth units will take place per year. And that is the case of many tropical species. We see it in the hevea but in all the species such as the oak which has several cycles per year or the beech, birch tree, sorry, or the individuals in chestnut trees for example. In plants like hevea this polycyclicism does not cause other heterogeneousness. In other species, polycyclic species, we will see the occurrence of another level of organisation that is the annual sprout or growth which corresponds to all the growth units formed during a year and which will have specific dynamics and which can also express specific morphological characteristics. For example, in most pine trees, not jus the maritime pine trees, but the pinus sp. , for example, the pinus pinaster…when there is a growth, bicyclic growth, so PA means annual growth…well, the first year you will get a first growth unit, a long one, which corresponds to the female cones and which may have also branches, the same year and the following year, and another growth unit, which, another one which is sterile, that is it has absolutely no female cones. And if we look at the structure the following year, you will see a specificity. The female cones will still be here. Of course, they will be one year older. They will have gone into maturity. They will be the structure here. And then sometimes we'll see that the largest branches that will be mono- or polycyclic moreover will be found mainly on the second growth unit which will therefore lead to what you call an acrotony. We will come back to this term which is very specific and which shows that the annual growth is a specific entity that is different from the growth unit, that is, the sum of two growth units within one year does not necessarily lead to this sum but can lead to a specific structure. In oaks, for example, the acorns are always on a growth unit and the leaves can be different on one growth unit than on a different and so on and so forth. I'll come back to this point later on with other examples. I will not insist on the notion of organogenesis. That will be illustrated again later on.

Let me finish with a notion that is essential in vegetals, which is linked to the growth, and to the organogenesis/elongation ratio or relationship, that is the notion of pre-formation and neo-formation.

The two notions are related to the time at which the leave and stem start grow. Let me explain myself. By the way, if I'm going to fast, let me know and I'll stop. In some cases, at the bud you will see all the organs or elements that will elongate in the next phase which are already formed in the bud. When Spring comes or when the conditions for elongation occur you will see that there is only an elongation of these structures already existing and the fact that they already exist in the bud is such that we talk about growth units or organs which are pre-formed. So we say a portion of a stem, to be sort of vague. In other cases, there will be the same thing, that is during the blooming the vegetal will elongate the elements which were already in the bud as a sort of…in a rough condition but after time often there is a drop in this speed of elongation and we will find in this axis other elements which were not in the bud.

So how do we see this? What we can do is take this vegetal, well, we will take 100 and out of the 100 the 50 first ones we'll look at the number of buds and we'll look at the anlages and on the other plants we'll look at the number of organs and we'll find the same distribution as here, that everything was pre-formed. And if we see a distribution which is significantly different with more organs here, well, we will say that the plant is formed, the axis, sorry, or the portion of the stem is composed of a pre-formed part plus a neo-formed part.

This is essential because these parts do not have the same characteristics. By way of example, the leaves can be different between the pre-formed and the neo-formed parts or, in some species, the blooming will take place in only one of the parts or in others only the internodes of the pre-formed part will be good for budding and others will not. So, you can see that in the case of the pre-formed buds the part that is elongated depends on the year +1 for external conditions whereas the pre-formed organs were formed previously and in a period before the neo-formed organs. For example, in a monocyclic plant that will stop, or will be sleeping all winter, there will be organs in the bud that formed in the Spring or the Autumn of the year N, whereas this part will have elongated during the Spring of N+1 whereas in the neo-formed part the organogenesis and the elongation take place almost simultaneously and in the same conditions. A third case, when we dissect the buds we see nothing inside, or, well, the dome only because, of course, there cannot be nothing. And when the plant is elongated it will form organs as it expands or becomes elongated and we are talking about a portion of the stem which is entirely neo-formed which is a very rare case, of course, observed correctly in an American ivy a couple years ago. But we will find this behaviour most often in the case of stump rejections when you cut a tree where buds will form and elongate the organs as they expand and develop them.

I will illustrate these various parameters. Of course, if you have questions don't hesitate to take them, to ask them. Well, first let me illustrate this with a mode of growth I did not talk about because it's quite simple. It is the growth which is defined or undefined. In a defined growth, there will be an apical meristem which at a certain time will turn into a structure which can no longer be elongated. This is the case, for example, of terminal flower transformation. There will be the same case for a Tulip, for example, the axis turns into a flower and can no longer elongate into a vegetative structure. In another case this axis will be finished by its so-called terminal inflorescence or by a thorn. This is the case for the Argana Spinosa in North Africa where once the axis has functioned for a while will turn into a thorn which can no longer grow. In other cases, this axis will transform into a spiral. This is the case in the African landolphia or this Gouania which is illustrated here. This would be the case for the vitaceae and the Vitis Vinifera vine which is constructed by successive models which all end up in spirals. Another case, frequent case, in other species they are the abscissions of the terminal meristem. This is a plane tree, for example. At each end of growth unit the plant finishes its elongation and afterwards the terminal meristem, sometimes with the last two nodes, will bud, become necrotic, die and fall and there will be a scar. And what you see here is not the terminal bud but, in fact, it is a lateral bud which is axillated by the leave that you see here and it fell because in the plane it's very different because there is a kind of a cap that comes on the bud hence the annular scar you see here and what you see here, in fact, is a lateral bud but which will take, which will grow in line with the initial stem and you won't see it unless you look at the scar here and you look at the pre-leaves because at the basis of the axis there will be the alpha and beta pre-leaves which will be in this position and which indicate that there has been a death of apex. These abscissions here are very frequent and we'll see that again. In the plane tree, for example, they are systematic at the end the elongation of a sprout, for example, or the bud. And it can be very frequent in an oak tree, for example. They're very frequent and they can occur.

Another phenomenon which is very specific, known only on tropical plants and especially in some families such as the apocynaceae or the solanaceae, like for the potato for the second one, the meristem having given leaves and twiglets and so on and so forth will be formed by vacuolised cells which can reproduce. And we therefore said that these meristems become parenchyma and we talk about the parenchymation which affects the meristem and this is notable in plants, vegetals such as Cordias for those of you who know them. And it's a very specific structure. The cocoa tree which has, of course, a high economic impact, this happens on the trunk hence its specific growth model. A cocoa tree that grows will have one stage of leaves and then branches and then the apical meristem will become paremchymed and the growth will be ensured only by a relay coming from a lateral bud that will start under that level, will go through it and will give this stage structure which is very specific of this cocoa tree which is the Theobroma cacao.

Next to these defined growth cases, that are in fact quite numerous, there will be many species which have an indefinite growth. This the case of specific palm trees, or this was the coconut tree, where growth is thus indefinite, that is one day it will stop because the tree will die and therefore there is this notion, this notion is relative. They will talk about indefinite growth when it goes over several years and throughout the life of the axis or the vegetal. Indefinite growth is what we find in many gymnosperms, for example in Araucaria but the same thing in pinus or fir trees where all axis are based on the same meristem which will function throughout the lifespan of the vegetal or axis.

Other type of growth: the growth that takes place as a function of the modes of expression of elongation. And as we've just seen, the continuous growth where length increases with time, this continuous growth is rare. It is found, it is found in some vegetals like most of the palm trees, again a coconut tree here or in mangroves such as the Rhizophoras or the Avicennia which have a continuous growth even though it can be modulated by external conditions. In the case of a palm tree, for example, you can see that if we were to dissect the tree from the oldest leaves up to the most recent leaves starting up to the mersitem and at every stage of the year we will see leaves at all stages growth or development which means that not only there is a continuous growth but there are also, there is also a continuous organogenesis which precedes or goes with the elongation. In most cases, when there is continuous growth where there will be an axis which is not heterogeneous which is formed only by the repetition of metameres with about the same characteristics as you can see here in this anonaceae. On the contrary, in some plants such as Hevea Brasiliensis, in equatorial conditions, well, there will be a meristem which goes through a rest phase and which at a given time will start elongating. You see the former portion of the stem with the three leaves and you can see the stem that is becoming elongated. When this takes place, well, this phenomenon goes very rapidly. You see this new portion of stem that takes place. You can see the cataphylls which correspond to the basis of this structure and within a few days this portion of stem has reached its final size and you can see young leaves here which, like in many tropical plants, at the beginning of their lives, are hanging and soft. Within a few days these leaves will have their limbs becoming bigger, thicker and harder and it will loose its red colour that turns green and we get to the same stage as the previous one, that is a meristem and a bud which is at rest. This will last about 45 days and the plant will therefore be contracted by accumulating portions of stem and each is constructed within a cycle of about 45, as I said. The cycles will repeat themselves. The plant is being constructed and we will see that the plant or vegetal is composed of the repetition or the reiteration of very similar entities which are all formed during a same period of time or duration and this is what we call growth units.
Again, this is essential because at the end of the course we will see that it is possible to define the development of a vegetal through four or five notions which are the same for all the vegetals, one of them being the notion of iteration or repetition. We repeat internodes or metameres in order to continue the growth and through rhythmic growth we see a new entity, botanic entity, called the growth unit and the vegetal here will be constructed through the repetition of these growth units. Again, depending on the condition of the elongation with time. We'll call elongation typical or typical rhythmic growth a vegetal which has been constructed through homogeneous waves of growth as we saw for the rubber tree. And we'll talk about atypical growth, although the word typical or atypical, I don't like them because it simply means that we don't understand the phenomenon. When you always hear something like pseudo or atypical it means that we don't know much about it. Anyway they indicate that the elongation will be rhythmic, there are phases of rest in the elongation, but it's fairly chaotic. It doesn't have the regularity of what we see in the first type of growth.

Rhythmic growth will be expressed by several phenomena. There will be alternating elongation and rest phases which translate through the occurrence of leaves you can see. There is a new crown of leaves that is being established and getting elongated and it's very spectacular.

Other specific phenomenon in tropical plants is the coloration of young leaves which can be soft and hanging as we saw earlier on and this is a pseudowintera from New Zealand and you can see that the new leaves are red. For those who have already flown over the Amazonian forest you see trees which are fully coloured and that you take for flower trees but, in fact, they are just trees that are establishing new leaves often red, sometimes yellowish, or purple and this is a criteria that is essential in tropics.

Where there is a rhythmic growth often the rhythmicity of the elongation is translated by a structural rhythm and the alternating zone of cataphylls leaves, long leaves, here, for example, we will see growth, successive growth units. It's always the case but do not forget that there are exceptions in biology and therefore we will see several expressions, for example, this protea. You can see this phenomenon which is exacerbated, several cataphylls which are membranous depending on their height and which are the basis of the growth unit and then the assimilating leaves which grow. When the leaves fall we can find the scars of the leaves here on another species you can see cataphyll zones and each has the scar of a leave and you know all these were successive growth units. And there for you can trace back the history of the tree if you know the rhytmicity, if it is let's say a yearly rhythmicity and the growth unit corresponds to a year, you can then find the age of the tree.

Other more subtle parameters exist such as the structure of the pith. This is a part that is below the apical meristem and it is the only primary tissue that remains in trees even when they are several thousand years of age. In a walnut, for example, tree you can see the small leaves' scars, and, but can't see very well here, but you will see scars of cataphylls and new leaves and so on and so forth. So we know here there's been a stoppage of growth. If we were to do a longitudinal cut, we would, or cross section, we would see the pith has a very different structure. The pith of the walnut is very specific. It is scalariform, that is just like the steps of a scale, you see, or the bars of a scale, it's the same thing except when there is a stoppage of growth. So when you do a longitudinal cross section, even with a large trunk, if you go though this pith, you will always find these growth units and you can find at the basis of a tree that is a 100 years old a stoppage of growth which occurred 99 years ago. Sometimes it is not as clear, for example for the oak tree, the Quercus Petraea, you can see the pith here which is beige or cream and you can see in the growth stoppage a slight narrowing of the pith and a colour that is different. So, criteria which are useful to understand the history of the tree.

In other species where the criteria are more difficult to evidence, this is a marine plant, the Posidonia Oceanica, and you will see that there are zones of branchings and zones without branching and to identify the rhythms, well, we have to look at the basis scales of the rhizome and we see there is a rhythmicity. Not only are the leaves larger and then smaller, but when you touch them (this has been validated by anatomical cross sections) we can see that depending on the season the folia basis are more or less thick or thin and this makes it possible to date the growth of these plants. This results from a study in which we tried to study the Posidonias to position their development to reconstitute the Posidonia field with a laboratory from the University of Nice and you know that they are being threatened by various problems such as the anchors of boats where there are the most richest zones for fish reproduction.

Another plant is the Azara Microphylla, a species from Patagonia, and you don't see any specific marker of the growth stoppage except for slightly smaller leaves at the base of the growth unit. And if you go in spring or in summer, you will see coloration of the leaves which are more shiny and lighter than elder parts. So, if you come afterwards it will be more difficult to see.

The modalities for elongation and growth are set for a species but can vary within the architecture of the vegetal or the function of time. For example, in the spruce species you see that the first year the growth is almost continuous throughout the year. It will last quite a long time during the vegetation period and the leaves produced on the stem have no difference. As of the second year, we can see that there is a slowing down. With respect to the question earlier on we can still talk about continuous growth. There is no stoppage, just a slow down. But you can see that this slowing down translates at the stem by a zone of leaves which are slightly different and the occurrence of leaves with a different structure after the slowing down. This becomes more obvious after the third year where there is true stoppage even if it is short and morphological markers are more obvious than before. And it's even more so the fourth year when there is a true polycyclism that takes place with noticeable differences between the leaves from the first growth unit and those of the second unit, with the limit between the two growth units which is very marked, and finally the plant will be essentially monocyclic at the end. Monocyclism, as I said, is the way according to which a vegetal will grow with only one growth unit per year, so every year there is one growth unit that takes place. In polycyclism there will be a set of variable number, but in excess of one, growth units that will take place and, for example here, on this example there is an annual growth with two growth units and the second one you can see UC1, UC2 and UC3. There will be three cyclic annual growth.

Therefore expression of polycyclism in time, we see elongation that can take place through a succession of cycles which are all identical one to another and in this case there is no morphological differentiation between the successive growth and to talk about a polycyclic species doesn't give much in terms of structure. But in other cases we could show that elongation could take place in a differentiated way, in a Callistemon here, for example, every year there are four growth units but you can see that the time of rest between two growth units increases between the beginning and the end of the growth year. Another example which has been evidenced is in Conte's thesis, in a Ryania, you can see that during a year, this is an equatorial vegetal from French Guiana, there are two waves, close waves, of growth and then a period of rest, a long period, and two other waves of growth. This polycyclism is found in the elongation but, of course, has an impact on the structure. For example here, for a Pinus, or in a green oak tree, two bicyclic (bicyclical) annual growths and you can see only the first of the year has a reproduction structure, which are female cones in the Pinus, and which are acorns in the oak, and there is another growth unit which takes place in the year which, there could be branchings or not, and you can see that the leaves here, especially in the case of the green oak, they can be very different from a growth unit to the next one. As you see there is a much more complex level of organisation that we will call the level of the annual growth. Illustration here with again a Pinus. You can see the growth of the bud from the year. You can see the first annual growth with the female cones and then there was branchings and you see needles which are different one unit to another one for the same year. And very often there will be a differentiation between the growth units of the same year. For example this is a Radiata Pinus. There is a vegetative bicyclic growth which did not lead to the female cone because there would be the inverted phenomenon and you can see a first growth unit which is much longer than the next one and the branches which are much thinner in the first growth unit than on the second one which will carry most of the most vigorous branches of the vegetal which, of course, has consequences in terms of nodes in the wood.

Now, just for reference to show to you that very often we talk about a polycyclic species or polycyclic vegetals, but things are often more complex. And the expression of growth, as we shall see the expression of branching, can be modulated by the development stage of a vegetal and by the location considered in the vegetal. For example here in a walnut, all range of vegetal sprouts, you can see the double lines show the stoppage at Winter, single lines the intra-annual growth stoppage and the sign here in S shows simply a slowing down of the growth. And you can see all the types of growth that you will find in a walnut tree from the one with only one very short growth unit to the one which has a very long unit growth which stops only at Fall and which is found only in a stump rejection or in bicyclic growth or tricyclic with only a slowing down and so on and so forth.

So, how can we identify this? Well, again, with a morphological marker which is very precise. Here Winter buds, lateral buds and terminal buds which will have only one or two leaves that will avort (abort) and will be like scales. When the leaves open up at springtime, you will see the leaves slightly scaled, the young leaves, and then the adult leaves that grow. And when the organs fall, in winter or in the following year, the following years, you will see the scars of the leaves, here for example, you see the scales here, scars, sorry, and scars of cataphylls that correspond to the organs here. So, this is a winter bud. When the vegetal has a bicyclic growth, well, we'll see that the bud that falls during the year has a very different structure. Here, for example, this bud that expanded at the end of spring but initiated at the beginning of spring and you can see that the cataphylls do exist but they are membranous, very thin and green and very different from those of winter and the scars, of course, are also different. And therefore, through the analysis we can show or retrace this growth dynamics. This is another example where you see only a very slight reduction of the internodes and an aborted leave, here about, with only a reduction of the elongation rate. And again, this elongation can only be characterised through weekly or bi-weekly control during the period. And it's only because we've studied this that we can understand the meaning of the markers I'm showing.

Finally, specific cases here. You can see a graft on a graft holder very lively and a growth that lasts from spring to fall. So, this is a bit of growth that we see almost exclusively on stumps or on grafts with very lively or healthy graft holders. When the walnut is blooming, when it is adult, well, it develops flowers and fruits in a terminal way and it will form a small relay which can be instantaneous and can grow with the flower and then it can grow as well in various ways, in which case we will find the same markers. This is a monocyclic growth you see with nuts and that will no longer grow. Here in winter you will find the scars of scales, the young leaves, the fallen leaves, and then here, the scar of the terminal inflorescence. So, this is a polycyclic growth and this is the type of growth we've mentioned. This is when there is a slowing down of the growth. There is not true stoppage but the growth rate is very low. In such cases, internodes are not so close and we can mark them or, as I showed earlier on, we'll just have a smaller leave. So when we monitor the shoots, you can see the varieties, we can have a stoppage of several weeks or a slowing down, there will be a very small growth and then the speed or the rate increases. You will find a scar of inflorescence and there will be what we call two structures here that make it possible for the plant to grow. And you can see that just with the structure of the buds that the buds will spend the winter because they are like winter buds. So, sympodial, terminal, these relays can expand. You can see more vigorous growth here and you will see the scar of terminal inflorescence where the flowers fell and there is a relay that will spend the winter whereas the other one is more vigorous. It has an intra-annual bud. You see the same scales as for the vegetative part and we start a second growth wave that will give the second growth unit of the year.

If I show you such examples to show you that everything is always moving, dynamic in a vegetal and we will see an evolution of the annual growth principle or the growth string development. In this Zelkova Serrata, from Japan, this tree is less than 10 years old. You see there is a specific structure. What is essential is the structure of the annual growth. They're always bicyclic, even three or tetracyclic and you see a first growth unit, the apex here, you see, and then the development of the second growth unit. These shoots can be as long as 10 centimetres for the young tree. If you look at the tree that is 100 years old and you look at the structure of the annual growth you see the scale is not the same. Each year, when the plant reaches that year, it only has monocyclic shoots with 10 to 15 internodes and 10 to 15 centimetres in size. All the parameters evolve and you will see that this is not by chance either.

Rapidly now because we don't have time to detail, relationship between elongation and organogenesis. When there is continuous growth, usually there is also the continuous organogenesis. In some cases, for example in mangrove trees in Florida, it was shown that even if the elongation was continuous it may have fluctuations and elongation rates which may vary. It has been shown that the organogenesis, therefore, has the same type of functioning but could be slightly offset in time. So, the fact that the organogenesis can be offset vis-à-vis the growth, I mean, for example in Hevea trees, or rubber trees, we can see that the elongation took place in 45 days on average. Now, if we look at when the organs are being formed, we can see that the meristem is starting its activity just before the start of the elongation and it will produce the organs that will then become elongated and therefore the morphogenesis unit is imbricated with the elongation unit. This phenomenon occurs next time there will be an elongation of part of the organs which have been formed previously and then we form the organs that will become elongated either during the same wave or during the next one. Another case, for example, in the ash tree, but in many other similar species it's the same, when there is the first wave of elongation taking place, we can see that this elongation wave expands the pieces that were in the bud which were pre-formed but the organogenesis of the staves or the shoots started beginning or middle of elongation. Organs will be formed and after a phase these organs will, in fact, expand and the process will continue from one period to another.

In the case of rhythmic elongation it has been shown that the organogenesis could be continuous. This is the case of the Camellia sinensis where there is an elongation which is rhythmic but the organogenesis is more or less continuous with fluctuations. Therefore, bear in mind that when we talk about rhythmic growth we do a shortcut. We only talk about elongation and the organogenesis could have its own dynamics.

To finish and then we'll have a break, there are notions related to the time when the elongated organs are initiated. First case, all the organs that will become elongated are present in the bud and we talk about pre-formation or pre-formed shoots. In other cases, there is the same thing, but instead of the plant stopping, it develops a new part which will elongate the organs as they are formed and we talk about a shoot that has a pre-formed part and a neo-formed part.

Finally, in other cases, when we dissect the buds, we look at the apex of the stems and we see no start or draught and the part that will be elongated results from an almost simultaneous organogenesis and we talk about shoots which are neo-formed.

So, how can we identify this? Well, simply we have to look at a population of buds that we dissected before the elongation. Then we look at the population which is equivalent and normally homogeneous of shoots and after the elongation we look at the two distributions and if they are identical, well, in this case we have identified that the shoots were entirely pre-formed. In other cases, well, there will be a pre-formed shoot that will develop, as I have shown you here, a phase which is generally of a weaker elongation and then leaves of different nature which are acclimated. Here in the poplar tree we cans see the structure of the leaves at the pre-formed part and the structure of the form of the leaves of the neo-formed part which are usually larger.

These notions of neo-formation and pre-formation are also important because there can be different functioning between the two parts, especially in the elm trees, for example, where inflorescence and therefore the reproduction function is ensured only by the pre-formed parts of the plants, whereas the neo-formed parts will be used mainly to explore the environment. Rare cases of neo-formation will be find, for example, will be found from stumps where a bud has very little draught, it might be a couple but then he will do organogenesis as he will, it will elongate the formed organs and you've understood that the elongation of neo-formed parts correspond roughly to what happens when there is a continuous growth and the organogenesis takes place at the same time.

So, we will now conclude this course with another characteristic which is what we call the morphologic differentiation of axes. And here we'll make a distinction mainly between four or five types of axis which will correspond to the construction of the vegetals. First, we'll find the orthotropic axis. The orthotropic axis are vertical ones with a radial symmetry, that is leaves or bearing axes that are distributed in all directions and I will give you examples, then so-called plagiotropic axes, that is there growth direction is slanted to horizontal and they have a bilateral symmetry usually anatomical but also through the distribution of the branches and leaves that they carry. You see this here. This is a bilateral symmetry.

So why don't we talk about vertical and horizontal axes? Well, simply because orthotropy and plagiotropy in fact correspond to syndromes. It's not just a direction but it is also to do with the distribution of the twigs and leaves and stems. In addition to the orthotropic and plagiotropic axes there are the mixed axes. So, mixed axes are very specific. These are axes which will not have the same properties from their proximal to their distal parts. For example there will be axes that will be plagiotropic and, sorry, orthotropic than radial symmetry in the proximal part and then they will become plagiotropic in the distal part. Or, on the opposite, axes which will be more plagiotropic in the proximal part and which will become orthotropic in the distal part.

As we shall see, through illustrations, some vegetals, some types of vegetals, like the strychnos in their young phase are constructed through the stacking of mixed axes like this one with a proximal part asymmetrical which is orthotropic and the distal is symmetrical and bilateral whereas some branches, as we shall see here, are constituted mainly by mixed modules. And this is the case for the plagiotropy through apposition and plagiotropy through substitution. Two modes of plagiotropy, very specific, which correspond to very specific morphological processes. So, plagiotropy through apposition. This is what you find species of terminalias, including the banana tree, the terminalia catappa, as well as many other species which are similar or in a tropical family which is essential which is the family of the sapotaceae. Let me remind you that the terminalia is a combretaceae. And therefore several sapotaceae will grow based on this model.

What does it mean? Well, in this case the branch will be constructed through the juxtaposition of mixed modules which will have a plagiotropic proximal part and a part which is distal orthotropic in which case the leaves are often distributed like this. And sexuality, that is inflorescences, are in lateral positions. Therefore they do not impede the subsequent growth of the various modules which may therefore continue. This is a very efficient mode to construct branches that will be well-suited to the capture of light energy and, for example, if I show this there will be a branch that will be zigzagging which may produce several twigs or branchlets and then will be able to stack successive rosettes which will form a very abundant mass of leaves and the rosettes will not superimpose and will not create shade. And therefore this gives birth to what we call the pagoda trees thanks to this very specific shape as we will see on the slides.

Next to plagiotropy by apposition there is plagiotropy by substitution. OK You don’t have to remember the terms that you’ll find in the book. What you remember is these processes exist and therefore it can be formed like this. Therefore in plagiotropy by substitution the situation is very close, very similar, except that the modules will have a terminal inflorescence or blooming. Otherwise the situation is also very close. And the difference here is the indefinite growth of modules, definite, sorry, of modules unlike what we had previously. This is something that you see more easily than the previous case and for tropical plants but in temperate climates you will find this phenomena in magnolias, in the magnolia grandiflora, or in the loquat tree, the Eriobotrya Japonica and there would be some specific cases which, for example in the cotton tree or pipers, there is reduction of the system which will lead to modules formed of only two leaves, the first being a cataphylls, the second being an assimilation leaf and each module therefore has two leaves, two internodes, and finishing with a terminal inflorescence. Those will be the piper, which all grow according to this mode, or the cotton trees, the gossypium in malvaceae which develop based on this model.

Finally I will finish with the position of sexuality. I will just illustrate it because it does not lead to any specific problem. The reproduction structures can be in lateral or terminal positions. The morphological differentiation of axes are the types of axes that exist in vegetals, first the orthotropic axis such as the trunk of a coconut tree and the orthotropy is characterised by a growth direction which is essentially vertical and symmetry which is radial. As opposed to this the plagiotropy characterised by oblique or horizontal axes and a symmetry which is bilateral. Next to these axes there are the mixed axes with different properties from the proximal to the distal part and for a same module, or same axis, there will be the orthotropic and more plagiotropic parts.

Orthotropy is characteristic of many trees or vegetals such as palm trees or here a Carnegia Gigantea. Plagiotropy will characterise branches, of course. It’d the ideal structure to capture light energy, be it a coffee tree or a Microphylla where leaves are small but the branching gives a large surface which can assimilate light, or the Breynia des Abies or Cornus, all examples of twigs and branches which are plagiotropic.

In vegetals or plants we’ll see types of axes, the Pinus, for example, all have orthotropic axes, or the mixed axes, orthotropic trunk and plagiotropic branches, such as, for example, in this Araucaria or in fir trees or spruces where for the same plant there are two types of axes or several types of axes.

Mixed axes are very specific because they are axes that have a proximal part with properties different from the distal part. One of the most striking examples is the strychnos gender when it is shrubby where you can see there is an orthotropic phase with very small leaves and then this strychnos axis when the vegetal is young it becomes curved horizontal and the twigs and leaves are brought in the same plane which will be, and they become plagiotropic. Likewise in anonaceae, for example, often there will be the apex that will remain tilted and the axis straightens up during the growth. It’s a very specific phenomenon which characterised many leguminous where the axes will always have the distal part that is horizontal and plagiotropic and slowly the trunk comes from this axis which becomes orthotropic whereas the distal part will always remain plagiotropic. I will show you other examples.

Two specific examples of plagiotropy, the one through apposition, well, there will be a juxtaposition of modules in the proximal and plagiotropic and the distal and orthotropic whereas in the plagiotropy through apposition, characteristic of pagoda trees, or what in the literature we call the terminalia branching, and there will be rosettes of leaves that will carry sexuality and which will be arranged, juxtaposed, next to one another. In magnolias and other species there is about the same type of structure but the inflorescence is terminal and therefore the modules have a defined growth.

How does it grow? Well, if we look at the terminalia catappa, we will see that all the module, this is another species, have a horizontal part which carries scales or cataphylls and long internodes which will ensure the edification of the branch whereas the distal part that you see very clearly here is composed of several leaves which are arranged in a rosette. This is this distal part which carries the elements of sexuality lateral here. You can see there is a high specialisation with proximal parts which form the structure of the branch and distal parts which are linked to the assimilation and reproduction function. Plagiotropy by apposition is specific of most of the species of the terminalia type but of many species of sapotaceae. This is an immediate branching. You can see the module even being formed with the relay axis which appears. These relay axes grow very rapidly usually and they are composed of cataphylls with long internodes. It will straighten at the end. You will see it carries the leaves and sexuality and therefore we end up with this very specific structure here sympodial. And the growth and thickness means that there will be a plagiotropic part which will ensure this structure.

In the plagiotropy by substitution we've got about the same phenomenon. You see it in a magnolia grandiflora. The axis is straightening up and again new relays appear in the proximal part, horizontal part, there are very few leaves or small leaves and long internodes whereas the old leaves are in the distal part. This is also in this distal part that the flowers or terminal inflorescence will grow and you can see the scars in all the parts.

Other examples in the American Byrsonima or in the fagreae, which are Asian trees, you can see this structure which is quite typical. Substitution plagiotropy will lead, is characteristic of many species such as the tabebuia or the Cornus and we can see in this case that some species are more specialised. In the Noni Morinda Citrifolia, widely used in medicine, each module is comprised of two internodes. You can see them here. A first internode which carries reduced leaves opposite a second one with a long leaf and a short leave and a terminal inflorescence. The module corresponds to this very specialised part.

Even more specialised, when we look at pipers, all constructed the same way, a piper branch comprises, you see, these articulations: a first short internode and a cataphyll, a long one, a flower, a leaf and terminal inflorescence and they're all fairly identical and they make it possible to easily identify species from that family.

To fish with the types of axes, we will see this afternoon that often there is a major differentiation within the architecture of vegetals and here in a gingko, for example, or in a birch tree, you can see that all axes are not the same. This why there is an architecture. And there are dominating axes and short ones. The dominating ones are here to form the structure of the tree, to explore it and explore the environment whereas the short axes will do photosynthesis and they reproduce and they're more exploitation axes. Short branches or short twigs are specific in the cactuses. Thorns are from leaves and they result from a shorter, short twig, sorry, which gives a very specific shape to this family. These short twigs are related to sexuality. Here, for example, a cedar tree has a male cone. Each branch or twig grows by 2 millimetres per year with a little rosette. This is about ten years old and in the meantime the tree may have grown by 2, 3 metres. For tropical plants the short twigs are structures that will make it possible for the cauliflori to appear, that is inflorescence or even fruits which are directly taking place on the trunk or the older part of the trees through successive blooming. In the artocarpus integrifolia, sorry, which is the jack fruit, and here you can see the pads which are short branches specialised in the cocoa tree, the theobroma cacao, which is a sterculiaceae.

To conclude, I will talk about the position of sexuality which does not leave many possibilities. This sexuality is lateral. It does not affect the indefinite growth or axes or it is terminal in which case we go to a sympodial system with definite growth. A couple of illustration of lateral sexuality in this Alchornea, an euphorbiaceae, and you can see blooming takes place but it does not prevent the ulterior growth of the main meristem which has experienced a rhythmic growth. Same thing for this Dictyosperma, a palmaceae, with lateral inflorescence or in an ash tree where inflorescence are male or female or hermaphrodites but always in lateral position. And therefore they do not impede the subsequent development of the terminal bud you see at the axis. Lateral sexuality, well, of course, will lead to a definite growth or the stoppage of the development of the axis. This is the case for this Calceolaria Uniflora from the south of Patagonia where the axis will no longer grow. Also the case for this aloe where there is terminal inflorescence that will stop the subsequent growth of this axis. In some cases this terminal blooming will cause the death of the vegetal and we talk about monocarpic vegetals. They're very specific cases, very spectacular too. For example, this case what we call the sabre vegetals. They're Argyroxiphiums, they're asteraceae compounds and they come from Hawaii volcanoes. They have a rosette you see here, very specific, which grows in altitude. The rosette grows for 20 to 30 years vegetative only and then it blooms, it has these capitula and then it will die and dry up. And this is what you see in a monocarpic palm tree. It bloomed and then it dries and dies. And you see the contrast between the intense level of branching, of inflorescence with respect to the non-branched part of the vegetative dimension. In some cases it is not that disastrous. There will be terminal blooming or, which will be followed by a sympodial branching for a, as you can see here, a relay will grow to ensure the continuation of the growth as you see here with inflorescence which are being deployed, remainings (remnants) of inflorescence and branch, sympodial branching which is a specific mode of development.

Finally, to conclude, blooming can be lateral and terminal on a same plane, on the same plant, sorry. For example, for the walnut there are female inflorescences which are terminal, you can see here, and male inflorescence or catkins which appear laterally on the axis of the previous year. You can see it here just before the growth of spring lateral catkins which are buds that will grow and the scar of the female inflorescence which grew the previous year.

So, we've finished with this part on the reminders of vegetal morphology. They were just reminders.

This afternoon we will look at all aspects of architecture of plants and vegetals. So, this is a fairly recent domain resulting from synthesis work Hallé and Oldeman, first book published in on the subject in 1970.

So what is the architecture in this case? Well, the architecture of a plant, in fact, is the specific disposition of all the structure of a plant at a given time. And it is also, at a given time, the expression of an equilibrium between endogenous growth processes, that is they are genetically determined, and external constraints from the environment. Constraints, of course, evolve throughout the life of a plant and especially a tree because it can live for several hundred years and the problem will be to extract from all individuals observed the general rules of development of an individual of the same species, but also more globally: are there generic laws which are specific to vegetal structures? Architecture of vegetals and plants is also a global and dynamic vision of vegetal growth. That is, we will analyse all the parts of a vegetal or plant and see how these parts change or rearrange themselves during the development with specific attention paid to specific events which will be the occurrence of branching or of blooming, and so and so forth, that will be landmarks for vegetal development. The architecture of plants is base on a few concepts including that of architectural models that we will cover rapidly.

Architectural models were defined by Hallé and Oldeman in 1970. Professor Hallé is now retired but was at the ORSTROM, IRD today, and in Montpellier II University whereas professor Oldeman was teaching at the Forestry University of Warenhingen.

What is the architectural model? Well, it is a growth strategy which is specific to the plant. The advantage of this notion of architectural model was to show that among all the strategies fro development observed in vegetals, it was possible to identify about 20 architectural models to which almost all vegetals observed could be linked. Each architectural model corresponds to a combination of the criteria we saw this morning including the growth modes, the branching modes, different morphological differentiation of axes, and position of sexuality. Therefore we will not analyse the 20 architectural models, of course, but we will look at four or five models which are rather different and we could classify them without having any presupposition of their position in architectural models.

And especially we'll look at the non-branched models. And in this group we'll find two models, but we'll analyse only one. It's a model that corresponds to monocarpic vegetals which are not branched off. They have no branches. They will grow over several years if we take the example of the Corypha umbraculifera which is a very well-known palm tree in Asia, this palm tree will grow for several years, 20, 30, years. It will produce leaves and, at a certain time, it will have a large inflorescence, terminal inflorescence, which, strangely enough, will be very, very significantly, richly branched off depending on the monocole structure, that is only one stem, of the vegetative system. So, with respect to this vegetative phase, blooming will produce a large number of seeds and the plant will die trying to reproduce itself as best as possible with all the seeds that will be disseminated.

So, this is the very specific model. It is the Holttum model. These architectural models could have received numbers 1, 2, 3, but the authors, Hallé and Oldeman, gave each model, in fact, the name of a scientist or botanist that made himself famous in the description of the mode of growth of vegetals which could be classified in such models. Holttum, for example, was a British botanist who did a lot of work in Southeast Asia in tropical zones. And I really invite you to read the books because they're all very interesting. This model of Holttum is found in monocparic vegetals such as the Corypha umbraculifera. It's called the Buri. And this is a palm tree found in India and it is on buri leaves that all the ancient sacred Hindu and Buddhist texts are written. We could also mention a surprising plant, the Puya raimondi, which is a terrestrial plant from the Andes which grows based on this model.

Next to those non-branched plants, but all non-branched plants are not polycarpic, no because the coconut tree is not branched but it does inflorescences lateral but that's another model. So they're not all monocarpic but conversely there are few cases, a few examples of very branched off plants which are monocarpic. In South America there is one species, Tachigalia diversicolor, which will give a tree with a lot of branches which will die about 10, 20 years and it blooms only once and then it dies.

Next to such models, there will be models of vegetals with braches, with branching, and in this group we'll find sympodial vegetals, fully sympodial vegetals, and in the case we will describe vegetals with only one type of module. This will be the Leeuwenberg model, very famous botanist from the Netherlands specialised in apocynaceae, a family which is essentially tropical in which we find many vegetals that correspond to this model. So the Leeuwenberg model corresponds to a vegetal which initially will produce an orthotropic trunk. The trunk after a certain stage of growth will give birth to a terminal inflorescence, or terminal flower, and the growth will be ensured by the growth of auxiliary buds. I will show you the flowers in red subsequently. And then the vegetal gives birth to a three dimensional system composed of successive modules. So, as you can see, it's a fully modular vegetal and what characterises this model is that all the modules are equivalent. You don't have long ones and shorts ones as we see in other types of models which are more complex and which correspond to more differentiated structures. I won't show you all the leaves, of course. This is a very spread out model in many shrubs, small trees. It is found very frequently in the solanaceae (the solanaceae, I remind you, are the families of tomatoes and aubergines) and often found in apocynaceae and especially in that family the model is that of the frangipani tree, the plumeria tree, that is the frangipani tree, and several species and hybrids. It will also be the model for pink laurel, nerium oleander of Mediterranean origin. In other families it would be the model of the manihot esculenta and, in the family of Euphorbiaceae, the ricinus cummunis, for example. All these are the euphorbiaceae, of course. As we shall see on slides this is a model highly represented by many shrubs or trees but if the first module is very long, for those who went to Guiana you will see the Didimopanax which has a long trunk with the crown and because the first module is very long.

Another type of model now with vegetals which are entirely monopodial. Again, if I erased the board too rapidly let me know. Now, fully monopodial vegetals that would be the RAUH model, a German botanist, very famous morphologist as well. Rauh's model, what is it? Well, this is a model of vegetal the axes of which are all orthotropic with a rhythmic growth and branchings, sorry. This is the model found in many forest species or pioneer species. You will find, for example, there the poplar trees, pinus, and various other species, monopodial species. And, of course, in this case the blooming is lateral because we have monopodes here. Moreover, it may affect all the axes of the structure or not in the Rauh's model. And we could mention all the pinus species, all the poplar trees, from the populus gender, the fraxinus, the ash tree, except the Fraxinus Ornus which has a terminal, excelsior which is the common ash tree, and we could also mention in tropical plants among the pioneers the Cecropia or Mussaenda both from the moraceae family.

I will illustrate the first three models here with a couple of examples. First the Holttum model, as I said, these are monocarpic vegetals with a single orthotropic trunk with a terminal flower. A very representative example, the Puya raimondi which is an altitude vegetal from the Andes so it has, you see a rosette or bough of flowers then there is a large flower that will produce thousands of seeds before the death of the plant. This is found in other bromeliaceae here the Tillandsia from Venezuela with a species and you can see three stages: the germination, a young plant, a more older plant with more vegetative. It has a large flower and then it dies. These are epiphyte plants and they are on a branch of the tree and you can see four stages of a plant from the Holttum model. Another specific case I talked about, the argyroxiphium or sabre plants from the summits of Hawaii, same family from the dandelion because they are compounds and they will have fruits and then the plant dies having dried and produced thousands of seeds. Same thing with the buri, the corypha umbraculifera which is a monocarpic palm tree, very spectacular, which blooms with huge flowers. This is what it, the result a couple of time later. This is a plant called the metroxilon in the aricaceae and you can see the structure of the plant with a terminal flower and the plant that dies, here in another species we saw earlier on. A specific case in a palm tree, quite easy to identify because it is the caryota gender in palm trees, it is the only one with bipinnate axis leaves and another gender which has a way of blooming that is quite specific. The plant will grow vegetatively for years and at a given time the terminal flower will grow. From then on all the axillae will bloom in descending series and therefore the oldest flowers will always be the tallest whereas the youngest ones will always be the ones at the bottom. It's quite unique in vegetals which means that buds are activated in series from top to bottom. You can see it in an older individual. So in the middle of the trunk, if not the base, you can see that fruits here and flowers and buds here and the other axillae will bloom down to the bottom of the trunk and this process can last up to 10 years sometimes. So, it's very specific.

Other specificity, in cactaceae this time with the cephalium of the Melocactus, the plant forms a bowl here you can see like many cacti and then, after a certain stage, it has this sort of drunkard's nose with very different structures. And this structure, specific structure will just produce flowers throughout the life of the plant which can last several years. And sometimes you end up with just the green part, which is a sphere, and a cephalium that could be tens of centimetres in height and again this is fairly unique in the vegetal world.

Other specific model, very stereotyped, the Leeuwenberg model corresponding to sympodial plants with only one type of module as you can see here. The Leeuwenberg model, of course, will be three dimensional and there will be more than one branching at each terminal blooming. This is frequently seen in small trees and shrubs. Easiest to see because they are ornamental tropical plants, the plumeria, the frangipani tree, which are very typical. Another emblematic plant Tournefortia Argentea, from the borraginaceae or the eriaceae depending on the classification, it grows often near the sea and you can see this structure here related to the sympodial branching. These are two vegetals belonging to this model which are constructed by a succession of modules which are all equivalent. You can see here the plumeria module with the flower and the relays here. Same thing here with the Tournefortia, the blue flower and the two relays on the side.

Earlier on we saw the brevifolia which after germination comes has a single trunk and a terminal flower at the basis of which relays or stumps will form to create the final structure of the plant which will form a small shrub from dessert areas composed of modules which are almost all equivalent. In this detail, here you can see the scars from the past flowers, one still present, and you see now that there can be between one and three relays each time. You don't have systematically three relays after each flower. Same thing in an araliaceae of the Sudan Sahel zone, Cussionia barteri, which belongs to the Leeuwenberg model. Other shrubs, typical shrubs, manioc, manioc esculenta, and I remind you this is essential in Amazonia as a food staple, you can see the first module from cuttings, development of the apex and the three relays under the blooming zone. In the Euphorbiaceae, Euphorbia dendroides, which are Mediterranean Euphorbiaceae, with arborescences found from Menton up to the North of Italy. You can see the same plant seen from the top and it shows the three dimensional structure of the plant. Another type of Leeuwenberg model plant, very specific, in the bromeliaceae, the abromeitiellas which are cushion plants from the Andes which resist snow cold and wind and when they are dissected inside they correspond to a small, highly grouped, Leeuwenberg model which forms a compact cushion. On the contrary it's the first module of plants from this model are highly developed and there is a kind of a trunk, like here, in a Dracæna Draco the Canary Island tree, which is disappearing, you can see the very schematic model or an aloe from South Africa which can form trunk though the growth of the first module.

Another type of model with similar axes it's the Rauh's model with orthotropic models with a rhythmic branching and lateral blooming. From such criteria you get the models for all the pinus, the pinus aristata, Pinus ponderosa, and Pinus caribaea on the right hand side. All those vegetals grow according to the same Rauh's model which is very frequent in trees found in Cecropias as well which are pioneers from tropical forests in the Americas and found as well in the ash tree on the left hand side or in poplar trees, the populus nigra. This model id also found in various specific vegetals especially the cacti with Opuntia and Carnegiea gigantea which, let me remind you, is the tallest cactus in the world. You can see it in old cowboy and Tex Avery films and cartoons. And the African equivalent, a cacti, the Euphorbia cooperi, with orthotropic axes as indicated.

I will conclude this series on models by looking at two other groups: another group of vegetals which combine sympode and monopode. In those cases either the trunk is sympodial or the branches are sympodial and we will look at one model which is very typical: the d'Aubreville model. Aubreville was a French botanist specialised in sapotaceae from Africa and this is a model which is often found in sapotaceae, but also several terminalias, the terminalia being, as you know the combretaceae as well. Aubreville's model is that of pagoda trees which have an orthotropic monopodial trunk with rhythmic growth and there are plagiotropic branches by apposition as we saw this morning. And you remember that they are composed of successive modules, mixed axes, each module being composed of a proximal plagiotropic part and a distal orthotropic part which carries rosettes of leaves and a lateral sexuality. Strange enough, this model is only known through tropical specimens. I don't know any specimen from the temperate climate of the d'Aubreville model. If you ever bump into one, please let me know. So far this has never been evidenced. Whereas a model with substitution plagiotropic leaves as we saw this morning, or branches we saw this morning, can be found, for example, in magnolias, for example, or the loquat tree.

OK I will spare you all the leaves otherwise we'll spend the afternoon there. So, the sexuality is lateral. Of course, to speed up the process a bit I'm just showing you for each model only one diagram but the model is more than just a snapshot in the life of the tree. It's a whole series of architecture that a plant or a vegetal will adopt though its growth.

To, finish let's look at another model which corresponds to a specific family of architectural models and this is the Troll architectural model. Troll is one of the most famous German botanists. He wrote many books on morphology and he described very well the growth of the elm tree which grows based on his model.

So, what is Troll's model? It is a model of vegetals which construct themselves from mixed or plagiotropic axes. It is a very strange model because when we look at germinations we'll see a small horizontal axis coming out of the ground with a symmetry which will be more or less radial at the base but which will be plagiotropic at the distal portions. How does it make a tree? Well, there will be two ways. The first way for the plant to produce a tree will be to stack up plagiotropic axes and therefore there will be a trunk made by the stacking of the plagiotropic portions that are sort of straightened up which gives us something like this. And the branches, or whatever serves as branches, that will correspond to the most distal part of the successive modules that grow during time. Subsequently the lowest branches will fall, will prune themselves, and basically the plant will end up with a rectilinear trunk whereas it is in fact the result of stacking of plagiotropic axes as you can see here. Therefore this is quite a frequent model found in many species and especially the beech trees, the fagus, the

Nothofagus, many species from the ulmaceae, and especially the birch tree or the elm, the ulmus, the Asian equivalent would be the Elkova, but also, the Zelkova, sorry, and the Celtis including the Celtis Australis which grows in the Mediterranean but in the under the tropics there are many Celtis that will grow in such a way. It is also the model of leguminous. And this model will be identified from far, often in forests, or in savannah, simply because there will be these funnel or sort of umbrella shapes, very typical. If you look old films with Clarke Gable such as the Kilimanjaro snows and you will see views of the savannah and all the trees you see which are, in fact, locust trees grow according to this model. Clarke Gable probably didn't know about it but you can see it and identify them very easily. This could be the forest with the Parkia, for example, or this could be many locust trees or acacias from the dryer areas.

There is the fact that there is a growth from axillary buds influences the mechanical characteristics of the tree. In principle no, except if the tree is growing in poor conditions and it cannot straighten up. But, in fact, it occurs very rapidly in the core, centre of the tree, and this is where we'll see the various connections of pith between the two. But, a priori, we have very good quality woods that, or trees that grow based on Troll's model and that does not affect them except if they are in difficult conditions and the trunk then does not then grow very well but that's not specific to that model. Then I would weigh this by saying that point has not been carefully studied and I don' think we could say more about it bearing in mind that the quality of the wood is often more related to the species than to the specific growth mode but afterwards trunks are usually rectilinear. Another possibility, because this is one, in some cases we'll start exactly from the same point, that is more or less horizontal axis, initially, and then instead of stacking horizontal short structures we will in fact straighten permanently the apical part of the tree here which will straighten up and therefore the next stage will be something like this. That is, the tree will have still the distal part, the most distal part is horizontal whereas the lower parts are straightening up. Of course, this will produce branches and you will end up with a vegetal looking like this. Now, of course, again this is a simplified diagram. And it is permanently straightening its trunk and this is found in many anonaceae, for example or in Tsuga, Tsuga Mertensiana, for example, which originate from North America and which may reach more than 45 metres and which correct or straighten their axis permanently. After a while, this does not straighten any more and then we move to a stacking phase which is quite equivalent to what we saw earlier on. And this is the case of what we see in cedar trees. When we said that the cedar produces its table in fact the trunk doesn't straighten up any more and it forms this kind of a table shape. So, the cedrus here and several other species, or course.

For the forestry part this is essential because often if there are trees based on Troll's model which grow in non-forest conditions they will tend to form something that creates a shrub more than a tree. And therefore they will need to be replaced in a sort of forest atmosphere so that they can produce a trunk. And this is essential if you do plantations, for example, that is exposed to the sun, well, the axes cannot really straighten up and you will just end up with a forest tree but which in fact cannot really become a tree and for a long time will remain a shrub. Whereas if you put it in more forest conditions or at least with a lateral sheathing, which is done often, and the axis will straighten up and therefore will give a trunk that is rectilinear and with a consequent height. This quite frequently observed when we see open plantations of leguminous with trees which do not grow. People often think "Well, it doesn't work in plantations" Well, it's not that it doesn't work. It is simply because conditions are not favourable to the straightening of the axis.

Let me illustrate the two models I've shown you and especially the d'Aubreville's model which corresponds to what we often call the pagoda trees you can see here. This is an orthotropic trunk with rhythmic branching and plagiotropic branches b apposition as we saw this morning. These are trees of high quality, a lot of African woods: *Fraques, Framirés,* Terminalia Ivorensis, and several species are used for their wood. They're very good timber and often used in plantations. In all these trees the trunk will be vertical orthotropic and you can see stages of branches which can be quite significant. The infrastructure of the branch is composed of the proximal parts of modules which comprises internodes and small scaly leaves whereas the sexuality and the assimilation function is dedicated to the straightened parts of the tree which creates rosettes of leaves which not superimpose one another and carry flowers. Another example the Terminalia Mantaly from Madagascar used as an ornamental tree, very specific as you can see, but it's very efficient to create structure that will capture light. These are very small leaves specific of this species and the Terminalia Catappa where you'll see the same structure, very emblematic tree in the tropics because it is used as an ornamental tree or it is found in many countries.

What should be looked at is that the architectural model results from the study of several specimens in non-stressed conditions. This is the Sudan Sahel zone in Africa where there are a lot of fires and we are dealing with the Terminalias Glaucescens which is regularly burnt and you can see that the tree has more difficulties getting a straight trunk but if you look at the structure of the branches you can see what the anglo-saxons call the terminalia branching and what are called the apposition plagiotropy which gives us elements to link up this vegetal to the d'Aubreville's model.

Now, if we look at non-stressed conditions in a botanical garden we could see it expresses a trunk easily. When the trees are old, this is a sapotaceae from the Mauritius Island, we don't see really the difference between the trunk and the branches but we can see the rosettes of leaves simply. And as we'll see later on, when the pant gets old the architectural model is less visible. Other phenomena occur and therefore we see only peripheral expressions of the model.

Another major model with mixed axis of vegetal is Troll's model resulting from the superposition of plagiotropic axes. And again, regardless of the name, what is to be remembered is that a tree can be constructed in such a way. As you can see here for an elm, there is typically the initial axis on which another axis started and another one and all this is very zigzagging but will become, will return cylindrical as it will grow and get bigger. You can see that the proximal part that will form the trunk has a large thickening in width to the distal part which will rather give structure that will be used as branches. In other cases it's not a stacking of axes but it is a permanent straightening of the axis you can see here. For a Soursop the axis straighten up but the most distal part is still plagiotropic.

How does it happen? Well, we star from a germ or an embryo the same in both cases even if it's quite an absurdity botanically speaking. This is an Anaxogorea dolichocarpa, from Guyana, from the undergrowth in Guyana, the ground would be here and you can see the plant is parallel to the ground which is not a condition to have a vertical trunk. Yet when we look at what happens in such plants, this is another species, and you will see that this axis can straighten up or it stack up other exes that will then come into the curvature zone and in the orthotropic proximal zone they will come in prolongation of the previous module. The process continues and in this diospyros from the botanical garden of Montpellier you can see the parts of trunks. The stump here of the plagiotropic portion that pruned itself, another axis, the part that was used as a branch which pruned itself and you can see this stacking which becomes more and more tightened as the vegetal gets old.

Same thing with the beech tree. And when it is in undergrowth, dark undergrowth, it could produce a kind of a nappe (canopy) it cannot straighten up because the environment doesn't allow for it but as soon as it can find a shaft of light the axis will straighten up and the trunk is rectilinear and if you come back the next spring you will always find the branches which are soft but which will straighten in good conditions during the same year of growth. This is again in older trees. This is a fully straightened tree and a tree that is much older and which now tends to collapse and this is also an altitude tree and it is in more stressful conditions and it has difficulties straightening up. This is a fairly old tree in open environment because usually beech trees form dense forests but you can the zigzagging shape of all the branches that is typical of this tropical model that will zigzag because the growth mode implies that. Another family which can be identified because of its growth model, the leguminous, this is a huge one from forest with a parasol or umbrella shape from Troll's model. This the Tipuana Tipu, which is an American leguminous and if you look a the periphery you can see la the zigzag and the stacking up. And here you have a very conventional view of a dry Southern Africa, Eastern Africa, with numerous locust trees which are all on Trolll's models and which gives this very typical shape of vegetal formations. Another example the Nothofagus of South America or the Celtis, this is the Celtis Australis, and most of the celtis in the world grow in exactly the same way.

Finally, in some cases, the successive relays do not stack up but will start at the bases of one another, for example in this phyllanthus of Mauritius, and there is a nappe (canopy) shape. The plant cannot create or form a trunk. Another mode of expression in this architectural model will go back to the germ of the plant we've seen earlier on, of the Anaxogorea dolichocarpa and we will have an axis that will straighten up and you will see here in an anonaceae and as you can see at several stages the plant is straightening up, can branch and we'll get exactly the same result eventually.

This is very typical of Tsuga and Tsuga Mertensiana from the Northwest of the US. Here you see a young germ, embryo, the proximal and the horizontal part. The young tree in undergrowth, same situation and this is a tree that is 30, 35 metres tall. You see it's a very good quality tree, wood and the trunk is more or less horizontal. In fact it's just straightening up until it reaches the final size of the tree.

This is what we'll find in cedrus and cedrus atlanitca here. We'll have the same thing in Cedrus Libani or Brevifolia. The trunk is rectilinear which results from progressive and permanent straightening throughout the life of the tree and you can see at the top that this trunk does no longer straighten up. It will remain horizontal. And we said that the cedar "makes its table" and that's an indication of the growth in height. The poorer the soil, the lower the position of the table and the better the conditions for growth, the taller the level of the table.

Another intermediate level in the locust tree or the Robinia Pseudoacacia the trunk will straighten up over several years and afterwards it will no longer stack up and will stack up axes as you can see here and therefore this is a typical model in many species. Many trees actually grow according to this model.

Now to conclude on this notion of architectural model, as you saw, each architectural model corresponds to a global growth strategy. Nevertheless, if you remember for the Rauh's model, we could see that it could be expressed in Pinus, Cecropias, Euphorbia Cooperi, and of course all these plants are different and you don't need to be a major botanist to define the difference. What does it mean? It means that in fact the notion of architectural model is useful to establish a typology of growth strategy of vegetals. But this notion is far too broad to really detail the specific architecture of a species. To complete this we will now analyse another concept which is that of architectural units.

The concept of architectural units described by Barthelemy, Edelin and Hallé in 1989 and which corresponds to what we called in the past the architectural diagram and defined for the first time Claude Edelin in his thesis on conifers in 1977. So, you will find the two terms bearing in mind that today we use the concept of architectural units.

So, what is an architectural unit? Well, it's rather difficult to teach that concept, well, at least in front of a blackboard. Because you can only understand the architectural unit of a vegetal by analysing it in a dynamic way and having seen tens or hundreds of specimens from the same species and by analysing the development from germination up to all the stages. Since we are in a room and we don't have time to go on site to look at it, and it takes a lot of time, I've tried to select two species which are very different and these will make it possible, we will illustrate several stages from germination to adult stage. They will illustrate the notion of architectural units.

The first species the monkey puzzle tree because of it's very painful thorns. This a primitive plant from the araucariaceae, the conifers, the Araucaria Araucana, which originates from Argentina and Chile in the southern parts of course. This is a temperate vegetal. Araucaria Araucana is a very old vegetal. It grows in some areas of Chile and in a specific area at the border between Chile and Argentina. It can form pure stands or mixed stands with Nothofagus here. For example this is a natural forest of Araucaria Araucana in Paso Tromen at the foot of the Lanin volcano that you see here where this species was studied by Xavier Grosfeld an Argentinian student.

How does it start, the story of this species, that we call the *Pehuén* in Mapuche language? Well, first the seed which you see is very bulky. It gives a flower which is a bit like a chestnut which is the basic food staple for the Mapuche natives of this region. It created an axis with leaves which are very small, very thin, you see thorny. And very often the first year the plant has a small axis of only 10 centimetres. It will be philotaxic with a spiral alternate. Sometimes it may branch off with a very short axis which has exactly the same leave, foliar characteristics as the bearing axis, that is the trunk except that it is a lateral axis slightly more oblique than the trunk. Now, if we look at this species when it grows, in all the drawings I will show you now the double lines here will represent the annual growth stoppage, and you can see that in germ of 2 to 4 years there is a rhythmic growth. The plant stops its growth in winter. There is no bud, scaly buds. It's the same bare bud that will be sort of asleep. The size of leaves will increase. Remember the size of the leaves of the young vegetal: 2 centimetres long and less than 1 centimetre wide and thorny. The growth is rhythmic but there is no scale bud and in order to identify the growth stoppage there are the rings which are annual but sometimes well-marked you can see the stenosis of the leaves you see which mark the pause of winter elongations. So, this is a real vegetal on site. You can see that these are 3, 4 years old. You can see initially it has very few branches. This a vegetal that is slightly 1 or 2 years older than the one I've shown in the drawing and which has 2 or 3 small branches at each branching stage. And the branching is acrotonic . In an undergrowth vegetal, which explains why there are very few living stage here, you can see the rhythmic growth and branching. You can see that annual shoots are taller when the vegetal is older. Leaves tend to increase in size as the vegetal grows. And there are always 2 to 3 branches at each branching stage of trunk bearing in mind that at this stage the branching off is more regular and every year the plant or the vegetal will grow one stage of branch. This is a vegetal in more garden condition therefore more favourable to growth. The architecture is typical. Note the size of the leaves which is now much longer, larger. Note that the successive annual growth of shoots are larger.

Note, as well, that the branching now is more or less stabilised around 3, 4 branches per sides of branching of the trunk. And for those who have very good eyesight you see something new that is the advent of a third branching order, branches which are borne by their branches. They're very scattered. They appear here and there on the most vigorous branches. Usually they appear in an isolated way at this stage. The vegetal will continue its growth. What should be noted is that you should understand the chrono-sequence and you remember the previous vegetal as I talk about the next vegetal. You can see that in an older vegetal you see again the growth of annual shoots getting more important. You see the zone where the plant had only 3 to 4 stages of branches. In the lower zone in the oldest one you find small branches which are scattered on branches. But you note as well that being the most recent part therefore this is a vegetal with a major development stage. You see more and more the stages with 4 to 5 branches, regular stages, they're not the branches themselves, pairs of branchlets which appear regularly. And therefore you can see that the development of the vegetal takes place according to a very precise sequence of events. This is a plant in good condition where the branches grow with the same rhythm of the trunk producing one unit per year. And in the dark undergrowth the trunk may stop growing and we've seen plants where the branches were 25 years of age where the trunk had not grown over 2 millimetres during that period.

So, all those are strategies which report on the architectural plasticities of plants but we won't have time to talk about it today. Please note here the branching more regular on the trunk and branches with pairs of branchlets which are more or less regular.

Next step this is Xavier Grosfeld who did his post graduate diploma on this species and this is what I'm talking about today. You can see regular stages here in regular situations here. You see leaves are larger, longer and far more painful than in the young vegetal. You can see the branches are bigger, branching off is more regular at all stages. And this is even more obvious in this specimen where you see the zone of the base with a shorter annual growth which explains that the branches are all together. And at this stage you can see that the annual growth of the trunk, more or less, has a constant size. You can see that there are between 4 and 6 branches regularly at each stage of the trunk. And you can see that the branching off of the branches themselves seem more regular with pairs of branchlets. So, at this stage the vegetal expresses regularly its elementary architecture. And for this species which is dioic that is we'll find individual male and female individuals. This is where we'll see the sexuality with male cones, 4, 6 of them around the branches. One has been removed here to show the others. And in one female specimen at about the same stage there will be female cones which are terminals. And you can see lateral sexuality in male and terminal sexuality in females. You can see the pairs of branches. And what is essential at this stage besides the criteria of regularity is to see that the cones, be they male or female, only appear on the branchlets. You don't find them on the branches and never on the trunk. Therefore the older tree here, on the same photo you can see a tree which is in the condition I've just described but you can see here a much older tree which looks more complex. In fact, if we were to detail this tallest tree we would see that, yes, indeed it has lost its lower branches through natural pruning but, just as the young specimen, it carries its reproductive structures on the A order 3 branching either in lateral position on male specimens or sympodial position on female specimen bearing in mind that each branchlet can produce between 4 to 6 groups of successive male cones whereas the female parts can produce sympodially between 3 and 4 successive cones. And you can see that the leaves are also different, much larger, and longer than on the younger tree. And we always find here the rhythmic growth expressed by a narrowing of the size of the leaves but that's not always obvious, less than the use of the scale buds. We now have an older tree here. This tree is more than 200 years old. The trunk much is thicker. You can see an individual here giving you the scale. You can see that it's a big vegetal. The leaves have pruned themselves and the architecture of the tip or the crown is more compact and we should take a look at it. Now, if we look at a female specimen we will see here, like earlier on, that there could be 3 to 4 series of productions of female cones before transformation of the terminal module that would look like a rat's tale. It's no longer thorny. Usually it's 20 meters tall so it doesn't help much but it shows the end of the growth of the branches. And afterwards you will see that the diameter of this termination will become thinner, the apex dies and the branch will die. On male specimens we'll see exactly the same thing, more or less the same thing, but we'll see the expression of the male cone. There will be between 4 to 6 productions of cone, of male cones, then the same terminal meristem here which gave the series will transform and will become a sterile part, a very similar, identical to the part which is found on the female individual which is the sterile zone and just as in the male individual, specimen, there will be a narrowing to the tip and the branch will die.

What' fascinating is that even at this stage there is always the same architecture. A slight difference is that in the oldest parts there will be isolated branches which will no longer be in pairs. So this is a tree more than 200 years old and you can see a general view of the foot, a detailed of the branches or branchlets. What you are seeing here are the remains of the male cones and you see how it finishes with a bud which is no longer thorny, broad leaves which narrow down before the dying of the branchlets. The same principle applies. You see the scars of the female cones. You can see the scars on the adult tree. On even older trees you can see that the tip is getting smaller. The trunk becomes conical. And you can see the only tip or crown of the vegetal and the tree will die at this stage with a trunk which is orthotropic, stages of 5 to 6 branches which are very close to one another, unlike what we had on the young tree. And there will be branches that are identical to what we saw on the young tree, that is, at the basis. There are pairs of branchlets which will carry other male or female cones. And that will then be isolated and will no longer be in pairs until the branchlets exhibit this sterile part and die eventually.

So, what are we going to say? Well, the development of the Araucaria Araucana could be expressed by a series of development stages throughout which the vegetal will establish its elementary architecture. It starts at the undergrowth with a vegetal, as you saw, that will give very short annual growth with little or no branching, or at least in a heterogeneous way. Then the branching will appear on a regular basis or a regular way. Then the tree will continue its growth, will have stages with 3 to 4 branches, the branchlets will appear, at the beginning scattered but then more regular, then, once the tree will have reached a certain size, once its branching is more regular, on the branches and on the trunk, that is 4 to 6 branches per stage of the trunk and pairs of branchlets on each branch, we will see that the sexuality appears with the advent on male or female specimen of the first cones, male or female, of course, you know, the first being lateral, the second being terminal. Then afterwards the vegetal will increase, grow. Natural pruning will continue. The tip will be getting narrower and narrower. The trunk will stop growing and branches will grow for years before there is another growth of the trunk. But globally speaking these are only quantitative differences and differences of size and of volume. The structure of the plant remains the same with a trunk, branches and branchlets which each have their own characteristics.

So, what does it mean? Well, it means that when we look at the whole development of the tree we could define the elementary architecture of the Araucaria Araucana through a, by means of a drawing and a table, the drawing showing in male or female specimens the general shape based on the architectural model of the model of the plant and the table giving the specific characteristics of all the axis morphologically, which can be differentiated morphologically in this species, for example the trunk which is the only orthotropic axis which adult carries stage of 4 to 6 branches, branches having pairs of branchlets. And the branchlets, let me remind you, are the only axis that will carry the sexuality. So, this is something that is significant.

Earlier on we were talking about repetition. This is not a photocopy as such. Axes by repeating themselves through branching lead to differentiation between axes and here we've got three categories of differentiated axes. In which case it is quite simple and this why, now that you've understood everything, we'll analyse a more complex vegetal. We'll change the zone. We're now back to Europe and we'll study the architectural development of the ash tree, the Fraxinus excelsior very representative of European temperate forests.

For ash trees we are no longer in conifers. We are dealing with angiosperms and leafy trees. And if we look at the growth in natural and undergrowth this is where it will take place. And there is one pair of two cotyledons which are very typical of the ash trees plus a small growth unit the first year of 1 or 2 centimetres with a pair of simple and full leaves. In undergrowth natural conditions this is what the ash tree does the first year. The second year it will form a pair of cataphylls and a pair of leaves. You see that these are very short growth units. What is interesting is that the leaves are, you know, are found in the oleaceae and you see they are trifoliate. And from one year to another in this species, well, there is a metamorphoses taking place. And in this case, is expressed by the structure of the leaves which changes from simple to composite. Still in the undergrowth, the vegetal remains monocole for a few years. It has annual growth which are very short with one or two pairs of cataphylls at the basis and one and sometimes two pairs of leaves at the tip which are the assimilating leaves which no longer have 3 leaflets but 5 and then 7 and then 9 and so on and so forth while the annual growth will be slightly longer. Note that the vegetal is still without branches and branching will only occur as of a certain stage. And you can see plantlets which live several years without branching. As these are young stages so just think that this is the first, second, third year etc. At this stage if you look at the vegetal which is 1 to 2 metres tall you can see growth units with 2 to 3 pairs of catphylls, the pairs of adult leaves, that is, 9 to 11 leaflets. And when the adult leaves appear on the trunk this is when the first branchlets will appear. You can see them on the photo. You can see here on the diagram. They're very short structures with 1 or 2 pairs of cataphylls and 1 or 2 pairs of adult leaves. And for the time being they are short branchlets.

When you take a stroll in the forest you look for older trees to see the result and this is a tree is about 3, 4 metres tall in forest undergrowth. The double lines correspond to the limits of annual growth. You will find on such a tree the young part where the tree doesn't have any branches. You can see he first growth units which gave branches but which only have short branches. And then in the central part, which corresponds more to the age of the tree as we know it or as we see it, we can see that the annual growth which are monocyclic are far more complex. Based on the well-developed acrotonic phenomenon we have at the top of the trunk branches which are vigorous with branchlets. And the branchlets carried by the branches have exactly the same structure as the branchlets which are in the middle at the basis of the trunk, of the middle of the trunk. So, you can see the branching is strong. The trunk with monocyclic annual growth with 2 to 4 pairs of cataphylls, 2 to 5 pairs of adult leaves at the tip of the annual shoots are branches which are composed of successions of annual shoots which have little branchlets with no branching off and they are found in the branches or in the trunks but not in any position. They are at the tip of the shoots, of the growth of the branches or the trunks due to the acrotony which is very strong in this species. And if we look at the real vegetal you have a branch of a vegetal on a tree of the age of the one shown. You can see first that the branchlets are of a structure very close to what we saw earlier directly on the trunk. This is what Ederlin called the intercalation process. That is the pant takes place slowly. We don' have first long branches and then branchlets. But first there will be small branches coming from the trunk then they can have branches that will carry branchlets. At this stage you can see one or two pairs of such branchlets which are not branching off. This is an older tree. Note that the shape is conical. If you look at the trunk you can't see much because you can see more pixels from PowerPoint than anything else so trust me on this one. On annual growth you can see the tip of the annual growth or shoots which are indicated by the larger branches. Due to acrotony the branches branch off themselves and then have branchlets at the tip of the annual growth which is also monocyclic. If we look at the detail of this structure you can see the annual growth which are much taller than before, or longer than before, branches that carry branchlets, the branchlets are also found at the basis of the growth units of the trunk. It is at this stage where the vegetal regularly branches off that it has a conical shape with strong branches with branchlets. They will have first a male or female or hermaphrodite inflorescence. Sexuality and reproduction in the ash tree is very complex. Therefore when we look at this structure we realise that its just like the Araucaria Araucana. The ash tree has an architectural unit composed of three categories of axes: trunk, branches and branchlets. I won't detail the characteristics; You will see this in many documents. What should be noted here, contrary to the Araucaria, is that the three types of categories of axes are not equivalent to the branching orders and the branches are found on branches and on the trunk but in very specific positions, or course, that is in the medial basal zone, medial to basal zone of the growth of the trunk and in the distal zones of the branches. Note as well that sexuality that is inflorescences can appear on all axes, on branchlets like on the Araucaria but also on the trunk and on branches and therefore we can understand this as another stage of differentiation which is lesser in the ash tree than in the Araucaria.

What should be noted in all this is that in all the species we look at, regardless of the appearing complexity of what is being looked at, the architectural unit of any species is composed of a small and finite number of categories of axes. We saw that there are three categories of axes in the Araucaria and in the ash tree. The maximum will be found in conifers bearing in mind that many of leafy trees have 3 to 4 categories of axes in their architecture. This is a cedar for example. Don't read the details but the cedar which has a very complex architecture will have 5 categories of axes and it's quite a lot already for one single tree bearing in mind that what you call the brachiblast for example are very short branchlets and they will be carried by all the other categories of axes but always in very precise positions. For example, on the shortest shoots of the order 4 branching or right at the base of the shoots or the growth of the trunk or branches, as you can see or not see, because it is not drawn and it would be here. Last example, are the cupressaceae and the Cupressus Sempervirens the evergreen cypress, and you can see that there could be 5, 6 sometimes, categories of axes and that's the maximum found in vegetals. Despite the appearing complexity seen from the observation of such vegetals we will be amazed to see that it is in vegetals with the smallest leaves, because for a cypress you have the one millimetre little fir, and this is where you have the highest level of branching and therefore we could consider that it could be a kind of compensation between the number of axes and the leave surface. You can see the difference between the two, the differences between the Araucaria that we saw earlier on and the ash tree we've just seen. And even if the two species have 3 categories of axes, well, the major difference is that the short branchlets, which are the most differentiated structures, in the Araucaria they carried the sexuality and always in the order 3 of branching off whereas in the ash tree sexuality is distributed in all types of axes but there is one category of axis which is found branching order 3 or in branching order 2 when they are carried by the trunk but in the medial zone. And therefore the notion of categories of axes is not just a branching order. It is a notion of differentiation of different axes and the notion of categories of axes could or could not be superimposed to the notion of branching order and this is something that must be understood and not necessarily easy because you have to see several vegetals to really understand this in a clear way.

The architectural unit, well, just to finish, is something very stable in the Araucaria Araucana. For example you can see three trees, different trees: one which grew in a dense forest, one which grew in a pastured open zone and another one which grew in rocky cliffs in therefore a very poor, stressed zone with very little food. And what's interesting is that in the three cases even if the shape of the vegetal when sexuality appeared is very different, well, what they have in common is that when the cones will appear, that is when the architectural unit of a species is expressed, there will be a trunk, branch and branches which will carry the cones. There is no reduction of the elementary architecture which means that even if quantitatively speaking the architecture can be strongly modified qualitatively the hierarchy remains the same. And this is what we will see at the end of the afternoon. Here we're dealing with a very important structure for the vegetals for the level of organisation that is frozen. Another example in a cypress, to show you applications to genetics, in the Cupressus Sempervirens there were three types of shapes. The Florentine or fastigated or what you call the graveyard cypress and the horizontal ones that foresters like very much because cypress doesn't burn as rapidly as the others so therefore the species can be used as firewalls. And there are also a sort of common shapes called intermediate, that is everything that could not be classified in one or the other. They have very little irritability and when wee studied the architecture we realised in fact the fastidious shape could result from different functioning. To be fastigated you could have a trunk and horizontal short branches. We could have medium but curved or vertical but with a very closed angle or you could have the reiteration, very specific reiteration processes. I'll come back to this later on. When I use these criteria, when I look at the insertion angle or the lengths of the branches relative to the length of the trunk or the possibility of replicating the architecture in early stages we can see that these parameters can be inherited. So, again the architectural unit has 5 categories of axes which remain but with forms or shapes that can be different and in which case are related to different genetic parameters.

I will finish this part on architectural units and we'll have a break of a few minutes. Again, what you should bear in mind from this first part is that each species can be represented by what we call an architectural unit which corresponds to the elementary architecture of the vegetal. This elementary architecture is characterised by the number of categories of axes which is fairly limited and which is finite for a given species. So, but you're going to tell me when there is an adult tree we feel that there are far more axes than you say and that there are not just 5 categories of axes and so on and so forth. Well, simply because we now have to look at one last process which is essential and that is a process that will enable to duplicate this elementary architecture and the axes that form it.

This is the phenomenon called reiteration which will enable basic architecture to be replicated. And for this we will have to include a new notion; that is the concept of reiteration developed by Oldeman in 1972.

What is reiteration then? Once again, the best way to understand this notion is to go on site or to look at images and real vegetals to understand them. So, let's look at the Araucaria we saw earlier on. You remember this Araucaria ha three categories of axis, small horizontal branch stages, 4 to 6, and then pairs of branchlets. And the vegetal dies after a while and this is what you see here: a plant, branches and so on. But if you look at this specimen, well you see the same thing. And it looks like what we saw earlier on but can see that at a certain level of the trunk we've got a feeling that we've grafted a small tree similar to the trunk that carries it. Likewise for those who went French Guiana or those who've already seen these species in West Africa, because it is in both zones, the Symphonia globulifera is a very typical of the Massart model: orthotropic trunk, plagiotropic branches and it has long branches with large leaves? The architectural unit of Symphonia globulifera has 5 categories of axis quite different and typical. Most often the trees are like this, with a trunk quite conform to the architectural unit and in some cases there are structures that are far more complex as you can see here. It's only one tree. It's not the forest as such. And though the structures are derived from another, but you can see that they are exactly the same architecture as the individual tree. Well this can be looked at, you know, of course.

So, what does it mean? It means that in some specimens instead of remaining conform with the architectural unit, a plant will duplicate the architecture and reproduce it, or replicate it and you can see it here and it's in quite a spectacular way. These species are shown first not by chance. It's simply because it's quite easy to see here. You can see, that following accidents, stresses, an individual history of the specimen where the vegetal will duplicate its elementary architecture. And if you look at each of these individual parts, you put them in the ground and you will have a feeling that they are identical vegetals. Likewise, in a wild cherry tree the, prunus avium, well, it's the same model. Branches will be straighter, 4 categories of axis. This is the young tree, pyramidal, very conventional. This is when it will carry its first flowers and fruits and this structure can last for a long time. You got this very beautiful wild cherry tree with the stages of branches which are far more complex than when it was young but little difference. And in some cases, there will be adult trees more complex and you can see again that the basic architecture ahs been replicated. The trunk was here and following a trauma, in this case, probably, the tree divided itself into two and gave two identical structures with the same characteristics than the young tree.

In other cases, a simpler case, the date palm, which is most often monocole **(monoecious)**, Phœnix Dactylifera, a monocole tree. With respect to the previous question, it has lateral flowers. This would be the Corner architectural model. If you take a walk in the south of Spain, and you go to the Elche enclosed garden in Andalusia, which is supposed to be the largest palm tree garden of Europe, you will see this specimen. You can see that it's not natural for it to have several trunks. I has to be supported with cables and steel braces. So an individual can replicate its architecture. This specimen can replicate its architecture.

So, now that your eye is more familiar, if you look at the tip of the trees, if you look at this Asian fagraea, you can see that the crown is not homogeneous. An in some species, as we saw earlier on, you know, it is a repletion of the basic structure. This is a Fagerlind's model with plagiotropic substitution model and something very specific in its crown. You can see the repetition of this elementary architecture.

Same thing if you look, if you walk around Montpellier, you will see several old specimens of Abies pinsapo, which is a Mediterranean fir tree and which, like fir trees, has a young trunk and then when they get old you can see that the apex died and you have the equivalent of 3, 4 small fir trees carried by the initial tree. Again, this could result from a trauma. The tree replicated its elementary architecture at the top. Likewise, in withering trees due to dryness, cold, or various conditions, the architecture will become dislocated and there will be just this structure and shoots, kind of survival shoots, as called by some tree gardeners, and they will reproduce the initial architecture and they will reproduce the architecture of the species until they reconstitute a crown of trees. This is quite significant and these reiterations, survival shoots are the phenomenon through which a tree can survive several years. This is another locust tree Robinia Pseudoacacia, in a botanical garden. You see it's very old. It's been braces because we don't want the tree to explode. The initial tree died for a long time. And you can see buds which have reproduced the initial Toll's model of the plant and which will restore the crown of the tree which had already lost its initial crown for a long time. Likewise, in the case of withering in older trees, for example this is, for example an ash tree, Fraxinus excelsior. You can see that it is almost dead but it survives through small reiterated complexes which occur, appear in several places of the vegetal. As is the case in this poplar, in a large branch of an older poplar and you can see a small Rauh's model, typical of this species. You can see with orthotropic braches with rhythmic growth and branching off. So, this is a duplication. As you can see the vegetal is going back though the initial stages of the vegetal.

Well, you could take my seat because this going to come in the next slide. This is manifestations of this phenomenon. We will see it now.

Reiteration is the process that will make it possible for us to understand the structure of adult trees. For example, this is an old terminalia malabatrica (?), for example, and you will see that we don't quite understand where is the basic architecture. But if you look at the branches and if you look at the architecture of some of the shoots you will see the typical Aubréville models of the terminalia. Same thing with this baobab, Adansonia digitata, in Botswana, considered as one of the largest in Africa, you can see a young one, which has already started duplicating its architecture, and this is a huge one. We don't quite understand when we look at this which was the development mode of the tree but if you look at, for the Africans who are there, here, sorry, and who know young baobabs you understand the typical model of the baobab here, Massart's model, you see here and there, that is, a vertical trunk with stages of plagiotropic branches which are characteristic of the baobab and of other bombacaceae. This specimen here was initially there. This is probably remains of the initial individual, specimen, sorry. It rejected its architecture, reiteration took place in the initial reiteration and therefore this is a tree where there is not much left of the initial structures and which is fully reiterated and which can only be interpreted thanks to this phenomenon and bearing in mind that such duplication may exist and appear during the development. Likewise, if you, one day you visit California do not miss the mountain range which is just behind East California where we will find the sequoia, what we call the White Mountains, just after the Owens valley, and limit of the dessert. They're very dry, cold, bare mountains and this is where you find the oldest pinus in the word, the pinus aristata or pinus longeava. You see this individual? It's only a couple hundred years old. The initial trunk is dead, dry. And since it is very dry, and cold they do not rot or very little so you can read the history of the tree which remains. You can see a shoot at the basis which has exactly the same architecture from a seed and which reproduces the initial architecture of the tree. The pinus aristata or pinus longeava is broadly used in dendrochronology. Why is that? Well, because we know specimens which are 4,700 years old. This one is young, for example. It's only 1,600 years old. And though the various rings we can find the climatic conditions of the zone. You can see here the same phenomenon being reproduced several times. This is probably the initial individual, specimen, a shoot which died and another one which died, another one which is partly dead and which only survives through a few partial reiterations which enables it to survive and reach this very old age. This phenomenon can start very early in young trees with reiteration at the basis of a young individual which will then form some kind of a shrub for the species and the architecture would need to be studied more in detail.

As your colleague insisted on earlier on, reiteration is just one word which gives a name to a process which is very well known, been very well known for a long time in many domains. Reiteration is what will happen when we will cut trees or even really trash them because in France we use the, you know, the mechanical saw even for ornamental saws, you know. I mean, we would have to, we would need a quality criteria for trees. But you see here they've been really damaged. This is called the pollarding cutting we see sometimes and the shoots that will start from the stumps and that will reproduce the initial architecture.

Reiteration is a reproduction of the development of the vegetal which means that we could expect to see at the bases of these reiterated complexes more juvenile characteristics that would be found on the branches or the peripheral parts of the trees. This is what we use in horticulture for ornamental trees. For example, in Japan, look, you see these are what we call the pollards of Zelkova serrata. And you see that what we'll take as cuttings are these reiterations which are better for roots at there bases and much better than what we would get from those trees. What will happen here when we cut a tree? This is a hybrid walnut which has just been cut. A few weeks later shoots grow and you know as well as I do that this could be a technique to grow a forest which is called the thicket forest. Montpellier, for example, is surrounded by a thicket forest for burning, for fuel wood. And these thickets are cut every 20, 30 years and then, you know, they grow and we can cut them again to get fuel wood.

We were talking about the suckers earlier on and you can see this Symphonia globulifera, which grows in swamps, that is, very asphyxiating ground. Well, it will grow roots that will make it possible to breathe which are called the pneumatophores with very specific structures in the pneumatophores some buds can grow and give shoots, suckers that will reproduce the architecture of the plant. That is initially the vegetal will have little branches, will have short branches and slowly will set up its architecture.

Now, if you haven't understood it yet, you have to see that the development of the vegetal is a kind of cartoon, it's a kind of reading of the alphabet in a given direction. Therefore reiteration as shown here is a phenomenon through which the vegetal in a given part will read again the alphabet. And we'll find in the reiterated complexes the same succession of phases, the same development stages, sometimes which are short-circuited, as found in the initial plant. It's a form of duplication, of repetition. It's not a photocopy. But it is the sequence of development which is reproduced. In some cases this sequence of development will be reproduced through layering in the nurseries will be triggered, for example here on the thuya. We think that the whole of the Canadian forest of thuya could be just a clone in the peat zone where trees are just simply layering themselves with the lower branches that go into the ground they produce their own roots and that's very specific because these branches have little branchlets on one plane. As soon as it touches the ground its apex goes up again and branches grow in all directions. This branch which has a bilateral symmetry will gain radial symmetry and we'll find again the characteristics of a trunk and we talk about dedifferentiation of a branch into a trunk structure. It will reproduce the architecture. So, it could be very specific and very spectacular, for example, here in this thuya. This is a tree you can see in the Harcourt botanical garden in Normandy. The initial trees have been cut and the layered trees which reproduce themselves. And of course when the link between the initial trunk and the branch is broken and the plant has its own root system then you will have the formation of a clone which is a phenomenon that is far more important and was neglected in the natural vegetal formations of the world.

As you can see reiteration, just as your colleague said, is a very frequent phenomenon which will make it possible to give a name to phenomena which are well-known. Reiterations are the stump shoots, the survival shoots, the buds, the suckers, and the structures that grow where you do a bending or when you do, for example, we do fruit trees, and the regeneration mechanisms through which the vegetal will regenerate a structure which has been damaged. In that sense we should always bear in mind that the vegetal is a living organism which has a continuous organogenesis whereas animals, at least animals that walk or crawl, are organisms in which organogenesis takes place in the embryo and then it is possible only in some organs, such as the liver, which can regenerate itself. But you never saw a human being with buds. I mean, if you behead an individual the head doesn't re-grow (grow back). A tree, if you cut the trunk it will reproduce a trunk. So, these are organisms that can be differentiated through this possibility of continuous morphogenesis through development.

So, reiteration is excessively important in Nature. We saw it for man through pruning, cutting, but in Nature too to produce trees with several trunks to repair and heal trunks which have been damaged. If there is only one relay where regeneration can be perfect and the forester will be able to reuse this part. If, on the contrary, there is a fork and there is no early formation this tree is no longer useful for the forester because the trunk part can be insufficient. So, as you can see, a true regeneration, a healing of the architecture or even its multiplication to give different shrubby forms or clones as in the case of a successful multiplication.

Yes. When there is reiteration at the cellular level is the tree juvenile or do the cells keep the age of the tree from which they are cloned? Well, I think it's a very good question but nobody has the answer today. A priori, you know that this is the experience of Gautheret with the little carrots he put in vitro and he did little pieces of carrots. Well, the cell is totipotent and could keep it juvenile criteria and a cell can fully reproduce the initial plant. In practice we also note that there are very poorly known phenomenon of clone aging. And so I don't know the answer. I think it's somewhere in between and more on one side in some cases and more on one side in other cases. We see reiteration and often reiteration of, for example, of stumps will produce structures which are smaller and smaller, which are pauperised with respect to the initial structures but they're also inserted on an aging root system in a soil that really hasn't been exploited. So, is a cell or can a little cutting which will change the environment and will have a new root system, is it going to age? We don't have the certain answer to this. Some arguments would tend to show this. Other arguments tend to show that cells tend to totipotency. It is always difficult to have a full control on the environment and even if you do in vitro culture, cultivation, there could be several phenomena that would lead to aging. So, the answer is somewhere in between. But, of course it's a very good question. But it is important to answer to this because especially when you tend, you wish to propagate vegetative species but vegetatively speaking.

This is an important phenomenon. Another one is the intervention of reiteration in the development of the tree. You can see here from Hallé, Oldeman and Tomlinson's book, you see that this has already been studied. The compared development of a pioneer species such as the sequoia, which has no reiteration, you see the size grows but after a while the crown that will grow goes into a cylinder whereas a forest tree will have a normal continuous expansion until its ultimate stage and until it reaches the maximum size with the shifting from a pyramidal shape for the tip crown to a rhomboid form and it will then be the adult shape with the umbrella shape for the canopy as we sill see later on.

Reiteration is important because depending on where it is present or absent the shape of the tree, adult tree, will change significantly. This is a laricio pine more than 100 years old. It's pyramidal. You can see that there could be reiteration, partial reiteration on the leaves, on the branches but there is also the domineering trunk. But in the pinus there will be the Pinus halepensis, for example or Pinus pinea which, on the right had side, which naturally will duplicate their architecture from a certain stage of development. And you can see that consequences for the two species with respect to this one are quite different. There is probably an evolutive meaning or an adaptative (adaptive) meaning. Again this is a domain which has not really been studied and not really explored either.

Reiteration can be expressed in different ways. Let's look at his papaya tree. You know that the papaya tree is monocole. It has lateral flowers. Most of the time it's monocole but of you give it too much organic elements or, like here, if you cut the trunk, well, it can branch off and reproduce the architectural unit of the species which is very simple in this case because it's a unique trunk with lateral papaya. And you see this is the structure which is reproduced on this tree where the trunk has been cut at several levels. Likewise, for this fouquieriaceae, a strange small family from the southwest of the U.S.A. and from the north of Mexico. These are dry zone plants. Fouquieria Columnaris is like an inverted carrot. What you see are not roots. They are, in fact, inflorescences. And you can see the normal structure of the vegetal which is a non-branched Corner model and if there is a trauma the plant will reproduce the structure and therefore there will be a total reproduction of the architecture and traumatic, we’re talking about total traumatic reiteration. Again here in anthocephalus which are arborescent pioneer rubiaceae from Asia. They have stereotypic architecture with a trunk and branches which are regularly spaced. And sometimes there are specimens where the apex has been broken. And this is a very spectacular one which duplicated in two its initial architecture whereas normally there would be a unique, straight, trunk.

Reiteration, as we saw, can duplicate the whole of the architectural unit of a species. In which was we would talk about total reiteration. In some cases, this reiteration will duplicate only a part of the architectural unit. For example, it will duplicate only the structure of the branchlets as the case for this Araucaria. And we’ll therefore talk about partial reiteration.

Partial reiteration is what you will see around you once you will have identified it. This is the trunk of a fir tree and you see the new branches coming out of the trunk after a trauma which has not been identified in this case. The structure of the branch is reproduced and we talk about partial reiteration, again, traumatic reiteration, for example in this prunus, ornamental prunus, which has weeping branches. You will see there’s been a wounding of the apex of the branch and you can see it reproduces its structure, initial structure and it will replace this structure which has been damaged here.

Reiteration can also be total or partial, as I said, but it can also be, just as branching, it can be delayed or immediate. And in some cases, well, we will have a trauma. If you cut this axis there will be a sleeping (dormant) bud, which might have remained sleeping, that will grow, will reproduce the initial architecture and in which case we’ll talk about delayed reiteration because there was a sleeping phase between the time when the bud formed and the time it grew. This reiteration can be very delayed. In old trees that all of a sudden you bring back to light, old forest trees, buds which have been there for tens of years can, all of a sudden grow to start reiterations.

Delayed reiteration is what you see in this example. This is a fir tree, the apex of which has been damaged. A bud between the stages of branches, which would have given nothing if the branch had stayed intact, it will have an orthotropic axis which will go through the large stages of branches and it will then grow with the same architecture as that of the trunk, the initial trunk. Of course, for foresters these are faults of form to be cut very early. You can see a bud that is growing. You can see buds which did not grow. The initial trunk is here and this one will replace it and it will reject this little structure and you can see that it is setting up, already, stages of branches just as the initial tree did. Same thing, of course, delayed reiteration can be caused by cutting. Here this is an Italian poplar, the black Italian poplar, of the italica species which has been fairly, rather savagely cut and you can see the total delayed reiteration resulting from buds which were sleeping until then.

More specifically we see the immediate branching, that is, an axis that was in position and which, for example, had a branch structure. This will be able to dedifferentiate itself and give a structure similar to the trunk and this is what we call the immediate reiteration. Why? Because it results from a bud which was growing which means that there was a dedifferentiation of the structure which gave a branch and which all of a sudden, following a trauma, which is shown, will reproduce the structure of the trunk. If there is no trauma, this is what we observed in thuya earlier on where a branch will grow roots and reproduce a trunk and in which case it would be an immediate reiteration without trauma.

Immediate reiteration or sylleptic or through differentiation, you can see it quite easily in this specific case. This is a fir tree. We saw earlier on that following a trauma a bud which was sleeping could give rise to a new trunk. It's the delayed reiteration. Here you see another case. A trauma which too place above a stage of branches, there is only one left by the way, you see this branch straightened up and it has exactly the same structure as the other branches, that is, is has all its branchlets in one plane but it has become vertical. Well, you say, you know, I mean for the functioning of a trunk it's not very good. Well, simply because this branch was already big when the trunk was traumatised and if we look at other examples we will see that the branch will get into another functioning; it's the same situation except here there is a branch that did not move. The trauma took place here and look at this structure. This is quite fascinating. Until about here you see that the branchlets are along one plane which corresponds to the structure of the branch which was horizontal with this branchlet on one side and at one stage you see the branchlets tend to have more orientations and here the meristem instead of forming branchlets on only one plane functions like a trunk and it is now producing branches in all directions just like a trunk would do. These are very specific, very spectacular examples of immediate reiteration or through dedifferentiation. And you understand why we say dedifferentiation because a structure which was differentiated in branch can re-function as the initial structure that gave its birth function. These are very spectacular cases but, you know, at the end you see the Abies lasiocarpa. The trauma took place here. Some branches stay there and will stay there as branches. One branch has straightened up but doesn't really make it and one of the branches that will take over the others and will turn into a trunk and grow like a trunk.

So, the summary of all this. We will see it in only one species that you know well which is the Araucaria Araucana and you saw that most often this species dies having elaborated a huge structure but in most cases this vegetal will die being in conformity with its architectural unit. This evidenced by a forest with a lot of old trees. You see that the trees that died with only one trunk, you know, and therefore vegetals which die exactly as saw earlier on. But now if you go further into the forest you will see trees that are difficult to understand because they have a structure which is far more complex. This is only one individual specimen but you see that there is the initial trunk but you see that there are branches that are straightening up or they came out here, others look like the initial trunk. These are small reiterated complexes which are quite apparent, so a structure which is more complex. So, in fact, if we take a stroll in this forest, you will find all cases of reiteration I mentioned and this is one of the sources of the plasticity of these old species again which, in fact, seems to have very constrained architecture that can be modulated especially through reiteration in different ways, as we saw earlier on through total reiteration which will reproduce all of the architecture or though partial reiteration which will reproduce only the structure of the branches. But they do not do it in any way. That is they will reproduce branches exactly as the architectural unit did it. They will have pairs of branchlets, will carry cones and so on and so forth.

Always bear in mind it's not a photocopy. It's a total or partial reproduction of the differentiation sequence. These are a few examples of typical specimens. An individual, you see the individual's trunk which was almost totally burned in a fire. You wee that it recovers and it survives thanks to a shoot which grew and reproduces the initial architecture in a total way. Individuals in undergrowth which may remain in undergrowth for tens of years and here the trunk has been fully damaged and it's lost almost all its branches. You see a total delayed reiteration from the development of the basal bud. And you can see here something very spectacular: total immediate reiteration through dedifferentiation. And if you look at the basis here you will see the horizontal scars of the branches or the branchlets. They were branches like other branches but, you know, as in the case of the fir tree earlier on, these branches will have a meristem which instead of giving branchlets along one plane will have branches in all directions. These branches will be 4 to 6 and so on and so forth and will reproduce the basic architecture.

In some cases there will be total reiteration on little pads here, scars of branches which died and then they pruned themselves, buds which remain there and they can grow to give partial reiteration. Another case here, more developed, you can see the same structure but older and after a while it will produce branchlets that can reproduce the basic architecture. Partial reiteration through dedifferentiation: this is a branchlet you can see. So, why do we know this? Because, if we look at the scars of the opposite branchlet it has survived. Don't ask me why. I can't tell you. But in the curvature zone it is not dedifferentiated to have the structure of a branch and itself, which was able to carry cones, will have a branch that will have branchlets and cones will be only on these branchlets. This is quite a surprising and amazing element. Another case on a tree which was damaged, I don't know by what, but the bark was thrown out, and you can see here the buds that started and reproduced the differentiation sequence of the initial vegetal with a phase which is not branched off, a phase where there are only branchlets and at the end you can see here this is a bud which started from another tree. I did not wait 20 years at the bottom of the tree to take this photo. You can see this architecture on another tree which is very similar to what we saw earlier on and which resulted from seeds. Note that this reiterated complex has not reached the adult stage, that is, it is not itself able to carry cones and it will do so only when the branching on trunks and branches will be regular, as would be the case for the plant coming from the trunk.

So, therefore in this kind of anarchical aspect of branchings, in fact there is a very deep organisation of the architecture of <u>vegetals</u> which is well organised and which can be explained in terms of differentiation sequences and which will reproduce true reiteration. Another spectacular example in this species here when it grows in dry zones and the root system is opened. OK, I've a wide angle but we are 15, 20 meters from the trunk. This is the root system from the tree which has been opened up. Cows helped a bit, the wind did a bit of erosion and this species will just have suckers directly on the roots. And therefore it can survive and if we look at the suckers on another specimen you can see the root which is just flush with the ground. You can see the same stages with a branching in branches which becomes more regular.

So, this is something that is well structured and which reproduces in a spectacular way. This is a tree which fell but which had a few roots alive. There is a true bush of reiteration at several stages: no branching, first branching and then the whole structure. So, on this tree which fell you can see all stages of development expressed by each reiterated complex.

In some cases during germination the plantlet breaks into two parts or separates and you've got the two cotyledon buds that will give an axis. One will be dominant. The other one will die. The other one will grow and in some cases it can last for 250 years. No one wants to give away and you end up with a bifid trunk, a tree which comes from the same seed but cut in two and which grew, the two trees grew, together.

Another example of an Araucaria in a wetter, more humid zone and you will see that some of the branches, we call them branches because we can see the opposite branching on the ground and then their transformation, and they will reproduce the architecture of the trunk through total immediate reiteration as I mentioned earlier on.

Even more spectacular, this tree where a branch which was about 20, 25 meters long, so at the limit of its mechanical strength, and you can see that at a certain stage this branch went up and reproduced the architecture of the trunk with the branches and the branchlets. You can see cones only on the structures which are carried here and which are the third categories of axis of this species. So, for an individual on the border between Argentina and Chile you will see the tree which has been heavily traumatised and which was a school case all by itself. Unfortunately we didn't have nice weather. We had shoots here, total reiteration of the stumps, total reiteration on the roots, total reiteration reproducing themselves several times through differentiation and so on and so forth. So, all types of reiteration that you could think of. What is of interest in this example is to see that this species expresses about all types of reiterations that are known in vegetals but it expresses it on one specimen or on another one. So, it is therefore an opportunistic expression. This species can have all sorts of reiterations but in a normal case it will express no reiteration and the tree will die with no reiteration. So, this is a phenomenon of opportunistic reiteration. It can also be related to the mode of growth of the species but it will also be related to the primitive, old nature.

In other cases this reiteration phenomenon can be programmed in the development sequence of the vegetal and, as of a certain level of differentiation, this reiteration will appear automatically. This can affect branchlets, branches or trunks and when it affects the trunks, well, it will be the process through which the top will take place. It's what we call the architectural metamorphosis. I will show you three examples which are complementary and which show types of reiteration we'll call sequential because they will be part of the normal development sequence of the tree. The first one will be the common epicea the, Picea excelsa, which has a model which conforms to Massart's model, that is, horizontal branches stages even if the extremity tends to straighten up. So, we are between Massart's and Rauh's models as we saw this morning. The architectural unit is composed of a certain number of categories of exes, about 4. The vegetal carries male and female cones. It is a monoic species and the vegetal expresses its architectural unit by having every year one or several growth units per year. This is the normal development of the spruce as you see it in nature. Now, if you look at the plant from the top you will see that, in fact, each bearing entity with a very marked acrotony will develop a new growth unit and new shoots. So, nothing very original. All vegetals grow the same way. When you look at the tree in conformity with its architectural unit you can see the various categories of axis, well distributed, precisely, just like in the ash tree earlier on and you see a category found in the medial part of the growth unit or carried by the branches. So, therefore the vegetal could continue its expansion for a long time by growing each time at the periphery but in adult trees we can see that as of a certain time, moment in time, buds which were sleeping will grow at the bases of the branchlets and will start growing and progressively they will grow exactly as the branchlets did. As the branchlets get old and die and go though natural pruning this phenomenon will increase and in the old part you will end up with the initial branchlets which have fell, which have fallen, and they are replaced by partial reiteration of the branchlets. What is very spectacular in the spruce is that, at least in some origins, often from more Nordic, because we show that this could be an adaptation to high latitude because the sun is far more horizontal and photosynthesis is better on a photosynthetic wall than on a flat surface, this phenomenon can be reproduced and this is what we will call the draperies of the spruce with several successive waves of partial reiteration which take place one after the other and replaces one another. And therefore in some specimens, in fact, there will be, all branches will be green and photosynthetic. Whereas if there was not this process of reiteration on several waves there would only be the distal part of the branch that would be green and the rest would have shed the branchlets. This process takes place automatically and can be called partial reiteration because it is only the branchlets which are reproduced and sequential because it appears automatically for the development of the trees.

Another species studied by Claude Edelin, the Araucaria hunsteinii, which is a tropical species which is conform with the Massart model when young like the Araucaria Araucana we studied earlier on, the growth unit which are getting longer and longer, branches which carry branchlets, branchlets which are grouped at the tip of the growth unit and so on and so forth. Nothing new here again. The tree grows. It tends to lose its lower branches. You will have more developed branches at the top, branchlets which become hanging and the tip of the branches always going up so therefore branchlets at the tip tends to distribute themselves in several directions. What is more original is when the vegetal gets old the initial branches shed and you can see that there are axes that will replace this structure which is being shed and therefore at the end there will be a reiterated top which is imbricated in the initial top and which will complete it. This phenomenon can be reproduced and at the bases of partial reiteration which are dying you will see the development of other partial reiterations that will replace them. And therefore there will be successive reiteration waves and even more recent, since you are in this tree, which is composed not just of its initial parts but it will be composed of imbricated systems which, of course, will give it a much higher size. So, this is how you can look at this. The vegetal which expresses its architectural unit here and, as of a certain time, on dying branches there will be reiterated complexes that will replace the structure and they will be replaced by others which will give the imbricated systems that we call the imbricated tops of Araucarias.

Let's look now at the spruce first and then we'll have the branches grow. This is the vegetal growing according to its architectural unit, the sequential branch with the branchlets which start dying here. And then mortality that increases with the occurrence of a partial reiteration phenomenon at the bases of the branches just before they die which will replace them like this. And then the branch will continue growing. Of course, if there was no reiteration you understand that the only green part would be the white part, so, I should have used green chalk, otherwise the others would be shed. The branches fell here and then the phenomenon is reproduced each time and as of a certain moment in time the branches will die and they are being replaced be another wave of partial reiteration which replaces them. This is what will give the, up to 5, 7 times, depending on the variety, and this forms what we call the draperies, spruce draperies. Knowing that the same phenomenon will be reproduced in the Araucaria but in order to, I'll start from the right hand side, yes, so, there will be a tree here, I'll do it very small first, which is setting up its whole architecture, then it will grow a trunk, with its sequential branches on the same level because they form stages. And then a phenomenon will start with branches that will start falling. A first reiteration wave that will appear and, of course, there will be only the stump now and the sequential crown first and then a second crown that results from reiteration wave and this phenomenon could be reproduced. Each time, of course, there are the stumps of the branches, on new parts, new tips that form, and, of course, they will in turn die and you can see the stumps here as well and a third reiteration wave here that will replace the structure and give a third top which is also imbricated. So this is the case of Araucaria hunsteinii. Two previous cases had been studied by Claude Edelin: the spruce during his thesis on conifers and the Araucaria in his thesis on Asian monopod trees.

In all these cases you understand that this is a partial reiteration because we reproduce only part of the architecture, delayed because it comes from sleeping buds and sequential because it is part of the reiteration of the normal development sequence of the species.

So, now that you have understood how it takes place at the branches and branchlets, how the same phenomenon can affect the total architecture of the plant or vegetal and this is the trunk structure that will be reproduced. If we take a look at the ash tree that we studied earlier on with the three categories of axis that, let me remind you, are a trunk, branches that carry from 2 to 6 pairs of branchlets, and branchlets which are on the branches bat also in the medial and lower part of the annual growth of the trunk. The plant will remain conform to its architectural unit for a long time and after a certain time we will realise that some of the branches are more developed than others. You can see it here. You can see the phenomenon starting here. And what do we see is that at this stage the branching order 4 which did not exist before have the same characteristics as the branching order 3 that we had before hand that you find in the annual growth of the trunk. And we can see that these branches are going up and instead of having 2 to 3 pairs of branchlets they start having 3 to 5 pairs of branches and in fact what happens, well, this structure will start functioning like the trunk and will produce or start producing a process called the architectural metamorphosis, that is we will progressively see a modification. This is a structure of a low branch and you can see in some cases there could be partial reiteration of the branchlets but roughly the branches are horizontal and only carry branchlets. Now, if we look at a specimen with a higher branch, we can see that it reproduces the architecture of the trunk and it carries branches that themselves carry branchlets. So, initially, this phenomenon is rather erratic. There's a branch here and a branch there…but globally it will propagate. You can see in this older specimen that all the top branches are straightening up whereas the low branches are straightened only at the most distal part. This is a low branch and you can see the straightened part but the rest of the branch functions like a normal branch as we saw in the summit part of the tree. And there there will be competition between the branches and the trunk and you can see the hierarchy is no longer clearly established. They all seem to function at the same level and branches seem to function like the initial trunk which tends to be lost. This is a specimen going through the transformation. You can see the low branches which are more or less horizontal, partial reiteration in the structures and here you can see in this zone branches which are straightening up which are becoming more general in the top part. The top will have now a rhomboid structure. It's not as pyramidal as it used to be on the young tree but the trunk is being duplicated automatically during the development stage. This phenomenon will be accentuated, repeated. You can see this single trunk at the base and the afterwards you can see the various reiterations which will duplicate the architecture and the top being rounder and rounder as you can see. On a much older tree now, you will see that we no longer have the pyramidal shape but pyramidal shapes for each complex and all said becoming more round and you see the structure that reproduced the architecture of the trunk and we can see on a diagram here, you can see a tree which is very similar to the previous one. The lower part has been shed. You can see partial reiterations and a few survival shoots which are total reiteration that do not lead to much. And all these straightened branches which reproduce the same architecture ad the trunk and they could be apex that will die and will favour the reiteration but this will take place anyway in an automatic way in the development sequence of the tree which is still growing and the top is getting rounder and it is composed more and more of duplication of the basic architecture and, of course, shedding continues. We see very few horizontal branches because they belong to the young tree and they fell. And you can see this reiteration which takes place which reproduces itself and you can see waves of reiteration which take place successively, the reiterated complex from the successive waves being each time smaller.

In some cases, well, the oldest trees may go through withering and we'll see the initial architecture with master branches which result from the reiteration process and the architecture will survive through small shoots which are delayed reiteration unlike the immediate duplications we've just seen which construct the global architecture of the tree.

Now, how can we summarise this? We will look at the development of the plant as fundamental stages. We see the appearance of key criteria such as blooming and so on and so forth. Then the plant will express its architectural unit. In the ash tree there are three categories of axes. I did not show you the categories here because I don't want to lake the diagram too busy. And after a while the vegetal will grow, branches will straighten up, erratically at the beginning and then on a more general basis. They will reproduce the architecture of the trunk. This will be favoured by the death of apex but, anyway, this will occur. And subsequently the plant will construct itself. Note the changes of shape of the crown which used to be pyramidal and now has become round and you see the successive waves of reiteration which are getting shorter or some other reiterations which are delayed will enable the lowest branches to survive. And you will see that from the plantlet that started from 2 cotyledons and 2 little leaves on the first year, now, this would be several tens of years, and you can see this architecture slowly will go through a metamorphosis to give the adult tree that you see afterwards in a forest.

As of 1978 this gave rise to a typology of the development stage of forest trees with the tree of the future which was basically the young tree expressing its architectural unit which will duplicate its architecture to give the tree of the present which is domineering which is in the forest canopy. That's the one the forester will cut because this is where you get the best quality wood and because if he waits too long there will be withering, local withering defects which is called rotting of the trunk. There will be a dislocation of the crown which will survive only through another type of reiteration which is the delayed reiteration which will reproduce the architecture of the plant but that will ensure simply the survival of the architecture.

Of course, what I've shown you is the summary of observations of hundreds of specimens for each species. It is the development sequence ideal for the vegetal without any trauma. Of course, in the forest it's not that easy and vegetals experience several stresses and traumas, that is, for thousands of specimens there will be only a few that survive. Why? Well, because there are branches that fall, cold years, dry years, insects, stresses and traumas and for a given specimen the trajectory will stop abruptly and the tree will die and disappear forever. In other cases what we'll find afterwards will be that, well, the trees fight against traumas through reiteration, through regeneration of the architecture as we saw earlier on. And again, at all stages trees will die but those that will go beyond a certain stage of growth will duplicate their architecture, initial architecture, will continue, if they don't die in the process, this architectural metamorphosis, will give reiterated complexes which succeed to one another and are getting smaller and smaller as the plant is getting old and this will give rise to a homogenous structure at the periphery of the adult tree which will then, eventually, have sort of a more umbrella shape. This reiteration, of course, goes through the same gradients as what went through the vegetal and Oldeman in his thesis in 1972 talked about arborescent reiteration or arbustive, suffrutescent, herbaceous and so on and so forth to indicate this pauperisation of the structure of successive reiterated complexes which take place during the development.

Therefore this reiteration has specific characteristics and somehow when we look at an adult top some events seem to show that reiteration, or the reiterated complexes that appear in the crown, have a certain autonomy. This is what seems to indicate what he called the "timidity" of the tops where within the same crown of tree there will be individual little tops that correspond to reiterated complexes and which are often separated by spaces, what you see here, for example, on a parinari, which also exists in dipterocarpaceae, or you find in the pinus when trees have reached a sufficient size.

Another argument for autonomy or partial autonomy of reiterated complexes are desynchronisms (desynchronisation) of blooming. Here you can see in Burkina Faso, a mango tree, quite significant, it is composed of several reiterated complexes and you can see that there are desynchronism in this crown, especially a part that corresponds to this trunk which is completely bloomed as the rest of the tree is just vegetatively resting. On a master branch which has been cut you can see exactly the same heterogeneity with shoots which are growing and others which are at rest and others that are full of flowers and those shoots started from the same stumps of the master branch.

This autonomy you will see it as well when trees die partially. This is an umbrella pine near La Grande Motte and you can see that this started, the, this was used by people, you know, hunters they shot the tree but you can see that it wasn't the whole tree that died but some parts of the tree died. Some reiterated complexes preferentially than others. Likewise, in the Peru square in Montpellier you've seen there are large magnolias. They were very thin and not very good a couple of years ago. You see Fagerlind's model with branches and their substitutions, some reiterated complexes would die, wither away and die on the trees.

Again, for the reiterated complex, at least for the delayed one, we can see the frequent occurrence in underwood, wet underwood, or of roots, at the bases of the complex you can see the Aucuba japonica and in the undergrowth where it is found you can see the root which starts at the basis of this reiterated complex just like a root would start at the basis of a plant. We see this again in various species in tropical undergrowth where conditions are ideal to have this rooting expressed and low on the dying trunk you can see the various reiterated complexes and the development of roots. This phenomenon is wide enough to not just be related to good conditions of rooting. You see a cactus in the desert. The head has been cut and the shoots have developed their own roots systems in totally desertic conditions. Sometimes, well, such root systems will give rise to some strange systems. Look at this Niaouli in Costa Rica. You can see that roots which started at the basis of the delayed complex, of the reiterated complex you see at the summit of this big trunk. And sometimes, as well, these reiterated complexes are not visible simply because they start inside the trunk and they digest the organic matter that is rotting. For example, this is a chestnut tree in Corsica. The trunk is dead and rotting and by scraping we could see the roots of the reiterated complex which were in the trunk and which were feeding on the trunk and without being in the open air. Same thing in this Judas tree from the botanical garden, and which was cut a couple of years ago, which was totally hollow and rotten. And when we tried to treat it by removing part of the trunk we realised that at the basis of the reiterated complex there was a huge pivoting root which had fed from this part and which had then gone into the ground.

Sometimes there are not root systems but they are like connection cords of vascular system of the reiterated complex to the bearing axis. This is an araliaceae. The system that will mimic a root and which will connect itself to the vascular system of the support stem or in this gnetum, this root system which seems to be crawling under the bark of the initial vegetal.

As I said there are several types of reiteration. And I talked about the sequential reiteration which occurs and which results into a duplication of the basic architecture. In other cases there will be a delayed reiteration and we have seen that juvenile characteristics such as the root system could reappear and there could be other criteria. You know that in a mimosaceae, which are leguminous with leaves, which are often bipinnate leaves, several locust trees have a philode structure. It is the leaf stalk of the, which becomes photosynthetic which becomes flat. You can see germination of acacia koa in Hawaii which gives leaf stalk and, a bipinnate leaf stalk and in philodes which become the adult leave. This is a transition phase between the two and you can see the two structures. Do not confuse the typical leave of the bipinnate family and the philode. In some cases there is a transition zone which shows that this philode results from the leaf stalk that in becoming flat. Here you can see a flat leaf stalk. It has the adult form and only the distal part of the leaf remains. On the adult tree, this is another acacia from the Reunion Island, and you can see only philodes and when you look at old trees with reiterated complexes which appeared on old parts you end up with these bipinnate leaves, juvenile characteristics which reappear in this reiterated delayed complex.

So, as I said, it's not a photocopy but it is simply a repetition of the development sequence, more or less complete depending on the, at which position it starts. What does it mean? Even if within the vegetal structure the reiterated complex can have a certain autonomy, they, like the rest of the vegetal, they are submitted to a strong hierarchy, to a strong organisation, and to what is called morphogenetic gradients such that these structures that will appear will have such or such aspect depending on the position on the plant, on the architectural stage of the plant and, of course, on the conditions in which the vegetal grows.

How can we look at a vegetal? A vegetal can be considered as a multi-scale organism and an organism inside which we will identify levels of organisation that will reproduce themselves and from which will go to other levels through some repetition phenomena which are not numerous and which do not necessarily express themselves in the whole plant. The elementary level when we look at our approach, which is a microscopic approach, is the metamere or phytomere that is a portion of the stem between two nodes: the node which carries either the leaf and the axillary bud, this elementary structure is the elementary organisation level which will be reproduced by several phenomena especially during rhythmic growth. And we will reproduce, as you saw earlier on, growth units. The growth units will then be included in annual growth that will form a new level of organisation. And if there is indefinite growth all this will give birth to axes that will have stacked up several successive levels of organisation. In some cases, as in a coconut tree, the metamere will repeat itself without any rest or non-elongation phase and there will be indefinite growth and we'll go directly from the metamere to the axis. Finally, in the case of definite growth, as we saw, there would be sympodial growth that could lead to linear sympodes and these linear sympodes are the equivalent of an axis we have here. The modules, furthermore, could be mono or polycyclic and so on and so forth. As you can see this is a first phenomenon we studied this morning, growth that can reproduce and construct the elementary organisation levels in a coconut tree. Well, we will not go beyond that stage but in others there will be another repetition process called the branching and which will make it possible to go from a, to go to a more complex structure, highly hierarchised (hierarchical). This is what we call the architectural unit and this architectural unit can be the maximum organisation level of the vegetal or could be itself duplicated to give the whole plant the metamorphosed tree through the phenomenon we call the reiteration.

So, as you can see, the vegetal can be seen as a stacking of levels of organisation from the simplest to the most complex through repetition processes and this repetition, however, should never, will never reproduce identical things but will produce structures, the nature and the parameters of which vary during autogenesis. I don't have time to detail but bear in mind, remember that the values of the parameters of an elementary structure, growth unit, here, for example, will evolve according to very precise morphogenetic gradients you see here with, for example, what we call the basic effect which will be the progressive increase of the complexity of the architecture of the vegetal and the length of the successive annual shoots or growth all depending on the, as a function like acrotony which is a local gradient. And, for example in the ash tree there will be branches at the top and short branchlets at the basis and you can reproduce the same structure through a phenomenon called reiteration.

And it is this vision of the vegetal and on this diagram you can see in the same colour and same size elementary entities which have exactly the same physiological age. It is from this vision of the plant and this identification that we've been able to develop samplings protocols and models and mathematical and computerised models for the quantification and simulation of architecture of vegetals that we developed in our laboratory but for which I would need as much time as what I had today, if not longer, to talk about. So, it will be another time. Thank you.