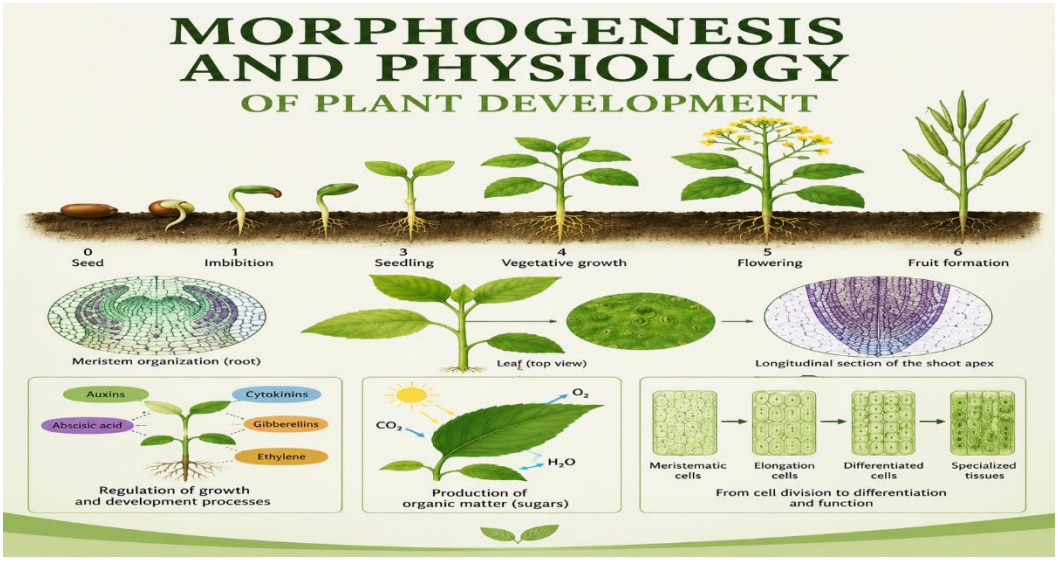
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People's Democratic Republic of Algeria
Ministry of Higher Education and Scientific Research

FACULTY OF NATURAL AND LIFE SCIENCES

DEPARTMENT OF PLANT BIOLOGY AND PHYSIOLOGY

COURSE NOTES



Intended for Master 1 (M1) students

Specialty: Plant biodiversity and physiology

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The course "Plant Morphogenesis and Developmental Physiology" is a core subject in semester 2, within the "Plant Biodiversity and Physiology" program's Core Unit. This subject has a weighting of 3 and is worth 8 credits, with a total of 90 hours of instruction spread over 14 to 16 weeks, including two lectures (3 hours) and two practical sessions (3 hours) per week. The aim of this course is to provide students with a theoretical and practical foundation enabling them to acquire fundamental knowledge about plant function and development. It emphasizes the mechanisms of morphogenesis and growth, as well as the structural and functional organization of plants, from the cellular and molecular level to the plant organism as a whole. This course material is intended for students in the natural and life sciences, particularly those specializing in plant biology, plant physiology, biotechnology, and biodiversity. This course can also be useful to Master's students in the life sciences, as well as to students in foundational biological and agricultural sciences, and to anyone wishing to delve deeper into the study of plant development. To effectively grasp this subject, a solid foundation in plant biology (morphology and anatomy), plant physiology, biochemistry, and genetics is necessary. This course covers the main aspects of plant morphogenesis and developmental physiology, integrating the cellular, molecular, and physiological bases of plant development. It also addresses the different stages of vegetative and reproductive growth, as well as the regulatory mechanisms that control them. Particular attention is paid to the interactions between genetic, hormonal, and environmental factors, which condition the expression of the plant development program and ensure the progressive organization of plant structures and its adaptation to the environment. Finally, this handout is structured into several chapters covering the essential concepts of plant morphogenesis, including growth, cell differentiation, organogenesis and the mechanisms regulating development in plants.

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Introduction

Morphogenesis and developmental physiology are two fundamental branches of plant biology that focus on the processes governing plant growth, structure, and differentiation. They allow us to understand how an undifferentiated cell or group of cells gradually evolves into a complex, organized, and functional plant organism. In plants, development is characterized by continuous and indeterminate growth, driven by meristematic tissues capable of producing new organs and specialized tissues throughout the life cycle.

Plant morphogenesis encompasses all the processes responsible for establishing the form and spatial organization of plant structures. It relies on a coordinated succession of biological events, including cell division, elongation, differentiation, and the organization of cells into tissues and organs such as roots, stems, leaves, flowers, and fruits. This process leads to the development of a modular and often repetitive plant architecture, characteristic of higher plants. It begins at the level of meristems, areas of undifferentiated cells capable of initiating the formation of new organs through finely regulated mechanisms.

Developmental physiology, for its part, focuses on the functional and biochemical mechanisms that control these morphological transformations. It highlights the central role of phytohormones, particularly auxins, gibberellins, cytokinins, abscisic acid, and ethylene, in controlling the growth and differentiation of plant tissues. It also incorporates the signaling mechanisms, metabolic processes, and energy flows that coordinate plant growth and ensure the proper progression of the various developmental stages.

This regulation is continuously influenced by environmental conditions such as light, temperature, water, and minerals. These factors interact with internal processes to modulate plant growth and organization. Thus, water stress can limit the development of vegetative organs, while temperature variations can affect germination, meristematic activity, or flowering. Despite these constraints, plants possess numerous strategies that allow them to respond to fluctuations in their environment and ensure their survival.

The life cycle of higher plants unfolds in several successive stages, from germination to senescence, passing through vegetative growth, organ differentiation, and reproduction. Each of these phases results from a close interaction between genetic, hormonal, and environmental factors, ensuring harmonious coordination of all developmental processes.

Thus, the study of morphogenesis and developmental physiology is of major importance in the fields of agronomy, biotechnology, and ecophysiology. It contributes to a better understanding of plant growth, differentiation, and adaptation processes, enabling improved agricultural production, the selection of varieties more tolerant to environmental stresses, and more sustainable management of natural resources in the context of climate change.

Chapter 1
Structure and Functioning of Meristems

Meristems are plant tissues composed of undifferentiated cells with high mitotic activity. They give rise to all the tissues and organs of the plant. Their activity ensures the continuous production of new cells, enabling plant growth, tissue formation (histogenesis), and the development of new organs (organogenesis).

Etymology

The term *meristem* derives from the ancient Greek *meristos* , meaning "divisible" or "capable of dividing," in reference to the intense cell division activity that characterizes these tissues.

Meristems occupy different positions in the plant and perform various functions depending on their location and activity.
Two main categories of meristems are distinguished (Fig. 1).

***** Primary meristems

Primary meristems are responsible for the longitudinal growth of vegetative axes. They are located at the tips of roots and stems and ensure the formation of the plant's primary tissues.

Primary meristematic cells exhibit several cytological characteristics: they are small, generally isodiametric (cuboidal or polygonal), have thin and poorly lignified cell walls, a high nucleocytoplasmic ratio, one or more well-developed nucleoli, poorly developed vacuoles, and a high ribosome density. Their cytoplasm is dense and their organelles are poorly differentiated.

Two main primary meristems are distinguished:

- The root apical meristem (MAR).
- The shoot apical meristem (MAC).

***** Secondary meristems
Secondary meristems play a role in the growth in thickness of organs, particularly in woody species. They generally derive from already differentiated tissues that regain meristematic activity.

The main secondary meristems are the cambiums, whose cell divisions produce secondary conducting tissues and contribute to the increase in diameter of stems and roots.

* Special meristems

Some meristems have specific locations or functions:

- Intercalary meristems: located at the base of the internodes or nodes, mainly in Poaceae, they allow the rapid resumption of growth after cutting or grazing.
- Adventitious meristems: responsible for the formation of roots or stems from tissues that do not usually participate in their origin.
- Axillary meristems: located in the leaf axils, they give rise to axillary buds and participate in the branching of the plant.

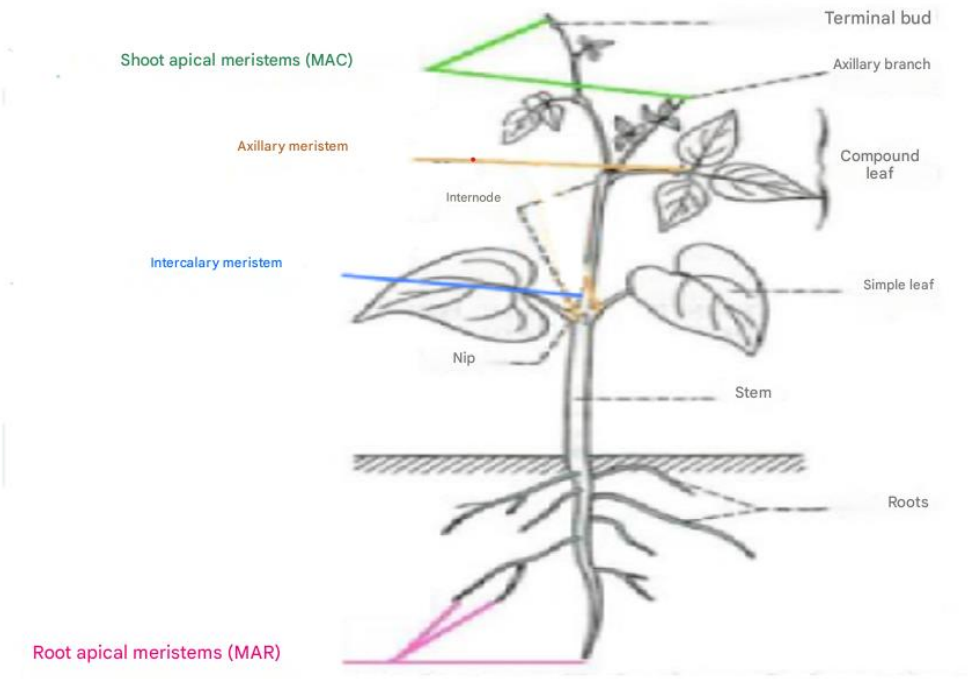


Figure 1: Distribution of different types of meristems at the plant level.

1.1. Root apical meristem

The root apical meristem develops during embryogenesis. It ensures the formation of the primary root tissues as well as the protective root cap. Unlike the shoot apical meristem, it is essentially histogenic, since it does not directly produce lateral organs. Lateral roots form endogenously, away from the apex , from the pericycle, a layer of cells located at the periphery of the central cylinder. Their development replicates the functional organization of the root apical meristem.

The root system is a fundamental element of the plant. Its morphology and architecture vary according to the species and environmental conditions. It fulfills several essential functions:

- Anchoring the plant in the soil;
- The absorption of water and mineral elements;
- The transport of substances to the aerial parts;
- The storage of nutrient reserves in certain species.

The root apical meristem is located immediately behind the root cap. It represents the growth zone responsible for producing the cells that will form the various root tissues. The root cap, composed of parenchyma cells, protects the meristem from the mechanical stresses of the soil and facilitates root growth through the secretion of mucilage. During root elongation, the peripheral cells of the root cap gradually detach. Covered with mucilage rich in pectic polysaccharides, they are continuously replaced by new cells produced by the root cap maintenance meristem, also called the calyptrogen.

Above this region lies the quiescent center, an area composed of cells with low mitotic activity. This center plays an important role in maintaining the organization of the meristem and in its regeneration after potential damage. Certain cells of the root cap, called statocytes, contain numerous specialized amyloplasts, or statoliths. Under the influence of gravity, these organelles sediment in the cytoplasm and participate in the perception of the gravitational stimulus, thus enabling the downward orientation of root growth (positive gravitropism) (Fig. 2).

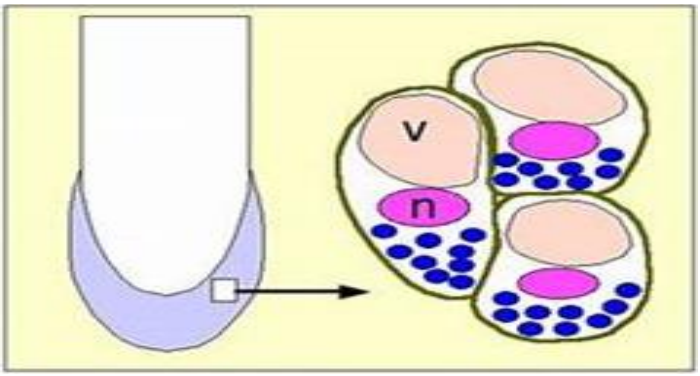


Figure 2: Representation of the phenomenon of sedimentation of statolytes, responsible for geoperception in the root.

The apical meristem is followed by an elongation zone, generally limited to a few millimeters, where cells gradually cease dividing and rapidly increase in size. This region is followed by a piliferous zone, or zone of cell differentiation. In this zone, root hairs appear, each consisting of a highly elongated epidermal cell containing a large vacuole. Their thin, uncutinized cell wall promotes the absorption of water and mineral salts from the soil, thus increasing the surface area for exchange between the root and its environment (Fig. 3).

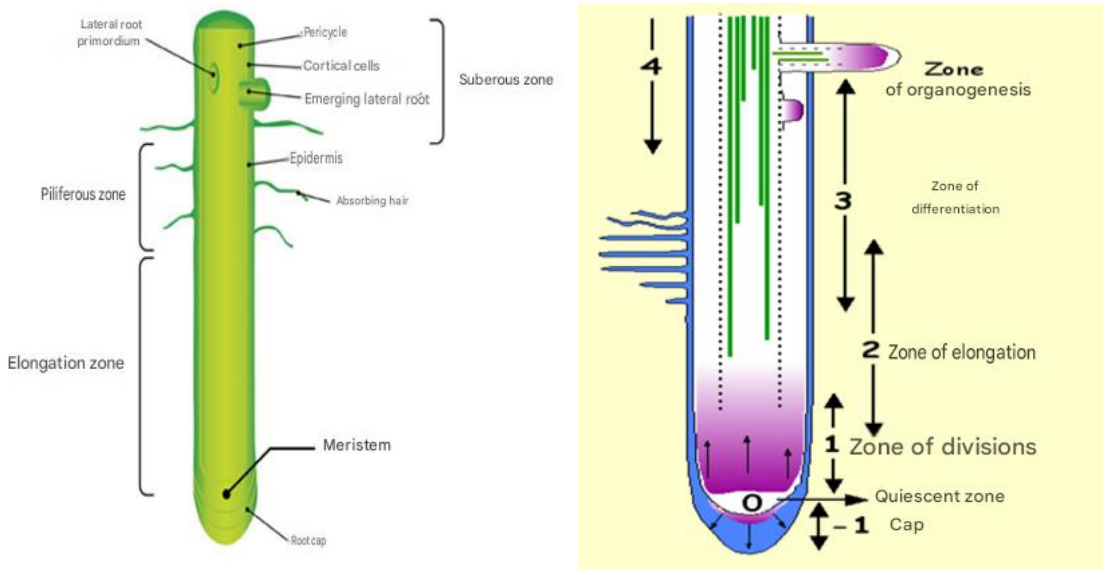


Figure 3: Root meristem.

1.2. Shoot meristem

The shoot apical meristem is a region composed of young, undifferentiated cells with a high capacity for division. Located at the tip of the stem, it ensures the plant's primary growth by allowing the elongation of aerial axes and the formation of new organs. It fulfills two essential functions: a histogenic function, responsible for establishing the primary stem tissues (epidermis, vascular tissue, and supporting tissues), and an organogenic function, giving rise to leaves, axillary buds, and future floral structures (Fig. 4).

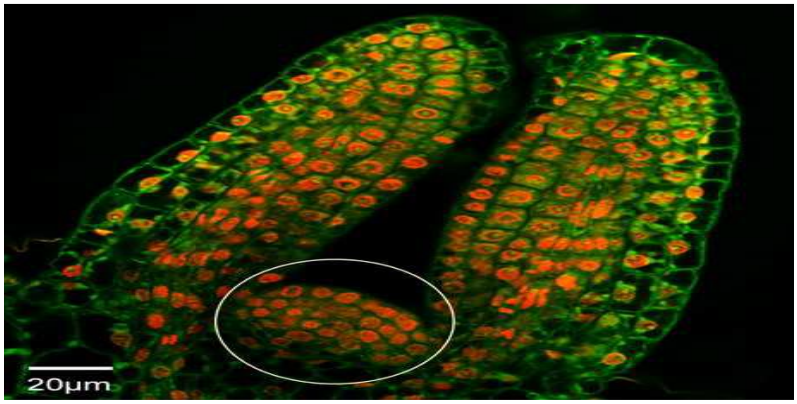


Figure 4. Confocal microscopy observation of the vegetative apical meristem *Arabidopsis* seedling at the 6-day post-germination stage.

In order to understand its organization, several models have been proposed. Among them, the zonal model and the cell layer (tunica-corpus) model are the most used to describe its functional and cytological structure.

A. The zoned model

The zonal model, proposed by René Buvat in 1952, considers the shoot apical meristem as a dome organized into three distinct functional zones: the central zone (CZ), the peripheral zone (PZ), and the medullary zone (MZ). This organization is based on cytological criteria such as cell size, cytoplasmic density, and especially the level of mitotic activity (Fig. 5).

* **The central zone** contains poorly differentiated initial cells with low mitotic activity and a long cell cycle. These cells are large, slightly vacuolated, poor in RNA and protein, and have small nucleoli. They primarily serve as a reserve and for the renewal of other meristem zones.

The **peripheral zone** exhibits very intense mitotic activity. The cells there are small, rich in RNA and proteins, with dense cytoplasm and large nuclei. The cell cycle is short, allowing for rapid proliferation. This zone is organogenic and gives rise to leaves, axillary buds, and floral parts.

***The medullary zone** has intermediate mitotic activity. The cells there are vacuolated and often contain reserves. Cell divisions there are predominantly periclinal, contributing to the formation of the internal tissues of the stem, particularly the pith.

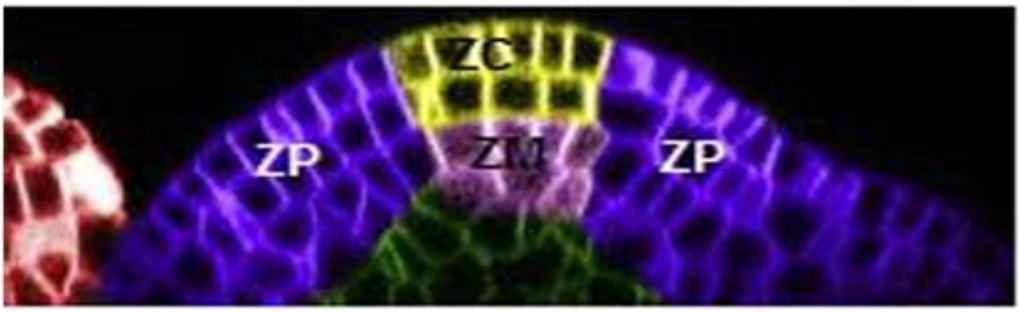


Figure 5: Schematic view of the development zones of the apical meristem cauline in *Arabidopsis* . (ZC. Central zone; ZP. Peripheral zone; ZM. Medullary zone).

B. The cell layer (tunica-corpus) model

The cell layer model, also called the tunica-corpus model, was proposed by Alexander Schmidt in 1924. According to this model, the shoot apical meristem is organized into superimposed cell layers: the tunica (L1 and L2) and the corpus (L3) (Fig. 6). Layers L1 and L2 divide primarily in an anticlinal manner (perpendicular to the cell wall surface), ensuring surface growth. Layer L1 forms the protoderm, which gives rise to the epidermis, while L2 contributes to the tissues of the leaves and reproductive organs. Layer L3, or the corpus, divides both in an anticlinal and periclinal manner (parallel to the cell wall surface), contributing to volume growth and the formation of the internal tissues of the stem.

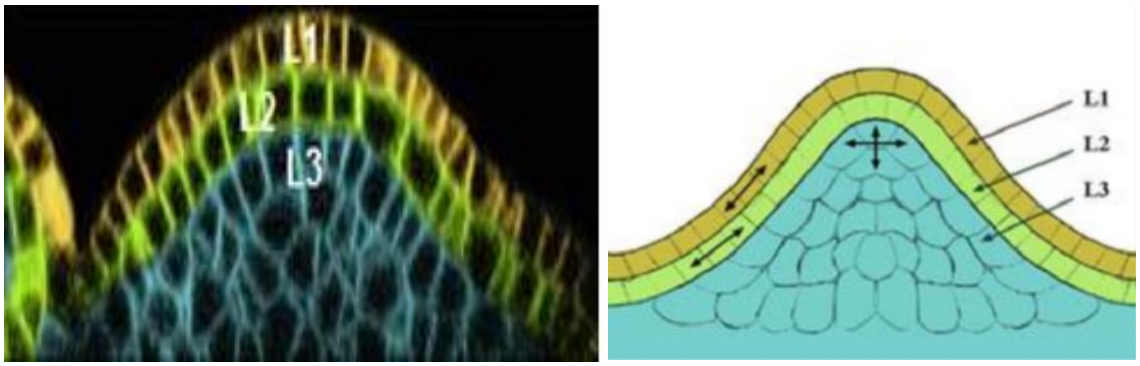


Figure 6. Tunica-Corpus Model of Apical Meristem Organization

1.2.1. Vegetative meristem

*** Mitotic activity of the various zones of the vegetative point**

Mitotic activity in the shoot apical meristem is unevenly distributed among the different zones, reflecting a functional specialization essential to the organization of the vegetative point. This

heterogeneity ensures the simultaneous maintenance of the cell reservoir, the production of new cells, and organ formation. Thus, cell dynamics vary according to region: some zones are characterized by low division intensity, guaranteeing the preservation of the initial cells, while others exhibit high proliferative activity, involved in organogenesis. An intermediate activity contributes to the structuring and differentiation of internal tissues.

This coordinated distribution of mitotic activity ensures the harmonious growth of the stem, the establishment of aerial organs, and the internal organization of the meristem.

*** Quantitative study of nucleic acid synthesis in the various zones of the vegetative point**

The different zones of the shoot apical meristem exhibit varying levels of nucleic acid synthesis, particularly DNA and RNA, reflecting their degree of mitotic and metabolic activity. DNA synthesis is directly linked to cell replication and occurs primarily in actively dividing cells, especially in the peripheral zone, where cell proliferation is most intense. This region is thus characterized by a high rate of DNA duplication. RNA synthesis is closely associated with metabolic activity and the production of proteins necessary for cell growth and differentiation. It is maximal in the peripheral zone, more moderate in the medullary zone, and relatively low in the central zone, consistent with the activity level of each meristem region.

*** Histogenesis and Organogenesis**

A. Histogenesis

Histogenesis is the process by which plant tissues are formed from meristematic cells. In the shoot apical meristem, undifferentiated cells divide and differentiate progressively to give rise to the main primary tissues of the stem. This process leads to the development of the covering tissues (epidermis), the ground tissues (parenchyma, collenchyma, and sclerenchyma), and the vascular tissues (primary xylem and phloem).

B. Organogenesis

Organogenesis refers to the formation of plant organs from the apical meristem. It primarily involves the initiation of leaves, axillary buds, and later, floral structures. In the shoot meristem, this process is particularly active in the peripheral zone, where cell divisions lead to the

development of leaf primordia. Organogenesis thus contributes to the establishment of the vegetative and reproductive systems, as well as to the branching of the plant.

*** Differentiation and dedifferentiation**

A. Differentiation

Differentiation is the process by which a non-specialized cell (often originating from the meristem) acquires:

- A shape.
- A structure and .
- A characteristic function of each type of tissue. It becomes a specialized cell (e.g., chlorophyll cell, xylem cell, phloem cell, etc.).

Example of a meristematic cell differentiating into a chlorophyll-containing cell (Fig. 7): In this case, cell differentiation is characterized by:

- Cell enlargement. It is this elongation that is responsible for the growth in length of the stem and root.
- A significant development of the vacuolar apparatus.
- Transformation of proplastids into chloroplasts.
- Adaptations to the specific function of photosynthesis.
- Thickening of the pectocellulosic cell wall.
- Loss of the ability to divide.

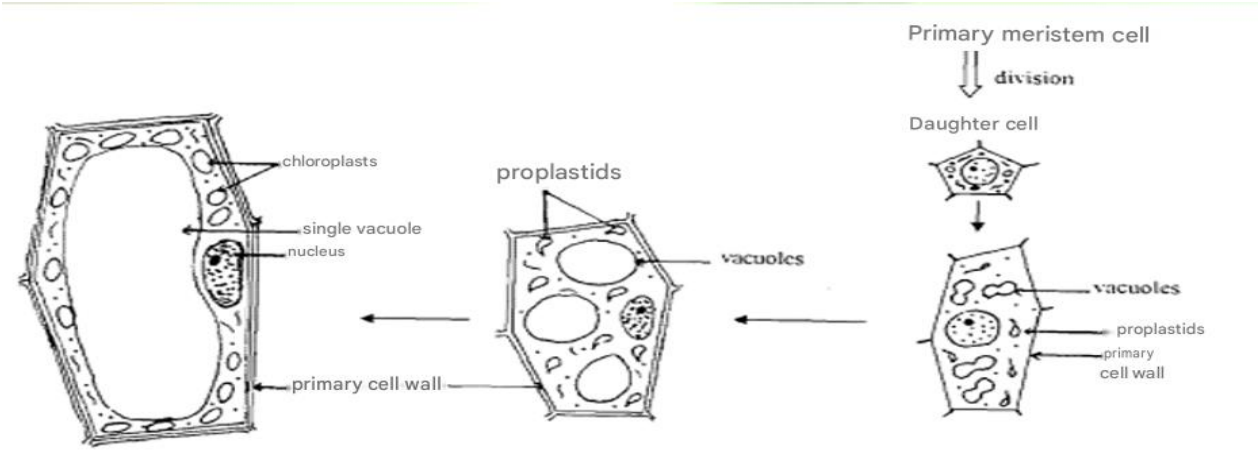


Figure 7: Differentiation of a young cell into a chlorophyll-containing cell

B. Dedifferentiation

Cell dedifferentiation corresponds to a process during which a differentiated cell gradually loses its specialized characteristics in order to return to a more undifferentiated state, exhibiting properties similar to those of meristematic cells, including the ability to re-enter the cell cycle and divide actively (Fig. 8).

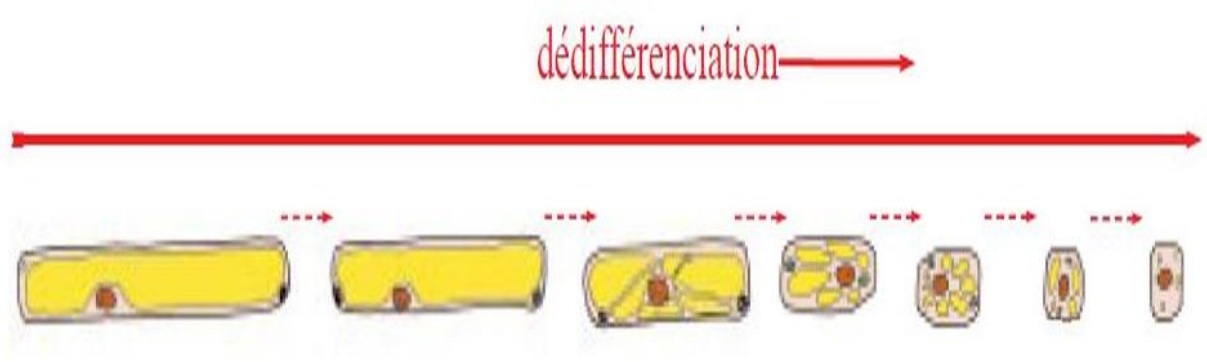


Figure 8: Differentiation phenomenon of differentiated cells

In plants, this phenomenon is particularly evident when certain parenchyma cells resume mitotic activity and acquire meristematic behavior. It also plays a role in the formation of a callus (Fig. 9) following injury, enabling the repair of damaged tissues. Furthermore, dedifferentiation is a fundamental mechanism in ***in vitro culture*** (totipotent cells), where it contributes to the regeneration of new tissues or organs from differentiated cells.

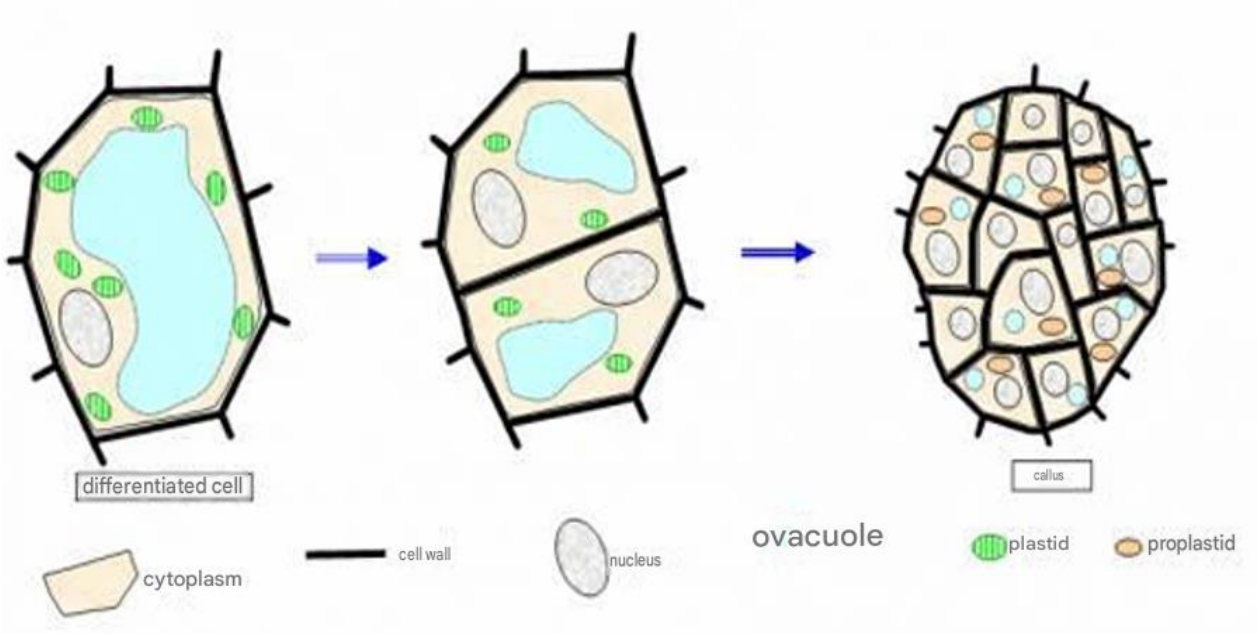


Figure 9: Formation of a callus from the differentiation of a cell.

* Growth and development

A. Growth

Plant growth corresponds to an irreversible increase in the dimensions of an organ or organism, resulting primarily from two complementary processes: cell division and cell elongation. In plants, this is a quantitative phenomenon, measurable through various parameters such as length, leaf area, volume, or biomass.

Growth is ensured by meristems, whether apical, lateral, or intercalary, which constitute the active zones of cell proliferation. Dynamically, it generally follows a sigmoid curve comprising a lag phase, an exponential phase characterized by strong mitotic activity and significant cell elongation, and then a slowdown phase associated with tissue differentiation and maturation.

Among the most representative models of this phenomenon, root elongation illustrates the meristematic activity and cell expansion responsible for the continuous elongation of organs in the soil (Fig.10).

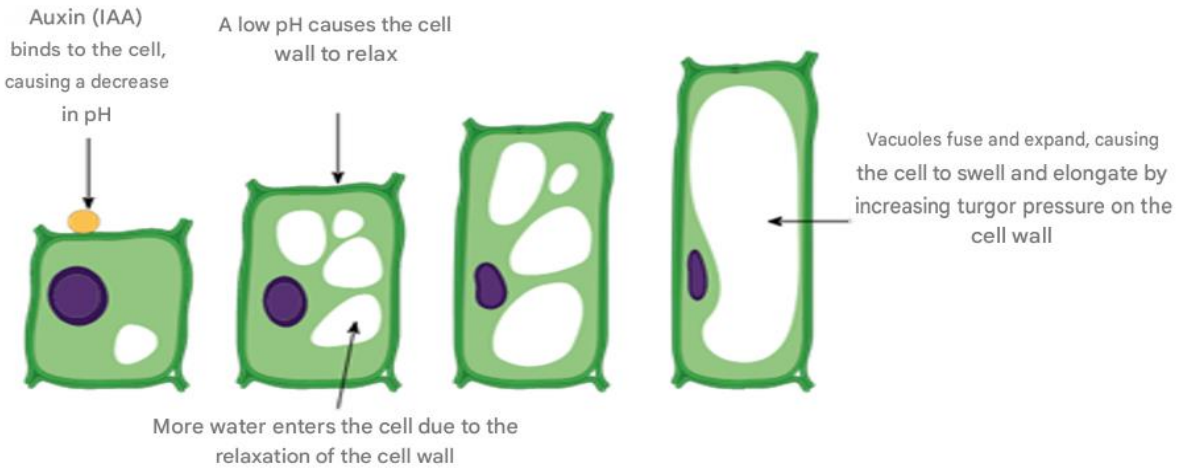


Figure 10: Elongation phenomenon at the level of the root meristem.

B. Development

Plant development corresponds to all the qualitative processes ensuring the progressive organization of the plant organism, from the embryonic stage to the adult stage (Fig. 11). It

encompasses morphogenesis, histogenesis and organogenesis, leading to the establishment of specialized and functional structures.

Unlike growth, which is a quantitative phenomenon, development is an essentially qualitative process, observable through morphological, anatomical, and physiological changes. It relies on the expression of the genetic program and is modulated by environmental factors, including light, temperature, water, and hormonal regulators

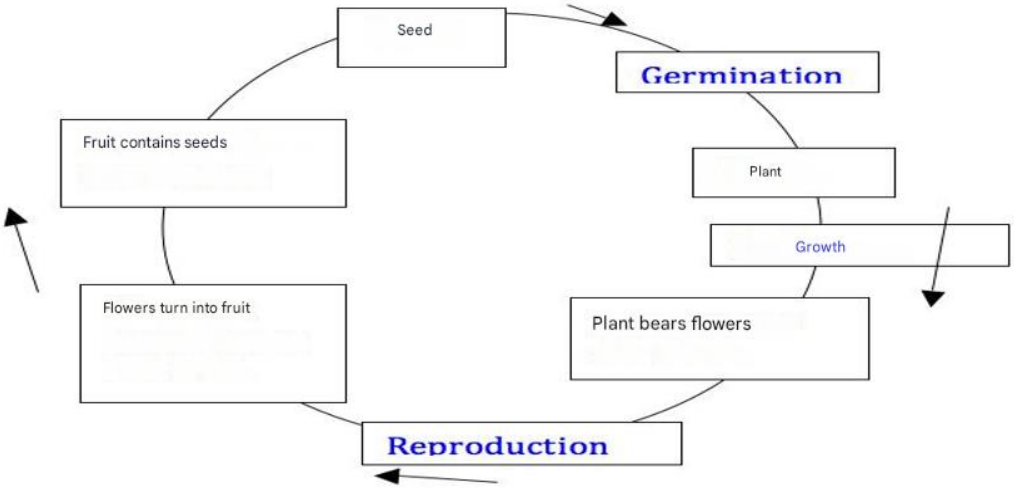


Figure 11: Plant development cycle.

Thus, development ensures the progressive formation of the form and functions of the plant, in coordination with growth, until the establishment of a mature and functional plant organism.

*** Phyllotaxis**

Phyllotaxis, from the Ancient Greek words *phýllon* (leaf) and *táxis* (arrangement), refers to the spatial organization in which leaves, or more generally lateral organs, are arranged on the stem of a plant. By extension, this concept also applies to the arrangement of the constituent elements of a fruit, flower, bud, or capitulum. It can be classified into different types, determined in particular by the number of leaves per node and their arrangement along the stem (Fig. 12).

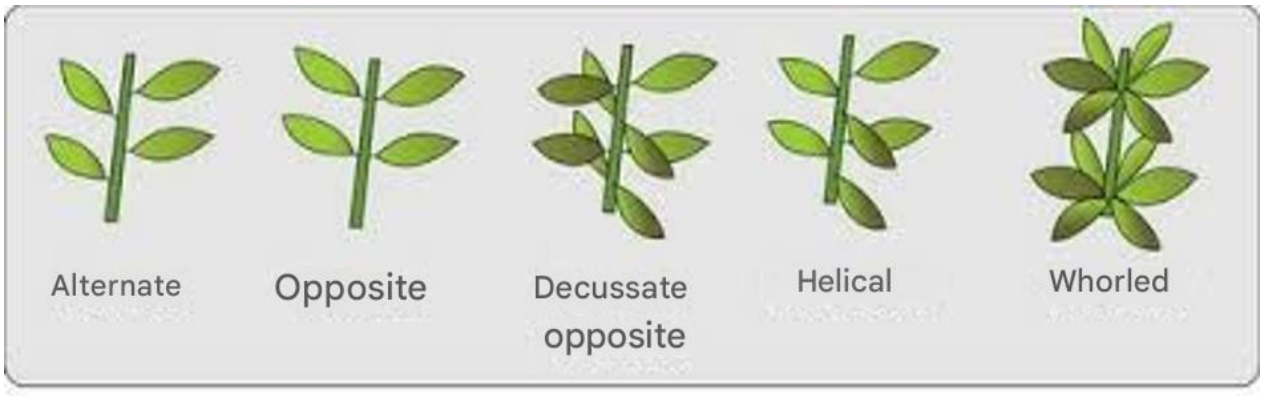


Figure 12: Main types of phyllotaxis in plants.

1.2.2. Floral meristem: morphological and structural modification of the vegetative meristem.

The plant transitions from a vegetative state, characterized by the formation of roots, stems, and leaves, to a reproductive state marked by the appearance of flowers and inflorescences. This change constitutes a major transition in the plant development program. It represents a key stage in the plant development program, corresponding to a reprogramming of the apical meristem, leading to the establishment of new reproductive structures. This transition is finely controlled by complex mechanisms involving genetic, physiological, and environmental factors. It occurs at the optimal time to ensure the reproduction of the species. It depends on several factors, including

- Environmental conditions (temperature, light, seasons)..
- The physiological state of the plant (age, maturity, development), as well as the expression .
- Specific genetic programs.

***Stages of transition from the vegetative meristem to the reproductive meristem**

The transition from the vegetative meristem to the reproductive meristem corresponds to a progressive and coordinated process of reprogramming of the apical meristem, resulting in its involvement in the formation of floral structures (Fig.13).

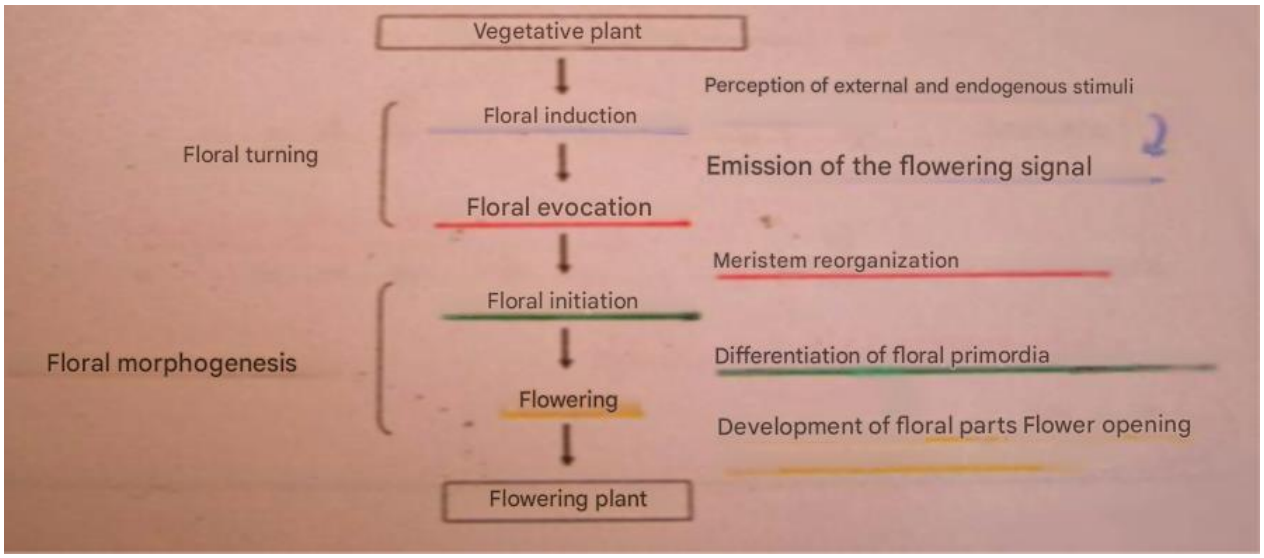


Figure 13: Transition from Vegetative to Reproductive Meristem.

The floral turning point corresponds to the transition phase during which the vegetative meristem gradually acquires a reproductive identity. This stage marks the meristem's commitment to the flowering program and prepares the development of future floral structures. It comprises two main phases: floral induction and floral evocation.

*** Floral induction**

Floral induction corresponds to the physiological decision-making phase to flower. It takes place primarily in the leaves, which perceive environmental signals and trigger the production of a flowering signal called **florigen** (Fig. 14). This signal is considered a mobile, hormonal substance capable of migrating to the apical meristem to induce its transition to a reproductive state.

The duration of this phase varies depending on the species, ranging from brief to several months. Floral induction is controlled by several factors, reflecting a multifactorial control.

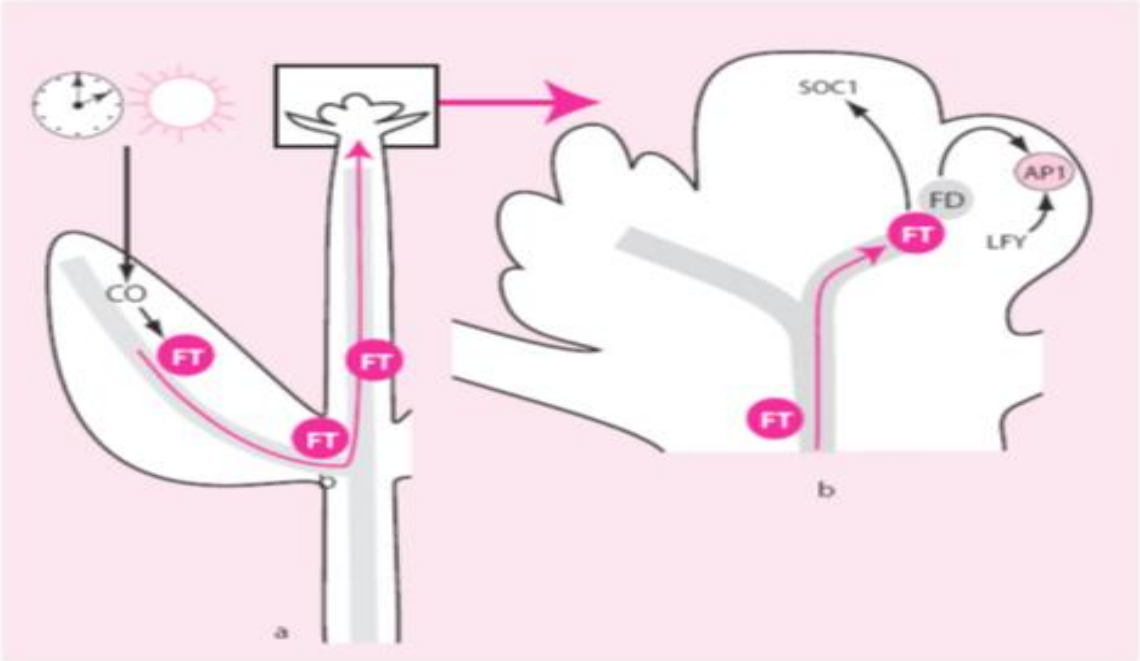


Figure 14: Florigenic signal produced by leaves

*** External stimuli**

External factors depend primarily on environmental conditions and the plant's geographical location. The main stimuli are:

- Temperature (vernalization).
- Light (Photoperiod) .
- Seasonal variations.

These environmental signals allow the plant to synchronize flowering with the most favorable environmental conditions.

*** Internal stimuli**

Internal factors correspond to the plant's physiological state and degree of maturity. These include age, vegetative size, stage of development, and trophic factors such as water availability, mineral availability, and the carbon/nitrogen (C/N) ratio. Hormonal factors, which will be discussed later, also play a role in regulating flowering.

The plant must reach a sufficient level of development, including a leaf area that allows for efficient photosynthetic activity and a meristem capable of perceiving and integrating floral induction signals. This physiological competence is essential for the acquisition of the floral state. In some species, this phase can be particularly long. When the stimuli are insufficient, flowering cannot be triggered; this phenomenon corresponds to the threshold effect.

*** Floral evocation**

This phase corresponds to the appearance of the first visible changes at the level of the shoot apical meristem, during which the vegetative meristem gradually transforms into a reproductive meristem.

This transition is accompanied by several morphological and structural changes (Fig. 15), including:

- An increase in the volume of the meristem:.
- A district of the meristematic apex:.
- A reorganization of the apex architecture:.
- Changes in cellular composition.

During this stage, the apical zone becomes highly active, and the different cell layers participate in the formation of the future floral organs, while the medullary zone tends to reduce its activity.

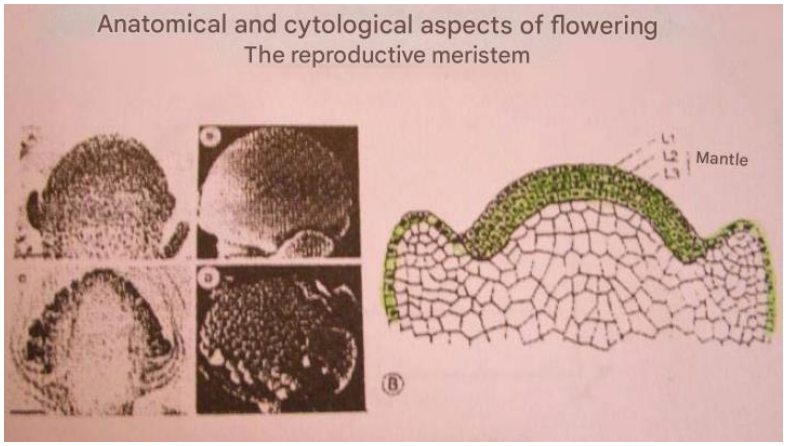


Figure 15: **Meristem Structural Changes During Reproductive Transition.**

Simultaneously, significant physiological changes are observed, including increased mitotic activity in the tunica cell layers, an increased supply of energy substrates, particularly sucrose, and an acceleration of energy metabolism associated with the activation of genes involved in floral induction. All of these transformations prepare the meristem for the development of floral structures.

***Floral morphogenesis**

Floral morphogenesis refers to the phase of formation and development of floral organs. It is primarily controlled by a specific genetic program, relatively independent of environmental conditions. This phase includes floral initiation and flowering.

***Floral initiation**

Floral initiation begins after the transformation of the vegetative meristem into a prefloral or inflorescence meristem. At this stage, the meristem acquires the capacity to produce reproductive structures. The inflorescence meristem gives rise either to the individual floral parts grouped within the flower bud, or to inflorescences bearing protected terminal floral meristems. In the case of a solitary flower, a single meristem gives rise to a single flower. This stage thus marks the beginning of floral organogenesis.

***Bloom**

Flowering corresponds to the complete formation of the flower and the opening of its various floral parts. This stage ensures the functional development of the reproductive organs. It includes, in particular, the development of the stamens and carpels, the formation of the gametes, the coloration of the petals, and the opening of the floral parts. The flower then reaches its final structure and becomes capable of reproduction.

1.2.3. Intercalated meristem

The intercalary meristem is a meristematic tissue located between already differentiated tissues and retaining mitotic activity. It corresponds to a portion of the primary apical meristem, some cells of which remain functional during plant development. This type of meristem is particularly characteristic of monocots, especially grasses. It is generally located at the base of internodes and

leaves, and sometimes at the nodes, particularly in Poaceae where it is frequently located at the base of young internodes and leaf sheaths.

The intercalary meristem originates from the primary apical meristem, some cells of which persist in an undifferentiated state between specialized tissues. It thus constitutes a meristematic remnant capable of continuing cell division after the differentiation of neighboring tissues. Its main role is to ensure the longitudinal growth of internodes and leaves. It also plays a role in the rapid regeneration of aerial parts after cutting or grazing, which explains the high regrowth capacity observed in many grasses such as wheat and maize.

1.3. Secondary Meristems

In dicotyledonous gymnosperms and angiosperms, the growth in thickness of long-lived organs (stems, roots, branches, etc.) is ensured by the functioning of secondary meristems, also called cambiums or generative layers. The tissues derived from these are called secondary, as opposed to tissues derived from primary meristems (Fig. 16).

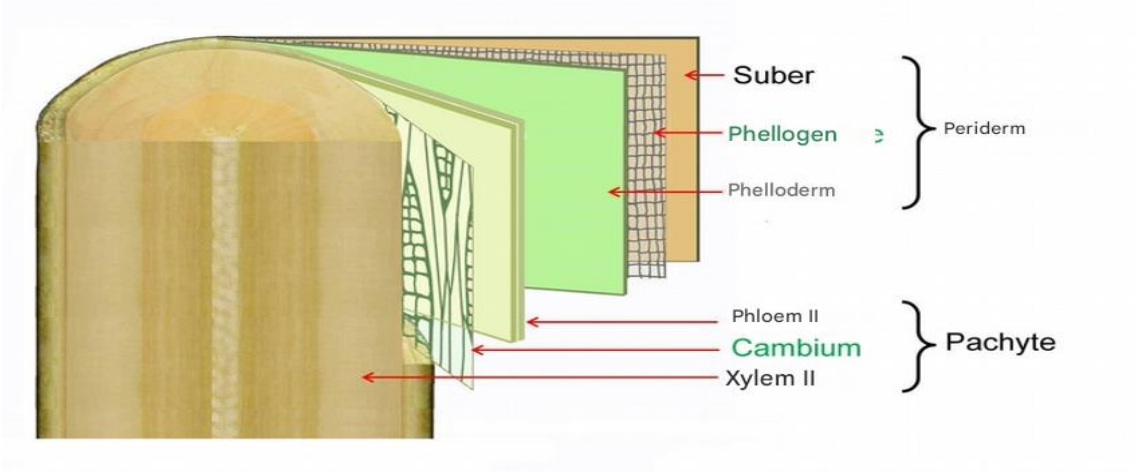


Figure 16: The different parts of the secondary meristem

1.3.1. The vascular cambium (or vascular cambium)

The vascular cambium plays an essential role in the growth in thickness of stems and roots in dicotyledonous angiosperms and gymnosperms. It constitutes a secondary meristem located between the primary xylem and the primary phloem.

Historically, the term *cambium* was introduced by Grew in 1682. Until the mid-19th century, it was considered a nutrient-rich fluid located between the phloem and the xylem. De Mirbel (1828) was the first to demonstrate that it was a tissue, the outer part of which gives rise to the phloem and the inner part to the xylem. Subsequently, Raatz (1892) proposed a multi-layered organization of the cambium. However, since Sanio's work (1873) on Scots pine, it has generally been accepted that the cambium is a generative layer consisting of a single cell layer.

This layer is composed of two types of meristematic cells: fusiform initials and radial initials. The former, elongated and longitudinally oriented, have a circular to elliptical cross-section, while the latter, less elongated, are arranged transversely and have a rectangular shape. The fusiform initials give rise inwardly to the elements of secondary xylem (vessels, tracheids in gymnosperms, fibers and xylem parenchyma in angiosperms) and outwardly to the elements of secondary phloem (sieve tubes, companion cells, and phloem parenchyma). The radial initials participate in the formation of medullary rays.

The activity of the cambium relies primarily on periclinal divisions, ensuring the production of secondary xylem inwards and secondary phloem outwards. Through its continuous functioning, the cambium contributes to the radial growth of organs and is progressively pushed outwards during growth (Fig. 17).

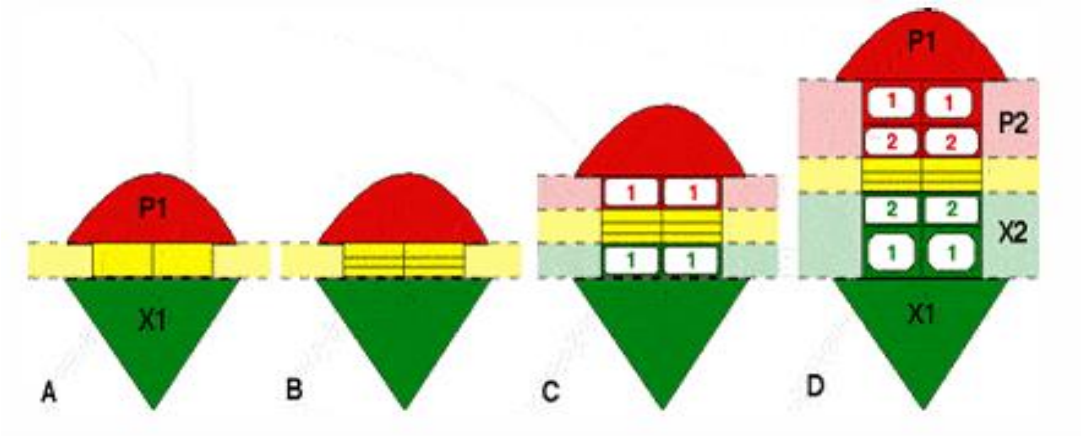


Figure 17: Representation of the functioning of the vascular cambium (P1. Phloem I ^{area} ; X1. Xylem I ^{area} ; P2. Phloem II ^{area} ; X2. Xylem II ^{area})

The cambium functions asymmetrically, with a greater production of secondary xylem than secondary phloem. Its activity, based primarily on periclinal divisions, establishes radial cell lines characteristic of secondary tissues.

The consequences of this cambial activity are observable in cross-section. The oldest cells are progressively pushed towards the periphery and towards the center of the organ, where they undergo progressive compression. In wood, only the areas close to the cambium remain functional and constitute the sapwood, which is lighter and softer than the central part called the heartwood, which no longer participates in the conduction of sap.

Furthermore, the generating base is progressively displaced towards the outside of the organ during growth.

1.3.2. The Phellogen (or suberophellodermic cambium)

The phellogen differentiates at the periphery of organs and gives rise to secondary protective tissues, collectively known as the periderm. Structurally, the periderm consists of three elements: the phellogen, the meristem responsible for its formation; the cork (or suber), a protective tissue produced externally; and the phelloderm, a living parenchymatous tissue formed internally.

During their differentiation, the inner cell walls of cork become impregnated with suberin, giving the tissue impermeability to water and gases. In some cases, lignification may also be observed. At maturity, cork cells are dead, while phelloderm cells remain alive and exhibit an organization comparable to that of parenchyma tissues, without suberin deposition.

Lenticels are air-bearing structures visible on the surface of stems, roots, and some fruits exhibiting secondary growth. They appear as small porous areas of the periderm and facilitate gas exchange between internal tissues and the external environment. Their formation begins during periderm development, generally near old stomata or groups of stomata. They thus play a crucial role in the aeration of secondary tissues.

Chapter 2
General factors of morphogenesis

2.1. Genetic factors

The development of plant organs relies on the action of coordinated gene networks that control the progressive establishment of the plant's form and organization. These genes are expressed according to precise spatial and temporal patterns, ensuring that each cell acquires a specific identity based on its position and stage of development. Thus, genetic information regulates growth, cell differentiation, and the organization of plant structures.

The importance of these genes in controlling plant development can be highlighted by studying mutations, the analysis of which makes it possible to identify their functions through the observed phenotypic modifications.

2.1.1. Mutation

A mutation in plants is an alteration of the genetic material (DNA) that results in a change in the expression or function of a gene. It can occur naturally or be induced experimentally by mutagens. Mutations are an essential tool for understanding the role of genes in plant development processes.

Depending on their origin, two main categories can be distinguished:

- **Natural or spontaneous mutations** occur without external intervention, generally as a result of DNA replication errors or repair defects. They are rare and most often involve point changes such as substitutions, insertions, or deletions, thus contributing to genetic diversity.
- **Induced mutations** are caused by chemical mutagens, such as EMS, or physical mutagens, such as UV, X-ray, or gamma radiation. They can lead to observable phenotypic changes.

Mutations can lead to a loss or gain of gene function, thus allowing researchers to identify their role in plant development. The study of mutants is therefore a key method for analyzing the mechanisms involved in embryogenesis, organ differentiation, and flowering. Much of our current knowledge about the genetic program of embryonic development comes from the study of mutants obtained in model plants such as *Arabidopsis thaliana* and *Zea mays* using various chemical or physical mutagenesis methods (Martensen, 1998; Parinov and Sundaresan, 2000; Lisch, 2002; Kamiya et *al*., 2003; van Enckevort et *al.,* 2005; Till et *al.,* 2007).

2.1.2. *Arabidopsis thaliana* (model plant)

The study of mutations affecting plant development relies heavily on the use of model plants, notably *Arabidopsis thaliana*, which is one of the most widely used reference organisms in this field.

2.1.2.1. General presentation and classification

Arabidopsis thaliana, also known as *Arabidopsis thaliana*, is a dicotyledonous plant belonging to the Brassicaceae family, native to Europe, Asia and northwestern Africa.

Classification :

- Kingdom : Plantae.
- Division : *Magnoliophyta*
- Class : *Magnoliopsida*.
- Order : *Capparales*
- Genre : *Arabidopsis*
- Binomial name: *Arabidopsis thaliana* (L.) Heynh., 1842.

2.1.2.2. Morphological and biological characteristics

Arabidopsis thaliana is a small annual plant, typically reaching 20 to 25 cm in height (Fig. 18). It has a raceme inflorescence and typical flowers composed of four sepals, four petals, six stamens, and two carpels. Its fruit is a silique containing approximately 30 to 60 seeds. Its development cycle is short, about two months under optimal conditions, and can be achieved under controlled conditions or in vitro. This species is primarily self-pollinating, which promotes the genetic stability of the lines.

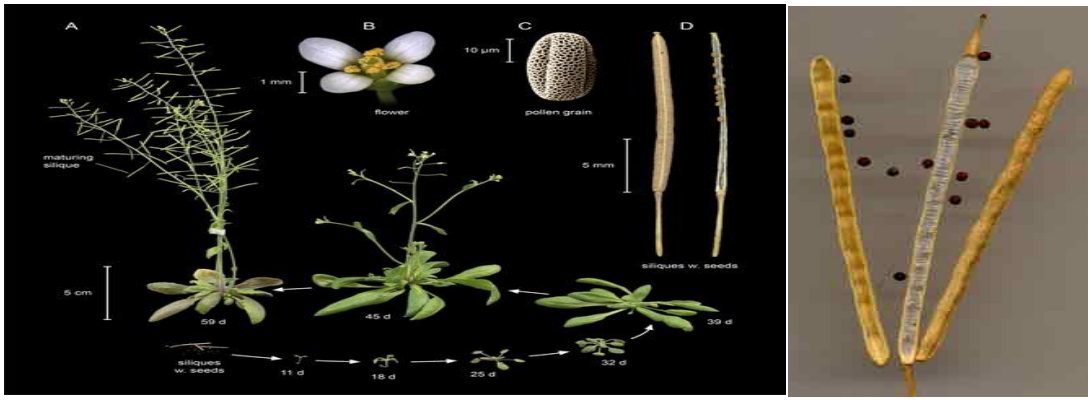


Figure 18: Botanical characteristics of the species *Arabidopsis thaliana*

2.1.2.3. Interest as a model organism

Arabidopsis thaliana is widely used as a model organism in plant research. This interest stems from several characteristics, including its small size, short life cycle, abundant seed production, and ease of cultivation. It also possesses a small, fully sequenced genome, which facilitates genetic studies. Thanks to these advantages, this species is a valuable tool for studying mutants and analyzing plant development mechanisms, particularly embryogenesis, morphogenesis, and flowering. Its use has thus enabled the identification and characterization of numerous genes involved in these processes.

2.1.3. Genes involved in plant development

Research conducted on *Arabidopsis thaliana* has greatly contributed to the understanding of the genetic mechanisms that govern plant development **(Table 1).**

Table 1: Genes involved in apico -basal polarity

Gene	Role	mutant phenotype
GNOM	Polarized transport of auxin, establishment of embryonic polarity	Loss of polarity, asymmetric division defect
MONOPTEROS **(MP)**	Formation of the basal part and the embryonic root	Absence of embryonic root, pituitary gland defect
FACKEL **(FK)**	Sterol biosynthesis, organization of embryonic tissues	Embryonic deformities, axial abnormalities
GURKE **(GK)**	Development of the apical region of the embryo	Defects in the formation of the apical region
HOBBIT **(HBT)**	Regulation of root cell division	Irregular cell divisions, root abnormalities
SHOOT MERISTEMLESS **(STM)**	Formation and maintenance of the apical meristem	Absence of apical meristem, stem/leaf defect
AUTEGUMENTA **(ANT)**	Cell proliferation, organ development	Reduced organs, small cotyledons

2.1.3.2. Genes involved in the root meristem (MAR) (Table 2).

Table 2: Genes involved in the root meristem (MAR).

Gene	Role	mutant phenotype
SHORT ROOT (SHR)	Controls the formation of the endodermis	Absence of endodermis
SCARECROW (SCR)	Regulates cortex/endoderm division	Poor cortex/endoderm separation
PLETHORA (PLT1/PLT2)	Maintenance of root stem cells	Reduced root meristem
PIN-FORMED (PIN)	Polarized transport of auxin	Disrupted root growth
WUSCHEL- related homeobox 5 (WOX5)	Maintaining the quiet center	Loss of stem cells

2.1.3.3. Genes involved in the shoot apical meristem (MAC) (Table 3).

Table 3 : Genes involved in the shoot apical meristem (MAC).

Gene	Main role	Location	mutant phenotype
WUS (WUSCHEL)	Maintenance of apical meristem stem cells	Vegetative and floral apical meristem	Disappearance of the meristem, cessation of apical growth
CLV1 / CLV2 / CLV3 (CLAVATA)	Limitation of stem cell proliferation	Apical meristem	Hypertrophied meristem, excess of stem cells
STM (SHOOT MERISTEMLESS)	Maintenance of apical meristem activity and inhibition of cell differentiation	shoot apical meristem	Absence of the apical meristem, defective formation of leaves and stem

2.1.3.4. Genes involved in leaf initiation (Table 4).

Table 4: Genes involved in leaf initiation

Gene	Role	mutant phenotype
ASYMMETRIC LEAVES1 (AS1)	Regulates leaf identity and inhibits KNOX genes in primordia	Asymmetrical and deformed leaves
ASYMMETRIC LEAVES2 (AS2)	Controls leaf morphogenesis with AS1	Leaf symmetry defects
CUP-SHAPED COTYLEDON (CUC1 / CUC2 / CUC3)	Delimits the leaf primordia and separates the organs	Fusion of the cotyledons or leaves

2.1.3.5. Genes involved in flowering (Table 5).

Table 5 : Genes involved in flowering.

Gene	Main role	mutant phenotype
SOC1	Integrator of floral signals (photoperiod, vernalization) and trigger of flowering	Delayed flowering
LFY	Triggers floral identity and the formation of floral primordia	Flowers replaced by leaves
AP1	Identify the flowers	Flowers partially transformed into leaf structures

Activation of integrator genes such as SOC1, LFY, and AP1 induces the transition to flowering, leading to the transformation of the apical meristem into a determinate floral meristem. At this stage, specific genes known as floral identity genes (Table 6) ensure flower formation and the specification of floral organs from floral primordia, according to an organized genetic program corresponding to the ABC model (Fig. 19).

Table 6: Genetic determination of floral parts according to the ABC model

Class	Main genes	Organ formed	mutant phenotype
Class A	APETALA1(AP1), APETALA2(AP2)	Sepals	AP1/AP2 mutants: sepals transformed into carpels, petals absent or malformed
A + B	APETALA3(AP3), PISTILLATA (PI)	Petals	AP3/PI mutants: petals transformed into sepals
B + C	AP3, PI + AGAMOUS	Stamens	Stamens transformed into carpels
C	AGAMOUS (AG)	Carpels	Indeterminate flowers, carpels transformed into leaf-like structures

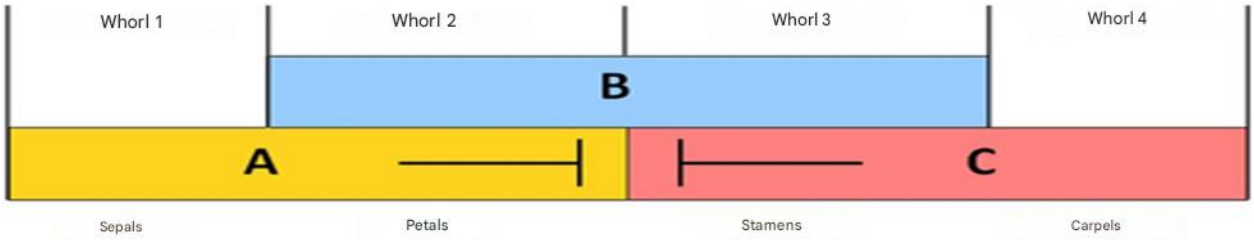


Figure 19: Representation of the ABC system

Genetic factors ensure the implementation of developmental programs by controlling the expression of genes involved in plant morphogenesis. The expression of these programs is then triggered by internal signals called endogenous factors, primarily phytohormones. These phytohormones are the main mediators of endogenous factors and regulate the growth, differentiation, and organization of organs.

2.2. Endogenous Factors

2.2.1. Hormonal factors

2.2.1.1. Definition of a phytohormone or plant hormone.

Phytohormones are organic substances produced by plants in small quantities. They are generally transported away from their site of synthesis, by the vascular system or by cellular pathways, and act at very low concentrations on specific physiological processes which they regulate in a coordinated manner.

Plant hormones play a role in regulating almost all plant growth and development processes. Their action ensures the plant's adaptation to internal and external conditions by modulating gene expression and controlling the various stages of development. They are present at different levels throughout the plant's life cycle, and their quantitative balance is essential for maintaining harmonious and coordinated growth. Phytohormones can be classified according to their main effects as growth hormones and stress hormones (Fig. 20).

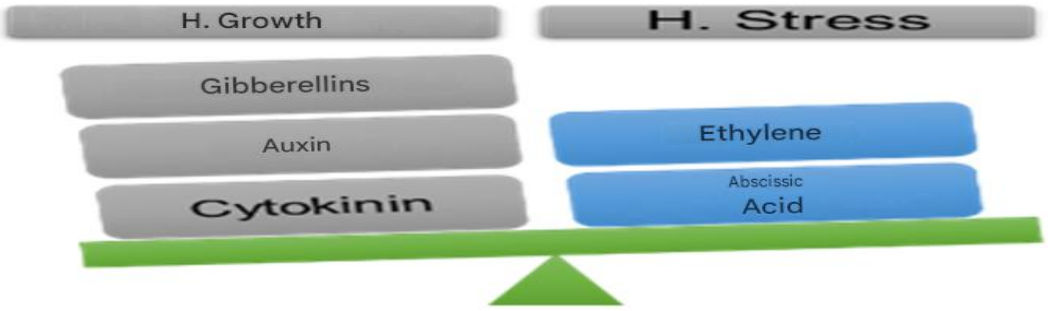


Figure 20: Classification of phytohormones (growth vs stress).

To better understand the diversity and specificity of hormonal actions, it is necessary to examine the main phytohormones individually. This analysis allows us to clarify their specific characteristics, their synthesis sites, and their physiological roles in regulating plant growth, development, and adaptation processes (Fig. 21 and Table 7).

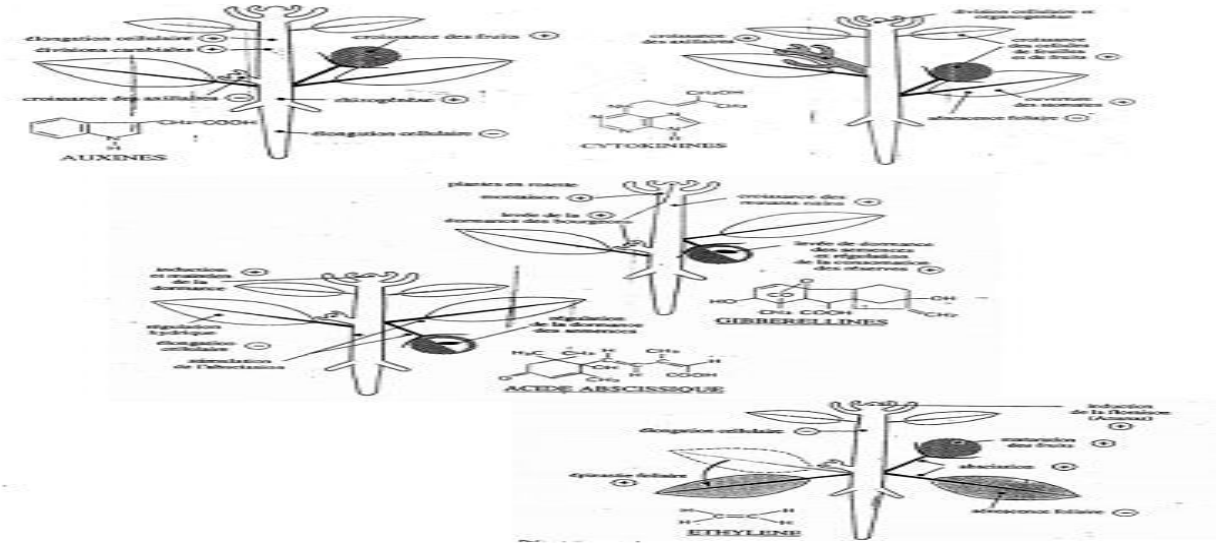
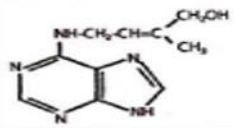
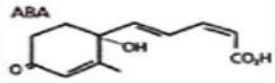
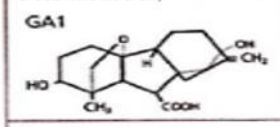
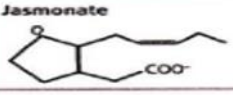
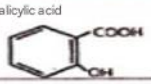
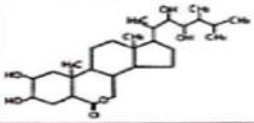


Figure 21: Effect of different phytohormones on physiological phenomena.

Table 7: Main characteristics of angiosperm phytohormones.

: Stimulation : Inhibition

Phytohormones	Biosynthesis and transport	Biological Effects
Auxin (IAA: indoleacetic acid) 	• Synthesis known from tryptophan in young leaves, primordia, and developing seeds, but other synthesis pathways exist. • Polarized cell-to-cell transport and long-distance transport via the phloem.	Shoot cell elongation, cambial activity, flower and fruit growth, rhizogenesis (adventitious roots) Apical dominance Root cell elongation, abscission Flowering of some species
Cytokinins (CK) Zeatin: 	• Synthesis via the terpene pathway from a CS precursor. • Cytokinins are derivatives of adenine (ATP) with an isoprene group at the N° position. • Synthesis in young or meristematic tissues (root apices, buds, cambium, developing seeds). • Transport via the xylem.	Cell growth of leaves, fruits, and axillary buds, cell division, organogenesis, stomatal opening Flowering of some species Leaf senescence, apical dominance
Ethylene Gas CH2 HC=CH	• Synthesized from methionine in senescent or stressed tissues. • Transport by diffusion.	Fruit ripening Abscission (leaf, fruit) Senescence (leaf, flower) Flower opening Shoot and root cell elongation
Abscisic acid (ABA) 	• Synthesis via the terpene pathway from a C40 precursor • ABA is a sesquiterpene synthesized from plastid carotenoids (non-mevalonic pathway) in mature leaves in response to abiotic stresses, stems, roots, developing seeds and fruits. Transport via the phloem and xylem.	Induction and maintenance of dormancy Stomatal closure Allocation of leaf assimilates to developing seeds Synthesis of storage proteins in seeds Cell elongation; antagonistic action of gibberellins
Gibberellins Gibberellic acid GA, GA1 	• Synthesis via the terpene pathway from a C20 precursor. GAs are cyclic diterpenes. • Synthesis in the leafy stem, young leaves of apical buds, developing seeds and fruits, and root apices. • Transport via the xylem and phloem.	Growth and cell elongation of the leafy stem (stem elongation) Growth of dwarf mutants Induction of seed germination Regulation of cereal seed reserve consumption Flowering of long-day plants
Jasmonate 	• Volatile derivative of unsaturated fatty acids (linolenic acid). • Synthesis in all parts of the plant.	Synthesis of defense proteins Accumulation of storage proteins Growth of stems and roots, Seed germination
Systemin Small peptide (18 AA)	• Small peptide produced in injured tissues.	Systemic defense
Salicylic acid 	• Synthesis via the shikimic acid pathway. • Salicylic acid is a phenolic compound	Activation of defense genes against pathogens Systemic defense Root growth
Brassinosteroids Brassinolides 	• Synthesis via the terpene pathway from a C30 precursor. • Brassinosteroids are steroid hormones. • Present in pollen, immature seeds, leaves, stems, roots, and flowers.	Cell division and elongation Pollen tube elongation Leafy stem elongation Leaf morphogenesis Ethylene production Root Growth and Development Vascular Differentiation
Polyamines Spermin $H_2N(CH_2)_3NH(CH_2)_4NH(CH_2)_3NH_2$ and putrescine $H_2N(CH)_4NH_2$	• Spermine is formed via the ethylene synthesis pathway. • Putrescine is formed by the decarboxylation of arginine and ornithine. • Present in all cells. Often conjugated to phenolic acids.	Cell Division Tuberization Initiation of Roots and Adventitious Stems Pryoge Embryogenesis Hypersensitivity Reaction Flowering of Certain Species Tissue Senescence

2.2.1.2. Phytohormonal balances

Although the analytical approach attributes specific functions to each phytohormone, plant morphogenesis never results from the action of an isolated molecule, but from hormonal balances and cross-talk expressed in space (Fig. 22). At the organismal level, the harmonious development

of the bidirectional architecture (stem/root axis) relies on spatial compartmentalization and a functional antagonism between auxin and cytokinins.

Auxin is primarily synthesized at the shoot apex, from where it is transported in a polarized manner to the root via a basipetal flow, while cytokinins, mainly produced in the root apices, are transported to the aerial parts via an acropetal flow. The interaction of these opposing flows establishes inverse hormonal gradients that regulate organogenesis: high concentrations of auxin in the basal zones promote rhizogenesis while inhibiting the action of cytokinins, whereas in the aerial zones, the relative increase in cytokinins promotes caulogenesis, leaf growth, and the development of axillary buds.

This hormonal interaction also plays a role in apical dominance, where auxin produced by the terminal bud inhibits the development of lateral buds, while cytokinins stimulate their growth. Thus, this hormonal balance contributes to the establishment and organization of the plant's vertical axis.

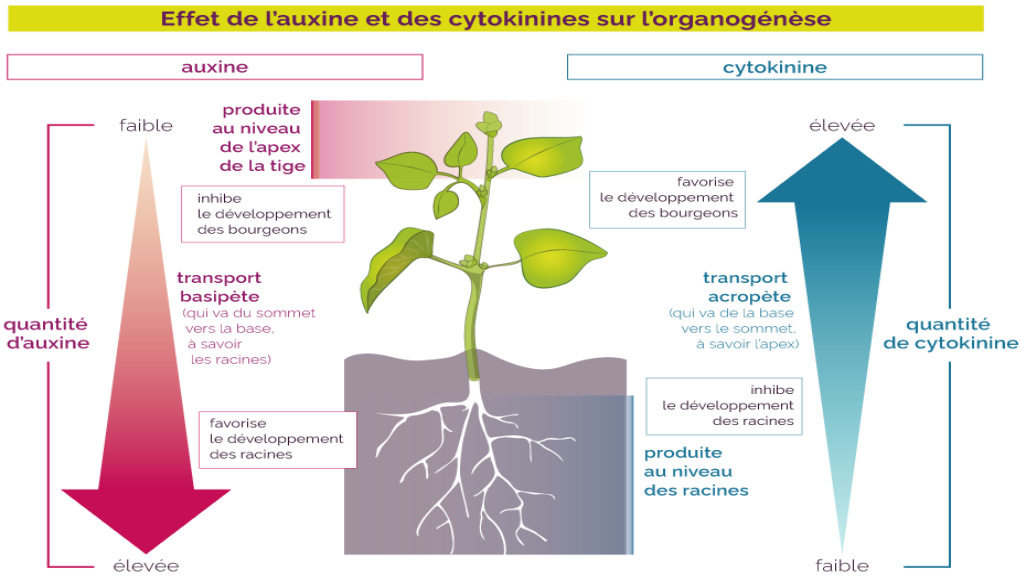


Figure 22: Inverse gradients and spatial control of organogenesis in angiosperm.

Beyond spatial compartmentalization, hormonal balances evolve dynamically over time to synchronize plant development with its biological cycle (Fig. 23). The main transitions in the life cycle of angiosperms are thus regulated by successive and coordinated hormonal waves. The graph

below illustrates the evolution of endogenous levels of five regulators during the different phenological stages of the plant.

We observe a strict chronological complementarity: the lifting of dormancy, induced by the switch between abscisic acid and gibberellins, is followed by a phase of vegetative growth ensured by cytokinins then auxin, before ethylene and abscisic acid dominate again during the terminal phases of maturation and senescence.

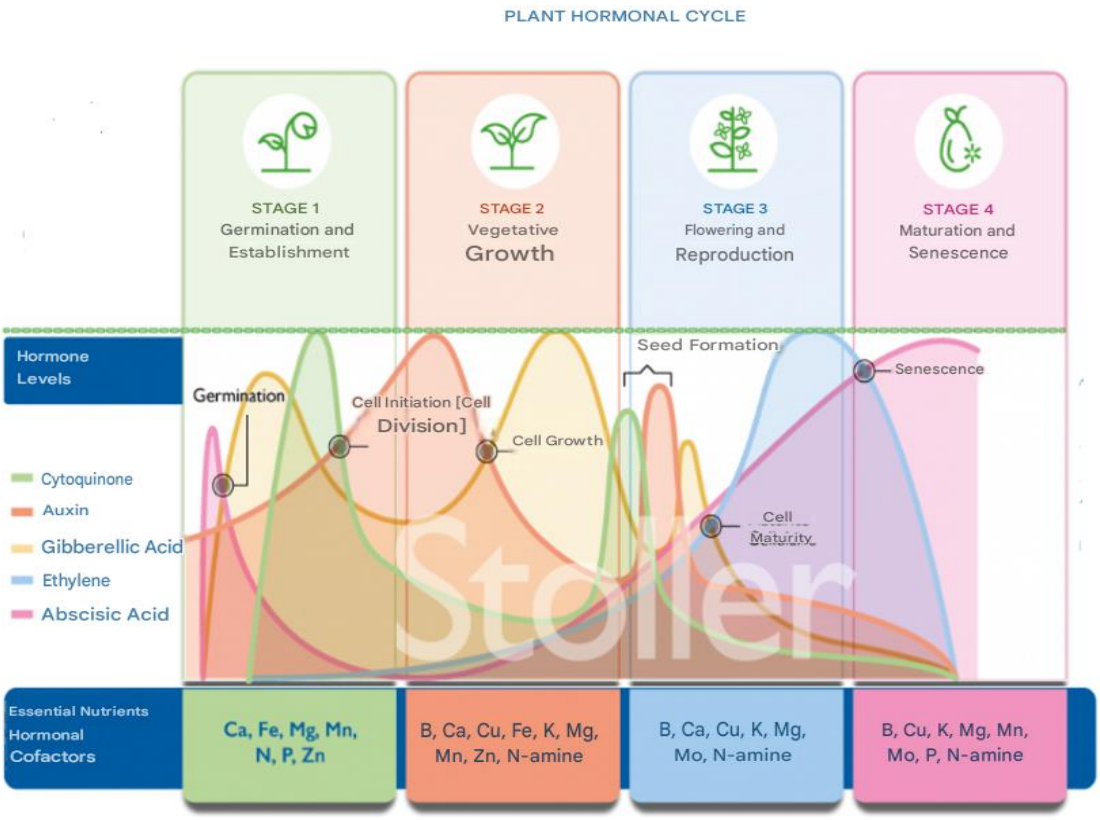


Figure 23: Evolution of phytohormonal balances during the phenological stages of the plant

In addition to hormonal regulation, plant morphogenesis also depends on trophic factors related to the plant's nutritional and metabolic state. These factors modulate growth and developmental direction according to available resources.

2.2.2. Trophic Factors

Trophic factors encompass all the nutrients and physical conditions necessary for the proper metabolic functioning of the plant and directly influencing its growth and morphogenesis. They primarilyinclude:

• Water, essential for maintaining cell turgor and growth processes • Mineral nutrients.. indispensable for the synthesis of biomolecules and enzymatic activity • The carbon/nitrogen (C/N) ratio, an indicator of the plant's nutritional balance and metabolic orientation

The carbon-to-nitrogen (C/N) ratio plays a crucial role in regulating growth and differentiation processes. A high C/N ratio is generally associated with carbon dominance and promotes differentiation, maturation, and flowering. Conversely, a low C/N ratio indicates high nitrogen availability and favors vegetative growth processes, particularly cell division and elongation.

2.3. Polarity

2.3.1. Definition

Plant polarity refers to the establishment of a directional axis during plant development, organizing the plant body according to a defined orientation. It allows us to distinguish an apical pole, oriented towards the aerial organs, and a basal pole, which gives rise to the root system. This fundamental organization appears as early as embryogenesis and is maintained throughout the plant's development.

2.3.2. Role of polarity in morphogenesis

This process plays a fundamental role in the organization of plant development. It ensures the establishment of growth axes, determines the position of organs, and controls tissue differentiation. It also contributes to the direction of growth and the coherence of the plant's overall body plan. These processes are primarily regulated by hormonal gradients, particularly those of auxin, as well as by differential gene expression and cellular organization.

2.3.3. The different types of polarity

2.3.3.1. Apico -basal polarity

It corresponds to the longitudinal axis of the plant, extending from the top to the base. The apical pole is responsible for the formation of aerial organs (stems, leaves, flowers), while the basal pole is the origin of the root system.

2.3.3.2. Radial polarity

This type of polarity corresponds to the organization of tissues along a center-periphery axis. It allows for the differentiation of internal organ tissues, such as the epidermis, cortex, and vascular tissues.

2.3.3.4. Origin of zygote polarity

Several hypotheses have been proposed regarding the origin of zygote polarity. Generally speaking, cellular asymmetry and different developmental potentials can result from the action of several factors:

- **External factors** : Environmental factors such as light or gravity can influence or modulate the orientation of the embryonic axis, intervening mainly in the adjustment of polarity rather than in its initial establishment.
- **Internal factors** : polarity may be linked to an asymmetric distribution of cytoplasmic reserves, organelles, RNAs and proteins, directing the first cell division and contributing to the establishment of the apico -basal axis.
- **Maternal factors** : signals present in the ovum, particularly those related to its polarity (micropylar pole and chalazion pole), can influence the initial organization of embryonic development (Fig. 24)

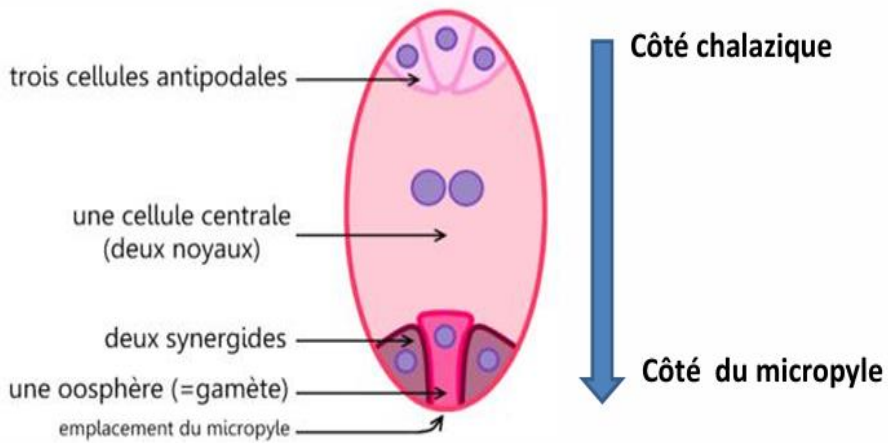


Figure 24: Embryo sac of an angiosperm

- **Influence of fertilization:** the position and fusion of gametes can also participate in determining the orientation of the embryonic axis.
- **Hormonal gradients:** phytohormones, in particular auxin, participate in the establishment of spatial gradients that direct cell differentiation and the establishment of embryonic structures.

Overall, plant polarity results from the interaction between internal determinants in the zygote and signals of maternal, hormonal and environmental origin.

2.4. Symmetry

2.4.1. Definition of symmetry

Symmetry refers to the regular organization of cells, tissues, or organs around a reference axis. It constitutes a fundamental element in the organization of the plant development plan.

The main distinctions are :

- **Radial symmetry:** the structures are organized around a central axis in a repetitive and equidistant arrangement. It is common in elongated organs such as roots and young stems.
- **Bilateral symmetry:** the organism or organ can be divided into two roughly equivalent halves on either side of a longitudinal axis. It is notably observed in leaves and certain embryos.

2.4.2. Role of symmetry in morphogenesis

This mechanism plays a crucial role in the organization of plant development. It determines the orientation of cell divisions and the formation of structured tissues. It also contributes to the establishment of the main developmental axes, notably the apico -basal axis and the radial organization of organs.

Furthermore, this mechanism is involved in the formation of organs, with certain transitions between radial and bilateral organization allowing for functional specialization of plant structures.

Finally, it provides a spatial framework in which hormonal gradients and genetic signals are expressed in a coordinated manner to direct morphogenesis.

2.5. Environmental Factors

Environmental factors are essential external regulators of plant morphogenesis. They constantly interact with endogenous mechanisms, particularly hormonal and genetic ones, to modulate plant

development and adaptation to environmental conditions. Generally, these factors can be classified into several categories according to their nature and mode of action on the plant.

We can thus distinguish between physical factors, including light, temperature, and water, which directly influence growth and fundamental physiological processes; orientation and shape factors, such as gravity, directional light, and mechanical stimuli, which control the spatial organization and architecture of plant organs; chemical factors, related to the availability of mineral elements and atmospheric gases; and biological factors, corresponding to the interactions between plants and other living organisms.

2.5.1. Physical Factors

2.5.1.1. The light

Light is a major ecological factor involved in plant morphogenesis, both as an energy source for photosynthesis and as an environmental signal regulating development. Its action, collectively known as photomorphogenesis , depends on several physical and biological parameters, including the direction of propagation, intensity, duration of exposure, and spectral quality. It thus plays a role in the spatial and temporal organization of growth, as well as in cell differentiation and the development of plant organs.

In an anisotropic environment, light induces directional responses resulting in the orientation of plant organs, while in an isotropic environment, its effect is primarily quantitative and qualitative, influencing overall growth and differentiation. Photoperiodism refers to the ability of plants to perceive and respond to the relative length of day and night. It constitutes a fundamental adaptation mechanism that synchronizes physiological processes with seasonal variations. The intensity of the photoperiodic response varies among species and is an important varietal characteristic. This phenomenon plays a key role in floral induction, but also in the regulation of seed and bud dormancy, as well as in certain phases of vegetative growth. Photoperiodic perception is based primarily on the duration of the dark phase, although the light phase can also be a factor in some species. Plants are classified according to their photoperiodic behavior into different functional types, presented in Table 8.

Table 8: Classification of plants according to photoperiodism

Classification	Features	Photoperiodic requirement	Examples
Short-day (nyctoperiodic) plants	Flowering is induced when the length of the night exceeds a critical value.	Long period of continuous darkness	Chrysanthemum
Long-day plants (hemeroperiodic)	Flowering is induced when the day length exceeds a critical value.	Long duration of illumination	Spinach, soy, hemp
Indifferent plants	Flowering is independent of the length of day or night	No photoperiodic requirement	Tomato, corn, peas

It is important to emphasize the existence of a critical photoperiod (CP), corresponding to the threshold duration of light or darkness required for floral induction in strictly photoperiodic species. Furthermore, the effectiveness of the photoperiodic response depends on a minimum illuminance, called the trophic minimum illuminance, which determines the plant's physiological vigor and its ability to respond appropriately to light signals.

At the molecular level, the regulation of flowering relies on a genetic cascade integrated with the circadian rhythm. The CONSTANS (CO) gene, expressed primarily in leaves, is controlled by the biological clock, and its expression varies throughout the daily cycle, leading to the synthesis of a CO protein whose stability depends on light conditions. When the amount of stable CO protein becomes sufficient, it induces the expression of the FLOWERING LOCUS T (FT) gene. The FT protein is then transported via the phloem to the apical meristem, where it interacts with the FD protein. This complex activates a set of genes responsible for the transition from the vegetative to the floral meristem, ensuring the initiation of flowering. Thus, flowering results from the fine-tuning of environmental signals, endogenous rhythms, and genetic regulation.

2.5.1.2. The Temperature

Temperature is a major ecological factor in plant morphogenesis. It directly influences the regulation of fundamental physiological processes such as enzymatic activity, metabolism, cell division, and tissue elongation, thus conditioning overall plant growth and the organization of its morphological structures. In general, it affects all aspects of plant development by modulating

vegetative growth and morphogenetic transitions, while interacting closely with other environmental factors, particularly light, to ensure the synchronization of biological cycles and the adaptation of plants to environmental variations.

In terms of daily variations, temperature exerts a specific effect called Thermopériodisme, corresponding to the alternation between daytime and nighttime temperatures. This phenomenon constitutes an important environmental signal influencing growth, cell elongation, and certain morphogenetic processes, notably the formation of storage organs such as tubers. It thus contributes to the adjustment of developmental rhythms in interaction with other abiotic factors. Furthermore, low temperatures play an essential role in regulating plant development, particularly through their involvement in dormancy states. They are involved in breaking seed and bud dormancy, allowing the resumption of vegetative activity when conditions become favorable, and also participate in processes preparatory to reproduction in certain species.

In species requiring prolonged exposure to cold, this phenomenon corresponds to vernalization (Fig. 25), defined as the physiological induction of floral competence following a period of low temperatures, generally at the seed or seedling stage. Depending on the species, this requirement may be obligatory, facultative, or absent. Vernalization relies on epigenetic control of gene expression, notably involving the FLOWERING LOCUS C (FLC) gene, which acts as a repressor of flowering by inhibiting genes that promote floral transition. Prolonged exposure to cold leads to stable repression of FLC, allowing this inhibition to be lifted through modifications of chromatin and histones, ensuring a lasting memory of the thermal signal. The FRIGIDA (FRI) gene promotes FLC expression and delays flowering in the absence of vernalization, while cold-induced proteins, such as VIN3, as well as VRN1 and VRN2, participate in establishing and maintaining this repressed state. Thus, temperature is a global factor in plant morphogenesis, acting at several levels: regulation of basic physiological processes, control of growth, synchronization of developmental rhythms, and induction of specific responses such as vernalization, making it an essential integrating factor in plant adaptation to their environment.



Figure 25: Effect of vernalization on flowering in *Arabidopsis thaliana*

2.5.1.3. Water (hydration factor)

Water is a fundamental ecological factor in plant morphogenesis. It plays a direct role in plant growth and development by ensuring cell turgor, which is essential for cell elongation and tissue expansion. It also contributes to maintaining metabolic activity as a major component of the protoplasm and a solvent for biochemical reactions, while simultaneously ensuring the transport of nutrients within the plant.

Variations in water availability strongly influence the morphological expression of plants. Under water-deficit conditions, plants develop xeromorphic adaptations characterized by a reduction in leaf surface area, a thickening of the cuticle, an increase in mechanical tissues, and deeper, more branched root development. Conversely, in water-rich or saturated environments, as in hydrophytic plants, a reduction in supporting tissues, a less developed root system, thinner cell walls, and an abundance of aerenchyma facilitating gas exchange are observed.

Thus, water acts as a major factor in regulating plant morphogenesis, modulating both growth, plant architecture and its structural adaptation to environmental conditions.

2.5.2. Orientation and Form Factors

Orientation factors encompass all environmental stimuli that determine the direction of growth and the spatial organization of plant organs. They play an essential role in establishing the plant's development plan by inducing differential growth in response to external signals such as gravity, light, or mechanical stimuli (thigmotropism).

Plant orientation responses to these stimuli are called tropisms. A tropism is a directed and irreversible growth reaction of a plant organ in response to a directional environmental signal. This response generally results from differential tissue growth under the influence of hormonal mechanisms, primarily related to the redistribution of auxin. Depending on the nature of the perceived stimulus, these mechanisms allow plant organs to adjust their orientation and development to environmental conditions.

2.5.2.1. Gravitropism

Gravitropism refers to the ability of plant organs to orient their growth under the influence of gravity. It ensures the characteristic spatial organization of the plant, notably by guiding the orientation of roots and stems. We distinguish between:

* Positive gravitropism in roots, which grow towards the center of the Earth.

*A negative gravitropism in the stems, which orient themselves in the opposite direction. Some organs, such as leaves, show low sensitivity to this stimulus and respond more to other environmental factors.

The perception of gravity relies on specialized cells called statocytes, located primarily in the root cap and stem tissues (Fig. 26). These cells contain amyloplasts (statoliths), whose movement under the influence of gravity allows the stimulus to be perceived. The gravitropic response is ensured by an asymmetric redistribution of auxin (AIA), responsible for the differential growth of tissues. In roots, an accumulation of auxin on the lower surface inhibits cell elongation, resulting in downward curvature. Conversely, in stems, this same accumulation stimulates cell elongation, directing growth upward. Thus, gravitropism relies on a hormonal signaling mechanism that coordinates differential growth and enables the functional orientation of organs in space.

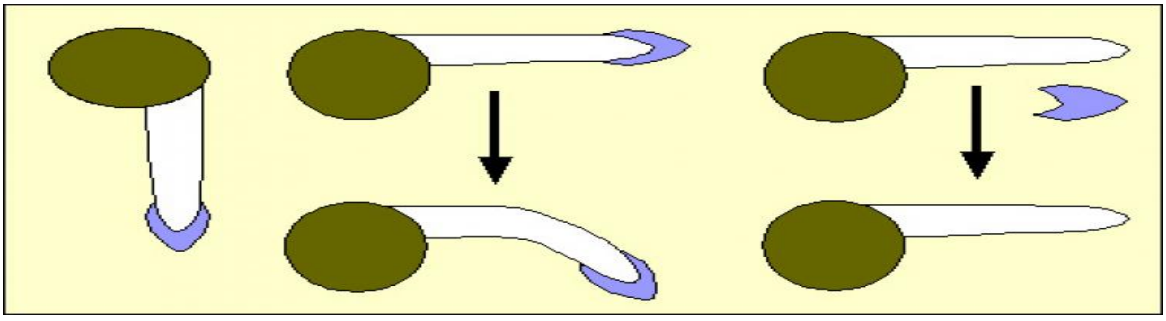


Figure 26: Importance of the root cap in the gravitropism of a root

Left : Germinated seed showing a young root, in its normal position, pointing downwards. **Center** : Seed with an (intact) root placed horizontally, showing a downward curve. **Right** : Root with its root cap removed, placed horizontally, no downward curve is observed.

2.5.2.2. Phototropism

Phototropism is a directional growth response of plant organs to a directional light stimulus (Fig. 27). It allows plants to adapt their development to their light environment by primarily orienting their aerial parts towards the light source to optimize the capture of energy needed for photosynthesis. This response is generally manifested as positive phototropism in stems and young shoots, while some roots exhibit negative phototropism by orienting themselves away from the light source.

The perception of light stimuli is mediated by specialized photoreceptors, notably phototropins , which are primarily sensitive to blue light. Absorption of the light signal leads to an asymmetric redistribution of auxin towards the shaded side of the organ. This hormonal accumulation stimulates cell elongation in this area, causing differential growth responsible for the curvature towards the light.

Phototropism thus constitutes an essential mechanism of morphogenetic adaptation allowing the optimization of the exposure of photosynthetic organs and promoting the physiological efficiency of the plant in its environment.

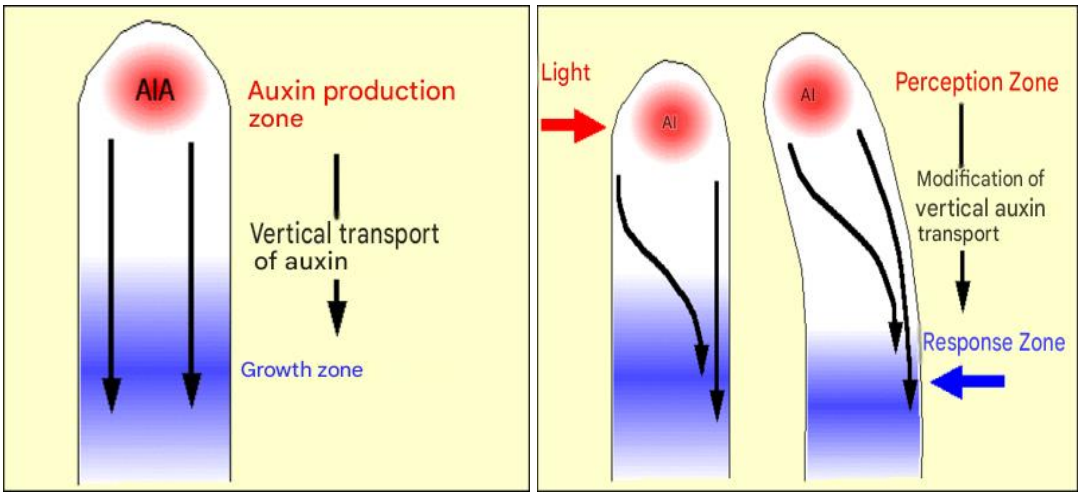


Figure 27: Phototropism in plant organs (curvature towards light)

2.5.2.3. Mechanical stimulation (Thigmotropism).

Mechanical stimuli are external physical signals capable of modifying the growth and organization of plant tissues. They encompass all the stresses exerted on the plant by wind, rain, contact, vibrations, or friction. These stimuli influence morphogenesis by modulating cell elongation, tissue differentiation, and the mechanical resistance of organs. Plant responses to mechanical stresses are

grouped under the term thigmomorphogenesis, which refers to the morphological changes induced by repeated mechanical stresses.

Plants subjected to these stresses generally exhibit reduced stem elongation, thickened axes, and strengthened mechanical tissues, thus improving their resistance to environmental conditions. When mechanical stimulation is localized and directional, it can induce movements or bends called thigmotropism (Fig. 28). This type of response is particularly noticeable in climbing plants, whose tendrils wrap around a support after contact. Some species also exhibit rapid movements called thigmonasty, independent of the stimulus direction, as in Mimosa pudica , whose leaflets fold after tactile stimulation.

At the physiological level, these responses involve changes in membrane permeability, ion fluxes, and hormonal redistribution, particularly of auxin and ethylene, leading to differential tissue growth. Thus, mechanical stimulation actively contributes to the morphological adaptation of plants by ensuring greater stability and optimizing their development in environments subject to physical constraints.



Figure 28: Yew tree with a flag-like crown

2.5.3. Other environmental factors

In addition to the physical and orientation factors previously discussed, other environmental factors also play a role in regulating plant morphogenesis. These elements, including nutrient availability, atmospheric gas composition, and biotic interactions, modulate growth, cell differentiation, and the organization of plant organs according to environmental conditions. Table 9 summarizes the main factors and their effects on plant morphogenesis.

Table 9: Complementary environmental factors of plant morphogenesis

Environmental factor	Type of stimulus	Role in morphogenesis
Nutrients / minerals	Nitrogen, phosphorus, potassium, iron	Affects the size, shape, color, and differentiation of organs
Atmospheric gases	CO_2, O_2	It influences photosynthesis and respiration, therefore the energy available for growth.
Biotic interactions	Microorganisms, herbivores, competition	Modifies root growth, stress resistance, and metabolite production

Chapter 3
Regenerative abilities

Unlike animals, plants possess a particularly well-developed capacity for regeneration, allowing them to restore damaged tissues, regenerate lost organs, or even reconstitute a complete individual from a tissue fragment or a single cell. This property is based primarily on cellular totipotency, that is, the ability of certain differentiated plant cells to return to a meristematic state, resume active divisions, and then redifferentiate into various specialized cell types.

Regenerative abilities are a fundamental phenomenon of plant morphogenesis, manifesting in both natural and experimental conditions. They play a role in several physiological processes, including wound healing, vegetative propagation, the formation of adventitious organs, and regrowth after injury. They also form the basis of numerous biotechnological applications in plant breeding and conservation. Studying regeneration mechanisms thus allows for a better understanding of the plasticity of plant development and the processes involved in plant adaptation to their environment.

3.1. Traditional Regeneration

All living beings possess the fundamental capacity to ensure their reproduction and the survival of the species. Although the mechanisms involved are varied and differ according to biological groups, they can be grouped into two main modes of reproduction.

3.1.1. Sexual reproduction.

It corresponds to a mode of reproduction involving specialized reproductive structures and the formation of male and female gametes. This process results in fertilization and the formation of a new individual with a genetic combination inherited from both parents.

3.1.2. Asexual reproduction or vegetative propagation.

3.1.2.1. Natural vegetative propagation.

Natural asexual reproduction in plants is a mode of multiplication in which a single plant is able to produce one or more new plants genetically identical to itself, without human intervention and without fertilization, therefore without seed formation.

Vegetative propagation is divided into two main types:

• **Natural vegetative propagation,** which occurs spontaneously in the plant from its own organs.

• **Artificial vegetative propagation,** which results from human interventions aimed at reproducing or multiplying plants.

Natural vegetative propagation relies on the use of various specialized or modified vegetative organs, ensuring the formation of new individuals from the parent plant. These structures can be aerial or underground and exhibit morphological and functional adaptations that promote the survival and propagation of the species. Among the main organs involved are stolons, rhizomes, tubers, bulbs, suckers, and shoots (Fig. 29).

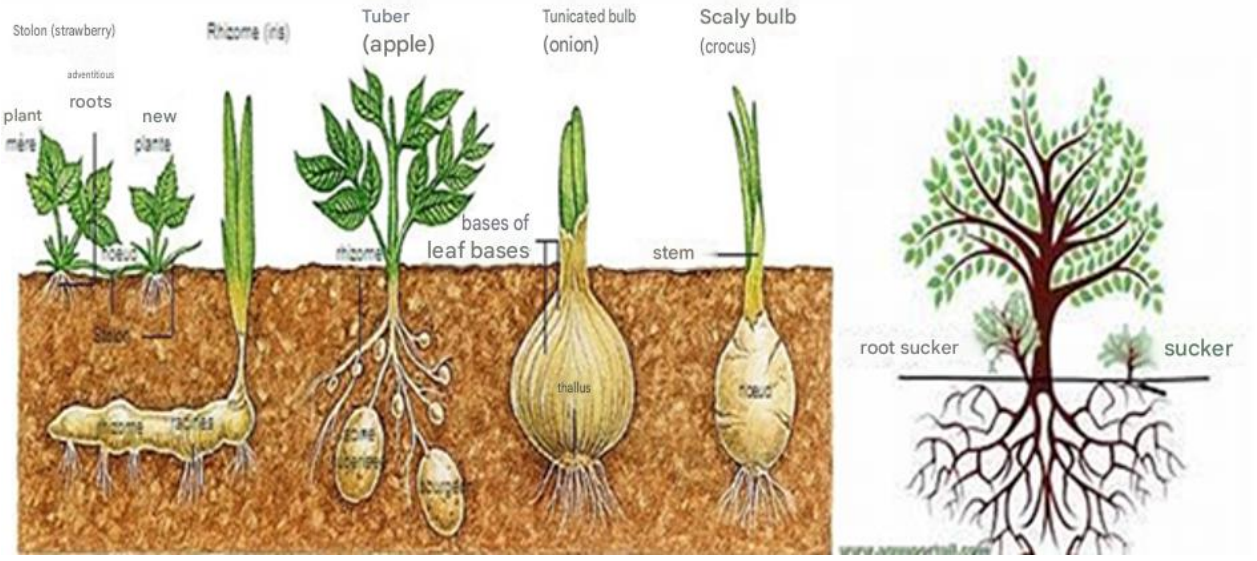


Figure 29: Organs of natural vegetative propagation.

This mode of asexual reproduction, present in many plant species, is characterized by high efficiency. It allows for rapid reproduction and promotes colonization of the environment through the formation of new individuals from vegetative organs. It has the advantage of occurring independently of pollination and fertilization processes, thus ensuring its survival even in the absence of pollinators or conditions favorable to sexual reproduction.

However, this method has significant limitations, notably the lack of genetic diversity between individuals from the same clone, which reduces their ability to adapt to environmental variations and increases their susceptibility to diseases as well as biotic and abiotic stresses.

3.1.2.2. Artificial vegetative propagation

A. Artificial vegetative propagation techniques

Artificial vegetative propagation is a plant reproduction technique carried out through human intervention. It consists of obtaining new individuals from fragments of existing plants, without resorting to sexual reproduction or seed formation. This method of propagation makes it possible to obtain plants genetically identical to the parent plant, thus forming clones that faithfully preserve its characteristics.

Widely used in horticulture, agriculture, and conservation programs, it is particularly well-suited to the preservation and propagation of varieties with desirable traits, such as disease resistance, high productivity, or specific morphological characteristics. It also provides an effective method for propagating species that are difficult to reproduce sexually.

This method of propagation relies on various techniques implemented by humans, such as cuttings, layering, and grafting.

- **Cuttings .**

Cuttings are an artificial vegetative propagation technique that involves taking a fragment of a plant, usually a stem, leaf, or root, and then placing it in a suitable substrate such as soil or water to induce root formation (Fig. 30). Once rooting is established, the new plant can be isolated and grown independently.

After the plant fragment is separated, it initiates healing mechanisms at the cut site. This physiological response results in intense cellular activity under the influence of growth regulators, leading to the formation of a protective tissue called a callus, composed of undifferentiated cells. Under favorable conditions, adventitious roots develop within this callus, allowing the plant fragment to nourish itself and continue growing until it forms a complete plant. This new plant faithfully retains the genetic characteristics of the parent plant, including its morphological and physiological traits.



Figure 30: Principle of vegetative propagation by cuttings

***The different types of cuttings.**

Generally speaking, there are several types of cuttings, adapted to the nature of the plant and the plant organ used to ensure the regeneration of a new individual.

- Stem cuttings

Stem cuttings are the most common method. They involve using a stem fragment, with or without leaves, capable of developing adventitious roots. Several subtypes exist:

- **Herbaceous cuttings:** taken from young, tender and non-lignified stems. Examples: basil, geranium, mint.
- **Semi-hardwood (or August-grown) cuttings:** taken from partially lignified stems, generally in late summer. Examples: lavender, fuchsia.
- **Hardwood cuttings:** taken from fully lignified stems during a period of dormancy. In deciduous species, this is done in autumn, while in evergreen species, it can be done in spring.

  Examples: grapevine, rose, fig tree.

- **Leaf cutting**

This type of cutting uses a whole or partial leaf capable of regenerating a new plant, either directly by the emission of roots, or by prior formation of buds (Fig. 31).

• **Leaf with blade and petiole:** example: African violet.

• **Leaf with blade only:** example: rex begonia.

• **Cut leaf:** example: sansevieria.



Figure 31: Leaf cutting

- **Root cutting**

It relies on the use of root segments capable of producing new buds and regenerating an entire plant. This technique, while less common, is nevertheless effective in certain species. Examples: raspberry, fig, lilac (Fig. 32).



Figure 32: Root cuttings

- **Bud cutting (or eye cutting)**

This technique involves taking a stem fragment containing a single bud, capable of developing into a new individual. Examples: rose, grapevine.

***Propagation methods**

Cuttings can also be propagated according to the environment in which the cutting is placed in order to promote rooting.

- **Cuttings in water**

The base of the cutting is immersed in water, allowing for easy and quick observation of root formation. Examples: some houseplants (Fig. 33).



Figure 33: Cuttings in water

- **Substrate cuttings**

The cutting is placed in a light and aerated substrate that promotes rooting, such as perlite, sand, vermiculite or a soil-sand mixture (Fig. 34).



Figure 34: Cuttings in substrate.

***Conditions for successful propagation by cuttings**

- ❖ Keep the cuttings in cool soil;
- ❖ Limit water loss to avoid excessive sweating;
- ❖ Reduce the leaf area by keeping the number of leaves low;

- ❖ Make clean cuts to promote healing;
- ❖ Use cuttings that are neither too young nor too old;
- ❖ Plant the cuttings in a well-aerated substrate.

- **Layering .**

Layering is an artificial vegetative propagation technique that involves inducing the rooting of a stem still attached to the parent plant. This method relies on bending a branch and placing it in contact with the soil or a substrate to encourage the development of adventitious roots while maintaining continuity with the main plant. Once the root system is sufficiently developed, the new plant is separated from the parent plant and can be grown independently.

***The different types of layering**

Layering comes in several types, differentiated according to the method of bending the stem and the rooting conditions.

- **Simple layering (or layering by layering).**

Simple layering involves laying a flexible stem in contact with the soil without detaching it from the parent plant, then partially burying it to encourage the development of adventitious roots (Fig. 35). Once rooting is established, the new plant is separated and cultivated independently. Example: jasmine.



Figure 35: Simple layering or layering.

- **Serpentine (or flat) layering .**

Serpentine layering involves burying several sections of the same stem alternately, leaving above-ground parts between the buried sections (Fig. 36). Each buried section can produce roots and give rise to several new plants. Example: grapevine.

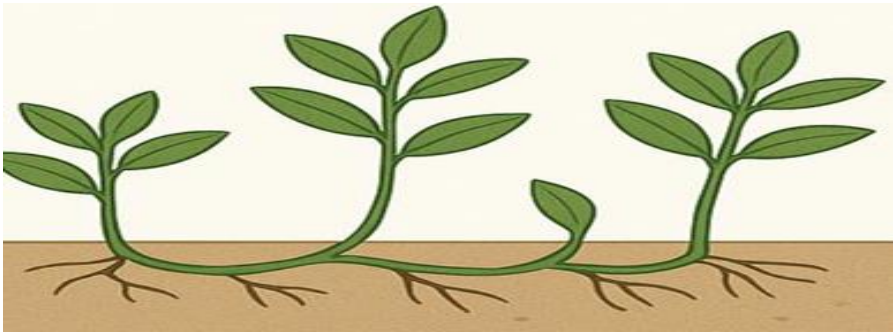


Figure 36: Serpentine or flat layering

- **Layering in a mound (in a clump).**

Mound layering involves cutting a mother plant at ground level and then covering the base with soil to stimulate the growth of new shoots that develop roots at their base (Fig. 37). The new plantlets are then separated. Example: fruit tree rootstocks.

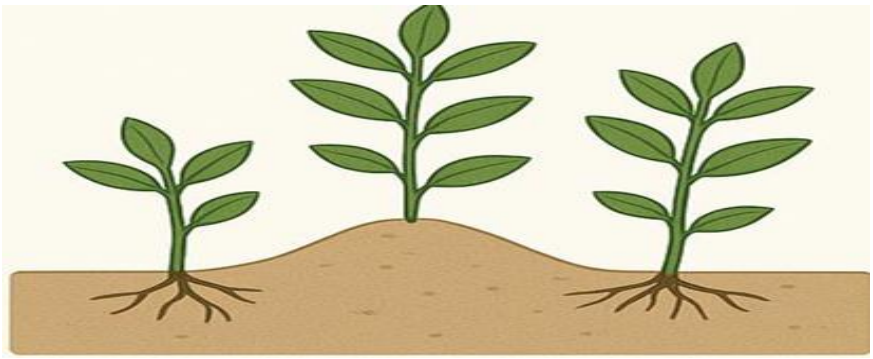


Figure 37: Layering in mounds or in coppices.

- **Aerial marketing .**

Air layering involves encouraging rooting of a stem without contact with the soil by making an incision in the stem and then surrounding it with a moist substrate held in place by a support (Fig. 38). After roots have formed, the stem is cut and planted. Example: ficus.

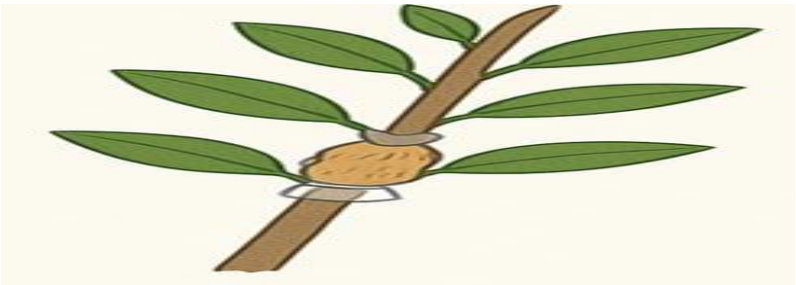


Figure 38: Aerial layering

*** Conditions and period for carrying out layering**

Depending on climatic conditions and the plant species involved, the layering period generally varies from late winter to spring, approximately from February to April. In both deciduous and evergreen species, this technique is most often carried out on shoots from the previous year's wood. In contrast, layering of herbaceous stems, corresponding to young shoots, is done during the summer, sometimes even until September, as with certain species such as the strawberry (*Fragaria spp.*).

***Conditions for successful layering**

- ❖ Maintain good humidity in the environment;
- ❖ Select branches bearing vigorous buds;
- ❖ Immobilize the branch to be layered before the appearance of new shoots;
- ❖ Carry out the weaning process carefully;
- ❖ Transplant the layering into moist soil.

- **Grafting .**

Grafting is an artificial vegetative propagation technique that involves joining two separate plant parts to form a single individual. The scion, usually a stem fragment or branch from a selected plant, is attached to another plant called the rootstock, which provides the root system and foundation for growth (Fig. 39). This association aims to combine the qualities of both partners, particularly by improving the vigor, productivity, or resistance of the resulting plant.

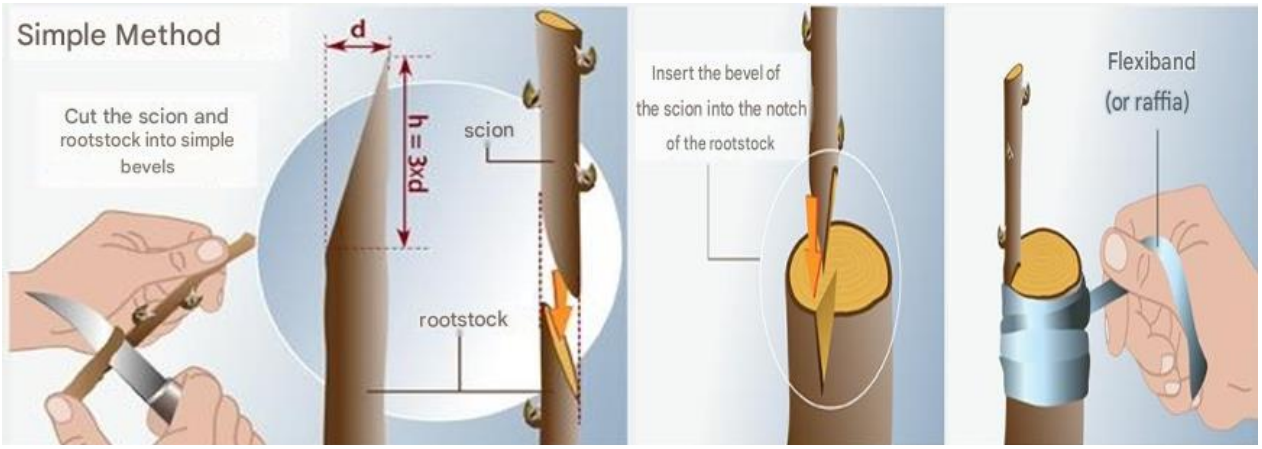


Figure 39: Grafting technique.

The success of grafting depends on the fusion of the vascular tissues of the rootstock and the scion, allowing for the rapid restoration of the continuous flow of raw and elaborated sap, essential for the scion's survival. This process is ensured by the cambium, a meristematic tissue located between the wood and the bark, which plays a crucial role in the formation of the phloem, responsible for the circulation of elaborated sap, and the sapwood, responsible for the transport of raw sap. It also plays a role in wound healing and the secondary growth in stem thickness. Thus, regardless of the grafting technique used, the fundamental principle is to bring the cambium layers of the rootstock and scion into close contact to allow them to fuse.

Furthermore, grafting offers the advantage of combining the characteristics of the scion and the rootstock. The rootstock can be selected for its vigor, its adaptation to soil conditions, or its resistance to diseases and pests, while the scion retains the desired varietal characteristics. The success of this combination, however, depends on their compatibility, which is generally ensured within the same species, such as between apple or pear varieties. In some cases, interspecific grafts are possible, notably between pear and quince, or between apricot and plum.

Grafting encompasses several techniques, differentiated according to the nature of the organs used, the timing of the procedure, and the desired objectives. Although all are based on the fundamental principle of the union between a graft and a rootstock, they differ in their implementation methods and the conditions under which they are applied.

- **The different types of grafting.**

- **Cleft grafting**

Cleft grafting involves making a vertical incision in the rootstock to insert one or more scions cut at an angle. The tissues are then held in close contact to promote union (Fig. 40). This technique is often used on mature trees. Examples: apple tree, cherry tree.

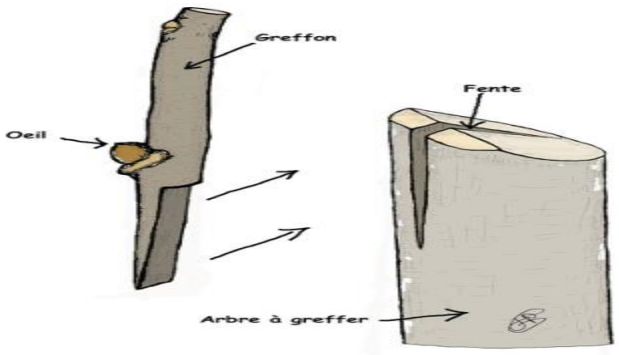


Figure 40: cleft grafting.

- **Crown grafting**

Crown grafting involves inserting several scions between the bark and the wood of a cut rootstock. The bark is slightly lifted to allow the insertion of the scions (Fig. 41). It is generally performed on large-diameter trees. Examples: walnut, apple.

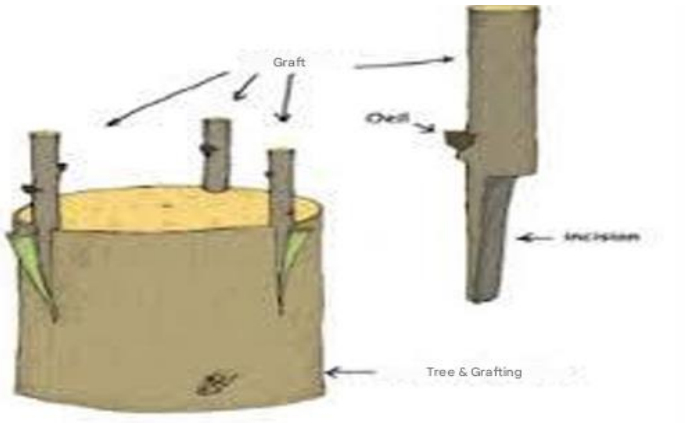


Figure 41: Crown grafting.

- **Bud grafting**

Bud grafting involves taking a single bud along with a shield-shaped piece of bark and inserting it under the bark of the rootstock. The entire assembly is held tightly until the graft union is complete (Fig. 42). This method is widely used in nurseries. Examples: roses, citrus trees.

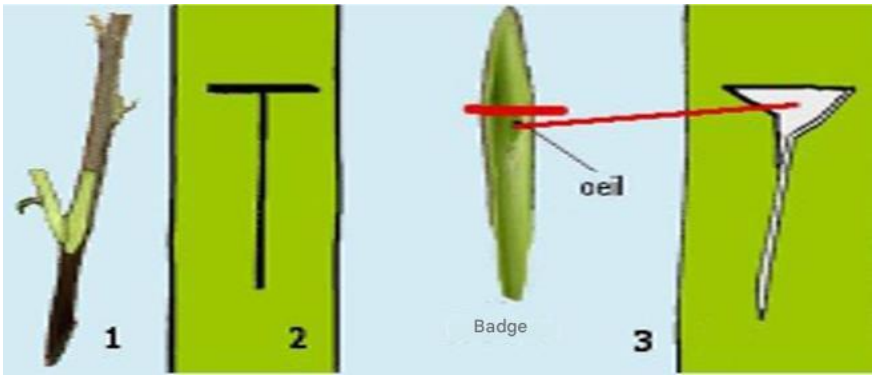


Figure 42: Shield grafting.

- **Grafting is approaching**

Approach grafting involves bringing two still-rooted plants together to allow their tissues to fuse. Once fusion has occurred, one of the plants is separated from its root system (Fig. 43). This technique is simple but time-consuming. Examples: grapevines, ornamental plants.

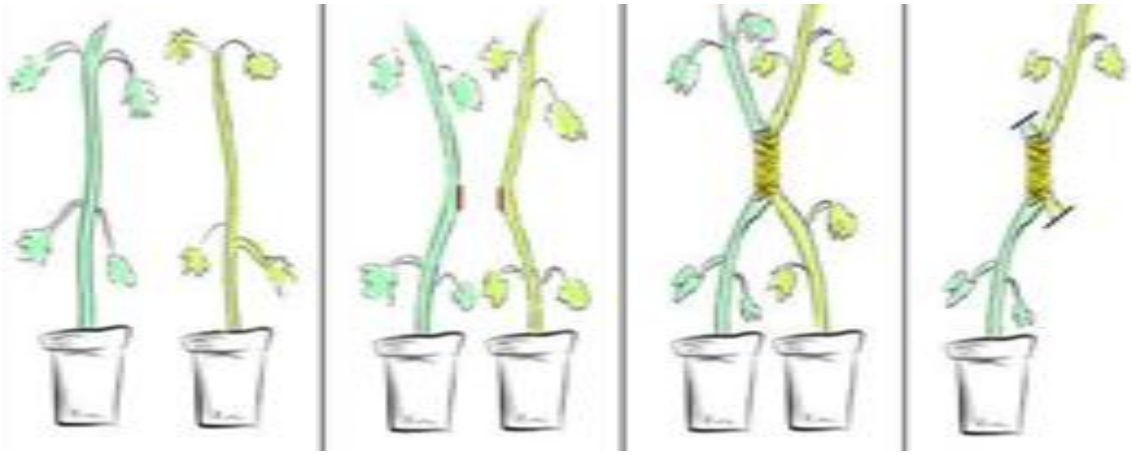


Figure 43: Grafting approach.

Other branch grafting techniques, such as English grafting and horse grafting, can also be used depending on the species and conditions of execution.

***Comparative study of different artificial vegetative propagation techniques**

To highlight the differences and specific characteristics of the main artificial vegetative propagation techniques, it is useful to compare cuttings, layering, and grafting. These methods are distinguished in particular by their method of execution, their relationship with the mother plant, the conditions necessary for their success, and their success rate (Table 10).

Table 10: Comparison of the main artificial vegetative propagation techniques

Criteria	Cuttings	Layering	Grafting
Connection with the mother plant	The cutting is cut from the mother plant right from the start.	The stem remains attached to the mother plant during rooting.	The graft is inserted onto the rootstock to ensure the exchange of sap and nutrients.
Part used	Fragment of stem, leaf or root	Flexible stem or still-living branch	Bud, stem or portion of branch constituting the graft
Time for rooting or union	Generally faster, but more delicate.	Generally slower, but safer	Variable depending on the compatibility between the scion and the rootstock.
Success rate	Variable depending on the species, sometimes low	Generally higher due to maintaining the link with the mother plant.	Generally high when compatibility and conditions are favorable.
Necessary conditions	Humidity, heat and sometimes rooting hormones.	Less demanding conditions thanks to the maintenance of exchanges with the mother plant.	Proper preparation of the graft and rootstock, humidity, tying and protection against infections.

3.2. Regeneration by *in vitro* culture.

A. Definition and principle of *in vitro culture*

In vitro vegetative propagation involves taking a fragment of a plant organ and placing it in a suitable culture medium to allow the regeneration of an entire plant. This fragment can be a piece of leaf blade, stem, or bud. The regeneration process is controlled by specific substances called growth regulators or phytohormones, which regulate and direct plant development.

B. Interest in *in vitro* culture

In vitro culture offers several major advantages, including accelerating the creation of new plant varieties and reducing the time required for their development. It also facilitates the exploitation of

genetic diversity and enables crossbreeding between different species. Furthermore, it ensures the production of healthy plants, free from viruses or diseases, and contributes to the conservation of rare or heirloom species.

C. Basic principles of *in vitro culture*

The implementation of in vitro culture relies on the availability and balance of several essential elements, the presence of which is indispensable for the proper progression of the plant regeneration process. The absence or insufficient control of any of these factors can compromise the development of explants and lead to culture failure.

***Totipotency**

Totipotency is the fundamental property of in vitro culture, defined as the intrinsic ability of any plant cell to regenerate and give rise to a complete plant when grown in a medium properly formulated with nutrients and phytohormones. This concept was initially demonstrated by Gottlieb Haberlandt in 1902.

***The MS midfield (Murashige and Skoog, 1962)**

They studied the vegetative propagation of tobacco and developed the first *in vitro culture medium (MS),* which today constitutes a standard reference medium for the *in vitro culture* of plants.

***Environmental conditions**

➢ **Macroelements**

Macronutrients include nitrogen (NO_3^-, NH_4^+), phosphorus (PO_4^{3-}), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), and sulfur (SO_4^{2-}). They are required in large quantities for plant growth. They play a role in the synthesis of proteins and nucleic acids, the formation of cell walls, photosynthesis, and energy metabolism. Calcium, in particular, contributes to the strength of the pecto-cellulosic cell wall.

➢ **Microelements (trace elements)** :

Iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), boron (B), molybdenum (Mo) and cobalt (Co). They are required in small quantities and act as enzymatic cofactors involved in numerous biochemical reactions, as well as in chloroplast synthesis and cell division. For example, iron is involved in photosynthesis, while zinc participates in enzymatic activity and cell division.

➢ **Vitamins:** thiamine (B1), nicotinamide (B3), pyridoxine (B6), nicotinic acid, etc. They play a role as growth stimulants and participate in cellular metabolism.

➢ **Carbon source:** sucrose or glucose. It provides the energy necessary for the development of explants, particularly in the absence of sufficient photosynthetic activity.

➢ **Phytohormones :** auxins, cytokinins, gibberellins, etc. They ensure the regulation of growth and the direction of development (roots, stems, buds, cell multiplication).

➢ **Agar-agar:** a gelling substance of algal origin, allowing the solidification of the culture medium.

➢ **Water, pH and general conditions**

The water used is distilled or demineralized. The pH of the medium is adjusted between 5.5 and 6.0. The plant material (explant) is carefully selected and sterilized. The culture is carried out under aseptic conditions (laminar flow hood, autoclave) and under controlled physical conditions (temperature, light, and humidity).

➢ **Sterility**

In vitro culture requires strictly aseptic conditions to prevent any microbial contamination (bacteria and fungi). This sterility applies to the explant, the culture medium, and all equipment used.

➢ **Physical conditions .**

Explant growth depends on controlled environmental parameters, including temperature (20–27 °C), light intensity, photoperiod, relative humidity and, in some cases, aeration of the culture medium.

***In vitro culture procedure**

In vitro culture relies on a series of successive and rigorously organized steps, enabling the regeneration and multiplication of plants under controlled conditions. Its execution is carried out according to fundamental principles essential to controlling culture conditions (Fig. 44).

- **Selection and preparation of the explant**

Selection of an appropriate plant tissue (bud, meristem, leaf, root) and removal of damaged or contaminated parts.

- **Sterilization of work equipment**

Disinfection of the explant to eliminate any microorganisms, generally by chemical treatments (alcohol, bleach), followed by rinsing with sterile water.

- **Preparation of the culture medium:**

Formulation of a nutrient medium containing mineral salts, sugars, vitamins and phytohormones, with adjustment of pH (5.5–6.0) and gelation, if necessary, then sterilization by autoclave.

- **Inoculation and culture:**

Aseptic transfer of the sterile explant into the prepared medium, under sterile conditions.

- **Culture and maintenance:**

Maintaining cultures under controlled conditions of temperature, light and humidity, with regular observation of tissue growth and development.

- **Multiplication and regeneration:**

Induction of the formation of new organs or buds via the manipulation of phytohormones, depending on the objective (organogenesis or somatic embryogenesis).

- **Acclimation:**

Gradual transition of regenerated plants to ex vitro conditions, with adaptation to open air, substrate and natural light before final transfer.

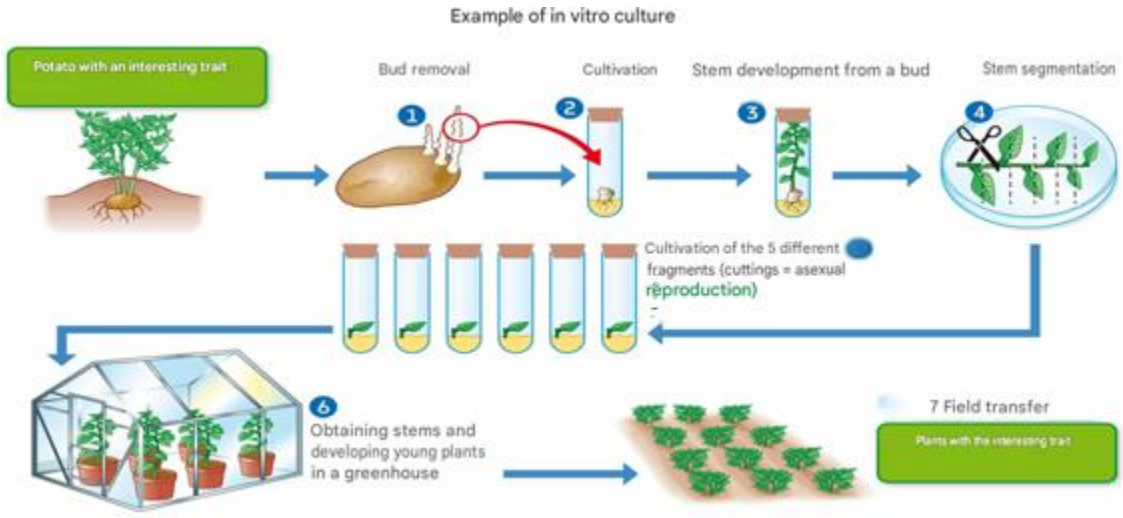


Figure 44: *In vitro* culture process (example of micropropagation in potato)

3.2.1. Meristem culture (in reversal)

Two approaches are distinguished in meristem culture: a classical form, used for the multiplication of healthy plants, and another form called reversion, aimed at obtaining healthy plants from contaminated plant material.

➢ Objective

The goal of reversionary meristem culture is to sanitize plant material by eliminating viruses and other pathogens present in the mother plant.

➢ Principle

This technique is based on the fact that the apical meristem is generally free of viruses. This is explained by its small size, its intense cellular activity and the absence of functional vascular tissues, which limits the arrival and circulation of pathogens in this area.

➢ Steps

• Careful removal of a small meristem (0.1 to 0.3 mm);

• Culturing on a sterile nutrient medium adapted to the needs of the meristem and it's *in vitro* regeneration, the composition of which varies according to the species and the objective of the culture (induction of calluses, organogenesis or direct regeneration of plantlets); • Regeneration

of a complete plant from the cultured meristem; • Verification of the health status by viral detection tests (PCR or ELISA).

➢ **Applications**

This technique is widely used for the sanitation of several species of agronomic interest, including potatoes, strawberries, bananas, and grapevines. It allows for the production of healthy plants, improves the sanitary quality of plant material, and ensures the production of disease-free propagation material.

3.2.2. Tissue culture (caulogenesis, rhizogenesis and calogenesis)

The success of micropropagation and plant regeneration relies on mastering in vitro morphogenesis. These processes involve cellular reprogramming characterized by dedifferentiation followed by a phase of tissue differentiation. Depending on the nature of the structures formed, we distinguish primarily between calogenesis, caulogenesis, and rhizogenesis.

3.2.2.1. Calogenesis

Callus formation, or a mass of undifferentiated cells, is the process of creating a callus from an explant grown in vitro. This process yields a totipotent tissue that can serve as a basis for the regeneration of new organs or entire plants. It is also used for initiating cell suspensions, producing secondary metabolites, and in certain plant breeding applications.

3.2.2.2. Caulogenesis

Caulogenesis refers to the formation of adventitious stems or buds from a callus or directly from an explant cultivated in vitro. It allows the regeneration of the aerial part of the plant and constitutes an essential step in vegetative micropropagation.

3.2.2.3. Rhizogenesis

Rhizogenesis refers to the formation of adventitious roots from a callus or explant cultivated in vitro. It ensures the development of a functional root system, essential for obtaining a complete seedling and for the survival of vitro plants during acclimatization.

3.2.3. Auxin/cytokinin ratio

Cell differentiation in in vitro culture depends primarily on the balance between auxins and cytokinins. Variations in the ratio between these two growth regulators can direct the morphogenetic development of cultured tissues (Table 11).

Table 11: Effect of the ratio of auxins and cytokinins on *in vitro* morphogenesis

Hormonal intercourse	Morphogenetic response
Balance between Auxins and Cytokinins (Auxins ≈ Cytokinins)	Callus formation: Calogenesis
Dominance of Auxins versus Cytokinins (Auxins > Cytokinins)	Root formation: Rhizogenesis
Cytokinin dominance over Auxin dominance (Cytokinins > Auxins)	Stem and bud formation: Caulogeny

Chapter 4
Morphogenetic correlations

Morphogenetic correlations refer to all the reciprocal influences that occur between the different parts of an organism during its development. They are based primarily on exchanges of physiological signals, particularly hormonal ones, ensuring the coordination of organ development.

These interactions allow:

• Stimulation or inhibition of organ development; • Coordination of growth between different parts of the plant; • Adaptation of development to environmental conditions.

They are expressed through various mechanisms, including morphogenetic gradients, mutual correlations between organs, and inhibitory phenomena. These mechanisms do not function in isolation, but are integrated into a global and coordinated system, ensuring the coherence of plant organ growth and differentiation.

4.1. Morphogenetic Gradients

A morphogenetic gradient corresponds to a non-uniform spatial distribution of regulatory substances, primarily phytohormones, within plant tissues. This heterogeneity in concentration constitutes a fundamental biological signal influencing growth, differentiation, and the direction of cell development. These gradients allow cells to interpret their position within the plant organism and to adopt a specific fate based on the signals received.

***Example of the gradient (IAA)**

The auxin gradient is a central mechanism of morphogenetic regulation. Auxin (IAA), primarily synthesized in apical meristems and young organs, is transported in a polarized manner towards the basal regions of the plant, thus establishing a concentration gradient along the vegetative axis. This differential distribution induces distinct effects in different plant regions.

- At the apical level, the high concentration of auxin stimulates cell elongation and promotes stem length growth.
- Conversely, in basal regions, the relative decrease in its concentration promotes the lifting of apical dominance and the activation of lateral buds.

Thus, this gradient plays an essential role in the architectural organization of the plant and in the coordination of its growth.

***Other hormonal gradients**

Besides auxin, other phytohormones participate in establishing hormonal gradients involved in regulating plant growth and development. Cytokinins, primarily synthesized in the roots and transported to the aerial parts via acropetal movement, play an important role in these gradients. Gibberellins, abscisic acid, and ethylene also contribute to regulating plant growth, development, and adaptation processes.

4.2. Mutual correlations between organs

The mutual correlations between organs correspond to the reciprocal interactions established between the different parts of the plant during its development. They ensure the functional coordination of the organs and contribute to the harmonious regulation of growth.

These correlations can be exerted:

- **Horizontally** , between organs at the same level (example: leaves between each other) .
- **Vertically** , between organs at different levels (apex, buds, roots, etc.) .

Communication between organs relies on several types of signals, including:

- Phytohormones (auxins, cytokinins, etc.) .
- Nutrients (sugars, assimilates) .
- Other chemical signals .

They allow:

- Coordinated plant growth .
- Better adaptation to environmental conditions .

- Optimizing resource utilization .

Two types of interactions are generally distinguished:

- **Cooperative** , when the organs stimulate each other .
- **Competitive** , when one organ dominates or inhibits the development of another .

❖ **Cooperative interactions**

Cooperative interactions correspond to positive relationships between organs, promoting their reciprocal development and ensuring coordinated plant growth.

Examples:

- **Leaf – bud:** a functional leaf provides assimilated substances (including sugars) that promote the development of the neighboring bud.
- **Roots – aerial parts:** nutrient and hormonal exchanges ensure the balance and harmonious growth of the plant.

❖ **Competitive interactions**

Competitive interactions correspond to situations in which one organ exerts dominance or inhibition over the development of another organ, resulting in a priority allocation of resources.

Examples:

- **Stem – buds (apical dominance):** the apical bud inhibits the development of axillary buds. Removal of the apex removes this inhibition and promotes their growth.
- **Fruits – flowers:** the development of fruits inhibits the formation of new flowers, the plant directing its resources towards the ripening of the fruits.

4.3. Inhibition

Inhibition refers to a negative interaction between organs, in which one organ limits or prevents the development of another. It results primarily from hormonal mechanisms and/or competition for resources, and contributes to the regulation of plant architecture and growth.

A. Inhibition between organs of the same type: apical dominance

Apical dominance corresponds to the inhibition of the growth of axillary buds by the apical bud.

Two complementary mechanisms are involved:

- **Hormonal mechanism:**

The apical bud synthesizes auxin (IAA), which is transported in a polarized manner to the basal regions. This hormone exerts an inhibitory effect on the development of axillary buds, either directly or indirectly via other growth regulators such as ethylene or abscisic acid.

- **Trophic mechanism:**

The apical bud constitutes a priority center for the consumption of resources (sugars, water, mineral elements), thus limiting their availability to the lateral buds and slowing their growth.

B. Inhibition between organs of different natures

- **Stem – leaves (foliar and fruiting abscission):**

Leaf and fruit fall results from abscission processes regulated by hormonal signals. An increase in ethylene combined with a decrease in auxins leads to the formation of a separation zone, resulting in senescence and then organ fall.

- **Leaf- bud:**

A leaf can exert a variable influence on the development of a neighboring bud depending on its physiological state and level of photosynthetic activity. A functional and well-lit leaf generally promotes the activity of the axillary bud through the supply of assimilates , while an old or deficient leaf can contribute to inhibiting this development.

Morphogenetic correlations constitute an integrated system for regulating plant development, based on coordinated interactions between the different organs of the plant. They ensure the organization of growth through complementary mechanisms such as morphogenetic gradients, mutual correlations, and inhibitory phenomena.

- These mechanisms allow the plant's architecture to be structured, the activity of organs to be modulated according to their functional hierarchy and the availability of resources, while ensuring dynamic adaptation to environmental conditions.

- Thus, plant development results from a global network functioning, where each organ participates in an integrated and coherent regulation of growth.

Chapter 5
Bud dormancy

5.1. Definition of dormancy

Dormancy is a reversible physiological state characterized by a marked reduction in metabolic activity and growth. It is an adaptive mechanism that allows plants to survive adverse environmental conditions, such as low temperatures, drought, or other abiotic stresses. This state can affect various plant organs, including seeds, buds, and certain vegetative organs. In the case of buds, it plays a crucial role in perennial plants by protecting meristems and synchronizing the resumption of growth with the return of favorable environmental conditions. It ends when appropriate internal and external signals allow the reactivation of growth and development processes.

5.1.2. Types of bud dormancy

In plant physiology, the modern classification proposed by Lang et al. (1987) distinguishes three fundamental types of bud dormancy: parodormancy, endodormancy, and ecodormancy. This typology is based on the origin of the signals responsible for the induction or maintenance of growth inhibition (Fig. 45).

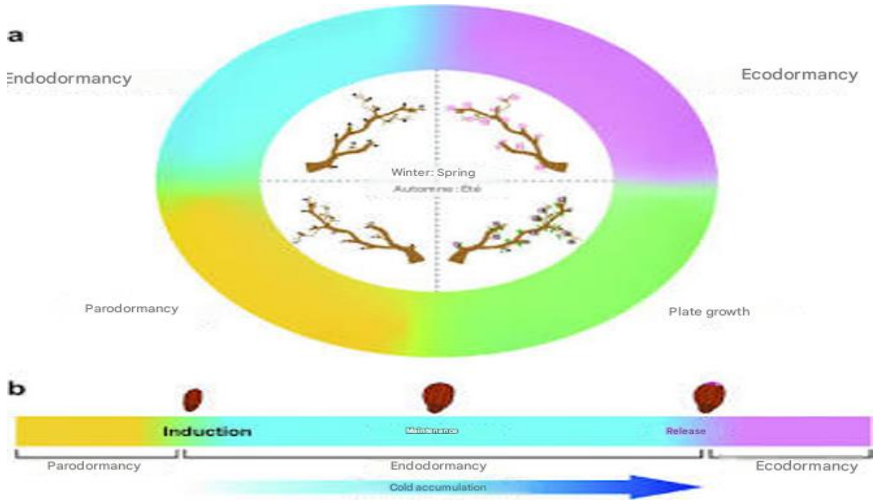


Figure 45: The three types of bud dormancy and their physiological succession.

A. Paradormancy (or correlative dormancy)

Paradormancy is the inhibition of bud development due to signals from other plant organs. The bud is physiologically capable of growth, but its development is inhibited by long-distance interactions within the plant. This phenomenon is primarily linked to apical dominance, in which the terminal

bud produces auxin, which is transported to the basal parts of the plant, thus inhibiting the development of axillary buds. This mechanism is modulated by strigolactones and antagonized by cytokinins.

B. Endodormancy (or true/innate dormancy) .

Endodormancy corresponds to a state of intrinsic inhibition of the bud itself, in which it cannot resume growth even if environmental conditions become favorable and in the absence of apical dominance. It is induced by seasonal signals such as decreased photoperiod and lower temperatures, leading to internal physiological changes. This process is associated with an accumulation of abscisic acid (ABA) and a reduction in intercellular exchange, notably through the closure of plasmodesmata.

C. Ecodormancy (or imposed dormancy).

Ecodormancy is a growth inhibition caused exclusively by unfavorable environmental conditions. The bud has already broken its endodormancy and is physiologically capable of growth, but its development is blocked by external factors such as low temperatures, water stress , or nutrient deficiencies. These conditions lead to a slowdown in metabolism and a temporary inhibition of cellular activity.

A comparative synthesis of the three types of bud dormancy is presented according to their origin, their mechanism and the factors involved in their emergence (Table 12).

Table 12: Summary of differences between the three types of bud dormancy

Type of dormancy	Origin of the inhibitory signal	Classic biological example	Main factor in raising
Paradormance	Exogenous to the bud, but endogenous to the plant	Apical dominance of branches in summer	Size / Decapitation of the apex
Endodormance	Endogenous to the bud	Fruit trees undergo a deep winter rest	Accumulation of cold (Chilling) requirement)
Ecodormancy	Exogenous to the plant (Environment)	Bud ready in spring but blocked by a late frost	Return of mild temperatures

5.1.2. Dormancy Installation

The onset of bud dormancy is a gradual process during which meristems cease growth activity and enter a physiological resting state. This phenomenon is primarily triggered by seasonal environmental signals, notably the decrease in photoperiod and the drop in temperatures as autumn and winter approach. These conditions allow the plant to synchronize its development with the seasons and ensure the survival of its vegetative organs.

Hormonally, the onset of dormancy is tightly regulated. It is generally associated with an increase in the concentration of abscisic acid (ABA), a key hormone in the induction and maintenance of the dormant state. Concurrently, there is a decrease in gibberellins (GA), hormones that promote growth and cell division. Ethylene may also play a role, particularly in modulating certain processes associated with developmental slowing.

At the physiological level, the onset of dormancy is accompanied by several internal changes. A progressive reduction in metabolic activity is observed, characterized by a decrease in cellular respiration and enzymatic activity. Cell division at the meristem level is strongly inhibited, leading to a cessation of growth. Simultaneously, changes in cell structure and membranes may occur, as well as a reorganization of protein metabolism with the synthesis of stress-related proteins and the degradation of non-essential proteins. Furthermore, the plant's overall metabolism slows down to limit energy consumption and ensure resource conservation.

At the molecular level, the onset of dormancy also involves the regulation of gene expression. Certain genes play a role in controlling the entry into dormancy by interacting with hormonal pathways, particularly those of ABA. This regulation stabilizes the dormant state until signals favorable to the resumption of growth are received.

Thus, the establishment of bud dormancy results from a fine coordination between environmental signals, hormonal regulations, physiological modifications and genetic control, leading to the establishment of a temporary resting state essential to the survival and seasonal development of perennial plants.

5.2. Types of dormancy measurement

Measuring bud dormancy is an essential step in plant physiology, allowing for the assessment of the functional state of meristematic tissues and their ability to resume growth. It relies on analyzing budburst capacity, response to dormancy-breaking treatments, and the indirect estimation of the level of physiological inhibition.

5.2.1. Observation of natural budburst

The first approach involves observing the budburst of buds placed in favorable environmental conditions (temperature, light, and water availability). This step allows for the assessment of the buds' intrinsic capacity to resume their growth.

The rate of breaking in can be expressed as:

$$D(\%) = \frac{\text{nombre de bourgeons débourrés}}{\text{nombre total de bourgeons}} \times 100$$

A low budburst rate generally indicates a high state of dormancy, while a high rate reflects low physiological inhibition.

5.2.2. Time-dependent monitoring of budburst

The budburst process is monitored over time to assess the dynamics of renewed growth. The average budburst time is an indirect indicator of the degree of dormancy: the longer this time, the greater the level of dormancy.

5.2.3. Dormancy Breakdown Tests

To distinguish between truly dormant buds and those simply inhibited by environmental conditions, specific treatments are applied. These treatments aim to lift the physiological inhibition and stimulate the resumption of growth.

The main treatments used are:

- Controlled cold (stratification) .
- Growth regulators (notably gibberellins, GA_3) .

- The modification of the photoperiod .
- The size or suppression of the sources of inhibition (apical dominance) .

The response of the buds to these treatments confirms the existence and intensity of dormancy.

5.2.4. Dormancy Index

Dormancy can be estimated relatively using an index based on the proportion of unbroken buds or the difference between control and treated conditions. This index allows for an assessment of the level of physiological inhibition, although it may vary depending on the species and experimental protocols.

Beyond morphological observations, dormancy can be studied at different levels of biological organization (Table 13).

Table 13: Methods for studying dormancy according to levels of biological organization

Level of analysis	Methods	Principle / role in the study of dormancy
Physiological	Chlorophyll fluorescence (Fv /Fm), respiration (CO_2/O_2), electrical conductivity, growth monitoring	Evaluation of metabolic activity and tissue functional status
Biochemical	Hormone levels (ABA, GA, auxins), enzyme activity (SOD, CAT, POD), ROS	Analysis of stress mechanisms and dormancy regulation
Molecular	Transcriptomics (RNA- seq , qPCR), proteomics, metabolomics, epigenetics (DNA methylation, microRNA)	Study of gene expression and dormancy signaling pathways
Imaging and advanced technologies	NIRS, plant MRI, micro-CT, growth sensors	Non-destructive monitoring of the structure and dynamics of growth recovery

These complementary approaches allow for an integrated understanding of dormancy mechanisms, linking the morphological, physiological and molecular levels.

5.3. Breaking dormancy

Dormancy breaking is a physiological process by which a plant organ (seed or bud) transitions from a state of metabolic inactivity to a gradual resumption of growth. It results from the release of internal physiological blockages through the combined action of physical, chemical, and environmental factors.

5.3.1. General principles of dormancy removal

Overcoming dormancy relies on three main types of complementary actions (Table 14), namely:

- **Physical actions:** modification of external structures or dominance relationships allowing resumption of growth.
- **Chemical actions:** modulation of hormonal balance and internal biochemical signals.
- **Environmental actions:** reproducing the natural conditions necessary for the emergence from dormancy.

Table 14: Main methods for breaking bud dormancy

Category	Method	Principle of action
Physics	Size / pruning	Suppression of apical dominance by reducing auxin production, promoting the lifting of paradormancy and the activation of axillary buds.
	Pinch	Removal of growing apices, leading to the lifting of the correlative inhibition and the stimulation of lateral buds
Chemicals	Gibberellins (GA_3)	Stimulation of cell division and elongation, antagonism of abscisic acid (ABA) and activation of budburst
	Cytokinins	Activation of cell division and reactivation of meristematic activity
	Calcium cyanamide ($CaCN_2$)	Acceleration and synchronization of bud break through action on enzymatic and hormonal processes
	Nitrates (KNO_3)	Stimulation of metabolism and activation of growth resumption processes
Environmental	Cold stratification	Prolonged exposure to low temperatures (1–5 °C) allows for the satisfaction of the need for cold and the lifting of endodor .
	Rising temperatures	Gradual activation of metabolism and resumption of growth in spring
	Increasing photoperiod	Lengthening of the day acts as a seasonal signal of renewed growth
	Water / humidity	Tissue rehydration and activation of cellular processes necessary for bud break

These different treatments allow the resumption of meristematic activity and the breaking of buds.

Chapter 6.

Aspects of the morphogenesis of woody plants

6.1. Rhythmic growth

The growth of woody plants is neither continuous nor uniform, but generally follows a seasonal or internal rhythm. This phenomenon, called rhythmic growth, is characterized by the alternation of phases of active growth and phases of slowing or resting.

6.1.1. Growth according to the life cycle

A. Annual plants

Annual plants complete their life cycle in a single growing season, from germination to flowering, fruiting, and then death. Growth is continuous over a short period, without a truly marked seasonal rhythm. Examples: wheat, peas, sunflower.

B. Biennial plants

Biennial plants complete their life cycle in two years:

- The first year is devoted to vegetative development (roots, stems, leaves).
- The second year involves flowering, fruiting, and then death. A winter dormancy period may occur between the two years. Examples: carrot, beet, parsley.

C. Woody plants

Woody plants (trees and shrubs) exhibit a multi-year cycle with marked rhythmic growth. This growth is characterized by:

- A phase of active growth (spring–summer).
- A phase of slowing down or rest (autumn–winter).

This alternation is the origin of the formation of growth rings.

6.1.2. Growth rings

Growth rings, also called annual rings or annual circles, are structures visible in the wood of trees when a cross-section of the trunk is observed. They result from the periodic activity of the cambium and constitute one of the most characteristic manifestations of rhythmic growth in woody plants.

The formation of tree rings is linked to the seasonal alternation of growing conditions. In spring, when conditions are favorable, cambial activity is intense and produces light-colored, less dense wood rich in vessels, called springwood. In late summer and autumn, growth slows and the cambium forms denser, darker wood, called summerwood or autumnwood **.** The alternation of these two zones constitutes a growth ring, generally corresponding to one year of development. The width and structure of the rings can also reflect the environmental conditions that have influenced the tree's growth (Fig. 46).

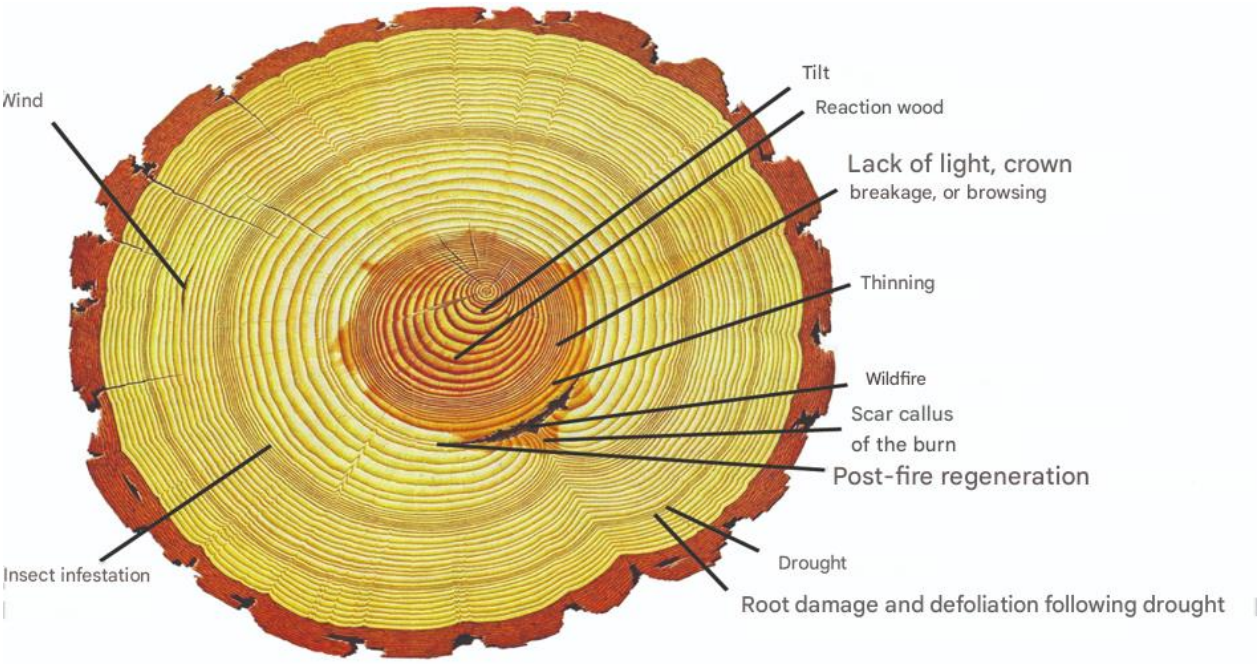


Figure 46: Organization of growth rings in the wood of a tree.

Analyzing tree rings reveals various events that have influenced a tree's development, such as periods of drought, insect infestations, mechanical damage, fires, and variations in light. Tree rings thus constitute veritable biological archives of past environmental conditions.

Tree rings allow us to estimate the age of a tree by simply counting from the heartwood to the bark. Each ring generally represents one year of life. The width of the rings varies depending on environmental conditions. Wide rings generally indicate favorable growing conditions (temperature, water and nutrient availability), while narrow rings can indicate periods of stress, such as drought, cold, or competition from other plants.

The study of growth rings forms the basis of dendrochronology, a discipline that allows us to reconstruct the age of trees as well as certain past climatic variations.

6.1.2. Main forms of growth in woody plants

6.1.2.1. Growth along the direction

A. Growth in length

Elongational growth, or primary growth, results from the activity of apical meristems located at the tips of stems and roots. It ensures the elongation of vegetative axes and the exploration of new spaces.

B. Growth in thickness

Thickness growth, or secondary growth, is mainly ensured by the cambium and the phellogen. It leads to an increase in the diameter of stems and roots and contributes to the formation of wood and bark.

6.1.2.2. Growth according to the progression over time

A. Continued growth

Continuous growth is characterized by prolonged meristematic activity without a clearly marked rest period. It is mainly observed in certain species of tropical regions where environmental conditions remain favorable throughout the year. Examples: certain palm trees and various tropical woody species

B. Rhythmic growth

Rhythmic growth corresponds to an alternation of phases of active growth and periods of rest or slowing down. It is the most frequent growth pattern in woody plants in regions subject to seasonal variations.

- **Growth in flow**

Flow growth, also called shoot growth, is characterized by alternating periods of active branch elongation and periods of temporary cessation. Each growth phase produces a well-defined shoot, separated from the next by a more or less pronounced rest period.

Depending on the species, only one shoot may be produced per year (monocyclic growth) or several successive shoots (polycyclic growth).

Examples: oak generally exhibits monocyclic growth, while maritime pine can exhibit polycyclic growth.

- **Relay growth**

Relay growth refers to a developmental pattern in which the continued elongation of the axis is not ensured by a single terminal bud, but successively by several buds that take over one after the other. This phenomenon allows the plant to maintain its growth despite the cessation or disappearance of activity in the preceding bud.
This type of growth contributes to the formation of complex axes and to the adaptation of the tree's architecture to environmental conditions.

Examples: certain conifers and various woody species exhibiting sequential growth of axes.

- **Endogenous rhythmic growth**

Endogenous rhythmic growth is controlled primarily by mechanisms internal to the plant, including genetic and hormonal factors. Even when environmental conditions remain relatively constant, the plant spontaneously alternates between phases of active growth and resting phases.
This internal rhythm can be likened to a true biological clock regulating the functioning of the meristem. Examples: some tropical species exhibit this type of growth.

6.2. The different types of branching

Branching refers to the architectural organization of a plant's aerial axes, that is, the way in which branches develop from the trunk or main stems. It is a fundamental characteristic of the architecture of trees and shrubs, influenced both by the genetic predisposition of the species and by the growth pattern (rhythmic or continuous), as well as by environmental and hormonal factors. Several major types of branching are distinguished in woody plants.

6.2.1. Fundamental types and evolution of branching

Two main fundamental types of branching are distinguished in plants: dichotomous branching and lateral branching.

Dichotomous branching refers to the division of the vegetative axis into two branches of equal or unequal value. It is characteristic of primitive plant forms and results from the activity of the apical meristem, which divides directly. This type of branching is primarily observed in the most evolutionarily ancient plants.

Lateral branching, on the other hand, is the most widespread mode of growth in modern plants. It originates from buds located on the side of the main axis, called axillary buds. This mode allows for a more complex organization of plant architecture and better use of space.

From an evolutionary perspective, plant branching has shifted from a terminal (dichotomous) mode to a lateral mode, marking an important step in the diversification of terrestrial plants, allowing for better exploration of space, an increase in photosynthetic surface area, and more efficient adaptation to environmental conditions.

6.2.2. Branching Modes

The branching patterns describe how the growth of the axes is ensured over time (Fig. 47).

A. Monopodial branching

Monopodial branching is characterized by the continued activity of the apical bud. This bud ensures the continuous growth of the main axis, while the lateral branches remain subordinate to this dominant axis. This branching pattern generally leads to the formation of a single, well-defined trunk and a hierarchical branching structure. Examples: pine, fir, spruce.

B. Sympodial ramification

Sympodial branching results from the cessation or disappearance of activity in the apical bud. Continued growth is then ensured by one or more lateral buds that successively take over.
The apparent main axis is thus composed of a succession of segments originating from different meristems. This branching pattern often produces more spread-out and complex structures than

those observed in monopodial branching. Examples include many deciduous trees and several fruit species.

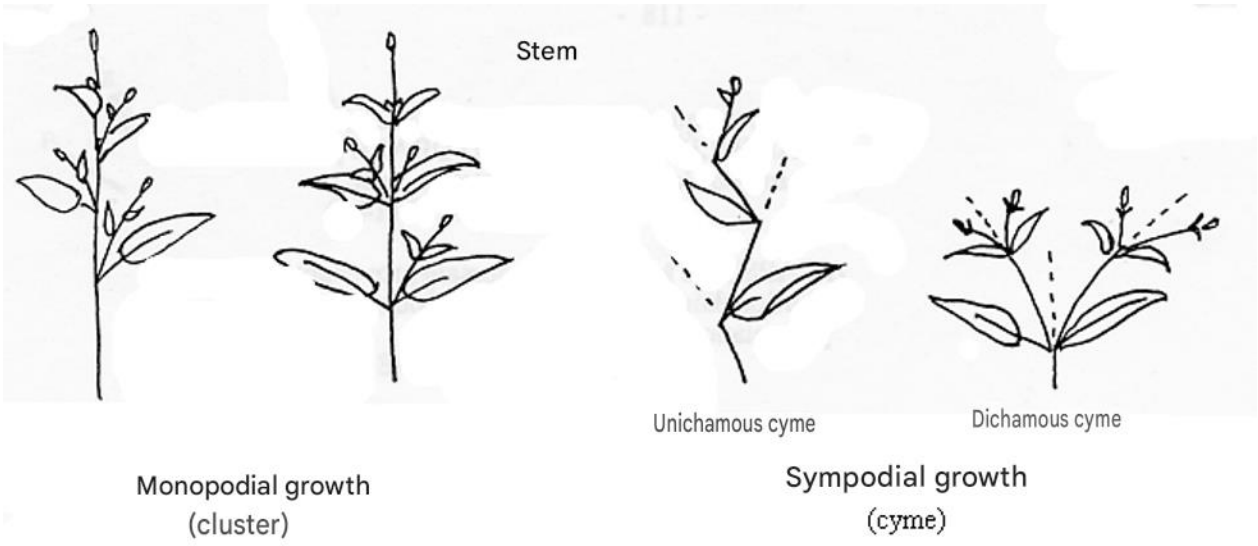


Figure 47: Type of branching: Monopodial, Sympodial.

6.3. Concepts of architectural model

Plant architecture refers to the spatial organization of a plant's axes and their development over time. It results from the interaction between the species' genetic makeup and environmental factors. In woody plants, this organization depends primarily on the growth pattern, branching type, bud activity, and axis orientation.

Each plant species thus expresses a set of growth and development rules that are repeated more or less constantly throughout its life. This set of rules constitutes what is called an architectural model.

6.3.1. Definition of the architectural model

The architectural model of a plant is a theoretical diagram describing the organization and development of its vegetative system in space and time. It represents the coordinated expression of the modes of growth, branching, and differentiation of the axes.

Each model is defined by a combination of several criteria, including:

- The nature of the axes (orthotropic or plagiotropic)..
- The growth pattern (continuous or rhythmic)..

- The type of branching (monopodial or sympodial)..
- The position of the reproductive organs.

6.3.2. Importance of architectural models

The study of architectural patterns allows us to understand the diversity of plant forms and to interpret the development strategies of woody species. It constitutes an essential tool for analyzing the organization of trees, their growth, and their adaptation to environmental conditions.

This approach highlights the fact that, despite the apparent diversity of forms, plants follow relatively constant construction rules, reflecting genetic control of architectural development.

6.3.3. General principles of architectural models

Architectural models are based on fundamental principles that structure the development of woody plants. These principles involve the repetition of successive growth units, the functional differentiation of axes, and the variation of their orientation in space. They also result from the interaction between internal factors, such as hormonal and genetic regulation, and external factors, including light, gravity, and environmental conditions. This interaction explains the diversity of tree forms while linking them to a limited number of developmental patterns.

6.3.4. The main architectural models

Architectural models of woody plants encompass various theoretical frameworks describing the organization of plant growth and branching (Fig. 48). They allow for the comparison of species' development strategies based on fundamental criteria such as growth type, branching, and the position of reproductive axes (Table 15).

Table 15: Characteristics of the main architectural models of woody plants

Architectural model	Growth type	Branching	Organization of the axes	Examples
Rauh	Monopodial rhythmic	Regular lateral	Dominant main trunk, hierarchical branches	Tropical trees
Massart	Monopodial rhythmic	Strong branching in crowns	Tiered structure with horizontal branches	Temperate trees
Troll	Mixed	Variable	Orthotropic and plagiotropic axes	Adaptive species
Leeuwen berg	Sympodial	Equivalent branching	Main axis replaced successively	Tropical shrubs

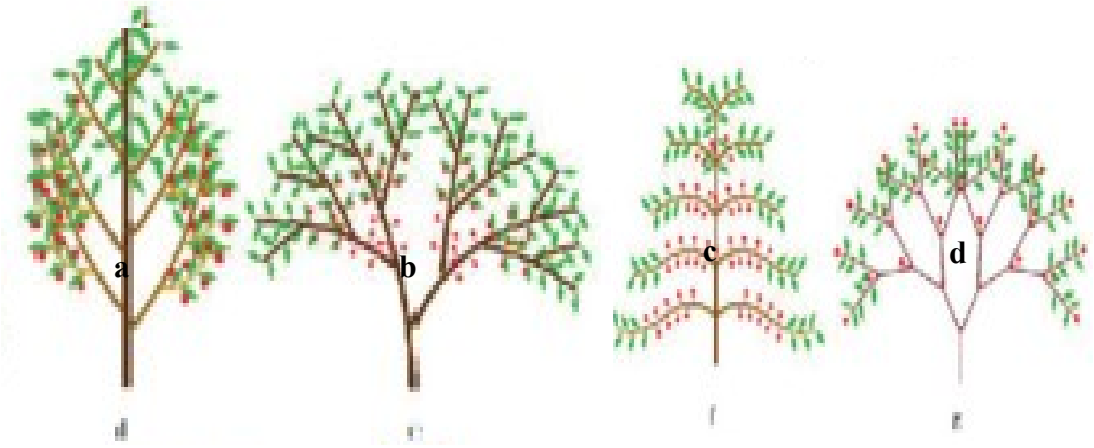


Figure 48: the different architectural models (a: Rauh, b: Troll, c: Massart, d: Leeuwenberg).

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