

Second part: Development

I. Seed formation

The seed is a reproductive organ that develops from an ovule, generally after fertilization. Ovules are produced by both angiosperms (true flowering plants) and gymnosperms (which include conifers). The seed provides the embryo with a favorable environment for its development and protects it until germination. The growth of the young seedling is largely determined by the reserve substances stored in the seed and by its ability to respond to the external environment.

Double fertilization in angiosperms

Angiosperms, or flowering plants, are characterized by double fertilization. One of the male gametes fuses with the egg cell to form a diploid zygote, which divides and develops into the embryo. The fusion of the second male gamete with the polar nuclei gives rise to a triploid storage tissue ($1n$ paternal chromosomes + $2n$ maternal chromosomes) called the **endosperm**. The endosperm fills the entire cavity of the ovule; it is a tissue rich in reserve substances, upon which the embryo develops.

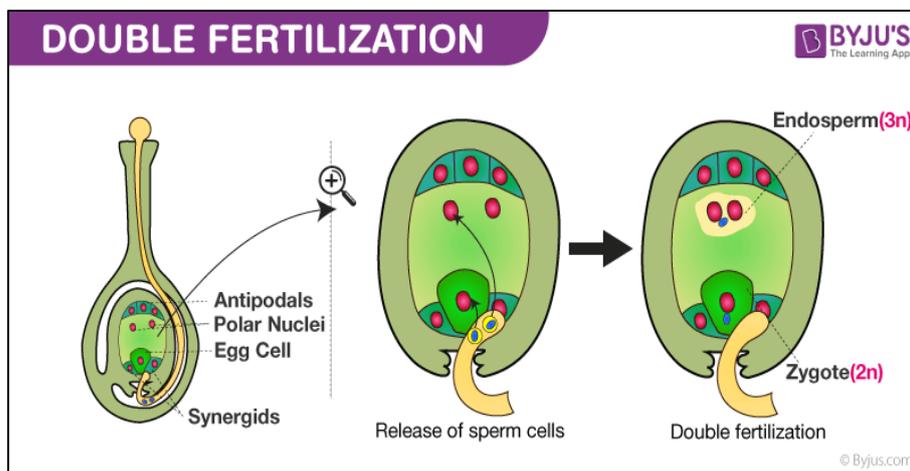


Figure 1 Double fertilization in angiosperms

Types of seeds

A seed is composed of a seed coat (single or double) and a kernel consisting of the embryo and reserve tissues forming the endosperm. The essential part of the kernel is the embryo, which includes a radicle, extended by a hypocotyl bearing the cotyledons.

Based on the presence or absence of endosperm, seeds are classified into three categories:

1. Perispermic seeds

The endosperm is very poorly developed and is surrounded by the **perisperm** (a remnant of the nucellus that has not been digested and serves as a reserve tissue). In this type of seed, the reserve substances are stored in the perisperm.

2. Albuminous (Endospermic) seeds

The nucellus disappears, the cotyledons are thin, and the endosperm is well developed and serves as the main reserve tissue.

3. Exalbuminous (Non-endospermic) seeds

The nucellus is digested by the endosperm, which is then absorbed during embryo development. The embryo and its cotyledons become fully developed and store the reserve substances, as in pea or bean seeds.

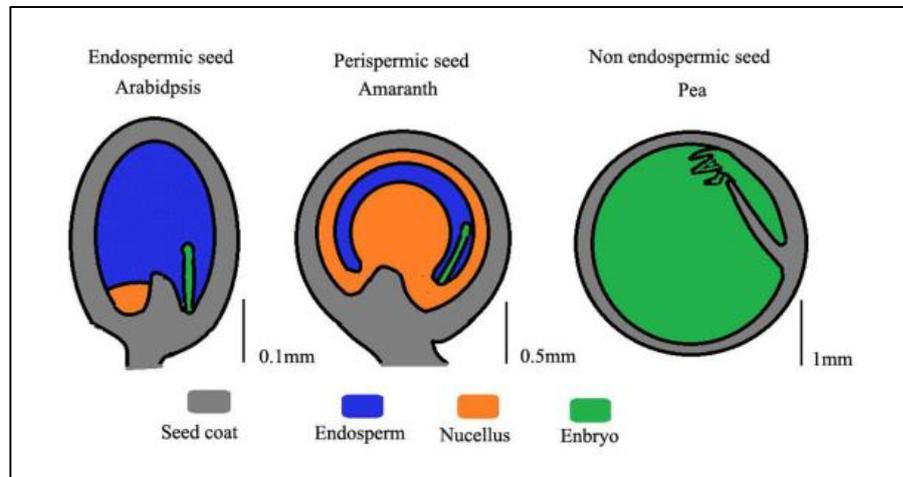


Figure 2 Types of seeds

Seed maturation

Seed maturation is generally accompanied by a significant and progressive decrease in water content. Water loss can reach up to 95% of the fresh weight, leading to the cessation of metabolic activities (a transition to a state of reduced metabolic activity or “quiescence”).

Seed dehydration is initially associated with an intense and transient synthesis of abscisic acid (ABA), which is known to be responsible for the establishment of desiccation tolerance and seed dormancy during seed development on the mother plant.

Seed longevity

Based on the lifespan of seeds under natural conditions, they are classified into three categories:

- **Macrobiontic seeds:** survive for more than 15 years.
- **Mesobiontic seeds:** remain viable for 3 to 15 years. This group includes the majority of species; wheat is a good example.
- **Microbiontic seeds:** do not survive for more than 3 years. Many of them do not tolerate desiccation. Numerous tropical or subtropical species belong to this group.

Seed dormancy

Seeds remain in a state of dormancy (a temporary blockage of growth and a momentary arrest of development) as long as environmental conditions are not suitable for germination. In some cases, even when seeds are placed under favorable germination conditions, they still fail to germinate. This is due to several types of dormancy, the most important being seed coat inhibition and embryonic dormancy.

Types of dormancy

1. Seed coat inhibition

The seed coats surrounding the embryo constitute barriers of varying effectiveness to the passage of water or oxygen, and their influence on germination can be considerable.

- **Water impermeability:** Some seeds cannot germinate because their seed coats do not allow water to pass through at all. In a humid environment, these seeds do not swell, remain dry, and resist crushing. For this reason, they are called **hard seeds**. Species producing hard seeds are commonly found among legumes (Caesalpinioideae, Mimosoideae, and Papilionoideae).
- **Oxygen impermeability:** This is due to the low permeability of the seed coats to oxygen.
- **Chemical inhibitors:** The seed coverings (seed coats or pericarp) very often contain germination or growth inhibitors, such as hydrocyanic acid, ammonia, ethylene and other sulfur-containing compounds, abscisic acid, as well as phenolic compounds.

2. Embryonic dormancy

Embryonic dormancy, by definition, originates within the embryo itself. It cannot be broken by treatments applied to the seed coverings and is expressed even when the embryo is isolated.

Primary dormancy

Primary dormancy is established during seed maturation and prevents the emergence of the radicle. Several forms can be distinguished:

- **Photolabile dormancy**, which is broken by light.
- **Scotolabile dormancy**, which is broken by darkness.
- **Xerolabile dormancy**, which is broken by prolonged exposure to dry conditions.
- **Psychrolabile dormancy**, which is broken by cold and moist conditions.

Secondary (Induced) dormancy

After dormancy has been broken, germination generally proceeds normally. However, in some cases, a **secondary dormancy** may persist or be induced, requiring a new dormancy-breaking treatment. In certain species, dormancy of the epicotyl (or plumule) may remain, preventing germination. In such cases, two successive winters may be required to break this secondary dormancy.

II. Germination

Germination is defined as the series of events that occur from the dry seed to radicle protrusion. It begins with water uptake, or imbibition, which allows metabolic activation, and ends with the emergence of the radicle through the seed coats.

Seed germination therefore requires favorable conditions (external conditions, including water availability, oxygen, and an optimal temperature) and internal conditions, namely the breaking of dormancy.

Germination consists of three successive phases: the imbibition phase, the germination phase *stricto sensu*, and the growth phase. Until the end of the germination phase *stricto sensu*, the seed can be dehydrated without being killed; however, once radicle growth has begun, dehydration becomes fatal.

1. Imbibition phase

The germination process begins with the entry of water into the dry seed. Rapid rehydration over a few hours leads to morphological changes expressed by an increase in seed volume. Water influx activates seed metabolism and resumes respiration. The mitochondria present in seeds contain enzymes that remain functional and are capable of providing sufficient ATP to sustain metabolic processes. In addition, protein synthesis is facilitated by the accumulation of mRNAs and the recruitment of ribosomes during the first minutes of imbibition.

2. Germination phase *Stricto Sensu*

This phase lasts from a few days to several months, depending on the dormancy status of the seeds. Water content remains nearly constant, all mechanisms initiated during phase 1 continue to operate, and protein synthesis is intensified. This phase prepares cellular growth that will allow elongation of the embryonic axis. DNA repair also occurs during this stage.

3. Radicle growth phase

This phase begins with the protrusion of the radicle through the seed coats, which represents the completion of germination. The radicle then undergoes rapid growth, respiratory activity increases again, and water content reaches its maximum at the emergence of the aerial parts. Metabolic events mainly involve the mobilization and degradation of reserve substances, followed progressively by the establishment of autotrophic nutrition.

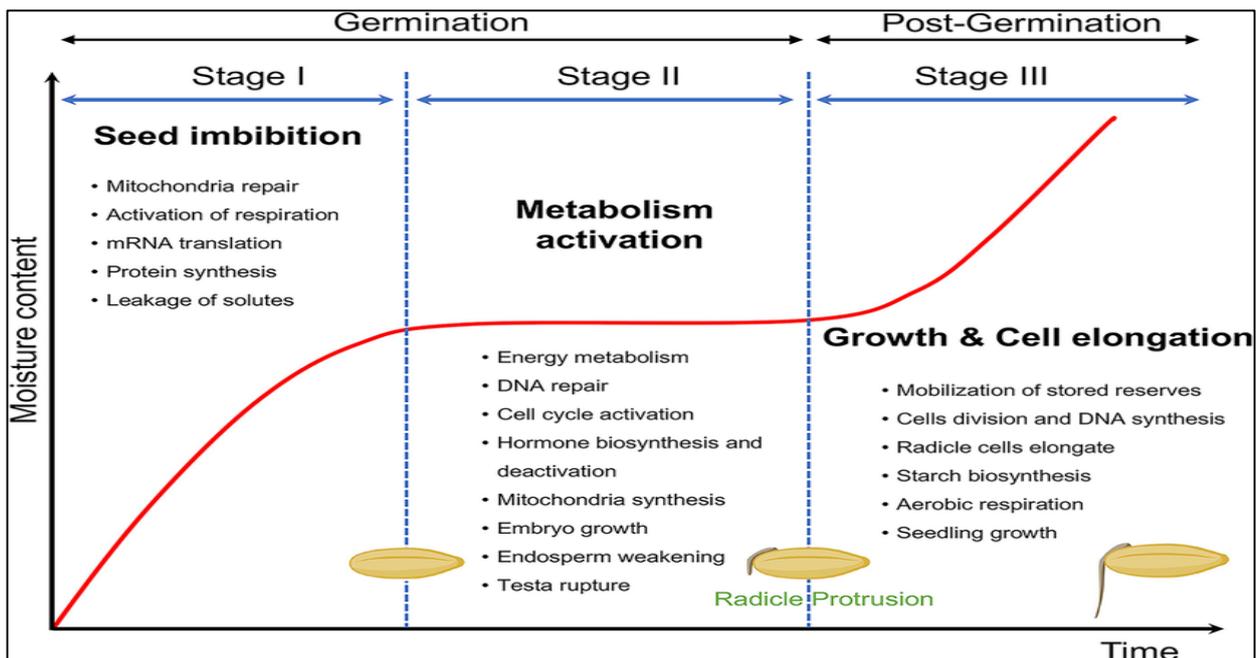


Figure 3 Germination's phases

Conditions for germination

A. Internal conditions

- **Maturity:** the seed coats and the kernel (endosperm and embryo) must be completely and morphologically differentiated.
- **Seed longevity:** the period during which seeds remain alive and retain their germination capacity.

B. External conditions

- **Water** is essential and must be supplied in liquid form. Seeds can absorb a small amount of water vapor, but never in sufficient quantities to ensure germination. Excess water is often harmful, which is why seeds generally do not germinate when completely submerged, except in aquatic plants.
- **Oxygen** is indispensable for germination and requires adequate soil aeration. In fact, the oxygen concentrations required by embryos are low; for most species, 2 to 5% oxygen is usually sufficient.
- **Temperature** directly affects germination by influencing the rate of metabolic reactions, but it may also interfere with oxygen availability, since oxygen solubility decreases as temperature increases (as in the case of apple trees). Species from temperate climates germinate easily at low temperatures, even around 0 °C. In contrast, tropical species require much higher temperatures and are unable to germinate below 20–25 °C. The optimal temperature is the one that allows the highest percentage of germination to be achieved in the shortest time.
- **Light** favors germination in most seeds, which are therefore described as having positive photosensitivity. Others germinate only in darkness and show negative photosensitivity.

Finally, some seeds are non-photosensitive; many species belong to this group, including most legumes, tomato, and squash.

Two types of germination:

There are two types of germination: **hypogeal** and **epigeal**.

In **hypogeal germination**, the cotyledons remain in the soil (for example, in peas), whereas in **epigeal germination**, the cotyledons emerge above the soil surface (for example, in beans).

The cotyledons have two successive roles:

- **Nutritional or storage tissue:** the future seedling uses these reserves to break through the seed coats.
- **Assimilatory tissue:** enrichment in chlorophyll allows photosynthesis to occur; in this case, they are referred to as cotyledonary leaves.

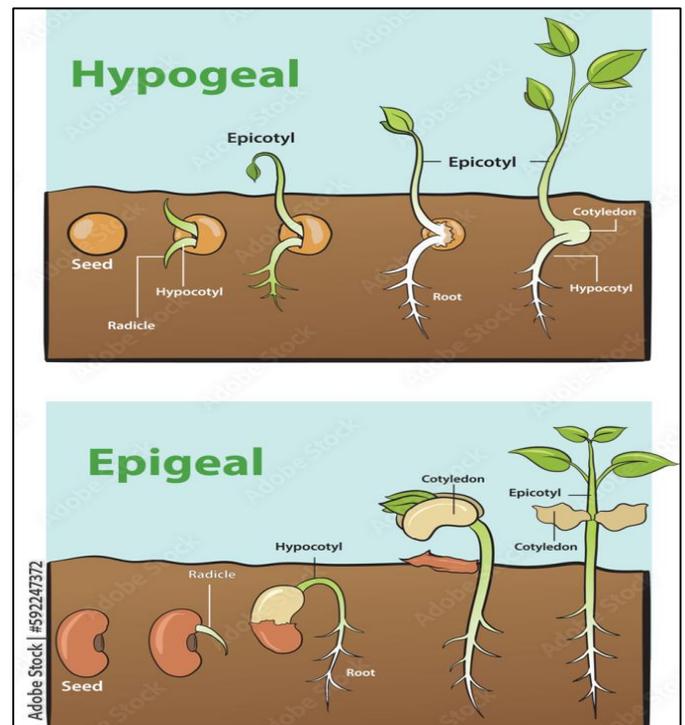


Figure 4 hypogeal and epigeal germination

III. Growth

Growth in the strict sense is a quantitative phenomenon corresponding to an increase in size, mass, and volume. Other qualitative changes, referred to as differentiation, involve the acquisition of new morphological and functional properties. These two sets of changes (quantitative and qualitative) are involved in the phenomenon of development, or growth in the broad sense.

Meriosis, Auxesis, and Differentiation

Meriosis, or cell proliferation, occurs in localized regions known as meristems, which ensure growth in length. Meristems are of two main types:

- **Primary meristems**, responsible for longitudinal growth, including:
 - **Apical meristems**, located at the root apex and in apical buds at the tips of stems and branches;
 - **Axillary meristems**, located in the axils of leaves.
- **Secondary meristems**, which ensure growth in thickness and develop in older organs. These include two generative tissues: the vascular cambium (libero-ligneous cambium) and the cork cambium (subero-phellodermic cambium).

Auxesis most often results in cell elongation due to the presence of a pecto-cellulosic cell wall.

Cell differentiation is the process by which cells acquire specific physiological functions, differing according to the tissue in which they are located. Differentiation corresponds to a progressive qualitative change of cells toward specialization, leading to the formation of specific organelles and cellular products.

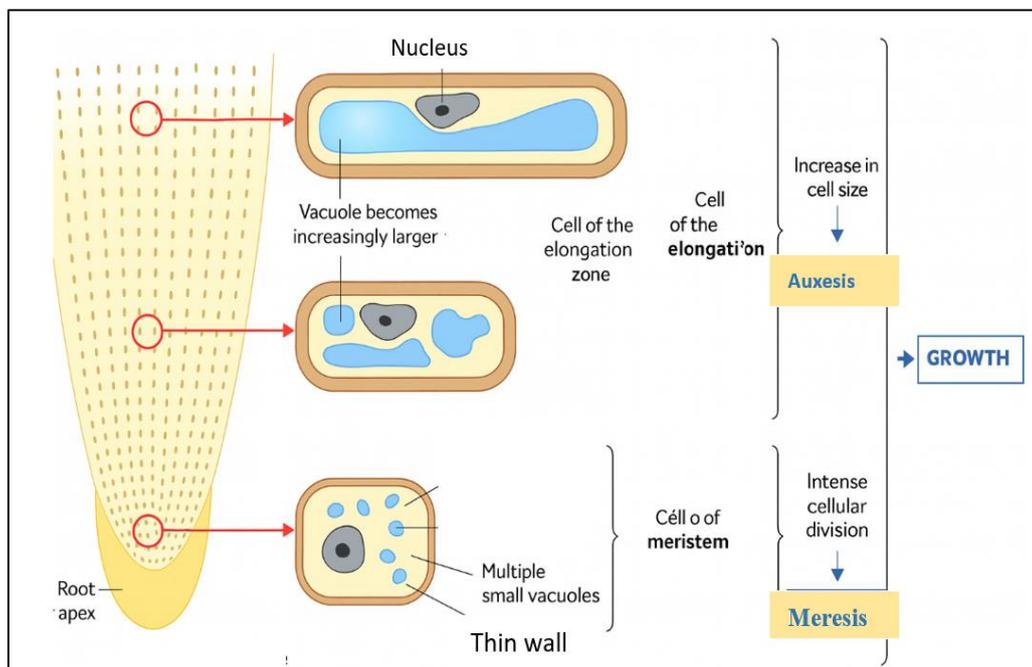


Figure 5 Meriosis and Auxesis

Growth of the different parts of the plant

Rhizogenesis

Ensured by the apical meristem located beneath the root cap. The cells derived from it elongate in the elongation zone, which is located a few centimeters behind the apex. It is in this zone that tissue differentiation occurs.

Caulogenesis

During seed formation, the embryo bears a small stem (hypocotyl) provided with a rudimentary terminal bud (plumule), as well as a radicle, which is responsible for the development of the root system.

The stem

The stem is composed of a series of units called phytomeres. These units consist of internodes and nodes, from which leaves emerge. An axillary bud is found at the base of each leaf.

The organization of the aerial parts depends on the activity of the buds. In perennial plants, bud activity continues throughout the life of the plant. The apical bud, in particular, breaks dormancy each spring, ensuring stem growth and branching.

The leaf

Leaves are inserted at the nodes, which bear an axillary bud. Lateral branches develop from this bud. The formation of leaves and their corresponding leaf segments mainly involves the peripheral zone (PZ) of the bud. This process involves changes in the frequency and polarity of cell divisions

Factors of growth: Phytohormones

Plant hormones, also called phytohormones, are natural organic substances that influence all physiological processes involved in plant growth, differentiation, and development. They confer on plants the ability to adapt to variations in environmental conditions. Phytohormones control and coordinate both the initiation and the growth and differentiation of newly formed organs.

The two cellular mechanisms responsible for growth are cell division and cell elongation. These two mechanisms are very tightly regulated by the combined action of several so-called growth phytohormones, including auxins, cytokinins, gibberellins, and brassinosteroids.

Other phytohormones, such as abscisic acid, jasmonic acid, ethylene, and salicylic acid, are more often classified as stress phytohormones because of their roles in responses to biotic or abiotic stresses. Nevertheless, these hormones can also be involved in the regulation of essential developmental stages, such as fruit ripening in the case of ethylene or pollen development in the case of jasmonates.

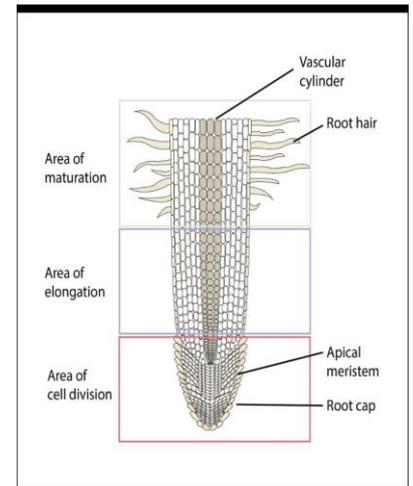


Figure 6 Rhizogenesis

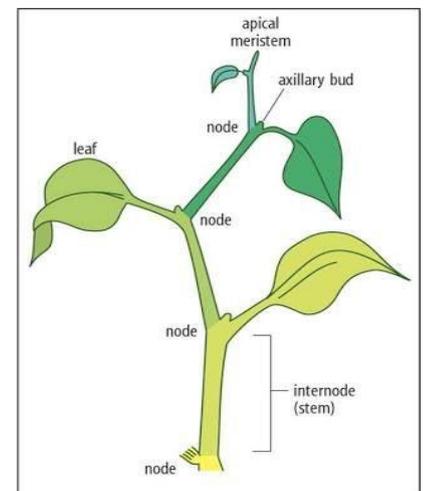


Figure 7 Construction of the aerial part

General overview of phytohormones

Auxins

Auxins are mainly synthesized in young leaves and are actively transported to other plant tissues, where they coordinate growth and facilitate responses to environmental variations.

They:

- stimulate elongation of coleoptiles and stems, and promote phototropism and gravitropism;
- play an important role in the initiation and formation of the primary root, lateral roots, and adventitious roots.

Auxin production is inhibited by zinc and phosphorus deficiency.

Cytokinins

Cytokinins are preferentially produced in the roots, from where they migrate to different plant organs. They promote cell division and cell growth.

They:

- play an important role in germination, stimulate cell division, and activate the initiation of leaves and stems;
- promote the expansion of leaves and cotyledons as well as nutrient transport;
- inhibit leaf senescence and allow the release of seed dormancy.

Water stress, high temperatures, and waterlogged (hydromorphic) conditions inhibit cytokinin production in roots and their transport to aerial parts.

Gibberellins

Gibberellins affect:

- the induction of germination through the production of enzymes;
- the induction of flowering;
- the growth of stems (elongation of internodes), shoots, and fruits;
- the functioning of meristems.

Stress hormones

Ethylene

Ethylene:

- promotes fruit ripening, leaf senescence, and organ abscission;
- inhibits cell division as well as gravitropism of stems and roots.

Ethylene production is stimulated by fruit ripening, leaf and flower senescence, and water stress. It is inhibited by light and anaerobic conditions. Ethylene synthesis occurs in meristems, young leaves, and the embryo.

Absciscic Acid (ABA)

Absciscic acid:

- promotes stomatal closure, leaf senescence, bud dormancy, and the formation of tubers and adventitious roots;
- inhibits seed germination, axillary bud growth, stem and root elongation, and floral initiation.

Water stress, excess water, mineral nutrient deficiency, and salinity increase the production of absciscic acid.

IV. Flowering

Flowering is the biological process of flower development. It is controlled by external environmental factors (light, humidity, temperature) as well as endogenous factors (genetics, phytohormones, age, etc.).

There are different types of plants:

- Annual plants: flower once and then die;
- Biennial plants: flower every two years;
- Perennial (or pluriannual) plants: flower every year.

Floral parts

- **Sepals** (together forming the **calyx**): usually green; they are the outermost floral parts and protect the flower bud.
- **Petals** (together forming the **corolla**): very often colored.
- **Stamens** (together forming the **androecium**).
- **Carpels** (together forming the **gynoecium**).
- **Floral peduncle**: vegetative organ connecting the flower to the stem.
- **Bracts**: small-modified leaves located in the axils of flowers.

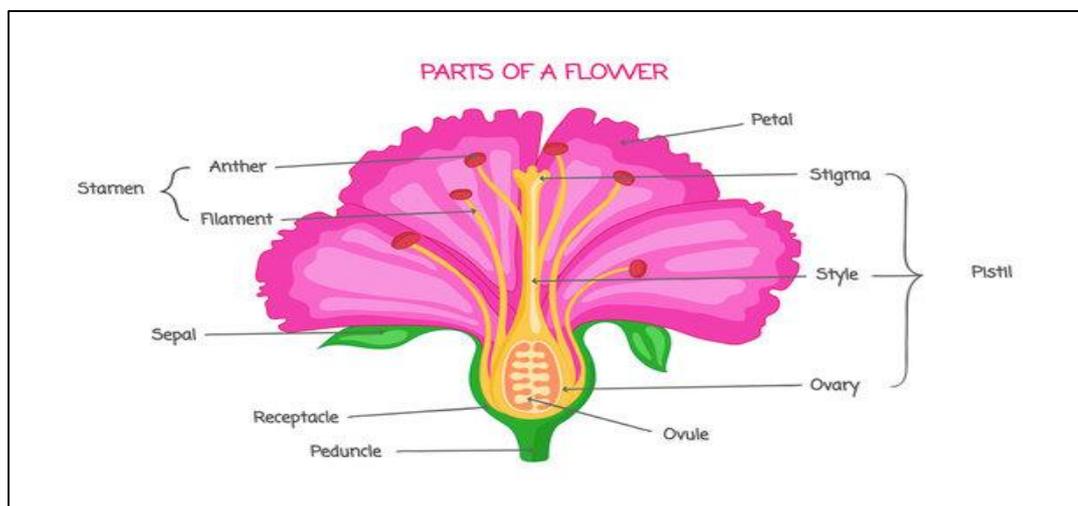


Figure 8 Floral parts

Types of flowers

- **Hermaphroditic plants:** each flower is bisexual, composed of both a pistil and stamens.
- **Monoecious plants:** male and female organs are located in different flowers borne on the same plant.
- **Dioecious plants:** male and female organs are borne on different plants.

Transition from the vegetative state to the floral state

The flowering process begins with floral induction, a preparatory stage during which certain plant organs, under the effect of external stimuli, send a flowering signal to the meristem, causing it to shift from a vegetative developmental program to a reproductive developmental program.

Floral evocation, which corresponds to the activation of the dormant meristem, is the period during which the architecture of the apex is modified in preparation for the differentiation of primordia. This stage is also characterized by an acceleration of energy metabolism and an increase in mitotic activity.

During **floral initiation**, the primordia of floral organs (perianth and sexual organs) differentiate. In other words, the vegetative bud becomes a floral bud, which explains the swelling of the bud. This stage is followed by flowering onset, marked by the development of floral organs, and finally by flower opening, accompanied by anther dehiscence. These last two processes together constitute flowering proper, also known as anthesis.

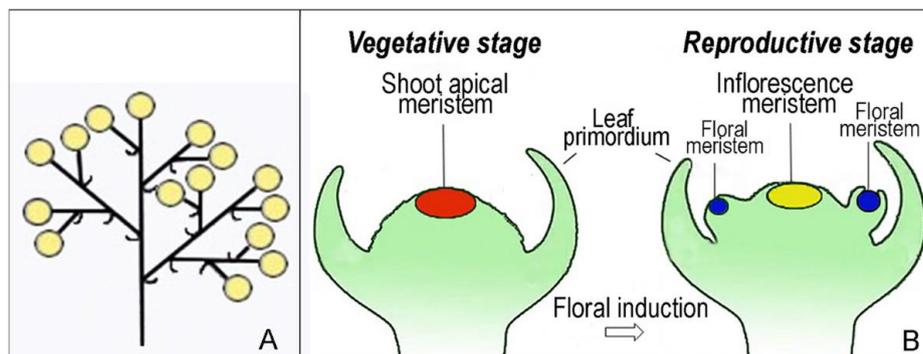


Figure 9 Transition to the floral stage

Control of flowering

Flowering depends on internal parameters (age, size, maturity, etc.) and external parameters (environmental conditions). In particular, the seasonal cycle, temperature, light, and stress can either promote or inhibit flowering.

The two most important factors are:

- **Cold treatment: vernalization**
- **Light exposure: photoperiodism**

1. Vernalization (cold treatment)

Vernalization is the process by which exposure to low temperatures for a certain period promotes the ability of a plant to flower. It is a physiological requirement in many species, especially biennial and winter annual plants.

- It occurs mainly in seeds, young seedlings, or apical meristems.
- Low temperatures (generally between 0–10 °C) must be applied for a specific duration.
- Vernalization does not directly cause flowering but induces floral competence, allowing the plant to flower later when favorable conditions return.
- After vernalization, flowering usually requires additional factors such as long days or suitable temperatures.

2. Photoperiodism (light exposure)

Photoperiodism refers to the response of plants to the relative length of day and night, which regulates flowering.

Plants perceive photoperiod through photoreceptors (mainly phytochromes) located in the leaves. The leaves then produce a flowering signal (historically called florigen) that is transported to the apical meristem.

V. Fruiting (fructification)

Fruits result from the transformation of the ovary of a fertilized flower; they contain seeds, which originate from the development of ovules. The development of the ovary, from its formation in a floral bud to the ripe fruit, is generally continuous when the flower has been pollinated.

In contrast, if the flower has not been pollinated, ovarian growth stops abruptly, and the unfertilized flower detaches and falls.

There are, however, some relatively rare exceptions: certain plants produce fruits without pollination. This phenomenon is known as parthenocarpy, which results in fruits that are completely seedless. This is the case in some species selected and cultivated by humans, such as seedless oranges.

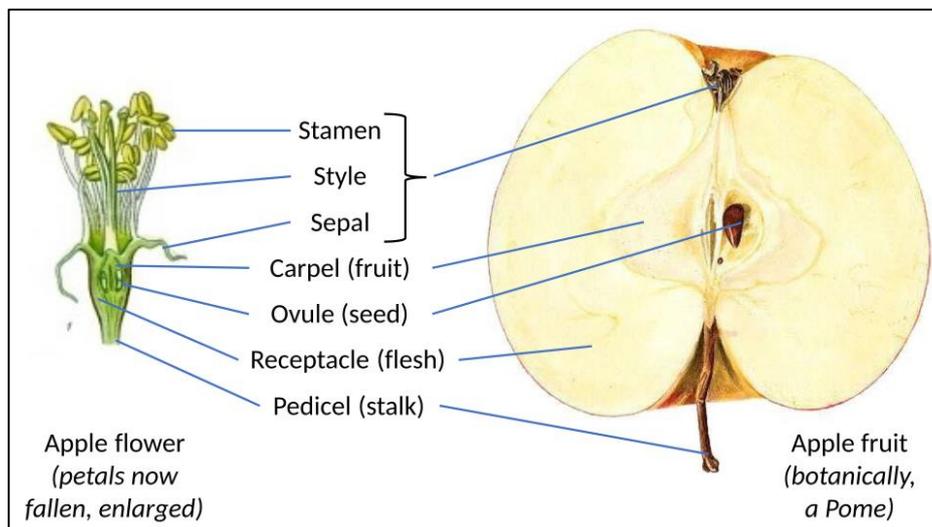


Figure 10 Transformation of a flower's ovary into a fruit

Types of fruits

A fruit may develop into a **succulent structure**, giving rise to **fleshy fruits**, such as:

- **Berries** (grape, banana, tomato, etc.);
- **Drupes** (olive, peach, cherry, etc.).

Alternatively, the fruit may develop into a lignified structure at maturity, in which case it is classified as a **dry fruit**.

Dry fruits can be:

- **Dehiscent**, meaning they open at maturity to release the seeds, such as:
 - **Follicles** (peony, magnolia, etc.);
 - **Legumes (pods)** (pea, fava bean);
 - **Siliques** (cabbage, radish, rapeseed).
- **Indehiscent**, meaning they do not open at maturity, such as:
 - **Achenes** (sunflower, buttercup);
 - **Caryopses** (grasses);
 - **Samaras** (maple, ash).

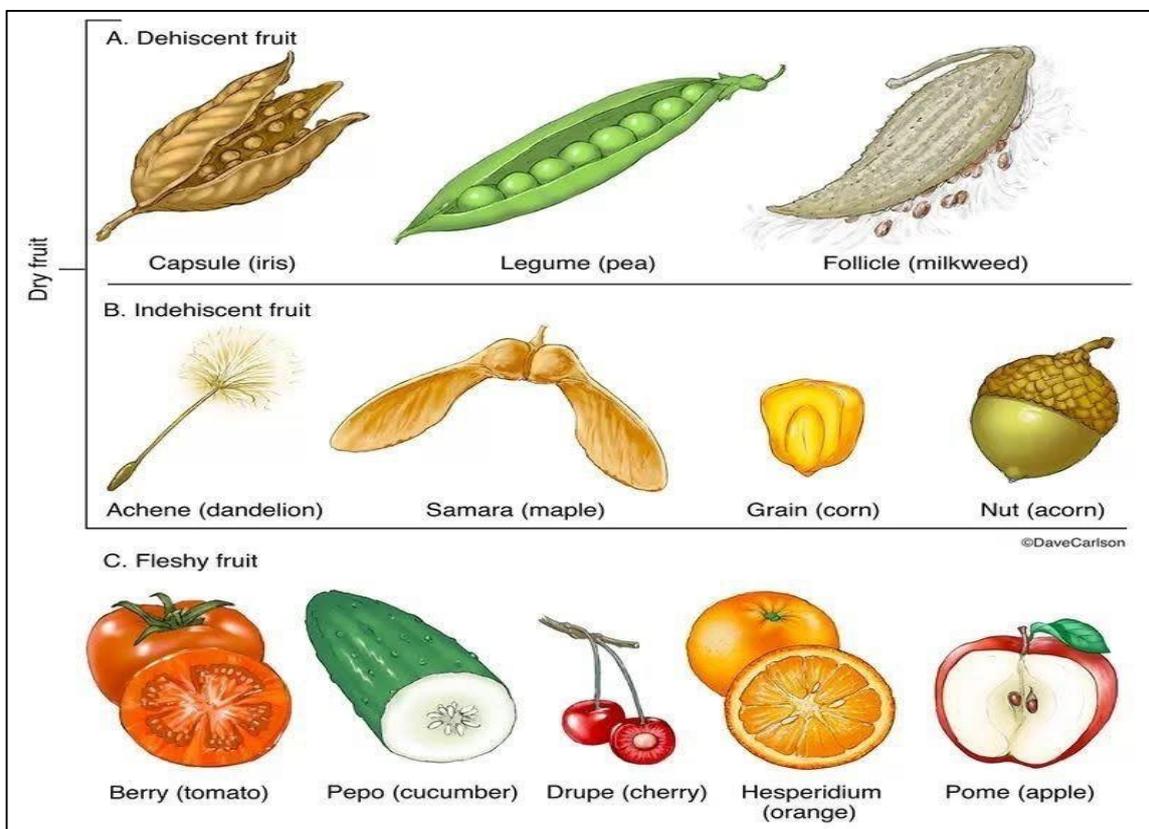


Figure 11 Types of fruits