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Université de Tissemsilt
Faculté des Sciences et de la Technologie

Polycopié de cours

Physiology of fruits development

Au profit des étudiants de Master 1 Production végétale

Filière : Sciences agronomiques

Domaine : Sciences de la nature et de la vie

Réalisé par : Dr. ZEMOUR Kamel

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Summary

Introduction

Introduction

The production of different fruits in the world exceeded one billion tones in 2017. This prodution depends on geographical areas, consumption and growing traditions.

The fruit is the result of the transformation of the flower after fertilization. The resumption of growth mainly concerns the female part (carpels). A complete flower consists of sepals, petals, stamen, and carpels. The sepals are the bud coverings, the petals are the petals, the stamen is the male part or parts, and the carpels (a.k.a., pistils) are the female part or parts. A carpel in turn consists of what is known as the stigma, style, and ovary, and the ovary contains one or more ovules. The ovules become the seeds and the ovaries usually will be what gives rise to the bulk of the fruit.

Botanically the fruit is a reproductive organ of a flowering plant, such a character for angiosperm. It can be edible or not (Inedible). It corresponding to the fertilizated ovary (or ovaries), that protect seed development and enssure its dispersal. Indeed, physiologically, seed is the organ for propagating plant species.

Besides the typical fruit components, this organ is a main and dominant source of phytochemicals that take significant place in human diets. Recently, the quality of fruits and vegetables has also attracted more attention, especially under the serious circumstances of the global COVID-19 pandemic, which is forcing people to rethink their lifestyles and diets. There is the recognition that the fruits can provide and are a good source of many energy, vitamins (vitamins A, C, and E…etc), minerals (calcium, phosphorus, magnesium…etc), fibers, pigments (carotene, xanthophylls, anthocyanins etc.), flavonoids, phenolics (Figure 1). In fact, these compounds (pigments and other phytochemicals) highligh antioxidizing capacity protective effects against several chronic disease, cancers, cardiacvascular diseases and other age-related problems. However, the amount of these coumpounds vary depending species, and within same species, this variation is related to the environmental conditions and production system (Figure 1).

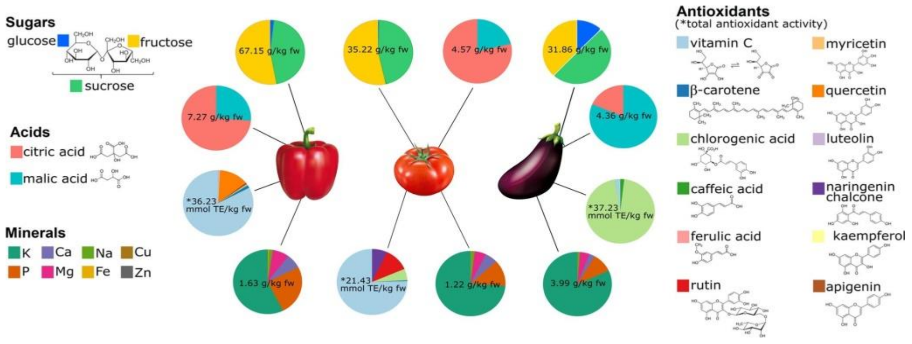


Figure 1. The main sources dieatry of fruit and vegetable

In nature, fruit is consumed from a wide range of plants, e.g. Rutaceae (citrus), Rosaceae (apples), Solanaceae (tomato), Cucurbitaceae (cucumbers), Ribaceae (berries), Vitaceae (grapes) and other species.

The fruit is a mature ovary (or ovaries) of one flower (or several flowers), developed after fertilization. After this stage, all floral organs naturally separate or detach, except the fertilized ovary which develops and becom a fruit. Sometimes, floral structures also develop, to become as fruit accessory. For exemple, Strawberry is a fruit resulte from the development of the floral receptacle (Figure 2). As well, a fruit may be produced without fertilization = parthenocarpic fruit.

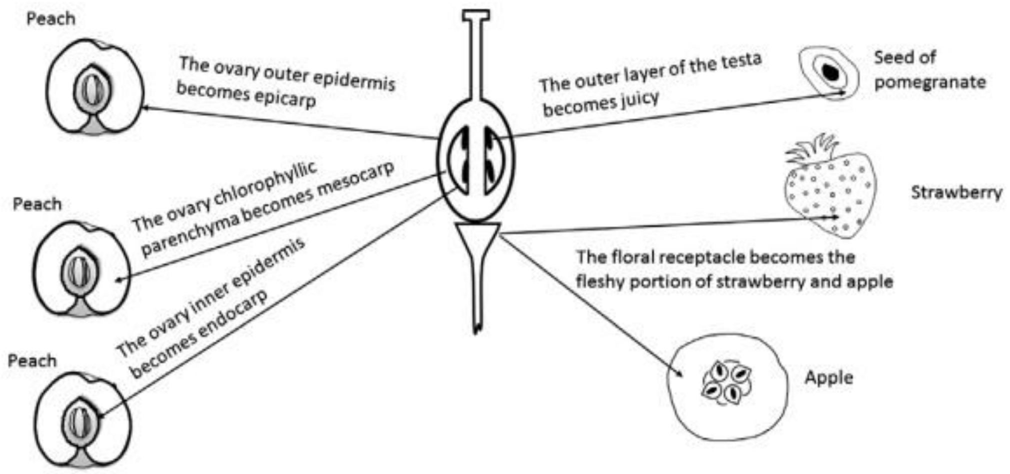


Figure 2. Fruit developement after fertilizeation and without fertilization of a ovary

1. The morphological composition of the Fruit

The fruit generally is made of two primary sections: pericarp and seed.

1.1. **The Pericarp**

The pericarp covers the fruit (dry or fleshy) and protects it from damage. It is composed of three layers not easily be recognized or be separated in dry fruits. However, if the pericarp is fleshy these layers may be easily distinguishable into epicarp, mesocarp, and endocarp (Figure 3).

1.1.1. The Epicarp

The epicarp or exocarp forms the outermost layer of the tough outer skin of the fruit. In the case of citrus fruits, the epicarp is called flavedo (Figure 4).

1.1.2. The Mesocarp

Typically the mesocarp is the edible part of the fruit and is the fleshy middle layer of the pericarp between the epicarp and the endocarp (e.g. peach). In the case of citrus fruits, this layer is called albedo. The epicarp (or flavedo) with the mesocarp (or albedo) is generally the nonedible part of the citrus fruit.

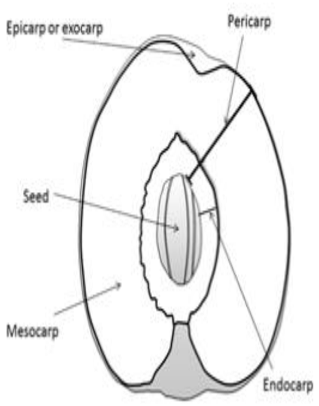


Figure 3. Parts of fruits

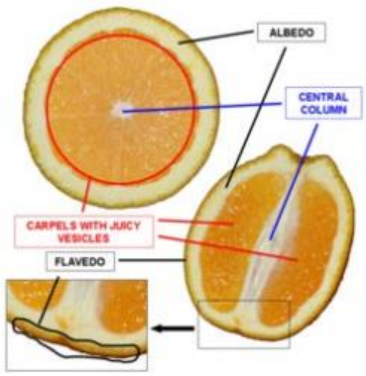


Figure 4. Citrus fruit section

1.1.3. The Endocarp

The endocarp, as the innermost layer, surrounds the seeds. It is may be inedible as in drupes (also called stone fruits) such as peaches, and cherries, or may be edible e.g. citrus.

1.2. The seed

The seeds are derived from fertilized ovule. Its coat has two layers, the outer testa and the inner tegme. Thus, the embryo is made up of radicle and plumule. Generally, ovule wall becomes the seed coat (Figure 5).

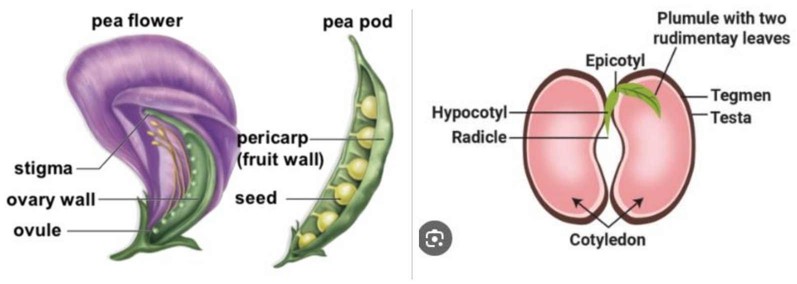


Figure 5. Seed formation from the flower and its composition

2. Fruit classification

Botanically, a fruit is derived either from a flower or an inflorescence. It can be classified into three major categories based on the number of ovaries and flowers involved in its development: simple, aggregate, and multiple or composite (figure 6).

- Simple fruits are derived from one flower of a simple or compound ovary.
  - A simple ovary is made up of a simple carpel.
  - whereas a compound ovary is made up of two or more simple fruit.

When Two types of transformations occur, it result consequently two types:

1) the cells develop thick walls which become lignified (sclerification). The organ becomes hard = dry fruit.
2) the cells gel their walls which become hydrophilic; intercellular cohesion weakens. A more or less melting pulp is formed = fleshy fruit.

The first rang (Dry fruits) may be either dehiscent or indehiscent. Dehiscent fruits are those fruits whose structure is split in order to release their mature seeds, a phenomenon named dehiscence, which is not observed in indehiscent fruits.

The second rang : Simple fleshy fruits are characterized by a broad range of sizes, shapes, and colors. Moreover, different species presents unique flavor characteristics that are of pivotal importance in several processes. It includes the berries (such as grapes and tomatoes), drupes (such as peaches, cherries, apricots and olives), pomes (such as apples and pears). Simple dry dehiscent fruits include the legumes (such as peas and peanuts). Simple dry indehiscent fruits include the achenes (such as caraway and sunflower) and balausta (such as pomegranates).

- Aggregate fruits develop from a single flower of numerous ovaries such as strawberries.
- Multiple fruits or infructescences develop from inflorescences which are clusters of many separate flowers of individual ovaries, such as fig, pineapple.
- Berries develop from compound ovaries, and possess a fleshy endocarp, and usually contain many seeds.

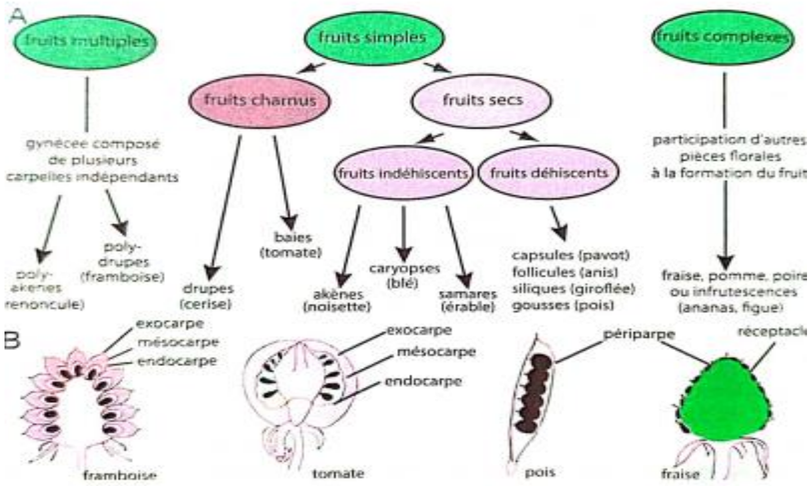


Figure 6. Fruit classification

3. Fruit quality as depended by shape, size, mass and softness

In general, the fruit shape is important quantitative trait that plays a role in determining its quality. While environmental conditions such as climate, soil, and cultivation methods can affect plant growth, the genetic makeup (DNA) of the plant has the greatest impact on the phenotypic variation of fruits.

The transformation from their wild characteristics that made fruits inedible to non-toxic, attractive and edible fruits for human consumption involved alterations through generations of domestication and selection, e.g. Corn (Figure 7).

Figure 7. Domestication of Corn

Currently, the fruit volume of the different varieties is bigger compared to their wild-type. The domestication present the main process which involve this variation.
For exemple, *Solanum lycopersicum* var. cerasiforme (wildtype) weighs only a few grams with two *loci*, while some of the domesticated tomato weighs as much as 1kg with manny *loci* (Figure 8).

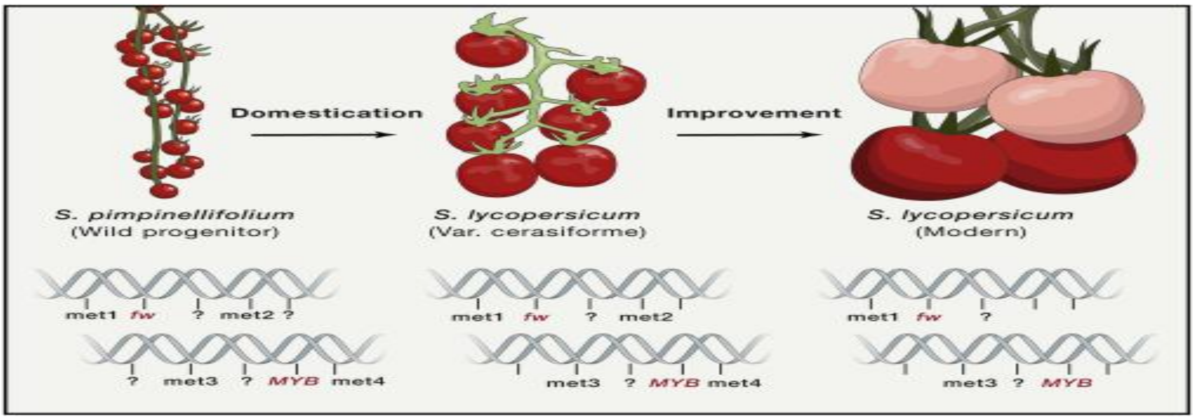


Figure 8. Comparaison between the tomato varities along the time after domestication

Actually, advancements in biotechnology and the identification of quantitative trait loci (QTL) have enabled researchers to point up the genomic regions and especially genes responsible for desirable fruit phenotypic traits.

The softening of fleshy fruits is one of the key determinants of quality and a primary target for manipulation to enhance postharvest storage. A complex structure consisting primarily of polysaccharides, surrounds plant cells and provides structure and stiffness. Cell walls consist of a rigid layer of sugars, called polysaccharides. A molecule composed of long chains of sugars, such as glucose, joined together to form linear or ramified chains, which cover the plasma membrane of each cell (Figure 9).

Softening of the fruit occurs due to a combination of structural changes to the cell wall and a reduction in turgor pressure. The initial changes in the cell wall at the onset of ripening involve the dissolution of the pectin matrix that makes up the middle lamellae, which form a connective layer between adjacent cells. Subsequently, alterations occur in the structure of the cell wall polysaccharides.

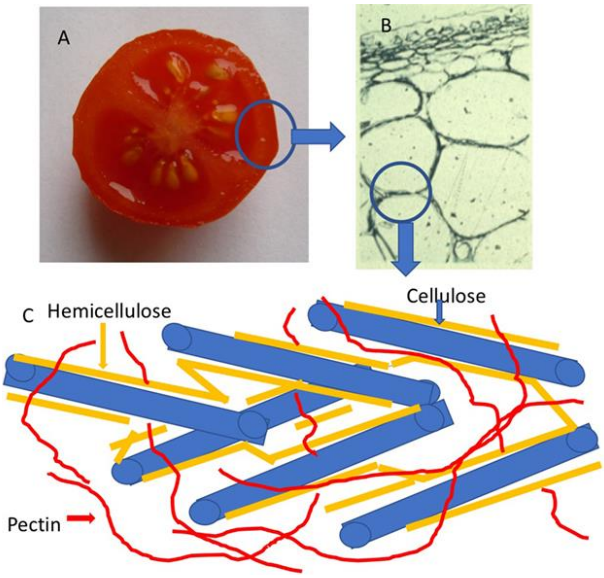


Figure 9. Plant cell wall structure (A). Section of cell wall using microscope (B). The cells can be seen to be surrounded by a polysaccharide cell wall, which is seen in the blue circle. The cell wall is composed of three main components, called cellulose, hemicellulose, and pectin (C).

4. Fruit nutrition and firmness

Firmness is an indicator of fruit ripeness. This feature is affected by various factors such as structural integrity of the primary cell wall, polysaccharide accumulation, turgor pressure, temperature, crop management and mineral nutrition. A positive correlation between dry matter and total soluble compounds and fruit firmness has been reported for kiwifruit.

- *Nitrogen :* An excessive or late nitrogen dosage makes the fruits less firm, more fragile during harvest and consequently leads to complications during post-harvest storage.
- *Phosphorus* : As a key role in producing more cells in fruit during cell division, phosphorus helps increase fruit size and firmness. It is therefore particularly important that the intakes are not limiting during the 6 weeks following flowering.
- *Calcium* : As has a role in the cohesion of cell membranes, calcium increases the duration and quality of preservation of fruits, in particular the reduction of bruising and internal browning. The higher the calcium value in the fruit, the firmer its flesh. Calcium nitrate applied to the soil improves the firmness of the fruit.

Pectins are the most important components of the primary cell wall that contribute to the texture and quality of the fruit. Cell wall changing during the ripening stage is a complex process. It's about an hydrolysis of cellulose and hemicelluloses, solubilisation and depolymerisation of the pectin polysaccharides, and rearrangements of their connection.

5. Pollination

Pollination is a crucial step for fruit set and fruit growth of most of species. The transfer of pollen to the stigmatic surface (e.g bees) followed by an adhesion of pollen grains to the stigmatic surface is the first step of successful pollination. After that, the pollen hydrates and germinates and then develop pollen tubes which penetrate the stigma and grow down the style to come into contact with an ovum inside the ovary.

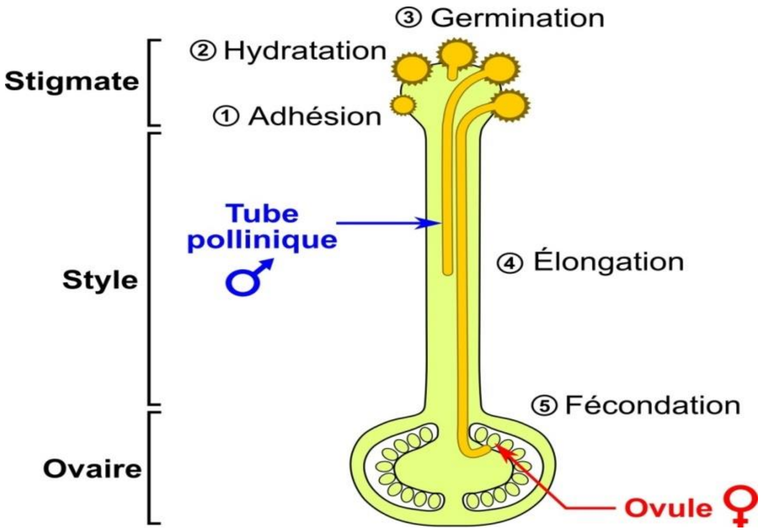


Figure 10. Pollination steps

As the pollen tube grows, the reproductive nucleus of the pollen splits into 2, in species for which this splitting has not already taken place during the maturation of the pollen grain. Having reached the ovum, the pollen tube penetrates, through a pore called the micropyle, to the embryo sac.

Figure 11. The pollen splits into 2

The two antherozoids will fuse, one with the oosphere or female gamete, the other with the central nucleus of the embryo sac.

- An egg is born from the first of these two fertilizations; it will generate thereafter, while dividing, a mass of cells; the seed embryo;
- the central nucleus of the embryo sac will give birth, after having received the second antherozoid, to an albumen egg whose division is at the origin of the nourishing tissue stored in the seed: the albumen.

The production of sufficient quantities of viable (autogamy) and compatible pollen and adequate pollen vectors (allogamy) are the main factors influencing pollination.

N.B : This part is consolidated by a video which perfectly illustrates the stages of pollination and fertilization *(https://youtu.be/78PzI9exMBo)*

6. Fruit set

Fruit set is a transition phase of the ovary from the flower which occurs after successful pollination and fertilization (Figure 12). Without fertilization, the carpel is unable to develop into fruit, no division takes place in the mesocarp and the endocarp does not lignify, except in the case of parthenocarpy, the fruit develops without pollination or fertilization. Indeed in some species, we can observe deformed fruits by the development of a portion of the fruit around the fertilized seeds. This suggests that the seeds communicate with the fruit tissues, via phytohormones of growth which they produce in large quantities, to ensure coordinated development.

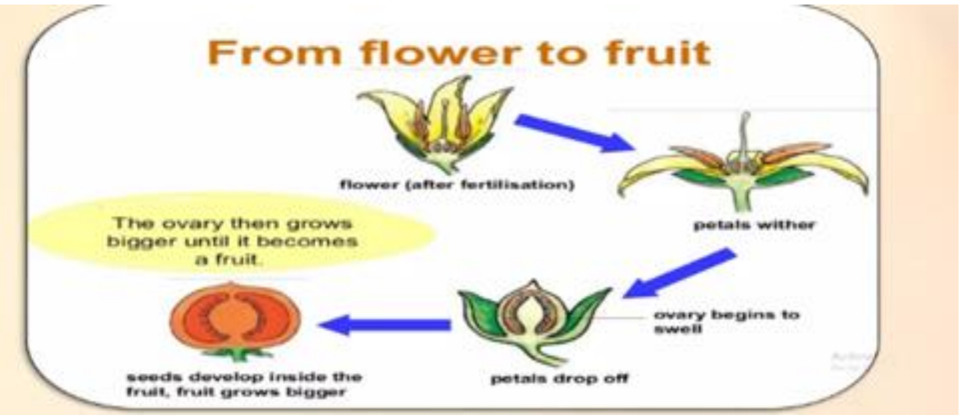


Figure 12. Fruit set step

Pollen germination

Generally, pollination is an essential process for fruit set and for fruit growth consequently. Pollen source is considered to be one of the most factors controling the fruit set. The density of pollen on the stigma is positively correlated with the growth of the pollen tube and fruit rate.

Pollen quality is important to growers and genetic improvers. It is not easy to measure pollen germination aptitude under natural (*in vivo*) conditions; however *in vitro* test is used to indicate pollen viability using lactophenol blue (Figure 13). In general, there is a linear relationship between pollen viability and germination ability in many fruit species.

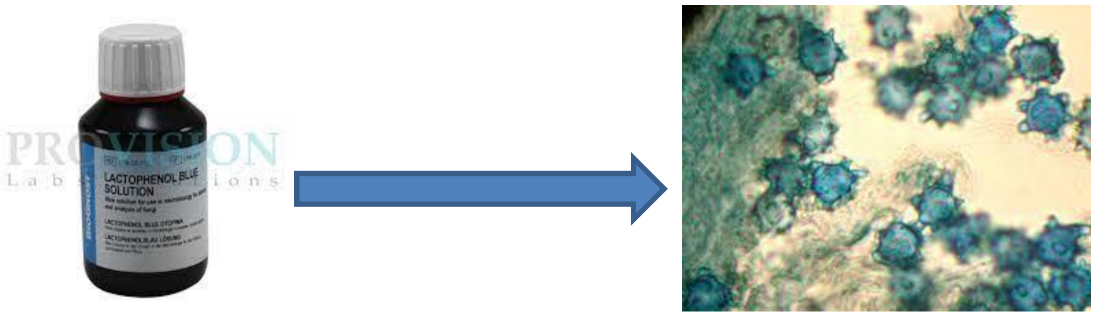


Figure 13. *In vitro* test of pollen viability

Practical control of pollen fertility in vitro

To carry out germination tests, Kobel (1938) recommends operating as follows :

- ✓ Harvest open flowers from a tree in full bloom but whose anthers (Part of the stamen that contains pollen) are still closed.
- ✓ Place them in the dry atmosphere of the laboratory, on black paper; the stamens open, the pollen is collected and mixed carefully to obtain a homogeneous sample.
- ✓ In a humid room, sucrose solutions at 5, 10 and 15% are prepared and droped on a slide. Using a fine brush, a trace of pollen is applied to the liquid.
- ✓ The slide is luted on the humid room with petroleum jelly (vaseline) and stored at 15 to 20°C. After 24 hours, the preparations can be examined. The germinated grains (germination capacity), and the length of the pollen tubes (germination energy) are mesured.

The use of phytohormones such as auxins, cytokinins, and gibberellins (see the details in the the section of phytohormones) could enhance fruit set.

These growth regulators can be provided naturally by the plant itself or by exogenous application. Other substances like thidiazuron, CPPU, Prohexadione calcium (P-Ca), and some micronutrients, especially the boron increases fruit set for exemple in apple.

7. Factors influencing the fruit set

The fruit set may be affected by two categories:

- Internal factors : Pollination process (Pollinating agents and Pollinizers), Sex distribution, Defective sex organs, Stigmatic receptivity, Incompatibility, Non-viable pollen.
    - Sterility: non-functional reproductive organs: malformed pistil or stamen, non-functional pollen or ovum.
    - Self-incompatibility: Lack of ability for a plant to set seed (seeds) when self-pollinated, although it can set normal seed through cross-fertilization. Its pollen is active on another plant.
- External factors: temperature, humidity, wind, light and nutrition…etc

Light

- Affects fruitfulness by its effect on photosynthetic
- Low light intensity or its duration can reduces the carbohydrates reserves.
- Poor light promote fruit abscission

Temperature

- the cold affects the activity of insects of pollination (Bees). Bees only forage when the temperature exceeds 18°C and in a particularly active way around 21°C, they would then be able to visit 10 to 15 flowers/minute.
- Also affects the growth rate of pollen tubes, pollen viability and fertility
- High temperature accelerates anthesis and shorten the bloom period
- Above 32°C, dessication of the stigmate surface and more deterioration of embryo sac occurs.
- Low temperature extends flowering period
- Low temperature kills flower buds (Frost)
- Low temperature decrease viability of pollen

Wind

- The wind plays little role for most species as a pollen transport agent. It is even sometimes harmful by drying the stigmas and slowing down the activity of the bees. Any protection against strong winds is therefore favorable to pollination.

Soil moisture statut

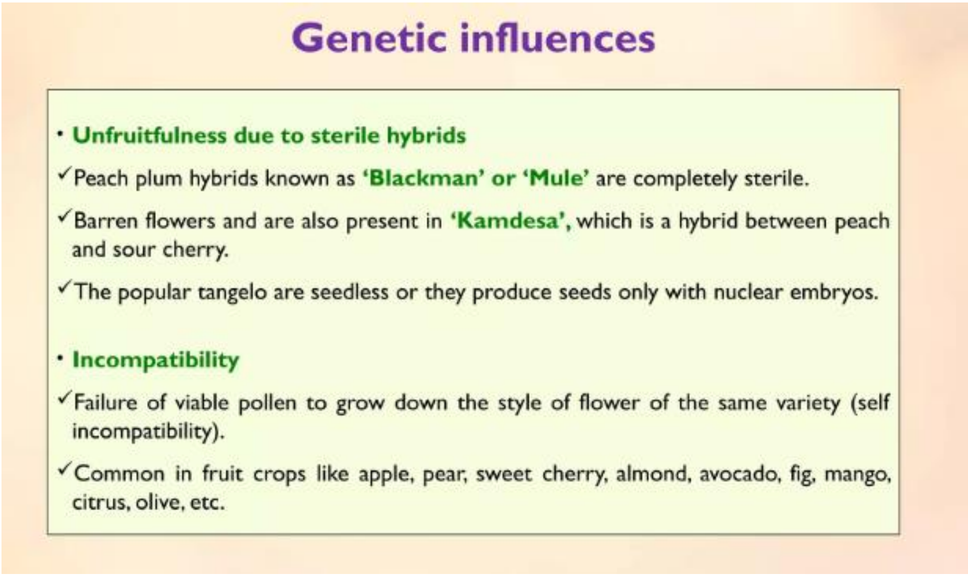
- Soil moisture stress causes pollen abortion

Chemicals and pesticides

- Can kill bees
- Cause abortion of flowers and lossing fruits
- Sprays can affect receptive stigmatic surface, showed varying degree of injury and range from minor surface wrinkling to degeneration of stigma papillae

Nutrition

- An adequate and balanced supply of all mineral nutrients is critical for optimumu fruit set
- Phosphorus, boron, Zinc, and molybdenum effect fruit set directly because they have various roles in pollen development, pollen germination, and pollen tube growth



8. Fruit Development stages

8.1. Cell devision

Growth is caused by cell division, or mitosis, and cell lengthening. The growth of an organ is the result of increasing the number of cells forming it and the size of individual cells. Cell multiplication and reproduction generally has an exponential rhythm (figure 14).

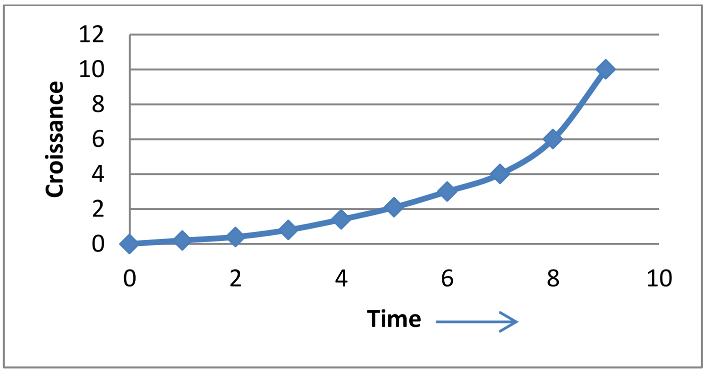


Figure 14. Relation between Croissance and time (Exponential fonction)

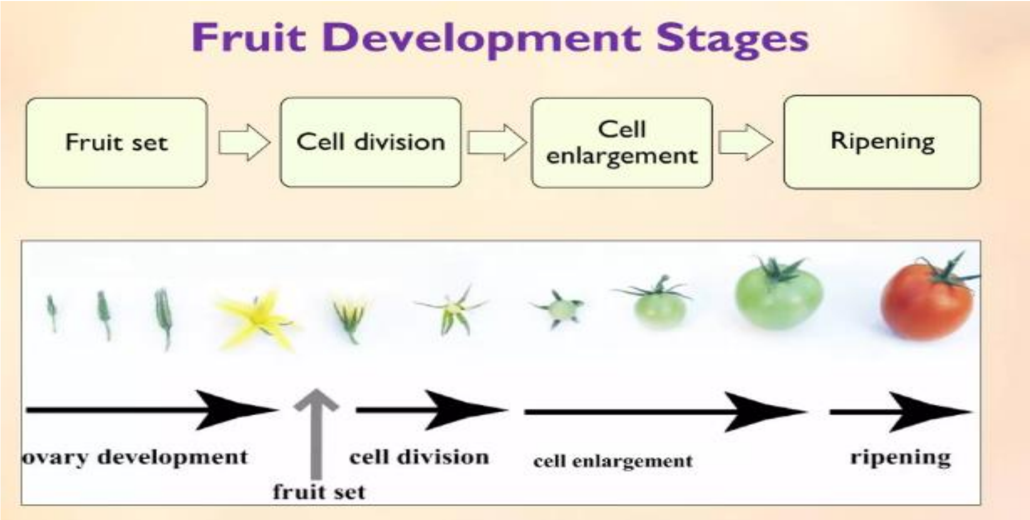


Figure 15. Fruit development of tomato

Early cell division Initiation happens following pollination: a phase that take a few days to more than a week (tomato, grape, and strawberry). After this step, the fruit growth is principally due to cell expansion (Fgure 15, 16).

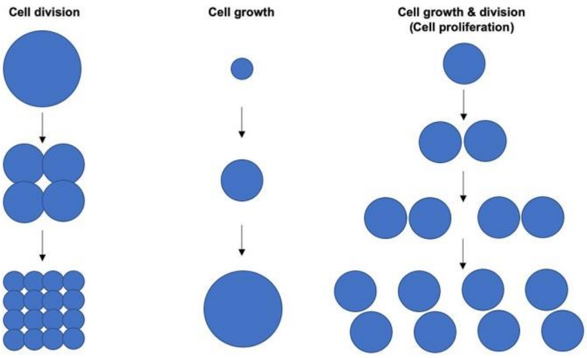


Figure 16. Cell division and growth model

In the case of fleshy fruits, following fruit set, the cell division phase continues until 7 to 10 days after fertilization. The cell divison is particularly active in the pericarp and placental tissue that surrounds the seeds. Anticlinical divisions (division plane perpendicular to the surface of the fruit) increase the number of cells per layer, while preclinical divisions (division plane parallel to the surface of the fruit) increase the number of cell layers.

Divisions of the cells of the epidermis continue until ripening to ensure the increase in volume of the fruit during the cell expansion phase, mainly in the mesocarp. The cytokinins produced by the seeds have been shown to condition the mitotic activity of the pericarp.

The importance of phytohormons such as auxin and GA during fruit growth has been previously revealed for many plant species. Indeed, In young cucumber fruit, an increase in auxin levels after fruit set leads to greater rates of cell division. Moreover, apple studies have indicated that auxin is the primary hormone influencing fruit size. Uncertainly, Cell elongation can take a more time than cell division (Figure 17).

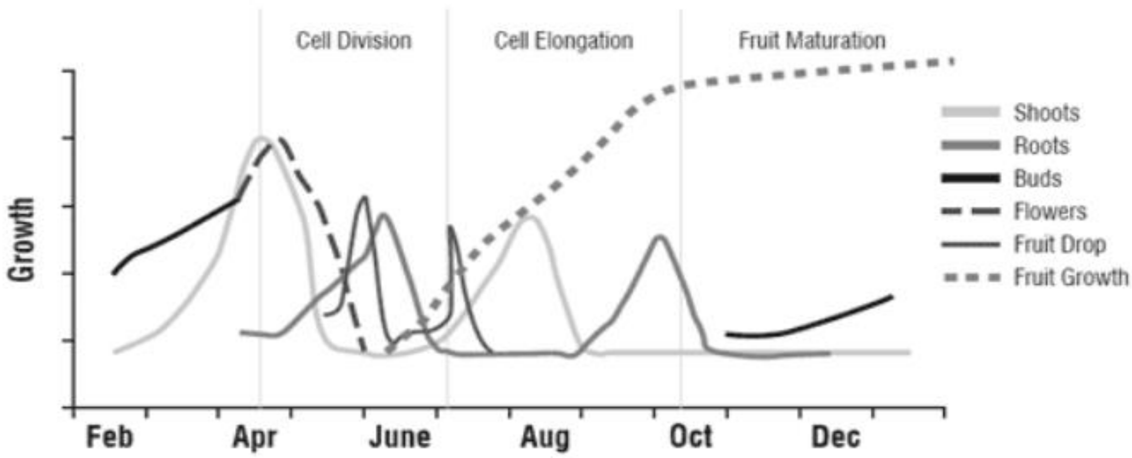


Figure 17. Phenological cycle of citrus including fruit development

8.2. Cell expansion

After this phase of cell division, the growth of the fleshy fruit is then mainly controlled by cell expansion which leads to the size of the fruit. In tomatoes, this phase extends from the second day after fertilization until the mature green stage (about 30 to 40 days later).

Expanding cells are characterized by an increase in the size of the vacuoles, due to the massive accumulation of sugars and organic acids which creates a pressure gradient and an influx of water allowing cell growth. These cells also show an increase in their DNA content. This variation in the diploid level is called polyploidy. This process, common to most eukaryotic organisms, results from the ability of cells to alter their classic cell cycle, to enter a cycle of DNA endoreduplication.

8.2.1. DNA endoreduplication : *Replication of ADN from the nucleus without division of cell itself.*

The phenomenon of endoreduplication would be one of the factors allowing the increase in cell size. Indeed, a positive correlation between the amount of DNA in the nucleus and cell size has been shown in many plant species.

8.2.2. Parthenocarpic fruit development

Some fruits can develop without fertilization of the ovules, these are the parthenocarpic fruits. These fruits do not contain seeds or the seeds do not contain embryos. Under these conditions, only vegetative propagation allows the plant to reproduce. Seedless fruits are highly prefered, on the one hand for their ease of consumption and on the other hand for their keeping quality. Natural parthenocarpy is either obligatory (in sterile species) or optional (in fertile species, self-incompatible). Many tomato mutants are good examples of facultative parthenocarpy where seedless fruits will be formed only if fertilization is absent. In species developing parthenocarpic fruits, signal transduction pathways are altered such that one or more signals act constitutively to produce high levels of hormones before or in the absence of fertilization. Thus, parthenocarpy can be induced by factors inhibiting fertilization such as low temperatures, light or chemical treatments.

Figure 18. Fruit developed by parthencarpy (e.g. watermelon)

By applying gibberellins, auxins or cytokinins to the unfertilized gynoecium, it is possible to trigger parthenocarpy, for example in *Arabidopsis Thaliana*. However, the addition of a single phytohormone does not allow the full development of the fruit to its final size.

9. Fruit ripening

Ripening initiates after the seed maturation process. It is behind the different properties of fruits such as flavour, texture, and colour. During this stage, metabolites are converted into sugars and acids, while in senescing leaves metabolites are mobilized and delivered to the fruit.

For a long time, ethylene was the only phytohormone considered to be responsible for triggering ripening in climacteric fruits. Phytohormones such as auxin were supposed to be mainly involved in controlling the ripening of non-climacteric fruit. More recently, auxin has also been shown to play an important role in climacteric fruits. Indeed, it has been observed that a low level of auxin is necessary for the initiation of maturation and that abscisic acid (ABA) intervenes just after ethylene.

Indeed, fleshy fruit tissues undergo changes in organoleptic characteristics such as:

- colour,
- texture,
- texture softening,
- production of flavour volatiles,
- transformation in carbohydrate composition, organic acids and proteins..

The change in color of the fruit is the first visible sign of ripening. This phenomenon is due to the simultaneous degradation of chlorophylls and the massive accumulation of carotenoids such as lycopene and anthocyanins. The accumulation of carotenoids occurs during the transformation of chloroplasts into chromoplasts. It is governed by genetic, hormonal (ethylene) and environmental (light, temperature) factors. Flavonoids including anthocyanins mainly accumulate in the skin of the fruit and play an important role in determining the color of the fruit.

Regarding the flavor, it depends mainly on the content of organic acids and sugars in the fruit. The acidity decreases following the degradation of the organic acids of the sugars from the leaves and, on the other hand, following the metabolic degradation of the starch reserves (Figure 19A). The loss of firmness is marked by a climacteric peak in ethylene production and an increase in respiration (Figure 19B). These texture changes involve coordinated and interdependent activities of several proteins: polygalacturonase (PG), pectin methyl esterase, B-galacttosidases (B-G) and B-galactanases (B-G2), and xyloglucan endotransglycosylases (XEs), which involved in the modification of cell walls. PG is induced by ethylene and its activity is responsible for the depolymerization and solubilization of pectins. The role of B-G and B-G2 is to cleave the galactose residues of the pectins of the walls, which has the effect of increasing the porosity of the wall and thus facilitating access to other enzymes. Finally, XETs are involved in the cleavage of the cellulose/hemicellulose network and allow the rearrangement of hemicellulose fibers. They thus contribute to the relaxation of the walls (Figure 19C)

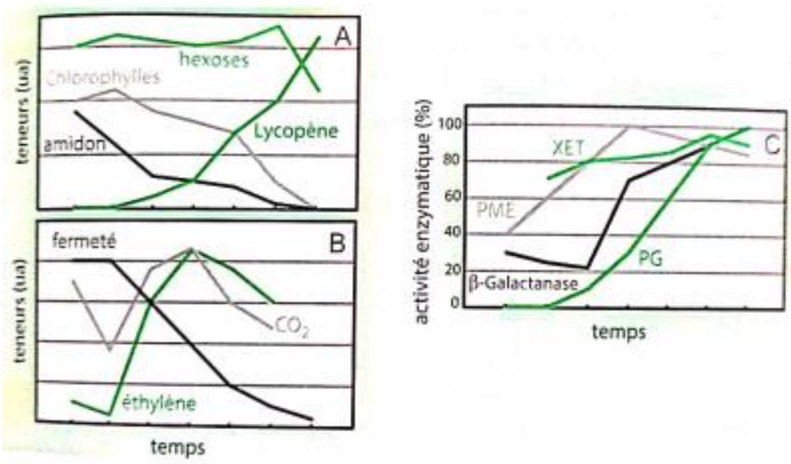
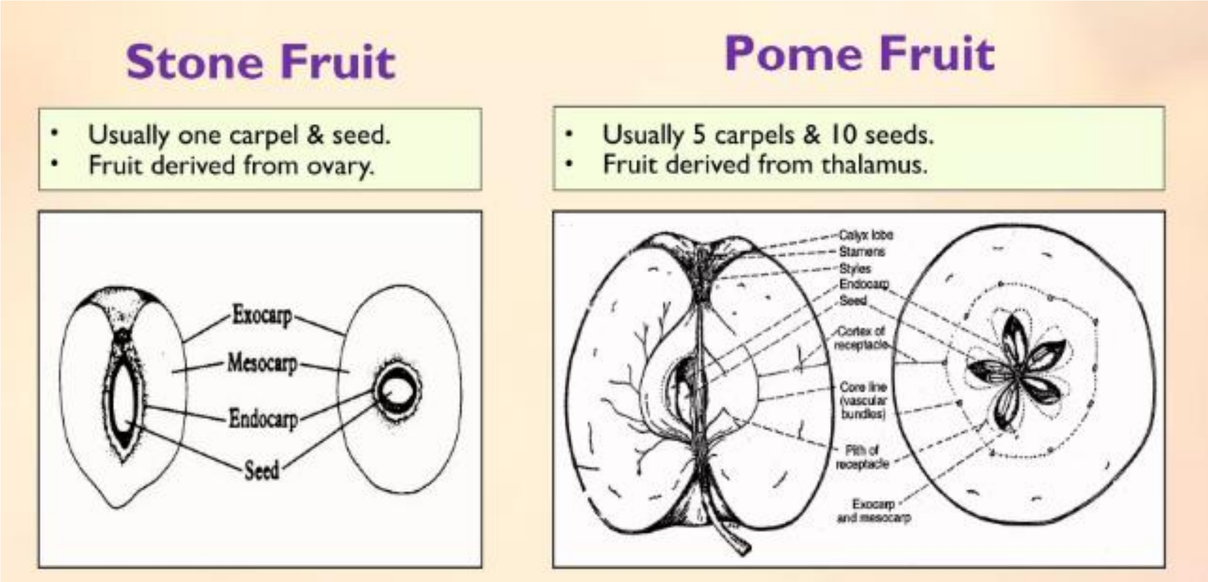
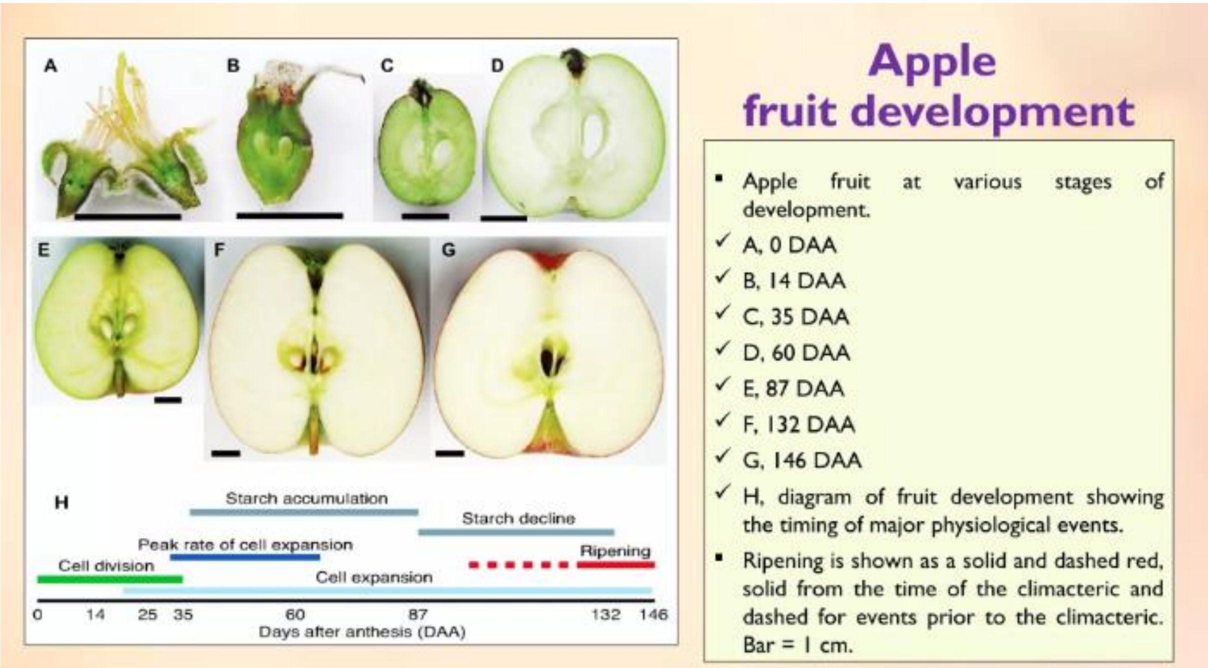


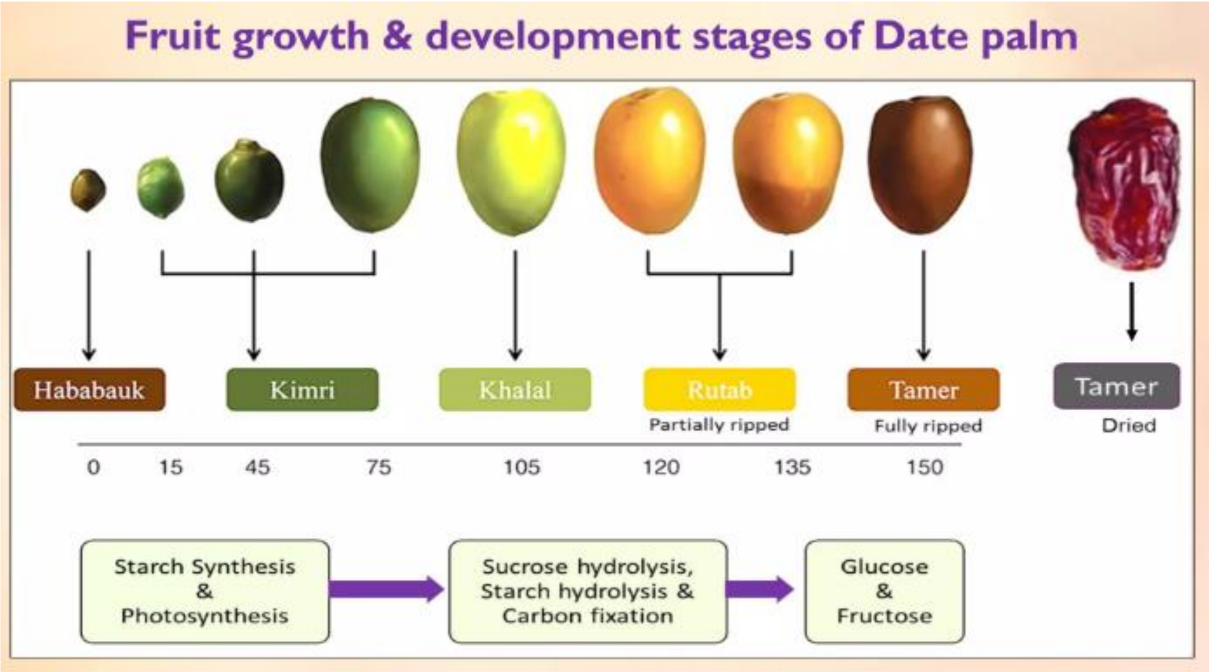
Figure 19. Biochimical activities changement during fruit repening. A. Modification of hexose, starch, chlorophyll and lycopene content during tomato ripening. B: variation of closure and tauw of carbon dioxide and ethylene during maturation. C: variation in the activity of the main pectin degradation enzymes.

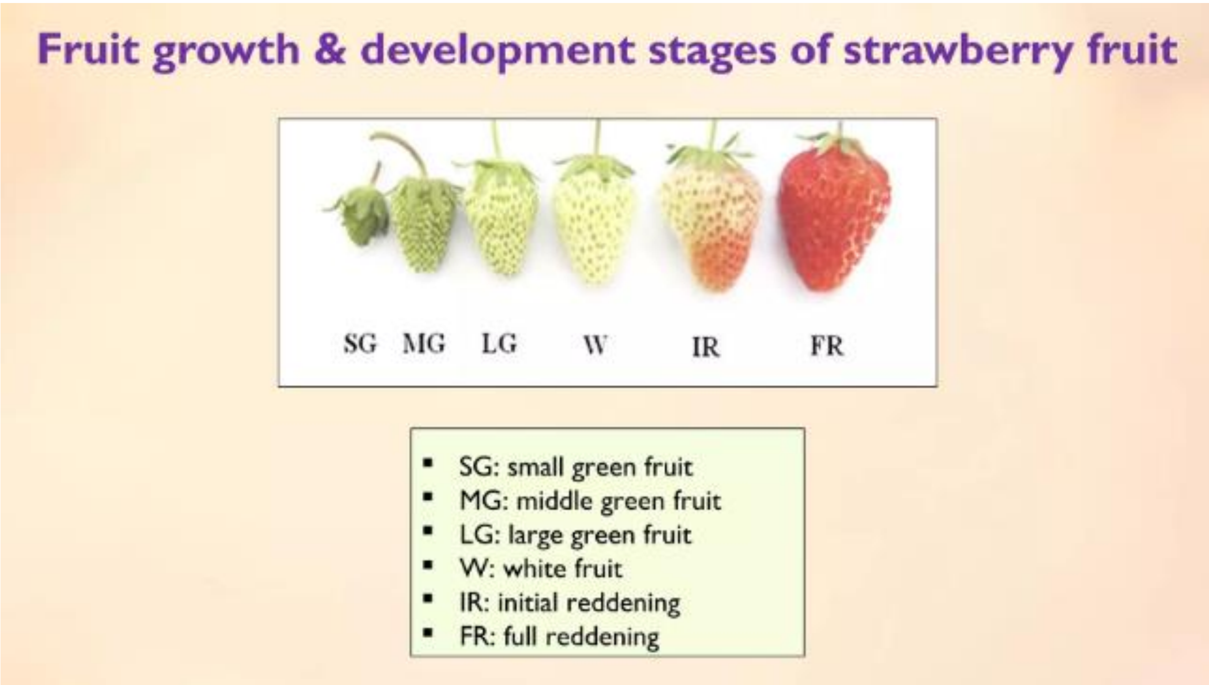
Conclusion regarding fruit development

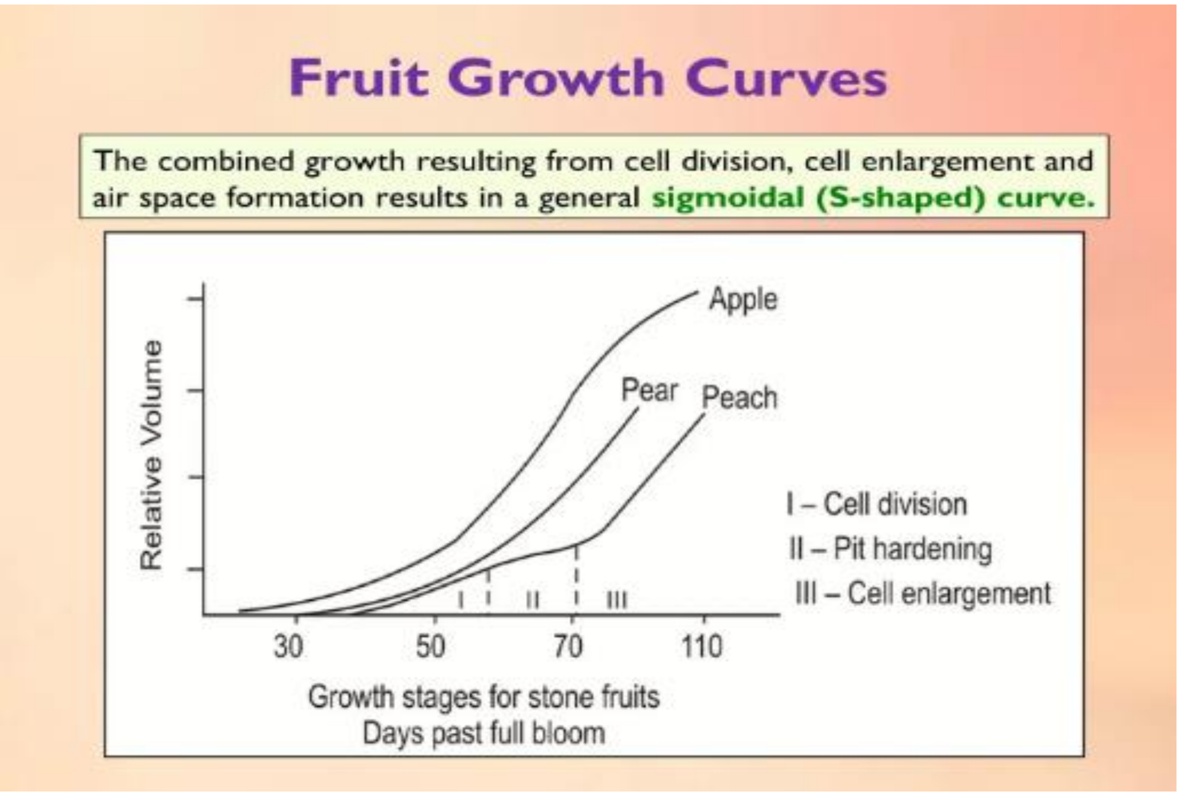
The fruit is probably the most complex organ produced by plants. Its development is at the origin of the reproductive success of angiosperms. However, each phase of fruit development and ripening involves specifics genes activity, such as the *Cnr* locus and several *MADS-box* genes expressed during the early stages of tomato fruit ripening.


Stone Fruit
Usually one carpel & seed.
Fruit derived from ovary.
Exocarp
Mesocarp
Endocarp
Seed
Pome Fruit
Usually 5 carpels & 10 seeds.
Fruit derived from thalamus.
Calyx lobe
Stamens
Styles
Endocarp
Seed
Cortex of receptacle
Core line (vascular bundles)
Pith of receptacle
Exocarp and mesocarp


A
B
C
D
E
F
G
H
Starch accumulation
Starch decline
Peak rate of cell expansion
Ripening
Cell division
Cell expansion
0 14 25 35 60 87 132 146
Days after anthesis (DAA)
Apple fruit development
Apple fruit at various stages of development.
A, 0 DAA
B, 14 DAA
C, 35 DAA
D, 60 DAA
E, 87 DAA
F, 132 DAA
G, 146 DAA
H, diagram of fruit development showing the timing of major physiological events.
Ripening is shown as a solid and dashed red, solid from the time of the climacteric and dashed for events prior to the climacteric. Bar = 1 cm.


Fruit growth & development stages of Date palm
Hababauk
Kimri
Khalal
Rutab
Partially ripped
Tamer
Fully ripped
Tamer
Dried
0
15
45
75
105
120
135
150
Starch Synthesis & Photosynthesis
Sucrose hydrolysis, Starch hydrolysis & Carbon fixation
Glucose & Fructose


Fruit growth & development stages of strawberry fruit
SG
MG
LG
W
IR
FR
SG: small green fruit
MG: middle green fruit
LG: large green fruit
W: white fruit
IR: initial reddening
FR: full reddening



10. Climacteric and Non-climacteric Fruit

Fruit ripening involves various biochemical and physiological changes, including loss of chlorophyll, synthesis of pigments such as anthocyanins and carotenoids, increased aroma and flavor, and alterations in sugar and acid components. These phenomena or changes vary significantly depending on the fruit's phenological cycle during the ripening.

Fruit ripening is traditionally classified into two groups based on the fruit's response to ethylene: climacteric and non-climacteric. Also, this classification of fruits depends on whether ripening associated increased respiration occurs in the fruit repening (Figure 20). Ethylene is a gas and is known as the "fruit-ripening hormone."

While all fruits produce a certain level of ethylene throughout their lifecycle, some fruits experience a sharp increase in ethylene levels during ripening.

- ❖ Climacteric fruits exhibit an increase in respiration and a rapid production of ethylene at the initiation of ripening, which accelerates the ripening process. Thise category includes fleshy fruits such as tomato, avocado, apple, melon, peach, kiwi, and banana.
- ❖ In contrast, climacteric fruits once harvested do not ripen further. Nonclimacteric fruits produce very small amount of ethylene and do not respond to ethylene treatment. There is not a characteristic increase in the rate of respiration or carbon dioxide production.

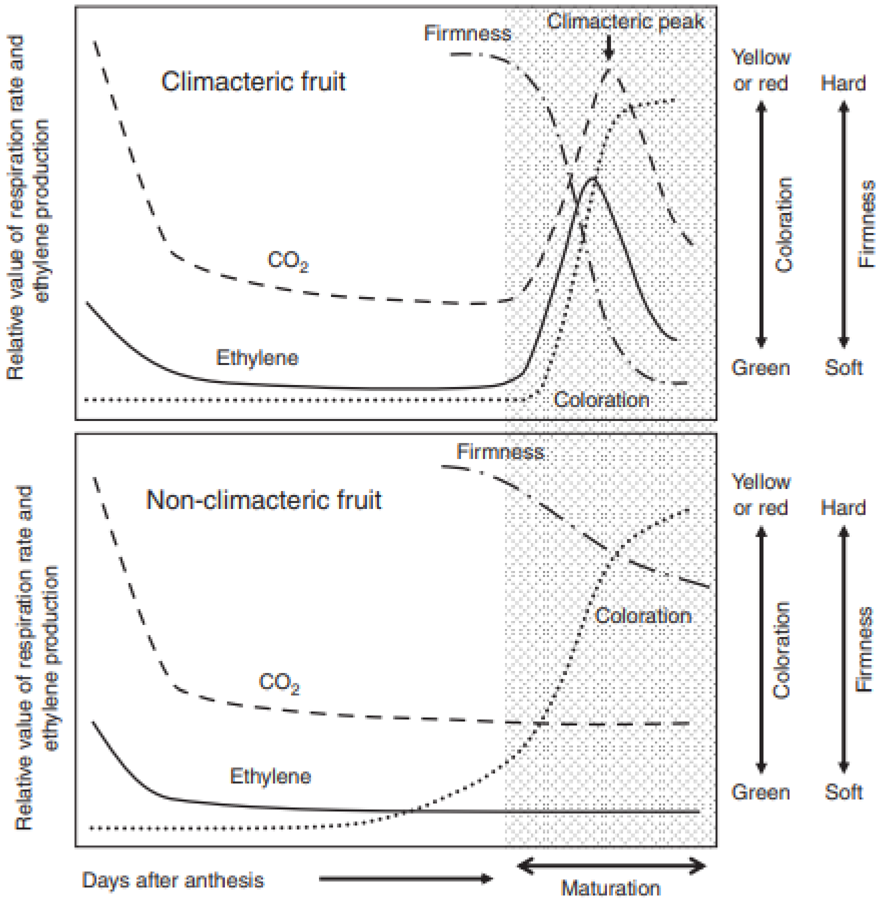


Figure 20. Characteristics of climacteric and non climacteric fruits

10.1. Ethylene and climacteric fruit ripening

Climacteric fruits rely on ethylene hormone for their ripening process. A high production of ethylene triggers changes in color, texture, aroma, flavor, and other physiological and biochemical characteristics of the fruit. Furthermore, enhanced ethylene biosynthesis are accompanied by increased levels of citrate, malate and glucose and fructose but decreased sorbitol and sucrose levels following harvesting. According to this definition, the shelf-life of climacteric fruits is shorter than the nonclimacteric fruits.

At the onset of ripening in climacteric fruits, various genes involved in cell-wall breakdown and carotenoid biosynthesis are stimulated to express and increase at the transcriptional and translational levels.

Exposure to exogenous ethylene can also pilot a rapid increase in the production of ethylene in climacteric fruits, even at the preclimacteric stage, leading to accelerated maturation. Low concentration of 0.1-1.0 microlitres is sufficient to trigger the ripening process in climacteric fruits. Conversely, treatment with inhibitors of ethylene action may promote and delay fruit ripening.

10.2. Characterization of non-climacteric fruit ripening

Non-climacteric fruits, such as strawberries, grapes, citrus, pineapples, and cherries, undergo maturation and ripening without a increase in ethylene production or respiration rate, unlike climacteric fruits. Generally, ethylene is not required for the ripening process. Recently, the possibility that ethylene is involved in the ripening process of non-climacteric fruit ripening has been proposed. In mature strawberry, exogenous ethylene applied after harvesting does not accelerate fruit ripening, and ethylene and 1-MCP treatments do not affect its storage life.

For more understanding the effects of ethylene :

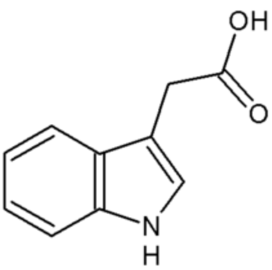
1- If you have for example an unripe avocado or other fruits, you can put them in a paper bag with a ripening banana to speed up their ripening process. The ethylene emitted by the ripening banana will trigger the climacteric response in the avocado and other fruits, resulting in faster ripening. It's important to note that this strategy works best when the ripening fruit emits a high concentration of ethylene, such as an apple, pear, banana, or passion fruit.

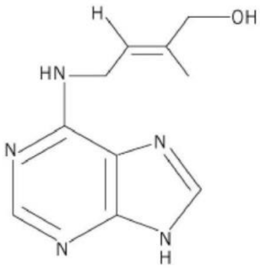
2- You can also observe the effects of ethylene on citrus fruits by putting a green lemon in a paper bag with a ripening banana. Ethylene is used to "de-green" citrus by triggering the breakdown of the green pigment (chlorophyll) in the peel, resulting in orange and yellow coloration.

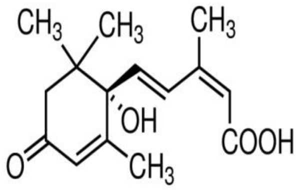
N.B : *It's important to conduct these experiments at room temperature, around 20°C, because low temperatures can inactivate important fruit-ripening enzymes. Avoid conducting these experiments in the refrigerator.*

11. Involvement of other Phytohormones in Fruit development

Fruit life is also notably affected by phytohormones, such as auxins [indole-3-acetic acid (IAA)], cytokinins (CKs), jasmonic acid (JA), abscisic acid (ABA), brassinosteroids (BRs).







Auxin Cytokinin abscisic acid

Hormonal molecules are involved in regulating various stages of fruit growth, including fruit set, development, maturation, and ripening by two or three hormones simultaneously.

For that, the combined action of auxins, gibberellins (GAs), and CKs is the major regulator of fruit set. Auxins and CKs modulate fruit development, although auxins also trigger fruit maturation. ABA and ethylene are the main ripening regulators.

Example:

- ✓ If the achenesare removed during the growth of the strawberry, there is an inhibition of its growth.
- ✓ If we remove the achenes from one side of the strawberry and leave them on the other side, the strawberry grows asymmetrically. Stronger development on the side still showing achenes.
- ✓ If all the achenes are removed from the strawberry and auxin is applied to the floral receptacle, strawberry growth is normal. Auxin application restores achene-deprived strawberry development.
- ✓ If auxin is applied to the fruit at the end of its growth, the fruit ripens: this is the senescence of the fruit. The synthesis of ethylene is stimulated which allows ripening.

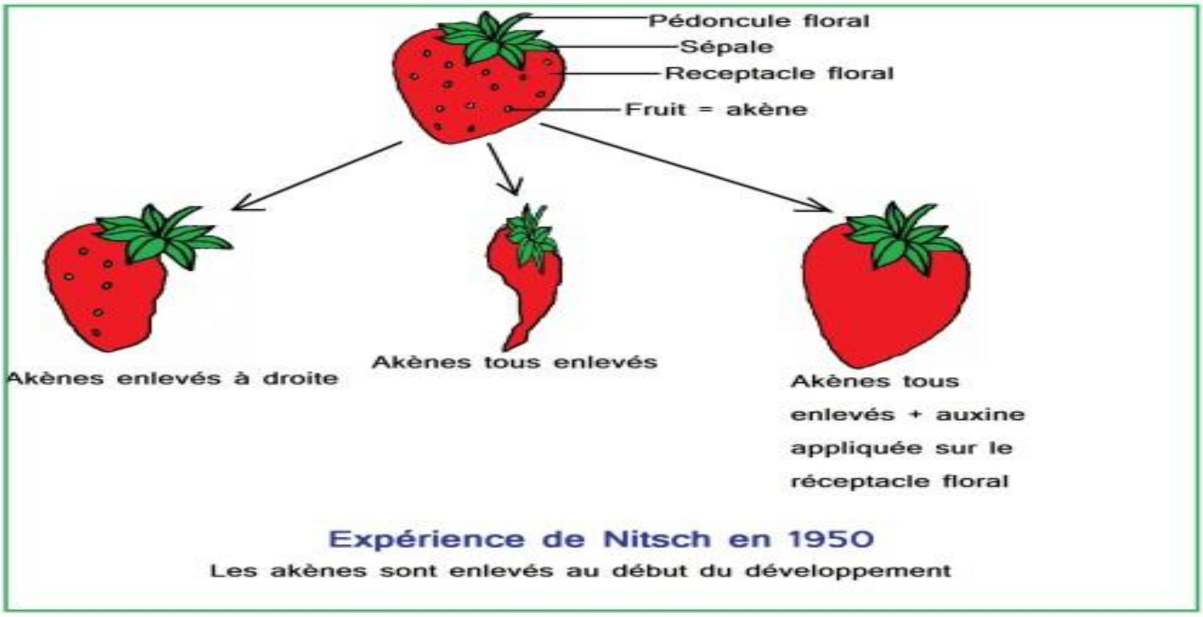


Figure 21. Experience's Nitsh and Auxin role in fruit development

11.1. Pollination

The communication between ethylene and auxin during pollination in tomato flowers is crucial for regulating pollen grain germination and tube growth. Ethylene precursor metabolites and the expression of ethylene biosynthesis and response genes (ACC synthase and ETR ethylene receptors, respectively) increase in pollen grains prior to anthesis.

Auxin accumulates in both the stigma and the pollen tube tip after pollination, while
Following pollination, auxin accumulates in both the stigma and the pollen tube tip, while ethylene emissions increase within the stigma, leading to the degeneration of transmission tissues that provide nutrients to surrounding tissues within the pistil and a low-resistance path for the pollen tube.

ABA and ethylene together co-regulate water transport in pollen tubes.

11.2. Fruit set

The initiation of fruit set is regulated by the accumulation of auxin and GA, however auxin being the primary regulator across different species of dry and fleshy fruits. The influence of both phytohormones has been widely demonstrated in studies comparing both pollinated and parthenocarpic fruits, including cucumbers and watermelons.

The ability of plants to accumulate and perceive these hormones is crucial for fertility and pollination. The growth and death phases in both types of fruits are modulated by the concentration of phytohormones, with auxins and gibberellic acids (GAs) playing a vital role. The application of exogenous auxins and GAs can induce fruit set and development even in the absence of fertilization (parthenocarpy). Ethylene and ABA also have the potential to influence pollination and fertilization by interacting with auxin and GA, as well as with each other.

11.3. Regulation via cytokinins, brassinosteroids, and jasmonic acid

Additional phytohormones such as cytokinins (CKs), brassinosteroids (BRs), and jasmonic acid (JA) have demonstrated capacity to influence fertilization and fruit initiation in some angiosperms. Both CKs and BRs generally increase after fertilization, and there is evidence in Japanese persimmon that exogenous application of BRs can significantly increase fruit set. CKs also proved to be functional in concert with auxin and GA during fruit set initiation in both pollinated and parthenocarpic cucumbers. Furthermore, within the transcriptome of set fruits, a significant overlap between genes responsive to auxin and those responsive to BRs, suggesting that the latter might also be influential in coordinating fruit set in cucumbers.

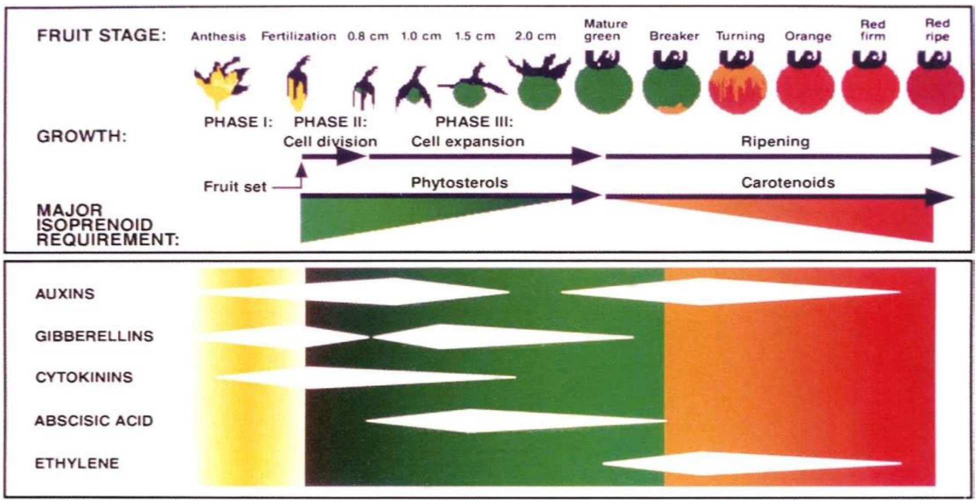


Figure 22. Fruit development and ripening in tomato (*Lycopersicon esculentum*)

12. Fruit water accumulation

Water transport into and accumulation in the fruits contribute significantly to yield and quality development of fleshy fruits. Fruit water accumulation is the result of water transport via the xylem and the phloem (Figure 23, A–C) and water loss by fruit transpiration via the fruit cuticle. Unlike leaves that have stomata the aperture of which is regulated by environmental conditions and plant water status, the tomato fruit surface has no stomata and transpiration through the cuticle is influenced mainly by the air humidity. It was estimated that ~80– 90% of water imported by tomato fruit was via the phloem and the remaining 10–20% via the xylem.

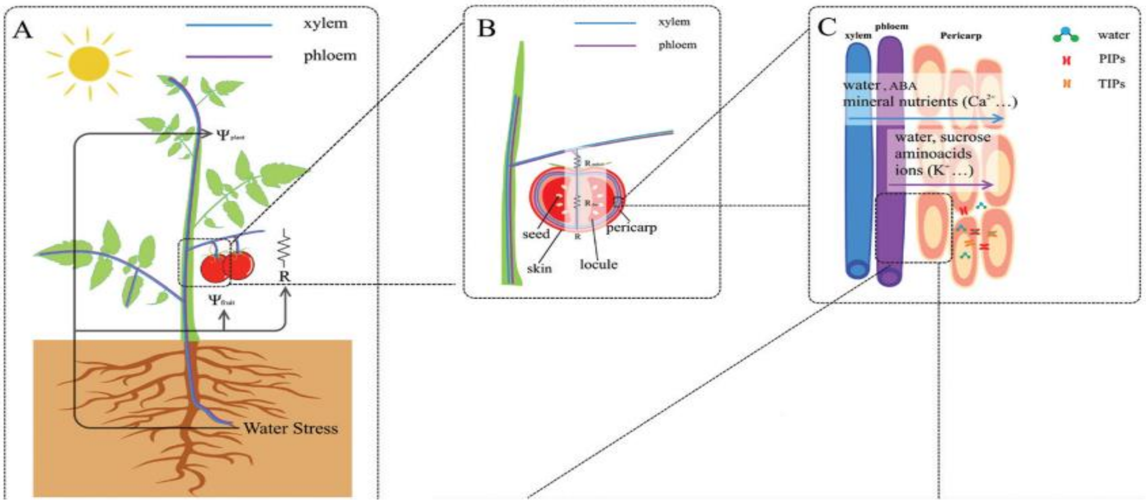


Figure 23. Water transport

Water enters the fruit through the xylem and then into fruit cells across cell membranes. Water transport into the fruit depends on the resistance of the pathway between the fruit and the parent plant, and the driving force for water flow.

Exemple :

In the vine, the berries are irrigated by xylem and phloem elements which are arranged parallel within the vascular bundles (Figure 24). There are two major vascular bundles within the berries. One is peripheral, located under the surface of the bays, and the other runs along their central axis. They are connected at the base of the fruiting peduncle (at the proximal end of the berry), and at the stylar end (distal) of the berry.

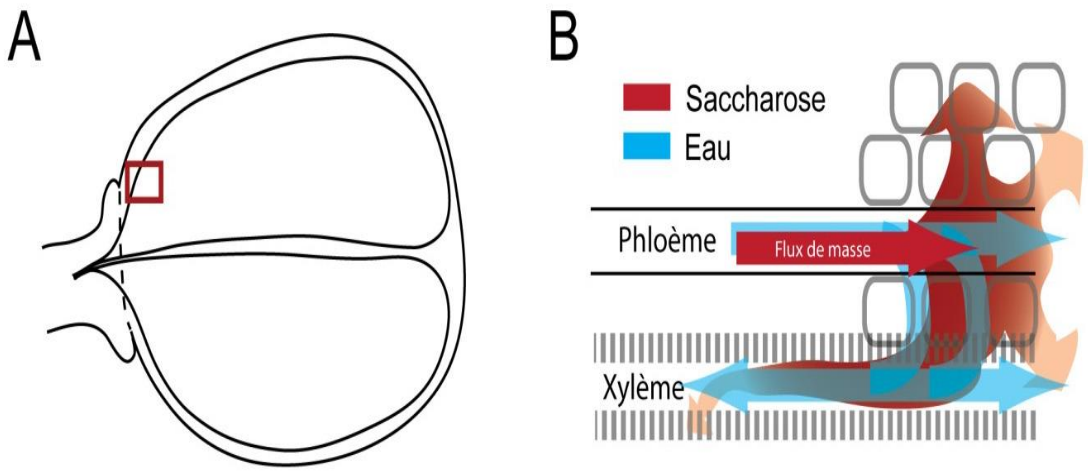


Figure 24. Vascularization and flow of substances within the bay. (A) There are two main vascular networks in the bay, one located below the surface, and the other extending through the central axis. They separate in the pedicel just before entering the bay and reconnect at the stylar (distal) end. (B) The berries are fed by xylem and phloem running parallel to each other in the vascular bundles. The phloem is the tissue

that transports sugars dissolved in water, while the xylem transports water and various mineral elements.

13. The influence of light on fruit development

The accumulation of brightly coloured pigments in fruits is one of the most dramatic events that accompanies ripening and serves as a key signal to seed-dispersing fauna of the ripeness and palatability of the fruit. Fleshy fruits predominantly accumulate carotenoids, anthocyanins and flavonoids and the de novo synthesis of these compounds at the onset of ripening is preceded by, or occurs concomitantly with, the degradation of chlorophyll. An exception to this generalization occurs in banana where the degradation of chlorophyll at the onset of ripening leads to the unmasking of the yellow-pigmented xanthophylls that are already present in immature fruit.

Physiological and genetic studies have also implicated light-signalling pathways in influencing carotenoid, flavonoid and anthocyanin accumulation during ripening in several species including tomato, apple and grape. For example, carotenoid synthesis in tomato can be stimulated by a short red light pulse and this is reversed by a far-red light pulse indicating that this effect is mediated by phytochrome.

14. Respiratory Metabolism

The rate of the metabolic reactions which occur in a cell has a significant affect on fruit development and its final quality consequenlty. For maximizing the longevity of the fruit this character could be useful. Carbon dioxide induces and suppresses the respiration and this is depending on its concentration *in situ*. Indeed, the respiration rate would be decreased as carbon dioxide concentration in the atmosphere surrounding plant tissues is increased.

The control of respiration in fruit can be regarded as the result of the interaction of three main processes, glycolysis, the TCA cycle (tricarboxylic acid) and the mitochondrial respiratory chain. However, several enzymes of the TCA cycle particularly SDH (succinate dehydrogenase), can be inhibited with elevated carbon dioxide leading to the accumulation of succinate.

Respiratory metabolism provides not only the energy required to conduct all these metabolic reactions, but it also produces the raw material used as substrates by these reactions. In its simplest context, respiration reacts with stored substrates (Typically a carbohydrate) and with oxygen to produce high-energy compound (e.g. ATP) and carbon dioxide (CO_2). However, the production of carbon fragments used in subsequent synthetic reactions is also of major importance.

The metabolic activity of fruits and vegetables follows shortly after harvest, where The energy required to maintain it comes from the respiratory process. This physiological process involves the oxidation of sugars to produce carbon dioxide.

After the initial healing of wounds during the harvest, there is usually a decrease in respiration in vegetative tissues and non-climacteric fruit (Figure 25). Conversely, the ripening of climacteric fruit is accompanied by a rapid increase in ethylene production and respiration. The required energy after this resperation for various metabolic processes, such as tissue softening, pigment synthesis, and volatile production that occur during ripening

Despite this, non-climacteric fruit undergo similar ripening changes without a corresponding increase in respiration. Additionally, climacteric fruit that remain attached to the parent plant exhibit a significantly lower rate of respiration during ripening compared to detached fruit, despite similar levels of ethylene production in both cases.

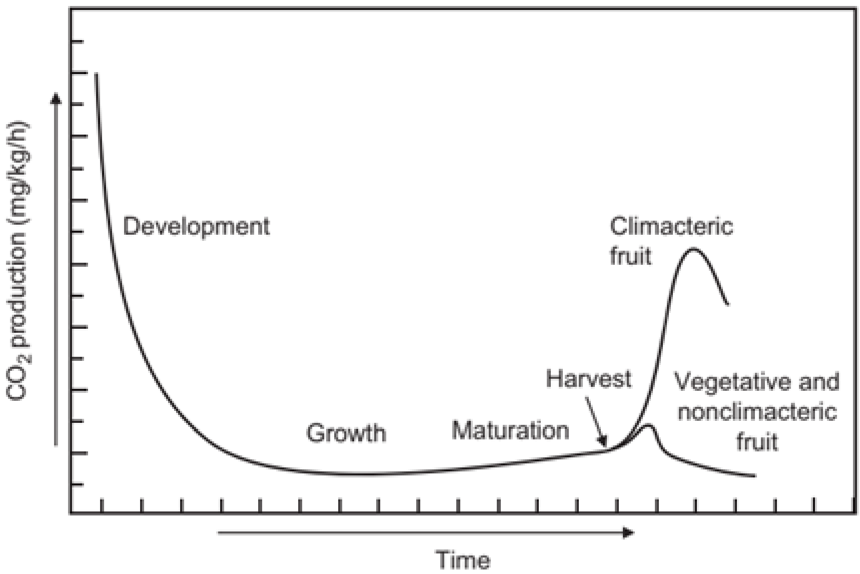


Figure 25. Change in respiration during development, growth and maturation fruit (Climacteric and nonclimacteric)

There are four primary metabolic pathways involved in respiratory metabolism, which include:

(1) glycolysis,

(2) the citric acid cycle (TCA cycle),

(3) electron transport,

(4) the pentosephosphate pathway

15. Action of carbon dioxide (CO_2) on fruit development

Generally, elevated CO_2 causes increased photosynthesis in plants, which leads to greater production of carbohydrates and biomass. These carbohydrates are a major energy source for plant growth, but they also act as signaling molecules and have a range of uses beyond being a source of carbon and energy.

The decrease in number of cell per area in the pericarp of mature fruits was associated with a significant enhancement in cell area, which in turn increased fruit yield and concentration of minerals. Moreover, the maximal fruit expansion rate was increased by CO_2 conditions, which was associated with enhanced of transcripts encoding expansin proteins in pericarp tissues of immature fruits. High amount of CO_2 increase potentially ethylene production and carotenoid contents during fruit ripening in tomato (Figure 26).

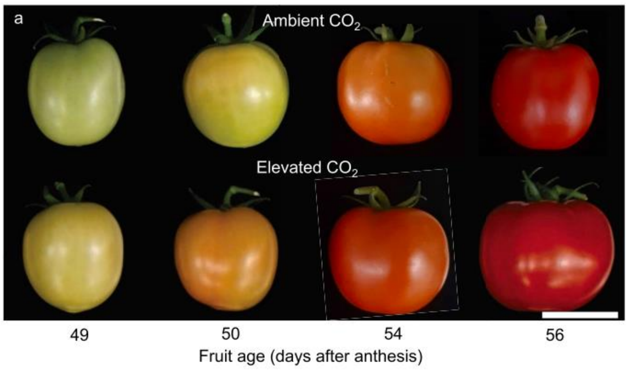


Figure 26. CO_2 concentration on fruit quality

The CO_2 absorption and fixation is undertaken from soil and atmosphere via leaves and roots.

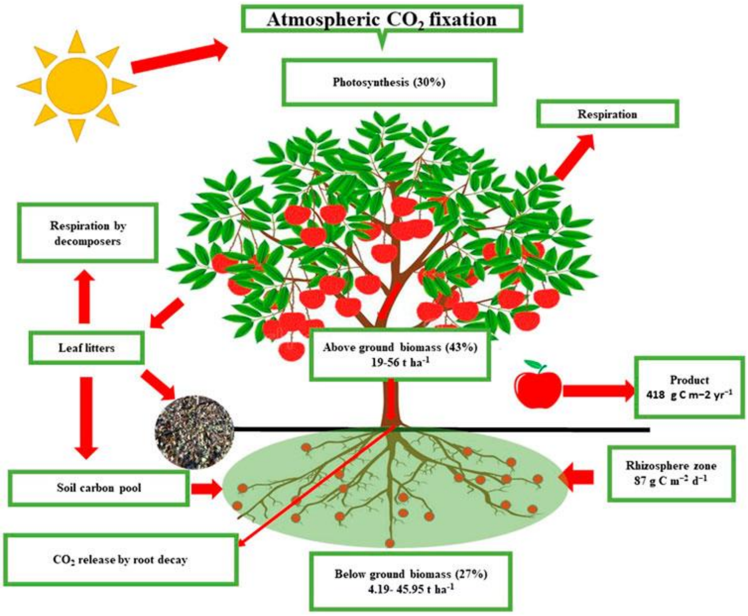


Figure 27. Schematic diagram of carbon pools in an apple tree

16. Mineral nutrititon

The minerals uptake could be a potential integrator and plays a crucial role in regulating fruit size. Mineral nutrition, such as N, P, and Fe, not only affects fruit quality directly but also affects the absorption of other nutrient elements

Potassium concentration is important for cell expansion and has a high positive correlation with fruit size and soluble solids content. Moreover, Ca is required for many structural processes in the cell wall and plasma membrane of fruits. The concentrations of minerals in fruits depends on uptake by the roots, xylem-to-phloem transfer and redistribution from vegetative tissues.

Table 1. Principal symptoms of deficiency and excess on nutreints in fruit (e.g Pear fruit)

Nutrient	Deficiency	Excess
N	low size, high firmness, early maturation, lack of flavor	Late maturation disorders (cork spot), pre and post harvest decay
P	High juiceness Low size and juice acidity	Late maturation, less aroma and sweetness
K	Low size	Low storage suitability, cork spot
Ca	Cork spot (bitter pit), black end, internal breackdown, senescent breackdown, watercore, alfalfa greening, high respiration, earlier maturation and peel yellowing	Delay in ethylene evolution
Zn	Low size, fruits are deformed, sour, early ripen	-
B	Low size, deformation, cracking, corking, pitting, black end,	Early maturation, Lower storage suitability

17. Regulation of pigment dynamics in fruit ripening

Amoung a genetic traits with ecological (seed dispersion) and nutritional role the fruit color is very important. The other adaptive challenges were entrusted on fruit color by environmental factors and domestication further resulting in diversification. The unprompted mutations occurring repeatedly in pigment biosynthetic pathways lead to variations in fruit color which were often propagated.

The emergence of pigments during fruit ripening has several advantages for the plant. During repining, the chlorophyll content and development of chloroplasts at mature green stage affects significatly the carbon content.

Amoung the photosynthetic pigments existed in plants which play a vital role in enhancing the net carbon yield of the plant, Chlorophyll and carotenoids are the most important. They are embedded in photosystems I and II and are involved in capturing and utilization of light energy by the plant, via the photosynthetic electron transfer and ultimately influencing the final yield of fruits

The process of pigment change during fruit ripening is precisely regulated, and it involves several factors such as plant growth hormone, transcription factors, gene families, enzymes of the pigment biosynthetic pathways, and environmental stimuli.

As fruit ripens, changes in pigment biosynthesis, degradation, and sequestration occur, with the aid the development of new structures such as fibrils in pepper and plastoglobules in other fruits.

Additionally, pigments may undergo various biochemical modifications after synthesis to enhance their stability, resulting in the production of novel cleaved pigment products that may have potential bioactivity.

18. Fruit de-greening process enhances carbon yield

At onset of fruit ripening, the degradation of the green pigment chlorophyll is initiated to accelarate both the remobilization of nutrient and the biosynthesis of vitamins. The decresae in green color of fruits is important to promote detoxification of chlorophyll released from its binding proteins.

Light, the growth hormones ethylene, ABA and jasmonic acid, signal specific transcription factors (TFs).

19. Pigments

The quality of fruit is primarily determined by its pigmentation, which undergoes significant changes during the ripening process. This transformation is caused by the upregulation of chlorophyll degradation and carotenoid biosynthesis, to form the unique color of the fruit.

In fruits such as tomato and pepper, the degradation of chlorophyll is accompanied by the regulated conversion of chloroplasts into chromoplasts (Figure 28) which accumulate carotenoids and cause a visible color change from green to yellow, orange, and finally red. Carotenoids are sequestered in plastids (chloroplast and chromoplast) at high levels. Xanthophylls are produced for photosynthetic purposes in the thylakoid membrane. However, during ripening, breakdown of the thylakoid takes place coupled with accumulation of carotenoids like lycopene in the membrane along with synthesis of membranes as sites for carotenoid biosynthesis, coupled with increased number and size of plastoglobules.

In the chromoplasts, the plastoglobules are highly enriched with esters of carotenoids and enzymes involved in carotenoid metabolism.

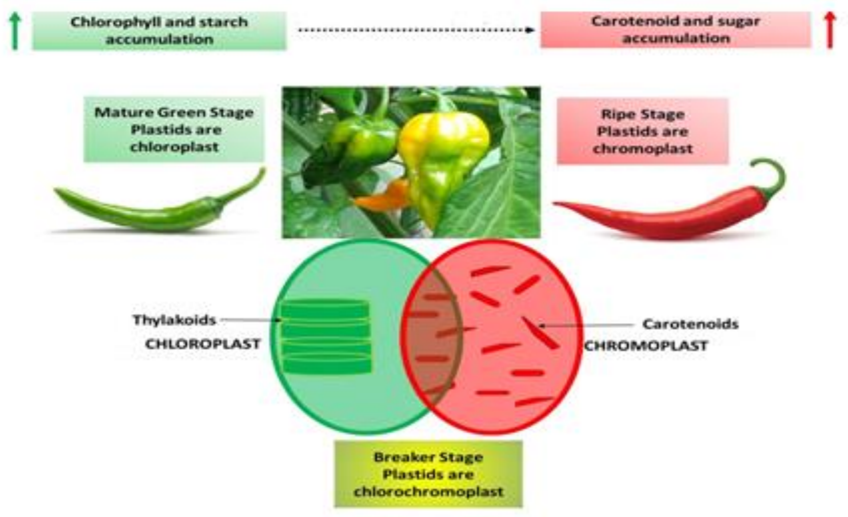


Figure 28. Conversion of chloroplast into chromoplast

20. Sugar signaling during fruit ripening

The role of sugars in fruit quality is crucial, as they directly impact the taste and overall consumer acceptance. Carbohydrates serve as the primary source of carbon and energy for the plant and have been implicated in various developmental processes, including embryogenesis, seed germination, stress responses, and vegetative and reproductive growth.

Additionally, research has demonstrated that both sucrose and its main hexose derivatives, produced through sucrose degradation, are involved in signaling and regulating plant development. Sugars can directly or indirectly control numerous processes, including photosynthesis, nitrogen uptake, defense mechanisms, hormone balance, and secondary metabolism.

20.1. Sugar Transport and Metabolism for Fruit development

Sucrose is the primary form of fixed carbon (C) form of carbohydrates for long-distance transport through the phloem from leaves sources to non-photosynthetic sink organs, including developing fruits.

The leaves are the sources and serve as a site of photosynthesis and assimilate production by importing carbohydrates from other parts of the plant. Nonobstant, over 90% and 85% of the required assimilates are imported for peach growth and for cherries respectively.

The transport and volume of the sugar are determined by the position and relative strength of the sink.

Carbohydrates produced in leaf mesophyll are loaded into the phloem systems and unloaded in energy-demanding or storage tissues (sinks); both the mechanisms can be apoplastic (sugars cross the cell membrane) or symplastic (exclusively through the plasmodesmata-connected cells. Among the sugars produced in plants, only a small number, usually highly soluble and chemically inert, are transported in the phloem over a long distance (Figure 29).

Once sucrose reaches the sink cells, sucrose is hydrolyzed by an enzym (sucrose synthases) or invertases into fructose and glucose, which help maintaining sink strength. This enzym is mainly involved in the synthesis of carbohydrate polymers, i.e. starch or cellulose, or in the generation of energy, necessary for the production of a myriad of compounds which help fruit development and seed dispersal.

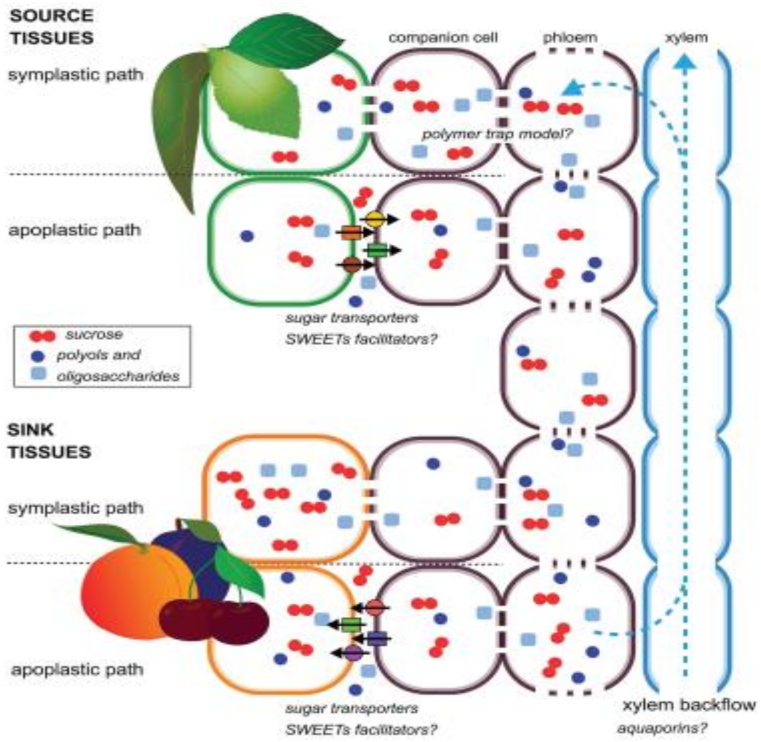


Figure 29. Sucrose mouvement necessary for the fruit development

21. Modifications in organic acid profiles during fruit development and ripening

Both maturity and ripening have been associated with metabolic alterations associated with multiple genetic and biochemical pathways. Although these changes have been observed in the context of reactions to hormones such as ethylene and ABA, the relationship between hormonal control and metabolite accumulation remains somewhat limited.

In general, fruits tend to accumulate organic acids primarily during the initial stages of development as an energy reserve. The accumulation of organic acids and amino acids moves towards sugar synthesis in subsequent fruit development. In citrus fruits, sucrose is transferred from leaves to fruit throughout development and accounts for around 50% of total soluble sugars. During the first half of fruit development, sucrose is hydrolyzed by cytosolic invertases or stored in the acidic vacuoles and hydrolyzed by vacuolar acidic invertases. Meanwhile, there is accumulation of the citrate (Figure 30).

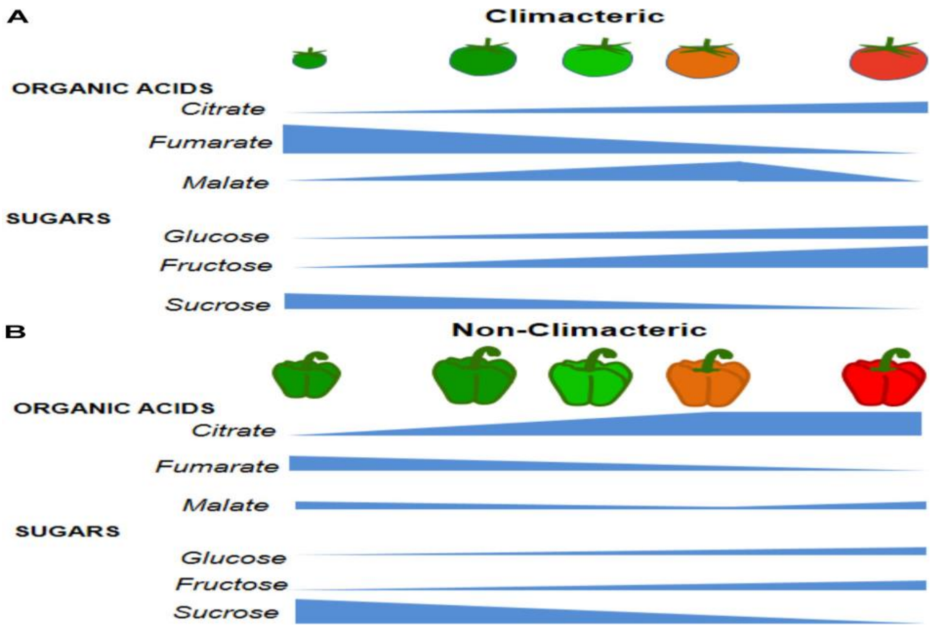


Figure 30. Comparative metabolite accumulation during fruit growth in two significant examples of climacteric (tomato, *Solanum lycopersicum*) and non-climacteric (pepper, Capsicum spp.) species.

22. Apomixis vs Parthenocarpy

Usually the seed and fruit develop after pollination and fertilization. Apomixis and parthenocarpy are two mechanisms involved in the production of seeds and fruits in angiosperms, respectively. Apomixis is a type of parthenocarpy. The main difference between apomixis and parthenocarpy is that apomixis is the production of seeds without fertilization while parthenocarpy is the production of fruits without seeds.

Apomixis is a type of asexual reproduction. The term apomixis is currently used as a synonym for agamosperms. The seed is formed by the tissues of the mother of the ovum and therefore apomixis avoids meiosis as well as fertilization (orange, rose). Apomixis uses the sexual parts of the plant for vegetative propagation or grafting.

23. Fruit ripening using calcium

In industry, most climacteric fruits are ripened with calcium carbide. Once dissolved in water, the calcium carbide produces acetylene which acts as an artificial ripening agent. However, this method steal used in some contries like India, and generally the only safe and worldwide accepted method is using ethylene, which is a natural hormone for ripening when done under controlled temperature and relative humidity conditions.

24. Seed filling

Seed filling is a main key that control the seed vigor, structure and and reserves accumulation (e.g starch) which depends on the supply of Carbon (C) and Nitrogen (N). Also, the remobilisation of these two elements from vegetative organs determine the seed filling process. The high supply for carbon depends on photosynthesis process. However, the nitrogen assimilation and N_2 fixation decline during seed filling, with newly acquired nitrogen generally insufficient for the high seed demand.

The remobilization of nitrogen from vegetative tissues to filling seeds interacts with photosynthesis since it induces senescence, which reduces the seed filling period. Therefore, improved grain legume seed filling requires either reduced dependency on nitrogen remobilisation or enhanced nitrogen supply. The nitrogen can might be obtained either by prolonging the activity of symbiotic fixation or increasing the potential for root assimilation of soil mineral nitrogen.

During seed filling, nitrogen assimilation primarily occurs in the source leaves and stems of some plant species. This element imported into the developing seeds is largely derived from the recycling of assimilated nitrogen sources before the onset of the reproductive phase.

Other compounds such as Zn and Fe have an significant role in seed filling for many species. After foliar application, these two elements can be absorbed by leaf epidermis and transferred into the rice grains through the phloem.

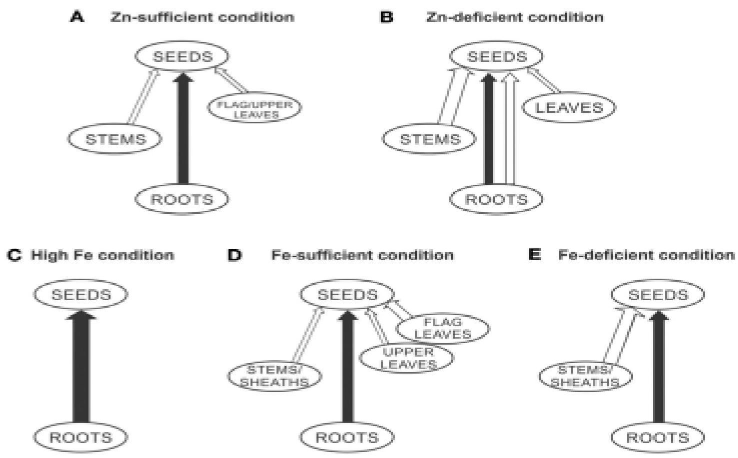


Figure 31. Model for Zn and Fe transfert to the rice seeds (A, Zn-sufficient condition; B, Zn-deficient condition; C, High Fe condition; D, Fe-sufficient condition; E, Fe-deficient

condition), through the xylem (continued root uptake, black lines) and through the phloem (mineral remobilization, white lines)

Generally, the seed filling is a criterion which is under the variation of the climatic conditions and the genetic factors of the species.

Conclusion

In order that students can come to understand the physiological mechanism of fruit development, a series of presentations and works should be carried out on:

- Tuberization ;
- Veraison ;
- Environmental factors effect on fruit deveopement by studying examples on different vegetable and fruit species.

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